NEST PREDATION AND BROOD PARASITISM OF TWO BOTTOMLAND HARDWOOD FOREST SONGBIRDS: THE IMPORTANCE OF HABITAT CHARACTERISTICS AT MULTIPLE SPATIAL SCALES

by

JILL J. GANNON

(Under the Direction of Robert J. Cooper)

ABSTRACT

Population declines of forest-interior neotropical migratory songbirds may be linked to a reduction and degradation of breeding habitat that result in increased nest predation and brood parasitism. Bottomland hardwood forests of the southeastern U.S. have undergone severe reductions in both the amount and quality of breeding habitat. The White River NWR is one of the largest remaining contiguous tracts of bottomland hardwood forest in the U.S.; however, songbirds breeding within the Refuge are subjected to high rates of nest predation and parasitism. I used a species-specific, multi-scale approach to investigate the relative importance of habitat characteristics to nest predation and parasitism of two neotropical migrant songbirds, the Acadian Flycatcher (*Empidonax virescens*) and the Prothonotary Warbler (*Protonotaria citrea*). Using proportional hazard and logistic regression models, I found that the risk of nest predation and the likelihood of brood parasitism were related to habitat characteristics at multiple spatial scales (micro, macro, and landscape). Water associated with seasonal flooding played an important role in reducing the risk of nest predation at all spatial scales, while a landscape-level factor describing proximity to cowbird foraging sites was strongly associated with increased brood parasitism. Additionally, human-induced disturbances within the forest interior that created edge and open canopy, namely roads and patch cuts, were associated with increased nest predation and parasitism. I conclude that 1) landscape-level management efforts may be most successful in reducing nest predation and brood parasitism within the Refuge and 2) anthropogenic disturbances that may alter the existing flooding pattern of the Refuge should be thoroughly investigated for their potential effects on the nesting success of bottomland forest songbirds.

INDEX WORDS: Bottomland hardwoods, Acadian Flycatcher, Prothonotary Warbler, Nest predation, Brood parasitism, Nest characteristics, Habitat characteristics, Flooding, Water, Multiple spatial scales, Cox regression, Logistic regression

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This dissertation is dedicated to

MY LOST TWENTIES

AND

THEN SOME

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CHAPTER

INTRODUCTION

Populations of many neotropical migratory songbirds have declined in recent decades (Robbins et al. 1989, Askins et al. 1990). Although the declines in many forest-dwelling neotropical migrant birds can be linked to a reduction in breeding and wintering habitats, the high degree of forest fragmentation and habitat loss in the eastern United States suggests that factors on the breeding grounds are the primary cause of migrant declines, presumably through decreased reproductive success (Robinson et al. 1995). Increased rates of nest predation (Wilcove 1985) and brood parasitism (Brittingham and Temple 1983) suffered by forest-interior songbirds in these fragmented landscapes may be a cause of their decline in North America (Robbins et al. 1989, Askins et al. 1990).

The pervasive nature of nest predation and parasitism indicate that the nesting season is a critical period for maintenance of bird populations (Martin 1993). Conservation of bird species depends on reducing the limiting nature of nest predation and parasitism through knowledge of the birds' breeding biology, understanding their habitat requirements, and identifying and preserving the habitat features that positively affect their breeding productivity and survival (Martin 1992). Physical features of the breeding habitat influence opportunities for nesting, foraging, and protection from enemies (Cody 1981) and may ultimately reflect the suitability of a site for the reproduction and survival of breeding birds (Hilden 1965). Hence, to effectively manage for the conservation of songbird populations, it is critical to identify the specific habitat features that directly influence fitness components of reproduction and survival (Martin 1992). Given that nest predation is the main factor causing reproductive failure in passerine birds (Ricklefs 1969, Martin 1992) and brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) significantly decreases the reproductive success of many neotropical migrants (Brittingham and

Temple 1983), it is imperative to identify the physical features of the nesting habitat that influence rates of nest predation and brood parasitism. Long-term solutions to maintaining populations of neotropical migrant birds include the identification of habitat features that directly impede the effectiveness of predators and brood parasites at locating nests (Martin 1992). In addition, the identification of and reduction of land use practices that augment predator and brood parasite populations are necessary.

As a result of reported declines, there has been a surge of research on neotropical migrant bird populations in recent years. Studies have documented that rates of nest predation and brood parasitism respond to habitat variation at several spatial scales, including the micro-scale (Martin 1993) and the nest-patch scale (Bowman and Harris 1980), as well as to edge proximity (Gates and Gysel 1978) and the pattern of forest and interstitial land use in the surrounding landscape (Donovan et al. 1997). Few studies have simultaneously investigated the relative importance of habitat characteristics at more than one spatial scale to the reproductive success of birds. Many ecological processes that might affect nest predation and parasitism operate at multiple spatial scales (Bergin et al. 2000) and are complex, potentially involving several interactions between variables at different spatial and temporal scales. Therefore, accurate interpretation of the mechanisms driving rates of nest predation and parasitism will require viewing these ecological processes at multiple scales (Donovan et al. 1997) and proper management of songbird populations will require more studies to use a multi-scale approach.

A drastic example of forest habitat loss in the southeastern United States has been in bottomland hardwood forests (MacDonald et al. 1979, Mitsch and Gosselink 1986). Bottomland hardwood forests are the most productive and ecologically important wetland ecosystems in the world today (Conner 1994), contain some of the richest and most diverse plant and animal life found in North America (Mitsch and Gosselink 1986), and are of hemispheric importance to neotropical migratory birds as prime breeding habitat (Hunter et al. 1993). It is estimated that 55% of the existing bottomland hardwoods are found in the Mississippi Alluvial Valley (MAV;

Mitsch and Gosselink 1986); however, only about 20% of the original 9 to 10 million hectares of bottomland hardwood forests in the MAV remain (Yin et al. 1997). Conversion to agriculture, timber removal, and the construction of flood control and navigation structures have eliminated bottomland hardwood forests from much of the MAV and, as a result, agriculture has replaced forest as the dominant land cover within the MAV. Most of the remaining bottomland forest within the MAV exists as small patches surrounded by a sea of agriculture; within such a landscape, forest-nesting birds are exposed to an abundance of generalist predators and Brown-headed Cowbirds. Breeding Bird Survey trends for the 38-year period from 1966-2003 reported that of 31 neotropical migrant species within the Mississippi Alluvial Plain, 39% showed declines (Sauer et al. 2004). Whether fragmentation, an altered hydrological regime, or a plant species composition that reflects silvicultural treatments rather than natural conditions are causing migratory bird population declines is unknown (Pashley and Barrow 1993). For the above reasons, and the predicted 18% increase in timber removal within bottomland hardwood forests for the next 30 years (Moorman et al. 2002), the bird conservation group Partners in Flight has identified bottomland hardwood forests as a habitat of regional concern (Hunter et al. 1993).

Despite the importance of and the imperiled state of bottomland hardwood forests, there is a lack of long-term data sets indicating the response of songbirds to silvicultural treatments applied to bottomland hardwood stands. Several papers have provided some guidance to land managers concerning silviculture for songbirds in bottomland hardwoods (Dickson et al. 1995, Hamel 1992, Pashley and Barrow 1993, Wigley and Roberts 1994, 1997); however, the authors of these papers note that existing monitoring data is comprised mostly of relative abundance information without data on reproductive success (Hamel et al. 2001). Assessment of avian densities and measurements of productivity are integral to conservation planning for forest birds within bottomland hardwood forests; however, there is a paucity of studies that have investigated the effects of fragmentation or edge on the reproductive success of birds breeding within bottomland hardwood forests in the southeastern US. Clearcutting (<20 ha) and patch-cutting (<4 ha) are the most proven and popular methods used to regenerate bottomland oaks in the South, while group cuts (<0.5 ha) are used to maintain uneven-aged stands (Clatterbuck and Meadows 1993, Dickson et al. 1993, Meadows and Stanturf 1997). All methods of timber removal cause internal fragmentation of otherwise contiguous forest while increasing the amount of internal edge. The forest openings created by the silvicultural practices may provide habitat for nest predators and parasites, thus increasing rates of nest predation and brood parasitism within the forest; however, the effects of current forestry practices within bottomland hardwood forests on the reproductive success of the birds that breed within them are largely unknown (Pashley and Barrow 1993). Additionally, there is an absence of research in the published literature on the effects of other types of edges within bottomland hardwood forests on the nesting success of forest-interior songbirds. The dearth of existing research, as well as the fact that fragmentation and edge effects may vary with species, habitat, landscape context, and region, indicates that further research within the bottomland hardwood forests of the southeastern US is warranted.

This study addresses the need for information on the reproductive success of neotropical migrant songbirds within bottomland hardwood forests of the MAV. The study was conducted within the White River National Wildlife Refuge, located in the MAV of southeast Arkansas, during the breeding seasons of 1996-2000. I focus on the nests of two common bottomland hardwood forest songbirds, the Acadian Flycatcher (*Empidonax virescens*) and Prothonotary Warbler (*Protonotaria citrea*), to examine nest survival from predation and the likelihood of brood parasitism in relation to the physical characteristics of the nesting habitat at the micro-, macro-, and landscape scale. These physical characteristics include descriptions of nest placement, vegetation structure, proximity and exposure to various internal edges such as roads, sloughs, and patch cuts, and proximity to external forest edges. Additionally, I investigate how characteristics of the water that describe the timing, duration, and spatial extent of the seasonal flooding are related to nest predation. I simultaneously assess the importance of the habitat and water characteristics on the risk of nest predation and simultaneously evaluate the relative importance of habitat features on the parasitism fate of nests.

This dissertation is organized into five chapters. Chapter 1 consists of a review of the published literature regarding nest predation and parasitism in relation to nesting habitat at local and landscape scales, including nest placement, vegetation characteristics, habitat fragmentation, external and internal edges, and forest management. Chapter 2 contains detailed background information, including accounts of the focal bird species, a description of the study area, and other essential background information on the number and the success of nests within the study. Chapters 3 and 4 are written in manuscript form. Chapter 3 explores the relationship between nest survival from predation and the habitat and water characteristics of the nesting habitat. Chapter 4 assesses the relative importance of habitat characteristics to nest parasitism status. Chapter 5 is a brief overall summary of the entire study and conclusions.

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CHAPTER 1

LITERATURE REVIEW

INTRODUCTION

Populations of many neotropical migratory songbirds have been declining in recent decades (Robbins et al. 1989, Terborgh 1989, 1992, Askins et al. 1990, Finch 1991, Robinson and Wilcove 1994). It is unclear whether these changes in population levels are attributable to habitat changes on the wintering grounds (Robbins et al. 1989, Terborgh 1989, Askins et al. 1990), breeding grounds (Sherry and Holmes 1992, Bohning-Gaese et al. 1993), or within the migration routes (Moore et al. 1995). Most likely, migratory bird populations are limited by a combination of factors within the three time periods (wintering, breeding, migration) of the annual cycle, but the relative contribution of the three remains a point of controversy (Sherry and Holmes 1995).

The declines in many neotropical migrant songbird species can be linked to a reduction in breeding and wintering habitat (Robinson et al. 1995). As a result of the high degree of forest fragmentation and habitat loss in the eastern United States, factors affecting the breeding grounds have been suggested as the primary cause of migrant declines, presumably through decreased reproductive success (Robbins 1979, Whitcomb et al. 1981, Ambuel and Temple 1983, Wilcove and Whitcomb 1983, Lynch and Whigham 1984, Wilcove and Robinson 1990, Robinson et al. 1995, Sherry and Holmes 1995). Increased rates of predation (Wilcove 1985, Yahner and Scott 1988) and brood parasitism (Brittingham and Temple 1983, Temple and Cary 1988) suffered by forest-interior neotropical migrant songbirds in these fragmented landscapes may be a cause of their decline in North America (Robbins et al. 1989, Askins et al. 1990, Wilcove and Robinson

1990, Bohning-Gaese et al. 1993, Robinson and Wilcove 1994, Donovan et al. 1995, Robinson et al. 1995).

As a result of reported population declines in forest-interior neotropical migrants, and the importance of having adequate breeding habitat for maintaining populations, research on these bird populations has expanded greatly in recent years. In the past, ecologists assumed that the most important ecological processes affecting animal populations operated at local spatial scales such as vegetation structure (e.g., Anderson and Shugart 1974). Along this line of thought, an influx of studies in the 1980's utilized multivariate statistics to model songbird habitat using vegetation characteristics (e.g., Capen et al. 1986). Subsequent studies expanded on these and investigated how vegetative characteristics modeled at the nest-site and nest-patch scale affected the reproductive success of birds. More recently, ecologists have become increasingly aware of the importance of examining ecological processes at spatial and temporal scales relevant to both the organisms and the processes under study (e.g., Wiens 1989). It is recognized that structural features of the vegetation and local habitat may not by themselves be adequate for understanding spatial variation in reproductive success of birds, but that larger scale features should also be considered (Saab 1999). In response, many studies have considered effects of vegetation structure, habitat fragmentation, forest edges, and other human-mediated changes at both local and landscape scales (see Keast and Morton 1980, Hagan and Johnston 1992, Martin and Finch 1995, Schmidt and Whelan 1999, Askins 2000).

Physical features of the breeding habitat influence opportunities for nesting, foraging, and protection from enemies (Cody 1981) and may ultimately reflect the suitability of a site for the reproduction and survival of breeding birds (Hilden 1965). Avian breeding success is higher in more suitable habitats (Dow 1969, Fretwell 1972, Holm 1973), suggesting that habitat selection is adaptive (Nettleship 1972). Fecundity is the primary demographic parameter influencing population dynamics of songbirds (Temple and Cary 1988). Hence, to effectively manage for the conservation of songbird populations, it is critical to identify the specific habitat features that directly influence fitness components of reproduction and survival (Martin 1992). Given that nest predation is the major cause of reproductive failure in most passerine birds (Ricklefs 1969, Martin 1992) and brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) significantly decreases the reproductive success of many neotropical migrants (Brittingham and Temple 1983), it is imperative to identify the physical features of the nesting habitat that influence rates of nest predation and brood parasitism.

The notion of identifying habitat features that directly influence the reproduction and survival of birds prompted numerous studies on breeding habitat attributes and their effects on the reproductive success of neotropical migrants, especially those of the forest-interior. Variables at several scales – micro-habitat, macro-habitat and landscape – have been investigated. However, further knowledge on the relative importance and the interaction of variables at multiple scales with respect to reproductive success is necessary for comprehensive management of songbird populations.

MICRO AND MACRO NEST-SITE CHARACTERISTICS

NEST PREDATION

Anti-predator strategies evolved by birds include direct effects of parental behavior (nest defense, predator distraction), as well as indirect effects such as selection of nest site (Weidinger 2002). Given the importance of nest predation to the reproductive success of birds, natural selection should favor birds that place their nests in sites that are less vulnerable to predation (Martin 1992). It has been documented that nest predation events affect re-nesting location, suggesting that nest predation may represent a proximate mechanism that governs a bird’s choice about where to nest (Rodewald and Yahner 2001b). Birds select nest sites non-randomly (Martin 1992; e.g., Petersen and Best 1985, Bekoff et al. 1987, Martin 1993b) and there is evidence that they can identify nest sites with characteristics that reduce the risk of predation (Stauffer and Best 1986, Martin and Roper 1988). The structural characteristics of the habitat surrounding nests may influence chances of nest success (Chasko and Gates 1982) and it has been documented that nest predation rates vary with attributes of nest sites (Nice 1957, Ricklefs 1969, Collias and Collias 1984, Martin and Roper 1988, Kulesza 1990, Martin and Li 1992, Martin 1993b). Nest-site characteristics influence predation rates via changes in nest encounter rates and recognition time (Schmidt 1999). By selecting safe nest sites, birds can either decrease nest encounter rates by incidental nest predators (Vickery et al. 1992a, Schmidt et al. 2001) or decrease nest detectability by actively searching predators (Weidinger 2002). Studies have suggested that nest-site selection within bird species, as well as differences in nest types between species, are important determinants of variation in nest predation risk (Martin 1993b, 1995, 1996, 1998). Nest predation varies in relation to vegetation layers (Best and Stauffer 1980, Martin 1993a) and nest types (Nice 1957, Moller 1989). Characteristics of the nesting micro-habitat and macro-habitat, such as nest concealment, nest height, percent canopy and ground cover, and vegetation density and heterogeneity, have been related to predation risk, although the evidence about their relative influence on predation likelihood is conflicting (Table 1.1).

Concealment by vegetation has received the most attention from investigators and may be a key habitat feature influencing predation, although the relationship between concealment and nest loss is not consistent (Martin 1992, Howlett and Stutchbury 1996, Rangen et al. 1999, Weidinger 2002). In a review of 56 studies, Martin (1992) concluded that in the majority (7 out of 11) of passerines studied, dense foliage directly around the nest reduced the probability of predation through concealment of the nest. Studies have found nest concealment to be significantly related to decreased predation rates (Nice 1937, Nolan 1978, Chasko and Gates 1982, Martin and Roper 1988, Flaspohler et al. 2000, Weidinger 2002). However, many other studies have found no relationship between nest concealment and predation (Bowman and Harris 1980, Holway 1991, Filliater et al. 1994, Howlett and Stutchbury 1996, Donovan et al. 1997, Wilson 1997, Huhta et al. 1998a, Flaspohler et al. 2000, Ricketts and Richison 2000). A significant positive relationship between nest concealment and predation rate that is dependent upon the type of predator (e.g., avian or mammalian) has been documented. For example, Rangen et al. (1999) found that small mammals depredated well-concealed nests, while birds depredated poorly concealed nests. Because many mammalian predators rely on both olfactory and visual cues while foraging, cover at the nest and surrounding vegetation may not be important unless it restricts movement, whereas, cover may decrease predation by avian predators that rely on visual cues (Cotterill and Hannon 1999). As a generalization, nests surrounded with more vegetative cover are less likely to be depredated (Martin 1992), but predator distribution and search methods (Martin 1987, Moller 1989) may be important factors.

The susceptibility of nests at various heights above ground to predation is also controversial, with some finding increased nest height related to decreased predation (Yahner and Cypher 1987, Martin and Roper 1988), others finding decreased predation for ground nests (Yahner et al. 1989, Rudnicky and Hunter 1993), and others finding no relationship (Filliater et al. 1994, Howlett and Stutchbury 1996, Wilson 1997). The relationship between nest height and susceptibility to nest predation may vary with the type of predator and the location of the nest (e.g., opening, edge, forest; with associated differences in vegetative structure; e.g., Rudnicky and Hunter 1993, Rangen et al. 1999, Tittler and Hannon 2000). For example, while arboreal nests may be less conspicuous and less accessible to large mammalian ground predators, they may be easily detected and accessed by visually oriented avian predators flying overhead or scanning from nearby perches (Yahner and Scott 1988, Huhta et al. 1996). This may be especially true if the nest is located within a forest opening as opposed to within the forest (Yahner et al. 1989); in a forest opening, avian predators will have a wider visual field, whereas large mammalian predators may experience inhibited movement and decreased foraging efficiency because of increased density of ground vegetation (Bowman and Harris 1980). Alternatively, a ground nest located within a forest opening, because of the same complex vegetative structure and dense ground cover, may benefit from increased nest concealment and experience decreased predation pressure from visually hunting avian predators (Yahner and Cypher 1987, Suarez et al. 1997).

These same ground nests, however, may experience increased predation from small mammalian predators that use the dense ground cover for their own protection while foraging in open areas (Rudnicky and Hunter 1993). Thus, the effect of nest height on predation rates may vary with nest location within the habitat and the abundance, diversity, and distribution of predators within the habitat. Ground nests may be subjected to greater predation in habitats where mammals are the dominant predators. If concealing cover is similar, avian predators are likely to be equally efficient at locating ground or above-ground nests (Ratti and Reese 1988), but there is some evidence that avian predators are more likely to prey on high nests that are more conspicuous (Darveau et al. 1997). Variable predation pressure on ground and above-ground nests is likely due to the suite of predators important to the particular study area and their respective foraging strategies (Ortega and Capen 2001).

Although predation studies at the scale of the nest-patch are few, results suggest that increased density, structural complexity, and heterogeneity/patchiness of vegetation in the surrounding nest-patch decrease predation rates (Bowman and Harris 1980, Chasko and Gates 1982, Martin and Roper 1988), however the mechanism by which this relationship occurs is debatable. Several hypotheses have been suggested to explain the link between the vegetation surrounding nests and the susceptibility to nest predation. Increased vegetation near the nest may conceal the nest by obscuring visual cues and may inhibit the transmission of auditory and olfactory cues produced by the nest, parents, and young, thereby decreasing predation risk (Howlett and Stutchbury 1996, Flaspohler et al. 2000). In addition, dense and structurally complex vegetation within the nest-patch may decrease predation risk by reducing predator search efficiency; the vegetation may impede predator movement and/or increase the number of potential nest sites that must be searched (Bowman and Harris 1980, Martin and Roper 1988). Along this same line of thought, Chasko and Gates (1982) suggested that predators may not be able to exploit patchily distributed nests and Morse and Robinson (1999) speculated that predators might search more efficiently in homogenous habitats.

The inconsistent relationship found between micro- and macro-habitat features of nest sites and the probability of predation has been attributed to spatial/temporal variation in the abundance and diversity of nest predators, as well as to interactions among the effects of nest sites and species-specific parental and predator behavior (Rangen et al. 1999, Schmidt 1999, Dion et al. 2000, Martin et al. 2000, Schmidt et al. 2001, Weidinger 2002). Factors influencing nesting success may vary according to whether predator communities are dominated by mammals, snakes, or birds, or whether predators use visual or olfactory cues to locate nests (Whelan et al. 1994). Interpretation of the observed patterns of predation is often limited by investigators' lack of knowledge concerning the identity of nest predators in their particular study system (Weidinger 2002). An environment with a variety of predators, each using different nest-searching strategies, may eliminate the existence of predictably safe nest sites (Filliater et al. 1994). Additionally, strong selection on nest-site choice may have occurred in an environment that differs from that currently found on the breeding grounds. That is, increased habitat loss and alteration may have subjected birds to a novel community of predators to which they are not adapted (Ricketts and Ritchison 2000). The different scales used by nest predation studies may also account for the highly variable and conflicting results.

BROOD PARASITISM

Specific habitat features of the nest site might also influence nest discovery by the parasitic Brown-headed Cowbird and thereby affect rates of nest parasitism. Differences in vegetation structure within the vicinity of host nests may influence the risk of parasitism by affecting the efficiency of the cowbird's nest-searching strategies. It is believed that cowbirds locate nests by visual and acoustic cues provided by hosts during nest-building activities (Friedmann 1929, Uyehara and Whitfield 2000) and that they use elevated perches from which they scan for potential hosts (Friedmann 1963). If so, then parasitism risk could be lower if vegetation within the nest-site, nest-patch, or territory concealed the nest as well as the behavioral cues of the nesting pair, thus impeding the cowbird's ability to observe host behavior and to locate nests. Vegetation structure within the nesting habitat may also affect the local variation of host densities, thus influencing where cowbirds will locally concentrate their nest-searching activities, assuming they are attracted to areas of high host abundance (Johnson and Temple 1990, Brittingham and Temple 1996).

Compared with nest predation, examinations of micro- and macro-habitat influences on nest parasitism are lacking. Similar to nest predation, however, the results of these studies are mixed and suggest that vegetation characteristics at the nest site itself are unreliable predictors of parasitism. Brittingham and Temple (1996) quantified the vegetation around parasitized and non-parasitized nests at the macro-scale and found that canopy openness was positively related to parasitism. They argued that the structural features that are associated with high levels of parasitism are also associated with both ease of observation and high host density. Similarly, Wolf (1987) categorized nesting habitats of Dark-eyed Juncos (*Junco hyemalis*) as open or closed canopy and reported increased frequencies of parasitism in open habitats. Smith (1981) found that Song Sparrows (*Melospiza melodia*) showed no correspondence between nest concealment and parasitism. A different study on Song Sparrows found that vegetation structure affected the probability of parasitism at two scales, broad (within 11 m of the nest) and local (within 5 m of the nest), and found that lateral cover was negatively associated with parasitism and foliage cover was positively associated with parasitism (Larison et al. 1998). A pre- and post-burn study within the breeding area of Yellow Warblers (*Dendroica petechia*) reported that parasitism rates did not increase post-burn when nests had comparatively less vegetative cover (Howe and Knopf 2000). Uyehara and Whitfield (2000) reported a negative relationship between the density of understory vegetation within the territory of the Southwestern Willow Flycatcher (*Epidonax traillii extimus*) and the parasitism of their nests.

It is hypothesized that a relatively open canopy and sub-canopy would enable cowbirds to attain an elevated perch with an unobstructed view of host nest-building activities below, thus improving their efficiency at locating nests (Freeman et al. 1990, Brittingham and Temple 1996).

However, lack of canopy cover does not always correlate with higher frequencies of parasitism and mixed results might occur if cowbirds search for and parasitize nests below the canopy (Uyehara and Whitfield 2000). It has also been suggested that cowbirds may locate nests by walking on the ground of forests and looking upwards at potential hosts (Lowther 1993, Uyehara and Whitfield 2000). If so, then the presence of dense ground vegetation or water may prevent or disrupt this type of search method (e.g., Moorman et al. 2002).

The pervasive nature of nest predation and parasitism and the influence of nest sites on risk of predation and parasitism indicate that nest sites are important habitat components and that the nesting season is a critical period for maintenance of bird populations (Martin 1993b). Conservation of bird species depends on reducing the limiting nature of nest predation and parasitism through knowledge of the birds' breeding biology, understanding their habitat requirements, and identifying and preserving the habitat features that affect their breeding productivity and survival (Martin 1992). Long-term solutions to maintaining populations of neotropical migrant birds includes the identification of habitat features that directly impede the effectiveness of predators and parasites at locating nests (Martin 1992). In addition, the reduction of land use practices that augment predator and brood parasite populations, such as agriculture and urban development that fragment breeding habitat, is necessary.

FOREST FRAGMENTATION

Studies at local scales confirm the importance of nest predation and brood parasitism and suggest that they have intensified as landscapes have become fragmented by human activity (Robinson 1992, Sherry and Holmes 1992). Fragmentation is the disruption of continuity of a habitat. This disruption creates edge, the ecotone between plant community types, successional stages, or land uses (Yahner 1988), reduces core area resulting in the loss of interior forest specialists (Temple 1986, Blake and Karr 1987), and increases the isolation of patches (Noss 1987). Fragmentation of extensive forests into smaller patches has occurred in many temperate forest regions due to conversion to agricultural or urban land uses. Forest fragments have a higher proportion of exterior edge than do larger, more intact forests and are thus more influenced by the matrix in which they are embedded (DeGraaf 1995). Such influences include higher rates of nest predation (Andren and Angelstam 1988) and brood parasitism (Wilcove 1985, Robinson 1988, Temple and Cary 1988), reduced pairing success, and lowered reproductive performance (Faaborg et al. 1995). Nest predation increases with fragmentation of forested habitat because many predators benefit from the increased ratio of edge habitat to forest interior; this is particularly true when fragmentation is accompanied by human residential developments and attendant food subsidies for populations of generalist predators such as corvids, skunks (*Mephitis mephitis, Spilogale putorius*), and raccoons (*Procyon lotor*; Wilcove 1985, Temple and Cary 1988, Yahner 1988, Small and Hunter 1988, Terborgh 1989, Finch 1991). Similarly, brood parasitism by Brown-headed Cowbirds increases with forest fragmentation and regional extent of agriculture (Brittingham and Temple 1983, Terborgh 1989, Robinson 1992, Robinson et al. 1993). Populations of cowbirds flourish in landscapes that offer a mixture of both feeding (agricultural) and breeding (forest) habitats (Donovan et al. 1997), and areas with high cowbird densities experience high parasitism rates (Hoover and Brittingham 1993).

The adverse effects of habitat fragmentation and decreased proportion of forest cover on rates of nest predation and parasitism are well documented on a landscape scale (Faaborg et al. 1995, Robinson et al. 1995, Donovan et al. 1997, Hartley and Hunter 1998). Andren (1992) reported that nest predation rates by corvids on artificial nests placed in forests increased as the proportion of agricultural land in the surrounding landscape increased from 4% to 80%. Similarly, Hoover and Brittingham (1993) found that the rate of cowbird parasitism on Wood Thrush (*Hylocichla mustelina*) nests is lower in the northeastern US than in regions with a higher proportion of agricultural land (e.g., the Midwestern and mid-Atlantic states). These studies suggest that forest fragmentation has a greater impact on breeding success of forest songbirds in predominantly agricultural landscapes than in heavily forested landscapes (Askins 1994).

The negative effects of forest fragmentation may depend on the spatial and temporal extent of the fragmentation and on the type of non-forest land use creating the fragmentation. Spatially, forest fragmentation ranges on a continuum from "intrusive fragmentation," where gaps are created in a continuous matrix, to "enveloping fragmentation," where continuous forest is broken into isolated fragments (Manolis et al. 2000). Temporally, forest fragmentation ranges from relatively temporary fragmentation of age-class, such as that caused by timber harvest, to more permanent conversion to non-forest habitats such as agriculture (Manolis et al. 2000). Most studies examining forest fragmentation effects on avian reproduction have been conducted in agricultural landscapes and have found increased predation and parasitism with increased fragmentation (Table 1.2; e.g., Donovan et al. 1995, Robinson et al. 1995). However, results from these studies may not be relevant to forested landscapes fragmented by silvicultural practices, as the majority of studies examining fragmentation effects within forest-dominated landscapes fragmented by timber harvests do not report increased predation or parasitism (Table 1.2; but see Yahner and Scott 1988, Yahner and Mahan 1996, Annand and Thompson 1997, Robinson and Robinson 1999). Forest fragmentation caused by small and/or temporary openings within areas that remain extensively forested may not lead to reduced reproductive success of birds (Small and Hunter 1988). Results from such studies as Ratti and Reese (1988), Thompson et al. (1992), and DeGraaf and Angelstam (1993) demonstrate that managed forest landscapes probably function differently from permanently fragmented landscapes and that fragmentation as a result of silviculture might have less deleterious effects on breeding birds than fragmentation by agriculture.

The dissimilarity of predation and parasitism rates between predominantly forested landscapes fragmented by silvicultural practices and landscapes fragmented by agriculture is often explained in terms of differences in productivity between habitats. Angelstam (1986) and Andren (1992) argued that the steepness in the productivity gradient between forest stands and the surrounding open matrix is the main cause increasing predation pressure at the edge zone of forest stands. Forestry practices tend to produce softer edges than does agriculture and produces landscapes characterized by a more complex mosaic of stands that vary by age, structure, and composition (Bourque and Villard 2001). These landscapes may contain lower abundances of nest predators than do forests embedded in an agricultural landscape (Bourque and Villard 2001). In addition, silvicultural openings within forest-dominated landscapes do not provide feeding opportunities for brood parasitic cowbirds and, unless within the home range of a cowbird feeding area, should not attract cowbirds or cause increased rates of nest parasitism. In contrast, agricultural landscapes are highly productive habitats that contain supplemental food for both generalist predators (e.g., corvids and raccoons) and parasitic cowbirds, leading to higher densities of potential nest predators and brood parasites that may infiltrate the adjacent forests and increase nest predation and parasitism rates (DeGraaf and Angelstam 1993). In essentially forested habitats managed for timber, where agricultural land is a minor component of the landscape, productivity is lower, the densities of generalist predators and cowbirds are lower, and thus predation and parasitism rates should be lower (DeGraaf and Angelstam 1993). Although the effect of silvicultural or agricultural fragmentation may depend on landscape-scale forest cover (Donovan et al. 1997), within a given landscape, different types and qualities of non-forest habitats or disturbances can influence predation and parasitism levels (Donovan et al. 1997). Thus, the composition of the entire landscape mosaic should be taken into account when examining effects of forest fragmentation and the external and internal edge that it creates.

EDGE EFFECTS

Phenomena associated with forest edges and the existence of “edge effects” has been well studied throughout the last 70 years (Leopold 1933, MacArthur and MacArthur 1961, Odum 1971). Originally, it was thought that the edge between adjacent habitat types was beneficial to wildlife because it increased plant and animal diversity, leading wildlife managers to widely prescribe the creation of edges (Leopold 1933, Temple and Flaspohler 1998). It was not until the late 1970's, that the beneficial edge paradigm was questioned by studies that looked at the effects of forest edges on non-game species, specifically songbirds (Gates and Gysel 1978, Brittingham and Temple 1983). Research that is more recent revealed that for some forest-nesting songbirds, the presence of forest edges might represent a hostile environment (Gates and Gysel 1978, Brittingham and Temple 1983). It has been hypothesized that the increase in predator diversity and density, as well as abundance of brood parasitic cowbirds, typically found at forest edges will result in elevated rates of nest predation and brood parasitism (Donovan et al. 1997) and reduce the productivity of birds nesting within/near the edges (Brittingham and Temple 1983, Wilcove 1985, Robinson et al. 1995). Since the 1980's, the negative effects of forest edges on forest-nesting songbirds have become a major conservation issue.

EXTERNAL EDGE EFFECTS

The effects of external edges, the edge created between forest and the enveloping non-forest land, on the reproductive success of forest-interior songbirds have been well studied (Table 1.3; Paton 1994, Andren 1995, Murcia 1995, Hartley and Hunter 1998, Lahti 2001). In reviewing 21 studies of nesting success at forest edges, Paton (1994) determined that in 70% of the cases, nest success declined near edges, with predation and parasitism rates being significantly greater within 50 meters of an edge. However, the generality of edge effects has been debated because results have been highly variable. A lack of consistency in experimental design among studies may be partly responsible for the variable results (e.g., distance intervals, nest types (artificial/natural), edge definition; Paton 1994). Furthermore, edge effects may be context-dependent and vary with differences in the type of edge (i.e., agriculture/silviculture, productive/non-productive, permanent/temporary, hard/soft), the landscape mosaic, the extent of fragmentation at the landscape scale, and the local predator assemblage.

NEST PREDATION AND PREDATORS

In his 1995 review, Andren found that edge-related increase in nest predation primarily occurred near forest-agriculture edges, and generally did not occur in forest-silviculture edges (but see Lahti 2001). Additionally, he reported that higher predation rates at forest-agriculture edges were more likely to occur in farmland-dominated landscapes than in forest-dominated landscapes (also see Table 1.3). In another review, Lahti (2001) reported that the existence of an edge effect is demonstrated more often in landscapes of high fragmentation (<50% forest) than in landscapes of low fragmentation (>75% forest; also see Donovan et al. 1997, Hartley and Hunter 1998). A meta-analysis of predator responses to edge (i.e., increased abundance, activity, or species richness) revealed that predator responses vary according to spatial scale, landscape context, and predator taxon (Chalfoun et al. 2002b). Predator effects were most frequently detected in tests at the landscape scale, followed by the local-scales of the patch and edge. Local-scale edge effects were more variable than landscape effects, and differed according to the surrounding land-cover type. Edge effects were found to be most common at forest-agriculture edges when tests were conducted within agricultural landscapes (Chalfoun et al. 2002b). This finding supports Donovan's et al. (1997) and Thompson's et al. (2002) hypothesis that local-scale edge effects are constrained by factors at the landscape scale (e.g., forest cover and surrounding land use). Results of Chalfoun's et al. (2002b) meta-analysis also parallel those studies that found edge effects to be inconsistent (Paton 1994), but most prevalent in more fragmented landscapes (Donovan et al. 1997, Hartley and Hunter 1998) and in agriculturally-dominated landscapes (Andren 1995). Previous research has documented that edges and/or landscapes that provide supplemental resources for potential predators are most likely to affect their distributions (Andren 1995).

Numerous hypotheses have been proposed to explain the observed increase in predator abundance and activity, and nest predation rates near habitat edges. The "ecological trap" hypothesis, originated by Gates and Gysel (1978), stated that edges would attract a high density of nesting birds and a commensurate increase in nest predation rates as predators increase their activity in response to increases in nest density (density-dependent predation; Krebs 1971, Fretwell 1972). Birds may be attracted to edges because they derive some benefit from the increased vegetative complexity found there related to food, nest-site cover, and singing or observation perches (Flaspohler et al. 2001a,b). Predators may show functional and numerical responses to high nest densities by increasing the time and intensity of their search efforts along edges (Martin 1988). Another widely espoused hypothesis involves the use of habitat edges by potential nest predators as natural traveling lanes because of the abrupt change in vertical vegetation structure found there (Bider 1968; but see Lariviere 2003). The travel-lane hypothesis predicts that predators traveling along edges, and the resultant increase in time spent at these edges, will bring about an increase in incidental predation along these edges (Angelstam 1986, Vickery et al. 1992a). It is also hypothesized that generalist predators (e.g., raccoons, opossums (*Didelphis virginiana*), skunks, corvids) associated with one type of habitat (e.g., agriculture), might "spillover", or penetrate, into the neighboring habitat (e.g., forest), thus increasing predation at the habitat edge (Wilcove 1985, Angelstam 1986, Oksanen et al. 1992). Chasko and Gates (1982) suggested that predators might increase activity at edges because of the presence of increased vegetative cover that may provide protection from their own predators. Additionally, predator activity may be higher near edges because it is the junction of two habitats and predators associated with both habitats will be more likely to occur there (Bider 1968). These predators may spend increased foraging time along edges because of the opportunity to simultaneously obtain prey from the two adjacent habitats. Lastly, abrupt-edge habitats are often associated with relatively recent environmental perturbations by humans, and birds may simply be poorly adapted to predation near artificial, human-made, edge zones (Ratti and Reese 1988). Recent and abrupt human-made edges may have greater predator abundance and lack a regenerating shrub layer, thus increasing nest visibility and resulting in higher predation rates (Suarez et al. 1997).

The intensity of the edge effect (i.e., the distance that the effect penetrates into the forest), may aid in elucidating which, if any, of the above mechanisms is occurring. If predation rate is related to increased prey density at the edge, the use of the edge as a travel lane, increased vegetative cover, or the junction of two habitats, then the edge-related increase in predation rate should be confined to the very edge. However, if predation rate at edges is related to predators entering from the surrounding habitat, the effect may penetrate considerable distances into the forest, thus allowing habitat generalists the largest potential to cause an increase in predation pressure at edges (Andren 1995).

Rates of nest loss reflect the cumulative pressure exerted by a suite of predator species, each exhibiting unique responses to the landscape, the habitat, and the presence of internal edges (Miller and Hobbs 2000). Although there is widespread concurrence that investigating the autecology of nest predators would facilitate a better understanding of nest predation patterns at edges (e.g., Paton 1994, Andren 1995, Sherry and Holmes 1995), few edge studies have identified the predators responsible for the nest predation (Chalfoun et al. 2002b). Although culpable predators are seldom identified, researchers regularly infer, yet make confident assertions, as to the responsible predator based on predator sightings within the study area or on characteristic signs of nest remains (Major and Kendal 1996). Both of these methods are unreliable sources of information (Major and Kendal 1996, Lariviere 1999) and are no substitute for actual identification of predators and sound natural history data. Despite this gap in knowledge, results are often explained by invoking causal mechanisms that employ species-specific predator behaviors and their relation to specific habitat and landscape features. These hypotheses, however, have rarely been tested empirically (Chalfoun et al. 2002b). For example, crows are adapted to edge habitats (Whitcomb et al. 1981), and their increased abundance in forested habitats containing considerable amounts of edge (Huhta et al. 1996) is often cited as being responsible for higher rates of predation without positive identification of the actual predator (e.g., Yahner et al. 1993). Similarly, the abundance of mammalian predators, such as raccoons, typically increases with greater amounts of edge and habitat diversity in the landscape (Heske 1995) and is evoked as an explanation for observed increases in predation rates.

Few studies have evaluated causal mechanisms for nest predation patterns via direct studies of nest predators and instead rely on describing patterns based on correlative nest-centered studies (Chalfoun et al. 2002b). Nest predation patterns observed from nest-centered studies may differ from those observed from predator-centered studies, especially when numerous potential nest predators exist (Lariviere 2003). Lariviere (2003) maintains that specific causal mechanisms cannot be inferred from patterns observed at depredated nests; rather, he argues that studies on the abundance, distribution, and diversity of predators in space and time are needed to transcend description of patterns and actually answer why these patterns exist. Identification of responsible nest predators and research on their behavioral ecology and foraging strategies are necessary to fully interpret the effects of forest habitat disturbances on avian nest success and would alleviate the need to infer cause from correlation (Schmidt 1999, Chalfoun et al. 2002b). For example, we cannot assume that all species (predators, parasites, and forest-nesting songbirds) perceive and respond to edges based on the same criteria (Rich et al. 1994). Investigating mechanisms of nest predation, rather than solely patterns, will enable managers to manage effectively (Lariviere 2003).

Edge studies that did consider predators typically focused on a single predator, for example raccoons (Pedlar et al. 1997) or black rat snakes (Weatherhead and Charland 1985, Durner and Gates 1993), or they pooled several species such as avian predators/corvids (Andren 1992), small mammals (Heske 1995, Bayne and Hobson 1998), or medium-sized mammals (Marini et al. 1995); however, results were then generalized across broader taxonomic groups (Chalfoun et al. 2002b). Studying only one or some of the predator species present may be misleading because it is unlikely that all species of a predator assemblage exhibit similar responses to edge (Fenske-Crawford and Niemi 1997). Thus, generalization about nest predators at edges should be avoided, especially when invoking mechanisms responsible for increased songbird nesting mortality. In a meta-analysis of predator responses (functional, numerical, or species richness) in relation to edge, Chalfoun et al. (2002b) found that predator responses to edge are taxon-specific; certain nest predator species are more abundant in forest edges while others are uniformly distributed or less abundant. In general, avian predators and snakes were more likely to respond positively to edge than were small- and medium-sized mammalian predators (mice, squirrels, skunks, opossums, and raccoons). The type of nest predator involved will largely influence the outcome of an edge-related predator-prey interaction, making it important to identify the predators and study their behavior in relation to the landscape mosaic and local edges.

In addition to studying the ecology of a specific nest predator species in relation to its environment, understanding a predator's foraging strategy is an important, but neglected, variable in our current conceptualization of nest predation (Schmidt 1999). Changes in the environment or to the predator-prey community manifest as measurable changes in nest encounter rates, nest vigilance or defense, and the predator's search effort and strategy, thus ultimately affecting the rate of nest predation (Schmidt 1999). Studies have typically documented the magnitude of nest predation and its patterns in relation to habitat characteristics (e.g., vegetation structure or edges), rather than investigate the process of nest predation as an interaction between predator and prey. Using theoretical concepts of predator foraging theory to investigate nest predation can elucidate mechanisms behind the process. Predator foraging behavior is influenced by properties of the environment, such as structure/composition of the habitat and abundance/distribution of food for both predators and prey, life-history traits of predators and prey that determine encounter rates, such as search strategy, nest-site selection, and nest vigilance, as well as interactions between properties of the environment, the predator, and the prey. Understanding nest predation rates entails more than identifying predators, measuring their abundance and activity within the nesting habitat, and describing patterns; the impact of the predator assemblage on nest predation rates of their songbird prey is complex and will require dissecting the individual interactions among the environment, the predator, and the prey (Schmidt 1999).

BROOD PARASITISM AND COWBIRDS

The effects of external edge on the rates of nest parasitism by brood parasitic cowbirds are far less studied than those of nest predation, partly because of the prevalent use of artificial nests, which are not susceptible to parasitism, in edge studies. Agricultural and residential areas provide foraging habitat for cowbirds and, although averaging less than 2 km, cowbird movement may extend up to 7 km between breeding and feeding sites (Thompson 1994). Thus, songbird nests located within forests adjacent to cowbird feeding areas are at increased risk of parasitism. Within a heterogeneous, managed forest in southern Illinois, Morse and Robinson (1999) found that the incidence of parasitism on ground-nesting Kentucky Warblers (*Oporornis formosus*) was inversely related to the distance from an external agricultural edge that functioned as a cowbird foraging area; however, parasitism rates were not related to forest type or proximity to internal edges within the study area. They documented that brood parasitism levels gradually decreased from 60% to 3% over a distance of 2 km from the agricultural edge proximal to the cowbird foraging site.

INTERNAL EDGE EFFECTS

The majority of forest edge studies have focused on permanently maintained external forest-agricultural edges within agriculturally dominated landscapes (see review by Paton 1994) where abundance of generalist predators is high (Wilcove 1985, Andren and Angelstam 1988, Andren 1992) and nests tend to be concentrated along forest edges (Wilcove et al. 1986, Andren and Angelstam 1988). The effects of internal forest edges, edges created by intrusive perforations within the forest, within forest-dominated landscapes have received far less attention from researchers interested in edge effects on nest predation and nest success of forest-interior songbirds (Flaspohler et al. 2001a,b). Internal edges exist along gaps in the forest canopy created by anthropogenic disturbance such as silvicultural activities (e.g., clearcutting), roads, and powerline right-of-way corridors. Natural forest openings, such as those found along streams or lakes, also create internal edge. Several studies have shown that predator and brood parasitic species, which can greatly reduce the breeding success of songbirds, increase in abundance near external forest edges (Brittingham and Temple 1983). Thus, the introduction of edge into the interior of a forest could have detrimental effects on the ability of songbirds to reproduce successfully (Robinson and Robinson 1999); however, it is unclear if internal edges in extensively forested landscapes cause similar edge effects. An understanding of nest predator and brood parasite responses to habitat disturbance and internal forest edges in extensively forested landscapes may be critical to efforts to conserve forest birds in these landscapes (King et al. 1998b).

Silvicultural Management – Distance From Edge

In many forested landscapes, timber harvesting represents the most common form of habitat alteration on the landscape (Flaspohler et al. 2001a). Intensive forest management creates mosaics of mature stands mixed with successional stands of various ages, thus increasing the amount of internal edge and having a major influence on landscape patterns. Concern has arisen that forest management practices that create internal edges are contributing to regional declines in neotropical migrant birds that inhabit forest interiors (Thompson et al. 1992), and reconciling timber harvesting with the conservation of forest-interior songbirds has become a major concern in applied ecology (Darveau et al. 1997). Clearcutting, a commonly employed harvesting technique, causes intrusive fragmentation in managed forest landscapes that creates temporary internal edges between stands of different age classes. Edges created by clearcutting are initially “abrupt” or “hard”, and as clearcuts regenerate, they become “soft”, and then nonexistent as contrast between the two ages classes diminishes (Manolis et al. 2002). The effect of forest harvest methods on the composition (abundance and richness) of breeding communities of songbirds has been well studied (e.g., Thompson et al. 1992, Faaborg et al. 1995, Hagan et al. 1997, Norton and Hannon 1997, Robinson and Robinson 1999), finding that silvicultural practices modify forest structure and in turn affect bird communities (Thompson et al. 1995). Various bird species respond differently to the same silvicultural treatments within a habitat type. In terms of abundance, some species appear to benefit from timber harvest whereas other species decline, are absent, or appear unaffected. However, abundance can be a misleading indicator of habitat quality and population status (Van Horne 1983, Vickery et al. 1992b); rather, productivity measurements are a better way to assess habitat conditions for sustainable populations (Donovan et al. 1995). In addition to changes in bird densities, lower reproductive success in managed forests could affect populations in these landscapes (Annand and Thompson 1997).

Fewer studies have looked at the relationship of silvicultural practices to the reproductive success of songbirds nesting within forest-dominated landscapes and thus, knowledge is limited on the effects of fragmentation and internal edges caused by timber harvest. A better understanding of the effect of clearcutting on nest predator and brood parasite abundance and distribution will help managers to more accurately assess the impact of forest practices on forest-nesting birds (King et al. 1998b). Despite this lack in information, some researchers have concluded that forest edge effects are less common in extensively forested landscapes managed for timber than in landscapes highly fragmented by non-forest land uses, especially agriculture (Andren 1995, Donovan et al. 1997, Hartley and Hunter 1998, Lahti 2001, but see review Manolis et al. 2000). In support of this conclusion, researchers have declared that forest-clearcut edges are younger, more abrupt, and less likely than forest-agricultural edges to have a higher concentration of nests and an increase in predator foraging activity along them (Rudnicky and Hunter 1993). However, the effects of clearcut-forest edges on potential nest predators and brood parasites and the risk of nest predation and parasitism are not well documented (Rudnicky and Hunter 1993). An increase in studies on edge effects within forest-dominated landscapes and a review of the recent literature on edge effects caused by clearcuts in these landscapes suggests that edge effects may also exist in extensively forested landscapes, however, the evidence is equivocal.

NEST PREDATION AND PREDATOR ABUNDANCE – Several studies within forest-dominated landscapes have reported edge-related increases in nest predation near clearcut edges as opposed to the forest interior (King et al. 1996, Fenske-Crawford and Niemi 1997; also see Table 1.4a). However, results may differ within fragmented habitats; for example, Morse and Robinson (1999) found no relationship between distance to clearcuts and predation rates on Kentucky Warbler nests located within a large, heterogeneously managed forest tract located within an agricultural matrix. Even within forest-dominated landscapes, results of edge effect studies are variable. Two studies within forest-dominated landscapes, both using artificial ground nests to compare nest predation rates in relation to distance from clearcut edges, reported contradictory results; Rudnicky and Hunter (1993) found no difference whereas Manolis et al. (2000) found higher nest predation along edges. In a study of Ovenbirds (*Seiurus aurocapillus*), King et al. (1996) reported increased nest predation rates closer to clearcut edges than within the forest interior. This is one of few studies that used data solely from natural nests of one species rather than composite data from natural nests of many species (e.g., Hanski et al. 1996) or data from artificial nests (e.g., Rudnicky and Hunter 1993). Flaspohler et al. (2001a) and Manolis et al. (2000) reported analogous results to King et al. (1996) in their research with Ovenbirds. In contrast, studies that have combined data among several species nesting at multiple vertical strata (e.g., Hanski et al. 1996, Rodewald and Yahner 2001a), or that have focused on the nests of one canopy-nesting species (e.g., Least Flycatcher or Red-eyed Vireo; Manolis et al. 2000), reported no evidence of edge effects. The different findings among these studies suggest the potential for masking edge-related increases in predation when nests from many species are pooled and highlights the importance of examining species-specific patterns of nest predation at edges.

In reviewing 37 studies of nest predation at clearcut edges within forested-dominated landscapes, 21 (57%) reported no increase in nest predation near the edge as compared to the forest interior (Table 1.4a). The majority of these studies were conducted within the North Eastern and Middle Western parts of the United States, as well as Canada. Of the 37 studies, artificial nests were employed more commonly (59%) than natural nests, and the greater parts of these were ground nests (59%; Table 1.4b). Studies using natural nests were equally biased toward above-ground (shrub or canopy) nests (Table 1.4b). Studies employing artificial nests tended to demonstrate no increase in predation at clearcut edges; however, the results varied with the vertical placement of the nests (Table 1.4a,b). Studies using artificial ground nests were more likely than studies using artificial above-ground nests to report no increase in predation (Table 1.4b). In contrast, studies using natural nests were more evenly divided between those demonstrating and not demonstrating an edge effect (Table 1.4b). Within natural nest studies, however, and opposite to artificial nest studies, ground nests suffered from increased predation near edges while above-ground nests showed no edge effect (Table 1.4b). Several of the studies reviewed were conducted by the same researchers, within the same study area (e.g., Flaspohler (3), Manolis (7), Rodewald (2), Rudnicky and Hunter (2), Vander Haegen (2), and Yahner (5); Table 1.4a). While this fact prevents the consideration of the 37 studies as independent, it provides the opportunity to directly compare results of the same studies that used both artificial and natural nests and, within a type of nest, ground and above-ground nests. For example, Manolis (1999) and Manolis et al. (2000) found increased predation at clearcut edges for both artificial and natural ground nests. Flaspohler et al. (2001a,b), Manolis (1999), and Manolis et al. (2000, 2002) reported increased predation at edges with natural ground nests, but not with natural shrub or canopy nests. In contrast, Rudnicky and Hunter (1993) and Vander Haegen and DeGraaf (1996), using solely artificial nests, reported no increase in predation at edges for ground nests, but an increase in predation for shrub nests. These comparisons are beneficial because they eliminate confounding factors attributable to comparing the results of studies with different experimental designs, conducted in different regions and landscapes, and subject to different predator communities.

In another review of the literature on edge effects caused by clearcuts within forest-dominated landscapes, Manolis et al. (2000) concluded that these edge effects may be common. Originally finding an equal division among those studies reporting elevated predation near clearcut edges and those reporting no edge effects (13 to 12, respectively), after excluding studies with low statistical power and psuedoreplication, they reported that 10 of the 13 studies conclusively found elevated predation near clearcut edges. Often, inconsistencies in edge-effect results are thought to be caused by habitat differences among studies, landscape context differences, problems with artificial nest studies, fluctuating and patchily distributed predator populations, and differences in predator communities (Paton 1994). Despite these inconsistencies, and taking into consideration differences in study design and statistical issues, there is strong evidence for clearcut edge effects as general phenomena in extensively forested regions (Manolis et al. 2000).

Artificial nests have been widely implemented to address variation in predation rates associated with nest type (e.g., open vs. closed), nest visibility, nest location (e.g., height), micro- and macro-habitat vegetation, spatial effects (e.g., fragmentation), habitat (e.g., forest vs. field), external edges, forestry practices, and internal edges. The use of artificial nests, however, has been criticized for many reasons (Roper 1992, Leimgruber et al. 1994, Haskell 1995, Major and Kendal 1996), suggesting that artificial nests may not be appropriate surrogates for studies of real songbird nests and that caution should be used when interpreting results of artificial nest studies.

The purpose of artificial nest studies is to infer something about the processes affecting natural nests; however, making this connection relies on the supposition that, from a predator's perspective, artificial and natural nests are the same (Major and Kendal 1996). If this were true, natural and artificial nests would: (a) have similar predation rates and (b) be attacked by a similar array of predators. It is generally acknowledged that artificial nests do not have daily predation rates similar to real nests (Storaas 1988, Willebrand and Marcstrom 1988, Reitsma et al. 1990, Haskell 1995, King et al. 1996, Sloan et al. 1998, Flaspohler et al. 2001b). Absence of sensory cues provided by parental and nestling activity (Wilson et al. 1998), lack of parental defense (King et al. 1999), and exclusion of certain predators (Haskell 1995, Buler and Hamilton 2000) are a few reasons why artificial nests may not accurately mimic natural nests. Although artificial nests do not provide an accurate estimate of predation rates at real nests, it is argued that they provide a relative index of nest predation (Reitsma et al. 1990, Paton 1994). However, further undermining the assumptions relating to the comparability of natural and artificial nests, there is evidence that separate predators, using distinct sensory cues, differentially attack artificial and natural nests. Avian predators, using visual cues, are believed to prey upon artificial nests while mammalian predators, using olfactory cues, prey more upon natural nests (Paton 1994, Major and Kendal 1996, Darveau et al. 1997). Despite this predilection, some researchers justify their artificial nest experiments on the grounds that whatever the biases, they will be the same across treatments; thus, nonetheless providing a relative index of predation (Andren and Angelstam 1988). However, there is some indication that relative rates of nest predation differ with the situation (e.g., nest type, location) and thus cannot be reliably ascertained (Major and Kendal 1996). Although artificial nests may provide an index of predation rates within a single habitat (Wilson et al. 1998) or among different habitats for a specific predator, they may not provide an accurate indication of predation rates when comparisons are made among habitats or along gradients where the composition of the nest predator community changes or one set of nest predators is replaced by another set of predators (Martin 1988, Haskell 1995, King et al. 1996, Donovan et al. 1997). How well artificial nests represent relative predation rates for passerine birds in various forest environments has not been thoroughly tested (Major and Kendal 1996); however, given the popularity of their use, especially in habitat edge studies, and the potential population effects of reduced reproductive success, confirming the results with real nests would be prudent (Steventon et al. 1999). Although the utility of artificial nests as a tool for elucidating factors influencing the predation of natural nests has been called into question, there is no doubt they have contributed to nest predation theory (Major and Kendal 1996).

In addition to actual nest predation studies, some researchers have focused on the relative abundance of potential nest predators in close proximity to clearcut edges as opposed to the forest interior. The objective of such studies is to assess whether clearcut openings within forest-dominated landscapes increase predator distributions in a manner analogous to the creation of non-forest habitat in human-dominated landscapes and to investigate whether nest predators concentrate at clearcut borders (King et al. 1998b). Underlying these studies is the assumption that increased predator abundance will result in increased nest predation by these predators, as suggested by some researchers (Angelstam 1986, Yahner and Scott 1988, Andren 1992, Hoover et al. 1995, Luginbuhl et al. 2001), and the idea that investigating the autecology of nest predators will facilitate a better understanding of nest predation patterns at edges (Paton 1994, Andren 1995, Sherry and Holmes 1995, Chalfoun et al. 2002a). Strelke and Dickson (1980) and King et al. (1998b) both reported that the relative abundance of an avian nest predator, the Blue Jay (*Cyanocitta cristata*), did not increase near clearcut edges; in fact, Blue Jays were found to be more abundant within the forest interior and absent within clearcut interior and clearcut-forest edge (Strelke and Dickson 1980). In contrast, the relative abundance of small mammalian nest predators, the eastern chipmunk (*Tamias striatus*) and red squirrel (*Tamiasciurus hudsonicus*), were found to increase at clearcut edges relative to the forest interior (King et al. 1998b). Similarly, higher numbers of deer mice were reported near the edges of 6-10 year old clearcut edges than at distances further away (Sekgororoane and Dilworth 1995). In a nest predation study that used artificial ground and shrub nests and identified responsible nest predators, Bayne and Hobson (1997) documented increased depredation of nests by avian predators, but not by small mammals, near clearcut edges. Although this finding contradicts what we might expect based on the relative abundance studies, the use of artificial nests and their vertical placement may influence the results because of differences in the foraging techniques and requirements of avian and small mammalian nest predators (visual/fly-over or perch sites versus olfactory/protective vegetative cover). Although providing insight, the relative abundance of potential nest predators without actual identification of the predators responsible for nest depredations and consideration of their foraging strategies offers an incomplete understanding of the factors influencing the presence/absence of edge effects.

BROOD PARASITISM AND COWBIRD ABUNDANCE – Nest parasitism by Brown-headed Cowbirds and abundance/distribution of cowbirds in relation to internal forest edges caused by timber harvesting within forest-dominated landscapes have received far less attention than predation. The need to study natural nests and the widespread belief that cowbirds are a threat associated with agricultural landscapes, not extensively forested areas (Donovan et al. 1997), may explain the dearth of research on this topic. A study of Hooded Warblers (*Wilsonia citrina*) within an extensively forested bottomland hardwood forest managed for timber found increased rates of nest parasitism near the edges of clearcuts, and extending up to 100 m into the adjacent forest (Moorman et al. 2002). Within smaller openings created by group cuts, cowbirds concentrated their nest-searching efforts near edges of openings greater than 0.26 ha in size; they were detected more frequently in and adjacent to 0.5-ha gaps than in unharvested areas or than within gaps of smaller size (Moorman et al. 2002). Strelke and Dickson (1980) reported increased abundance of cowbirds within clearcuts and at clearcut-forest edge and an absence of cowbirds within the forest interior. Based on these findings and the assertion that areas with higher cowbird densities experience higher rates of parasitism (Hoover and Brittingham 1993), it is suggested that the probability of parasitism is higher near edges created by timber harvesting techniques within forest-dominated landscapes. However, results may vary within agriculturally dominated landscapes where forest tracts are already saturated with cowbirds. In such a landscape, Morse and Robinson (1999) reported no evidence that cowbirds were more abundant nor that parasitism was increased near internal edges caused by timber harvesting. Instead, they found that rates of parasitism were driven by proximity to an external agricultural edge that functioned as a cowbird-feeding site.

SILVICULTURAL MANAGEMENT – STANDS OF VARYING TIMBER CLASS

In addition to examining local-scale effects by focusing on distance from internal silvicultural edges on patterns of nest predation/parasitism and predator/parasite distributions, research has also investigated other local- and broad-scale effects of timber harvesting. Local-effect studies of timber size/class compare nest predation/parasitism and predator/parasite distribution within stands of varying age since harvest (Table 1.4a, footnote j). This approach explores not only the effects of disturbance caused by harvesting practices, but, through following the regeneration process, the temporal scale at which the effects change and are possibly mitigated.

Several studies have investigated the rates of nest predation and the distribution/abundance of potential nest predators within stands of varying age created by timber harvesting practices (Table 1.4a). Within extensively forested landscapes managed for timber, the general consensus of studies using artificial ground and shrub nests is that predation is not higher in younger stands (e.g., DeGraaf and Angelstam 1993). In fact, most studies reported higher rates of predation within mature forest than within regenerating clearcuts (Ratti and Reese 1998, Rudnicky and Hunter 1993, Yahner and Cypher 1987, Yahner and Wright 1985). Hanski et al. (1996) reported the same result with natural nests of ground-, shrub-, and canopy-nesting species. Lending support to these findings, researchers have documented that abundances of potential avian predators (Blue Jay, American Crow (*Corvus brachyrhynchos*), and Common Grackle (*Quiscalus quiscula*); King and DeGraaf 2000, Moorman and Guynn 2001, Thompson et al. 1992) and small mammalian predators (eastern chipmunk and red squirrel; King and DeGraaf 2000) are not relatively higher within regenerating clearcut stands than within mature forest. In fact, King and DeGraaf (2000) reported that the major nest predators of their study site (eastern chipmunk, red squirrel, and Blue Jay) were forest-associated and actually reached their greatest abundances within the interior of the mature forest. In contrast, other studies have reported higher relative abundance of small mammals within regenerating clearcuts compared to mature forest. Kirkland (1990) reviewed 21 studies that examined small mammal abundance in recent clearcuts (<6 years after cutting) and adjacent mature forest and found that overall abundance of small mammals was higher in clearcuts than mature forest in 15 of 21 studies. In addition, Potvin et al. (1999) and Sullivan et al. (1999) found higher numbers of deer mice in clearcut versus mature forest. In addition to these studies conducted in forest-dominated landscapes, a study within a heterogeneously managed forest tract within an agriculture matrix reported increased depredation of Kentucky Warbler nests located within younger, more recent clearcuts than within more mature forest (Morse and Robinson 1999). Within this study area, clearcutting was demonstrated to increase rates of nest predation; however, this increase in predation rate was shown to diminish through time with the re-growth of the forest and consequent increased heterogeneity of vegetative structure. Predators responsible for the nest depredations were not identified in this study, however generalist predators often associated with agricultural landscapes (e.g., raccoons, opossums, skunks, Blue Jays) were pervasive throughout the study area (Morse and Robinson 1999) and may have increased rates of predation within the younger, more recently disturbed, and more homogeneous forest stands (Bowman and Harris 1980).

SILVICULTURAL MANAGEMENT – TREATMENT PLOTS

Harvesting practices, such as clearcutting, not only create internal edge but also markedly change vegetative structure compared to unharvested adjacent habitat within the landscape (Yahner et al. 2001). With this in mind, researchers have gone beyond studying local-scale effects and have investigated the consequences of timber harvesting practices at a broader spatial scale, the experimental plot, comparing patterns of nest predation/parasitism and predator/parasite distributions between treated an untreated plots (Table 1.4a, footnote m). Using this broader-scale approach, researchers focus on fragmentation effects of timber harvesting rather than edge effects per se. An edge effect is defined as an increase in nest predation near gap-created edges, whereas a fragmentation effect is an increase in nest predation along a gradient from less to more fragmented. While edge and fragmentation effects are often correlated, it is important to distinguish between them because the two effects may be expressed at different spatial scales; for example, an edge effect may be absent at a smaller scale, but if a larger landscape including less fragmented areas is sampled, a fragmentation effect may be revealed (Manolis et al. 2000).

NEST PREDATION – Examination of nest predation in relation to timber management at the scale of the treatment plot (the larger area within which smaller-sized stands are treated), rather than the treated stand, reveals parallel results. Several studies, conducted within forest-dominated landscapes and employing artificial ground and shrub nests, have reported no significant difference in rates of predation within plots fragmented by clearcuts in comparison to uncut plots (DeGraaf 1995, King and DeGraaf 2000, Steventon et al. 1999, Yahner and Mahan 1996). However, when examining effects of fragmentation caused by varying intensities of timber management at an even broader landscape-level spatial scale, higher predation rates were reported on artificial nests located in landscapes subjected to extensive clearcutting and containing considerable edge habitat compared with landscapes exposed to less clearcutting and containing reduced edge habitat (Yahner and Scott 1988; Table 1.2). Comparable studies with natural nests are lacking and tend to focus on nest success rather than predation. Nest success may be an acceptable surrogate for predation because predation is the most important mortality factor affecting nesting success in most passerine birds (Ricklefs 1969). A pre- and post-treatment study within extensive bottomland hardwood forests reported that nests of various forest-interior songbird species were not preyed upon more heavily within treatment plots when compared to pre-treatment predation levels and pre- and post-treatment predation levels of untreated plots (Twedt et al. 2001). A similar study by Wood (1999), also conducted within an extensive bottomland hardwood forest and with pre- and post-treatments, reported no significant difference in the daily nest success of Prothonotary Warblers among post-treatment plots, pre-treatment plots, and untreated plots. The same harvesting techniques, while inconsequential to the nesting success of some songbirds, may be detrimental to others. For example, when compared with untreated plots, the daily nest success of Ovenbirds on plots treated with selection-cuts was reduced; however, Black-throated Blue Warblers (*Dendroica caerulescens*) exhibited no significant difference in daily nest success (Bourque and Villard 2001). Robinson and Robinson (2001) conducted a similar study on the daily nest success of the Acadian Flycatcher (*Empidonax virescens*), Kentucky Warbler, Northern Cardinal (*Cardinalis cardinalis*), and Wood Thrush within treated and untreated plots of a forest tract embedded in an agricultural matrix. Contrary to what might be expected, they found no differences in nest success between treated and untreated plots for all four species. Because of the extant high level of regional fragmentation, additional fragmentation caused by timber harvesting may have added little to the assiduously high rates of nest predation suffered within this study area (Robinson and Robinson 2001).

PREDATOR ABUNDANCE – Abundance of potential nest predators within plots treated for timber harvesting and untreated plots has also been examined. Studies of this nature, however, are far fewer and are strongly biased toward avian nest predators. Corroborating the nest predation studies conducted within extensive forests, the relative abundance of Blue Jays and American Crows was not higher in treated than untreated plots (Annand and Thompson 1997, Thompson et al. 1992). However, when expanding the spatial scale beyond the plot to include the entire landscape, Yahner and Scott (1988) found higher densities of Blue Jays and American Crows in forested areas fragmented by higher intensities of clearcutting compared to those of lower intensity. Within an agricultural landscape, the highly fragmented forest studied by Robinson and Robinson (1999) displayed higher relative abundance of Blue Jays within plots treated with group cuts (timber cuts 0.02 - 0.4 ha in size) as opposed to untreated plots. Blue Jays are habitat generalists known to thrive in fragmented and second-growth habitats of mixed forest-farmland landscapes and to be far less abundant in predominantly forested landscapes (Whitcomb et al. 1981, Wilcove 1985, Hickman 1990, Hoover et al. 1995, Chalfoun et al. 2002a, Thompson et al. 2002). Thus, this finding is in accord with the low regional forest cover and the agriculturally dominated landscape. More studies on predator distribution and abundance in relation to timber management are needed, especially those of large mammalian predators and snakes. In addition, it is essential to identify the perpetrating nest predators and to create a link between predator abundance and nest predation rates in order to understand factors influencing the presence/absence of edge effects in certain landscapes.

BROOD PARASITISM – The effects of timber harvesting practices on levels of brood parasitism have rarely been studied and exhibit variable results. Results may vary with landscape-scale forest cover (Donovan et al. 1997). Within an extensive bottomland hardwood forest tract (60,000 ha), Prothonotary Warbler nests located within the forested portion of clearcut treated plots did not suffer increased rates of parasitism compared with untreated plots (Wood 1999). In a similar study of several forest-nesting species, Twedt et al. (2001) also found that parasitism rates were not higher within plots treated with group cuts compared with untreated plots. In contrast, a study within a much smaller forest tract (2,000 ha), managed for multiple purposes and surrounded by agriculture, reported increased brood parasitism on Acadian Flycatcher and Kentucky Warbler nests located within plots that were recently treated with small group cuts compared to uncut plots (Robinson and Robinson 2001). They did not, however, find increased parasitism on the nests of Northern Cardinal or Wood Thrush. In these three instances, internal fragmentation resulting from timber harvesting did not increase parasitism rates within a forest-dominated landscape, but did increase rates for some species nesting within the forest of an agriculturally dominated landscape with decreased forest cover. Even within a fragmented landscape in which levels of brood parasitism were already chronically high (Robinson and Robinson 2001), additional fragmentation caused by timber harvesting exacerbated the rates of parasitism, though in a species-specific manner.

COWBIRD ABUNDANCE – More common than studies of parasitism rates in relation to timber harvesting are studies of cowbird distribution and abundance. Within forest-dominated landscapes managed for timber and consisting of a mosaic of age-classes, studies have reported higher relative abundance of cowbirds within regenerating stands compared with within older stands (Thompson et al. 1992, Moorman and Guynn 2001) and within treated rather than untreated plots (Annand and Thompson 1997). Within the same study area, Thompson et al. (1992) reported an increase in cowbird abundance within actual treated stands (local-scale), however, not within treatment plots (broad-scale), revealing the need to look at more than one spatial scale. Within a fragmented study area, Robinson and Robinson (1999) reported abundance of cowbirds was not relatively higher within openings created by group cuts compared with uncut portions of the same treated plot. This result may seem contradictory to the findings of their same-site study that reported increased parasitism rates within treated plots compared with untreated plots (Robinson and Robinson 2001). However, rather than being incongruous, this result may instead highlight the importance of investigating timber harvesting effects at more than one spatial scale (local and broad), considering the annual variation in cowbird abundance and consequent need for long-term studies, and elucidating the relationship between cowbird abundance and parasitism rates.

SILVICULTURAL MANAGEMENT – HYPOTHESES FOR PRESENCE/ABSENCE OF EDGE EFFECTS

Several explanations have been proposed to account for a lack of edge effects at internal edges created by timber harvesting within forested landscapes. In contrast to agricultural edges, openings created by timber harvesting do not produce isolation (King et al. 1996), regenerate quickly (i.e., are ephemeral) and are relatively small making them unsuitable to support resident predator populations that are specialized to living in logged openings (Suarez et al. 1997), have more abrupt edge zones (i.e., have little transition zone vegetation and lack a shub-layer) making them less attractive to nesting birds and subsequently to nest predators (Rudnicky and Hunter 1993), don’t provide the habitat or food subsidy for generalist nest predators typically associated with more productive agricultural fields or suburban habitats and thus lack the population augmentation of generalist predators (DeGraaf 1995, Hanski et al. 1996, Huhta et al. 1996, Huhta et al. 1998a), and are free of cowbirds unless within the proximity of agriculture or human habitation (DeGraaf 1992, King et al. 1996). Increases in nest predation near forest edges will depend on the diversity of the predator community, their densities, and their habitat use (Cotterill and Hannon 1999), all of which will vary between agricultural and forest-dominated landscapes. Predator behavior and the location of the nest site relative to predator distribution will also affect patterns of nest predation in relation to edges (Reitsma et al. 1990). Bayne and Hobson (1997) suggested that fragmentation caused by logging may result in little change in predator assemblages and might be similar to fragmentation caused by natural disturbance regimes such as fire. Thus, the general fragmentation theory associated with agricultural landscapes may not be applicable in forested landscapes fragmented by logging. Much of the difficulty in evaluating whether the effects of fragmentation on nest predation are influenced differently by logging and agriculture results from differences in methodology, forest types, and predator communities among studies (Paton 1994).

Outside of comparisons between internal timber harvest-induced edges and external agricultural edges, other hypotheses have been proposed to explain a lack of edge effects within forest-dominated landscapes. Openings created by timber harvests are unproductive compared with forested stands and thus support a lower prey density and a subsequent lower concentration of predators (Huhta et al. 1998a). Fewer predators in clearcut areas and in young successional stands (Hanski et al. 1996) suggest unequal use of the forested and non-forested habitats, which may circumvent an increase in predation pressure at the edge zone (Andren 1995). Additionally, increased vegetative complexity at clearcut edges may reduce the foraging efficiency of nest predators (Yahner 1988) and increase nest concealment (Burhans 1997), thus dissuading an increase in predation at edges. Within studies focused on effects of logging, determining the generality of edge effects is difficult due to differences in study regions and landscape types, as well as inconsistencies in edge structure, edge age, focal avian species, and research design (Ratti and Reese 1988).

Although few, explanations for the existence of increased nest predation at internal edges created by timber harvesting within forested landscapes have also been put forth. The most frequently expounded hypothesis suggests that abrupt human-made edges lack regenerating shrubs and have sparse vegetative cover, resulting in increased visibility of nests located at these edges and facilitating the detection of nests by predators (Bowman and Harris 1980, Rudnicky and Hunter 1993, Huhta et al. 1998a). Additionally, it is hypothesized that predators may favor abrupt and often linear clearcut edges as travel lines; thus, spending more time along edges and resulting in greater incidental predation (Gates and Gysel 1978, Ratti and Reese 1988). Increased abundance of small mammals near clearcut edges has been explained by the juxtaposition of two different habitat types; edges may provide forest-dwelling small mammals with simultaneous access to cover within the forest and food resources within the adjacent clearcuts (Strelke and Dickson 1980, King et al. 1998b). Other explanations are derived from the findings that some small mammals are more abundant within the interior of clearcuts. If rodents are more abundant within clearcuts, a spillover effect may cause increased predation near clearcut edges within the adjacent forest. The extent of the edge effect, however, would be restricted by the small home range size of small mammals (Manolis et al. 2002). Additionally, if clearcuts generate increased numbers of small mammals, predators that prey upon small mammals may also be attracted to clearcuts. If these larger predators, with their larger home ranges, also prey upon bird nests, nest predation may increase along the clearcut edges and extend into the forest interior (e.g., Wiens et al. 1993; Manolis et al. 2002).

The absence of increased nest predation within younger stands of regenerating forest than within mature forested stands has predominantly been explained with differences in vegetation structure. Younger, regenerating stands contain a higher density of ground-level vegetation than do stands of mature forest (Yahner and Cypher 1987). Because the density of understory vegetation is generally positively related to nest survival (Martin 1992), one might expect lower predation on ground nests within regenerating stands than within mature forest (King and DeGraaf 2000). Dense ground vegetation may conceal low nests and reduce detection from visually oriented avian predators (Yahner and Wright 1985). In addition, younger stands have fewer large trees and a low frequency of perching sites, thereby hindering detection of nests by avian predators (Yahner and Wright 1985). High nests, or nests located within mature forested stands may be more conspicuous to avian predators perched above or flying over (Yahner and Wright 1985). Where mammals are the main predators, high density of shrubs may not only conceal nests, but also obstruct foraging movements and impede foraging efficiency (Bowman and Harris 1980, Yahner and Wright 1985). Lastly, young stands have relatively simple vegetative structure and lack the multiple vertical layers and complex vegetative structure of older forest stands; thus, predators may forage less often in younger stands because they afford fewer foraging microenvironments (Yahner and Cypher 1987). For the above reasons, nest predators would be expected to forage more often in mature forested stands and we would not expect to find increased predation within younger, regenerating forest stands.

Effects of timber harvesting on rates of brood parasitism may vary among species and landscapes, probably in response to cowbird abundance, host preferences, and the local features cowbirds use as feeding sites (Gates and Griffen 1991). Cowbirds require simultaneous access to breeding and feeding sites (Donovan et al. 1997); therefore, rather than responding to edge types or proximity to edges, cowbirds may select habitats with high host densities (Rothstein et al. 1986, Thompson et al. 2000) within the vicinity of feeding areas. Thus, cowbird abundance is determined by host abundance and availability/accessibility of feeding areas (Thompson 1994). Forest-dominated landscapes do not offer feeding opportunities for cowbirds; thus, unless a feeding site is within the home range of a cowbird (~ 7 km), nests within extensive forests should experience low rates of parasitism and should not suffer from increased parasitism due to openings created by timber harvesting. Cowbird nest searching techniques in combination with the vegetation structure of timber harvest openings will also affect rates of parasitism. To locate nests, cowbirds observe adult host behavior from prominent perch sites or by walking along the ground and looking upward (Lowther 1993). Regenerating clearcuts and young forested stands do not provide the necessary perch sites, and their dense ground-level vegetation may conceal adult behavior as well as prevent nest searching from the ground. Thus, openings created by timber harvesting within forest-dominated landscapes may not be conducive to increased rates of brood parasitism.

It has been argued that the effects of timber harvesting must be interpreted in the context of the composition of the regional landscape (Robinson et al. 1995, Donovan et al. 1997). Much of the geographic variation in levels of nest predation and brood parasitism experienced by forest birds appears to be closely linked to the amount of regional forest cover, landscape-level patterns of fragmentation, and the type of surrounding non-forest land use (Robinson et al. 1995, Donovan et al. 1997). Harvesting practices that cause intrusive fragmentation and create gaps and internal edge within the forest may substantially increase the risks faced by forest birds; however, the characteristics of the regional landscape may influence predation and parasitism dynamics at the local scale (Robinson et al. 1995, Donovan et al. 1997). For example, a forested tract within an agricultural area of low regional forest cover (≤ 15%; Donovan et al. 1997) may be so fragmented and saturated with generalist predators and cowbirds that additional perforation of the forest may have little effect on the already chronically high rates of predation and brood parasitism (Robinson and Robinson 1999, 2001). In contrast, in extensively forested landscapes that are insulated from agricultural land-use in an area of high regional forest cover (≥ 90%; Donovan et al. 1997), generalist predators and cowbirds may be absent (e.g., DeGraaf 1992); thus, internal fragmentation caused by timber harvesting would not be expected to increase levels of nest predation or brood parasitism. In comparison, a large forested tract within the proximity of agriculture in an area of moderate regional forest cover (45-55%; Donovan et al. 1997) may be susceptible to increased levels of nest predation and brood parasitism if gaps created by internal fragmentation facilitate generalist predators and cowbirds to penetrate into the forest interior from the surrounding non-forest matrix. Although regional and landscape-scale habitat composition may have a large effect on the nesting success of forest-interior songbirds, local management practices may have an equally strong impact (Morse and Robinson 1999), suggesting that multiple spatial scales need to be considered when patterns of nest predation and brood parasitism are examined.

In addition to variations in regional forest cover, distinctions in the predator community within different landscapes highlight the importance of evaluating edge effects on a region-by-region basis (Flaspohler et al. 2001b). Landscape structure as well as the local assemblage of nest predators and brood parasites influence avian nest success (Robinson and Robinson 2001). Although predator and parasite assemblages are associated with landscape structure, they will also vary by region (Tittler and Hannon 2000). Inconsistent results among research projects designed to investigate the effects of edge on avian reproductive success may be due to regional or landscape-level variation in vegetation structure, predator communities, and bird communities (Robinson et al. 1993, Donovan et al. 1997), warranting regional and species-specific studies (Hoover and Brittingham 1993).

NARROW CORRIDORS

Most studies examining effects of internal edge within forests have focused on the extensive openings created by silvicultural practices, disregarding narrow breaks in the forest canopy created by anthropogenic disturbance such as recreational trails, roads, and utility right-of-way corridors or natural forest openings created by streams. Narrow forest-dividing corridors are not generally viewed as sources of fragmentation (Rich et al. 1994). Regarding forest fragmentation, the definition of what constitutes an edge has been inconsistent within the literature; researchers have defined a tract of forest as discrete if it is separated from other forest by 10 meters of open land (Askins et al. 1987), others use a 100 meter-wide section of open land as the definition (Whitcomb et al. 1981, Ambuel and Temple 1983, Robbins et al. 1989), while others use a silviculturally-derived definition of twice the width of the height of the adjacent forest trees (Paton 1994). Despite these inconsistencies, criteria for defining edges should be framed within the context of the specific ecological processes under question (e.g., bird abundance, habitat use, nest predation; Ortega and Capen 2001). Although forest edges are frequently associated with increases in edge-related nest predation and brood parasitism, it is unclear whether narrow internal edges, man-made or natural, create the same edge conditions that concentrate predators near edges adjacent to large, human-induced openings (King and DeGraaf 2002). Furthermore, few studies have compared predation effects along different types of edges (Boulet and Darveau 2000). Studies have examined avian use, abundance, distribution, and diversity along narrow internal edges (Hickman 1990, Gates and Giffen 1991, Rich et al. 1994); however, these studies did not evaluate nesting success. From the perspective of population viability and management, habitat quality for forest birds must be evaluated by considering both their density and reproductive success (Van Horne 1983, Martin 1992).

TRAILS – There is increasing evidence that non-consumptive outdoor activities can have negative effects on forest-living wildlife (Boyle and Samson 1985, Knight and Cole 1995; as cited in Miller et al. 1998). Coinciding with rising levels of recreational activities is an increase in the number of trails crossing natural areas; because trails bisect forest habitats, they may create habitat edges (Miller et al. 1998). Human activity associated with recreational trails may affect the habitat use of breeding birds and nest predators (Miller and Hobbs 2000). Forest-interior bird species could suffer decreased reproductive successes as a result of increased nest predation, brood parasitism, and interspecific competition near nature trails if the trails create edge habitat (Hickman 1990). Of the few studies that have examined the effects of trails on forest-nesting songbirds (Table 1.5), some have found decreased nest success (Miller et al. 1998), increased nest predation (Miller and Hobbs 2000), and increased abundance of nest predators and brood parasites (Hickman 1980) near trails, while others have found no such effects (Boag et al. 1984).

ROADS – Potentially more harmful than recreational trails is the creation of roads within the forest interior. Roads are associated with negative effects on the biotic integrity of terrestrial ecosystems (Trombulak and Frissell 2000). In addition to causing wildlife mortality from construction and collision with vehicles, altering the physical and chemical environment, spreading exotic species, and modifying animal behavior, the construction of roads within the forest facilitates increased use by humans, who themselves often cause diverse and persistent effects detrimental to forest ecology (Forman 1998, Trombulak and Frissell 2000). Several studies have highlighted the negative effects of generalist predators (e.g., corvids, raccoons, skunks) and brood parasites associated with open areas and human settlement (Wilcove 1985, Andren 1992, Hoover and Brittingham 1993, Andren 1995, Huhta et al. 1996, Hannon and Cotterill 1998). Roads often connect the forest to open habitat, thus potentially serving as a conduit bringing generalist predators and cowbirds into the forest interior (Schonewald-Cox and

Buechner 1992). In addition to linking the forest interior to external, non-forest habitats, vegetation structure of forest-road borders may concentrate activity of nest predators and cowbirds as has been described for other types of edges (Bider 1968, Chasko and Gates 1982, King et al. 1998b). Although the creation of roads within the forest may break the continuity of the canopy and change vegetative structure along the narrow corridor, it is questionable whether these openings create edge effects comparable to those caused by larger forest openings (Askins 1994).

Most studies that examined nest predation levels relative to road edges reported no difference in predation rates at varying distances from the edge (Table 1.5; Latta et al. 1995, Bergin et al. 1997, Yahner and Mahan 1997, Lindenmayer et al. 1999, Manolis et al. 2000, Ortega and Capen 2001, Rodewald 2002). King and DeGraaf (2002) also documented that nest success of ground-nesting Ovenbirds did not vary with proximity to interior forest roads. An increase in nest predation with close proximity to road edges was reported in only two studies (Burkey 1993, Marini et al. 1995). Roads evaluated within the above studies varied in width, surface type, density, intensity of use, and changes in vegetative structure. Road width (Haskell 2000) and density (Forman 1998), as well as other characteristics of the road, may influence the type and extent of the edge effects that occur. In a comparison of predation rates along different types of roads, Boulet and Darveau (2000) documented that predation levels were higher along wide, high-use highways than along more narrow and lower intensity-use logging roads. Similarly, the relative abundance of potential avian and small mammalian nest predators, as well as cowbirds, did not increase at close proximity to 8-10-m wide unsurfaced roads (Rich et al. 1994, Ortega and Capen 2001). Whereas, within the same study area, Rich et al. (1994) reported increased relative abundance of cowbirds near 16-m wide paved roads containing mowed grass on either side. Assuming that predation and parasitism pressure are proportional to predator and cowbird abundance (Andren 1992, Hoover and Brittingham 1993, respectively), the study of Rich et al. (1994) suggests that edge effects may vary with road characteristics.

UTILITY RIGHTS-OF-WAY – Research to date suggests that small-width, forest-dividing corridors created by utility rights-of-way may also generate detrimental edge effects. Differential attraction of potential nest predators and brood parasites to these edges, without edge-avoidance by forest-nesting songbirds, may cause an increase in rates of nest predation and parasitism and subsequent lower nesting success ("ecological trap" hypothesis of Gates and Gysel 1978; Chasko and Gates 1982, Rich et al. 1994). Chasko and Gates (1982) documented increased nest predation and parasitism and decreased nesting success with decreasing distance from utility corridor edges. A predator-focused study at the same site found increased activity of potential mammalian predators (esp. eastern chipmunk) and snakes at the corridor-forest ecotone (Ladino 1980; as cited in Chasko and Gates 1982). Parasitism was highest at the edges of grassy forest-dividing corridors (Chasko and Gates 1982) where simultaneous access to both foraging and breeding opportunities, as well as prominent perches from which to observe host activities and perform courtship displays, provided optimal cowbird habitat (Rich et al. 1994). Similarly, Rich et al. (1994) reported that increased abundance of potential avian nest predators and cowbirds were associated with narrow (23 m) forest-dividing utility corridors; avian predators reached their greatest abundances along the edges of corridors containing shrubby vegetation and cowbirds preferentially selected corridors with mowed grass.

STREAMS/RIVERS – Natural internal edge caused by water courses has been a lesser-studied subject. Few studies have investigated the potential of riparian ecotones to have a detrimental effect on forest-interior breeding birds; however, streams may function similarly to human-made corridors within forested landscapes (Gates and Giffen 1991). Bodies of water create openings within forests that cause changes in the physical and biotic characteristics of the interior (Gates and Giffen 1991). Natural forest-stream edges share some characteristics in common with narrow forest-dividing edges created by human disturbance; they are narrow, they create high-contrast, shrubby, and multi-layered vegetation, and they attract a high density and diversity of forest-interior birds (Gates and Giffen 1991). Given these similarities between forest-stream edges and human-made edges, there is the expectation that birds nesting near forest-stream edges may suffer comparably high rates of nest predation and parasitism. Gates and Giffen (1991) found a higher diversity of neotropical migrants, as well as potential nest predators and cowbirds, along forest-stream edges, suggesting that conditions at forest-stream edges might be conducive to increased nest predation and parasitism within forested landscapes. In support of this finding, Marini et al. (1995) reported increased predation rates on artificial nests located directly adjacent to a forest-stream edge as opposed to a short distance away from the stream. These results are consistent with the notion that streams concentrate predator activity and are frequently used as travel corridors by mammals (e.g., raccoons and mink; Harris 1984, Forman and Godron 1986; as cited in Gates and Giffen 1991). Additionally, the presence of canopy gaps and snags, as well as increased host-density, at forest-stream edges may differentially attract cowbirds (Brittingham and Temple 1983, Robbins et al. 1989). Although the effect of forest-stream edges is not thought to be as great as terrestrial openings (e.g., Boulet and Darveau 2000), the above findings suggest that forest-stream edges may foster increased rates of predation and parasitism.

WATER BODIES

In addition to internal forest edges caused by streams, edges of natural forest openings caused by larger bodies of water (e.g., lakes, marshes, swamps), may potentially affect rates of predation on the nests of birds breeding within the adjacent forest. Bodies of water within or adjacent to forests create riparian or lacustrine edges that may lead to elevated rates of nest predation (Bollinger and Peak 1995). The few studies that have examined nest predation in relation to distance from water bodies have not found elevated rates of predation near, as opposed to far from, the forest-water edge (Huhta et al. 1998a, Manolis et al. 2000, Pierre et al. 2001; Table 1.6). However, when comparing nest predation rates between natural forest-water edge and anthropogenic internal edges such as fields, clearcuts, and logging roads, other researchers found no difference between them (Bollinger and Peak 1995, Huhta et al. 1998a, Boulet and Darveau

2000; Table 1.6). These findings suggest that avian nests located near forest-water body edges, like those near other internal forest edges, may experience elevated predation rates in comparison to nests located in the forest interior. Potential predators may be attracted to edges of water bodies as travel lanes (Bollinger and Peak 1995) and/or foraging grounds. For example, Boulet and Darveau (2000) suggested that crows and raccoons might be attracted to forest-lake edges to feed on mollusks, crustaceans, and fish. Conversely, Small and Hunter (1988) reported decreased predation rates on nests located within forest fragments bordered on one side by a large water body, as opposed to those located within fragments surrounded by non-forested land. However, results of their study may not be applicable because they focused on the matrix surrounding forest fragments, not on openings created within contiguous forest.

NARROW CORRIDORS – HYPOTHESES FOR PRESENCE/ABSENCE OF EDGE EFFECTS

Several hypotheses have been proposed to explain the anticipation of increased nest predation along narrow, forest-dividing internal edges within forested landscapes. Most frequently invoked is the travel-lane hypothesis (Bider 1968; but see Lariviere 2003), which suggests that potential nest predators will incidentally take nests while traveling along linear corridors. Coyotes (*Canis latrans*) are known to have an affinity for linear habitat features and use of trails (Miller and Hobbs 2000), and other mammalian predators such as foxes (*Urocyon cinereoargenteus, Vulpes vulpes*), skunks, and raccoons are suspected to use linear corridors while foraging (Small and Hunter 1988). Further, several authors have speculated that roads may provide a conduit for the movement of generalist predators, allowing them to invade forest interiors from surrounding non-forested habitats (Schonewald-Cox and Buechner 1992, Lindenmayer et al. 1999). Increased human activity within forested habitats is associated with the presence of trails and roads. Trash and road-kills provide supplemental food for generalist mammalian and avian predators and thus may influence their presence and their foraging behavior in forested areas (Boulet and Darveau 2000) and may lead to elevated predation pressure on the nests located within forested areas. Lastly, increased structural complexity of the vegetation at edges may attract a higher density of nesting birds (James 1971, Shugart 1984), and result in increased nest predation (density-dependent predation; Fretwell 1972) as predators increase their search intensity in response to discovering occupied nests (Martin 1988).

Effects of narrow, forest-dividing corridors on rates of nest parasitism may vary in response to cowbird abundance, the extent to which cowbirds forage in specific openings, the local features cowbirds use as travel lanes and feeding sites, and host preferences (Gates and Giffen 1991). Similar to hypotheses concerning predators, it has been suggested that cowbirds are attracted to and use open corridors as access routes to penetrate into forest interiors (Small and Hunter 1988, Askins 1994). This is especially true if these corridors provide feeding sites, such as grassy areas beside roads or within utility corridors. Because cowbirds maintain separate foraging and breeding ranges (Brittingham and Temple 1983) and forest habitat does not provide sufficient foraging sites for cowbirds, their utilization of forest habitat is dependent upon locating appropriate foraging sites within the vicinity (Gates and Giffen 1991). The best strategy for a female cowbird would be to search for nests as close as possible to feeding and breeding areas, thus spending the least amount of time and energy acquiring food and mates and allowing more time for locating host nests and laying eggs (Rich et al. 1994). Grassy, forest-dividing corridors, then, provide optimal habitat for cowbirds. Also similar to generalist predators, the presence of cowbirds is positively associated with human activity because of the supplemental food and foraging opportunities humans provide (e.g., Trine 1996; as cited in Morse and Robinson 1999). Additionally, like generalist predators, the presence of cowbirds is thought to be dependent upon host-nest density (McGeen 1972), suggesting increased nest parasitism may exist at internal forest edges that attract a high density of nesting birds. Poles within utility corridors and snags along streams and lakes provide perches for cowbirds to search for nests and perform courtship displays; thus, increased rates of parasitism may be found adjacent to these internal forest edges (Rich et al. 1994). Lastly, it has been proposed that, when given the opportunity, cowbirds may prefer to breed within forest-interiors over their usual open habitats to take advantage of nontraditional hosts that lack defense strategies (Hahn and Hatfield 1995).

Reasons for a lack of increased nest predation and parasitism at narrow, forest-dividing internal edges also abound. The most common explanations refer to the hypotheses proposed for edge effects at external agricultural-forest edges and show how they do not apply to narrow, forest-dividing internal edges. The explanation most often called upon is a lack of generalist predators and cowbirds found within forest-dominated landscapes (Hartley and Hunter 1998, Boulet and Darveau 2000, Ortega and Capen 2001). Another explanation refers to the idea that narrow internal edges, such as trails, roads, and streams, do not actually create edge habitat, as defined as the junction or ecotone between two different habitat types; rather, they are simply a break in the continuity of one habitat type (Lariviere 2003). As such, narrow internal edges would not be expected to attract a higher density and/or activity of predators/parasites to take advantage of simultaneous access to two different habitat types. Additionally, narrow internal edges would not sustain distinct populations of predators or cowbirds; therefore, one would not expect a spillover effect of predators or parasites from internal edge habitat into the adjacent forest (Lariviere 2003). It has also been suggested that some narrow forest-dividing internal edges, while permanent, do not create large gaps in the forest canopy and thus are not associated with differences in vegetative composition and/or structure. Thus, they would not be expected to attract an increased density of breeding birds nor to concentrate nest predators as do edges near more extensive forms of disturbance (King and DeGraaf 2002). Lastly, supplemental food resources that attract nest predators to edges adjacent to suburban or agricultural development are generally absent at narrow internal edges (King and DeGraaf 2002).

The effects of internal forest edges on nest predation may differ between human-made and natural edges. Human-induced edges are often abrupt, usually possessing less vegetative cover than natural edges and creating a sharp gradient (Huhta et al. 1998a). These edges may be more damaging to forest-nesting songbirds than are natural edges which are often more structurally complex, with a well-developed shrub layer (Huhta et al. 1998a, Huhta and Jokimaki 2001). The increased vegetative complexity at natural edges may provide better nest concealment from visually-oriented predators, as well as more potential nest sites, both of which may reduce rates of predation on nests located within these edges (Martin 1992, Martin 1993b) as compared to anthropogenic edges. In addition, increased complexity of the vegetation may reduce nest predation by hindering the movement of potential predators (Bowman and Harris 1980) or blocking the transmission of auditory or olfactory cues used by predators to locate nests (Howlett and Stutchbury 1996). For these reasons, in addition to the association between human activity and predator activity, an increase in nest predation at narrow forest-dividing internal edges may be more likely to occur at human-made trails and roads than natural streams.

WATER AND NEST PREDATION

In addition to its potential to create edge effects, surface water can be a dominant feature affecting plant and animal communities (Swift et al. 1984). Although documentation of breeding bird habitat relationships within wetland forests is limited, some studies have demonstrated hydrology to have a major influence on breeding bird communities (Smith 1977, Swift et al. 1984, Wakeley and Roberts 1996). Hydrology has the potential to influence breeding birds at multiple temporal and spatial scales (micro-, macro-, and landscape) and may play a key role in their reproductive success; however, information on the relationship between hydrology and reproductive success of birds is lacking. Given the primary importance of nest predation to the reproductive success of passerine birds (Ricklefs 1969), the effect of water on rates of nest predation is of major interest.

Water has the potential to positively and negatively affect rates of nest predation. Water may influence rates of nest predation by providing alternative/additional prey to potential nest predators and to breeding songbirds. The abundance and distribution of food sources is important in predator-prey relationships (Byers 1974, Hogstad 1995, Schmidt 1999). Alternative prey for predators may affect predation on nests by buffering nest losses (Byers 1974), altering the foraging strategies of predators (Crabtree and Wolfe 1988), or changing the habitat used by predators (Darrow 1945, Stickney 1991). However, these effects may have limited affect on rates of nest predation where the predator community is complex (Greenwood et al. 1998). Increases in prey availability for breeding birds may lead to increased vigilance at the nest and decreased nest predation (Martin 1992, Schmidt 1999). Abiotic factors, such as water, that cause change in the environment and the foraging behavior of predators are important to predator-prey relationships.

Although predator foraging behavior will be influenced by life-history traits of the predator and the prey that influence encounter rates such as nest-site selection (Martin 1993b) and nest vigilance (Martin 1992), the environment will also influence foraging behavior of the predator. Changes in the environment, such as in the abundance and distribution of alternative foods, may manifest as measurable changes in nest encounter rates and predator search effort and strategy, thus affecting rates of nest predation (Schmidt 1999). When alternative food to predators is scarce, foraging for nests is profitable relative to other opportunities even when nests are at low densities (Schmidt 1999). This notion is well supported by empirical studies in mammals (e.g., Dunn 1977, Brown et al. 1992, Bowers et al. 1993, Morgan et al. 1997) and birds (Kohlman and Risenhoover 1996; as reviewed in Schmidt 1999). However, when alternative prey are abundant, concentrating foraging efforts on nests is not profitable, and predation on nests may simply occur incidentally (Schmidt 1999). When evaluating predator-prey interactions, however, the abundance of alternative food sources must be considered within the context of their temporal and spatial distribution. For example, over short time scales the presence of alternative prey tends to correlate negatively with predation rates on bird nests (Angelstam et al. 1984). However, at longer time scales, where reproductive responses can occur, alternative food may increase predator densities (i.e., a numerical response) and result in positive correlations with predation rates. Within a spatial context, alternative food that co-occurs with nesting birds will increase total prey availability and may cause predators to have a functional response; an aggregation of predators at sites with high overall prey density or an increase in predator foraging effort at these sites may result in increased predation on nests ("enemy-mediated apparent competition," Holt 1977; Holt and Kotler 1987, Vickery et al. 1992a, Holt and Lawton 1994, Schmidt and Whelan 1998). Predators are known to increase their foraging effort in response to successfully obtaining prey (Martin 1988). Additionally, when a predator increases foraging effort within one stratum (e.g., water at ground level), it will likely result in greater search effort within all strata of the macro-habitat (e.g., shrubs and trees above ground level) and increase incidental take of non-focal prey such as nests (Schmidt and Whelan 1998; e.g., Hoover 2001). Alternative prey that occurs in a spatially separate habitat from nesting birds may result in apparent mutualism through predator emigration (Holt and Lawton 1994) or through buffering and diverting predators from nesting habitat (Crabtree and Wolfe 1988). Large increases in alternative food may alter the marginal value of the focal food and decrease predation regardless of spatial context (Schmidt 1999). Predator-prey interactions must be considered over the appropriate temporal and spatial scales (Holt and Lawton 1994, Morgan et al. 1997), their placement within the community, and their likelihood of generating feedback via indirect effects (Schmidt 1999).

In addition to indirectly affecting (increasing and decreasing) rates of nest predation as a source of alternative prey, water may directly decrease nest predation frequency in another way. Water may act as a deterrent to some nest predators (Picman et al. 1993), thus affording protection to nests located over water. Studies have reported that water acts as a barrier to some predators (terrestrial mammals; esp. raccoons), preventing foraging within flooded areas and depredation of nests located over deep water (Jobin and Picman 1997). Jobin and Picman (1997) reported that water depth was the most important predictor of nest predation. They also linked nest predation rates with temporal fluctuations in water depth during the breeding season; seasonal increases in predation pressure were associated with decreasing water level. Picman

(1993) studied the relative importance of water depth and distance from dry land on nest predation rates and on determining the predator community. He found that successful nests had greater mean water depth and distance from dry land than did depredated nests. Using fixed distances (30, 90, 110 m) with varying water depths (0, 0-10, 10-20, 20-30, 30-40, and 40-120 cm) and vice versa, he found that predation on bird nests decreased with increasing water depth while distance to dry land was relatively unimportant. For example, he documented that predation by raccoons decreased from 64% in an area with 0-40 cm water to 4% in areas with more than 40 cm of water, regardless of distance from dry land. He also reported that predator diversity decreased with increasing water depth and concluded that dry-land areas have a more diverse predatory community and that lower predation in deep-water areas was the result of the exclusion of many predators that occur on dry-land areas. Similarly, a study of Prothonotary Warblers nesting in nest boxes reported a decrease to 0% predation when nest boxes were placed over water that was 30-50 cm deep (Petit 1989). These studies, however, were conducted in marsh-like habitats and may not be representative of results found within forested wetlands, where nest predators such as snakes (e.g., rat snakes (*Elaphe obsolete*); Mullin and Cooper 2000), squirrels, and birds are capable of leading an arboreal existence. However, parallel results were described by Hoover (2001) within the seasonally flooded bottomland hardwood forest of the Cache River Watershed of southern Illinois. Hoover (2001) documented a decrease in daily predation rates on Prothonotary Warbler nests as water depth increased. Nests located over shallow (0-20 cm) water suffered nearly 4.5 times greater rates of predation than did nests located over deep (>30 cm) water. Differential rates of nest predation by raccoons were identified as the driving force, while rates of predation by other nest predators such as snakes, flying squirrels (*Glaucomys volans*), and avian species were not associated with water depth and contributed little to the overall trend of increased nest predation with decreased water depth. Hoover (2001) concluded that, with the exception of raccoons, other predators within his study area were able to move form tree to tree without having to use the ground (or water) and were thus less hindered by deeper water than were raccoons. More research is needed on the relationship between water and nest predation, especially within seasonally flooded forests. Because water can span multiple spatial scales (micro-, macro-, and landscape) and temporal scales, studies investigating the depth and spatial extent, as well as the timing and duration, of flooding are in order.

IMPORTANCE OF SPATIAL SCALE

It is important to examine the reproductive success of birds at the appropriate spatial and temporal scales. To effectively manage for the conservation of songbird populations, we need to identify the features of the nesting habitat that most directly influence fitness components of reproduction and survival (Martin 1992). Nest predation and brood parasitism are the primary sources of nest failure (Ricklefs 1969), therefore, we need to investigate features of the nesting habitat at various spatial scales to determine which ones are most closely associated with predation and parasitism rates. Ovenbird population parameters have been shown to respond to habitat variation at the micro-scale (e.g., nest concealment; Flaspohler 1998, as cited in Flaspohler et al. 2001a), the local habitat patch (e.g., forest edge; Kroodsma 1984), and the pattern of forest and interstitial land use in the surrounding landscape (Brittingham and Temple 1983, Gibbs and Faaborg 1990, Villard et al. 1993). Other studies have also demonstrated that habitat structure at the micro-, macro-, and territory-scale (Bowman and Harris 1980, Martin and Roper 1988, Martin 1992), distribution of nests relative to edges (Gates and Gysel 1978, Wilcove 1985, Andren and Angelstam 1988), and characteristics of the landscape (Donovan et al. 1997) affect rates of nest predation or brood parasitism. A more complete understanding of the factors that control populations of forest-nesting songbirds on their breeding grounds will require information on responses to habitat features at multiple scales. Although an increasing number of studies are showing that both localized and landscape-level factors can have a profound effect on avian predation rates, few studies have simultaneously investigated the relative importance of habitat characteristics at more than one spatial scale to the reproductive success of birds.

How ecological processes are related to different spatial scales in a hierarchically structured landscape is not well studied (Huhta et al. 1996). In a study of Wood Thrush, Hoover and Brittingham (1998) investigated the relative importance of local-scale vegetation features and landscape-scale patch size on nest fate and found that the best predictor of nest fate (successful/depredated) was patch size, the landscape-scale variable. Similarly, Huhta et al. (1998b) examined two spatial scales, local vegetation and landscape patch size, in a study of Pied Flycatcher reproductive success; however, they found that variables at both spatial scales were important. Saab (1999) used a hierarchical approach to investigate the relative importance of three spatial scales (micro-, macro-, and landscape) to the habitat use of breeding songbirds. She found that variables of all three scales were important; however, landscape variables (composition and pattern of the surrounding non-forest land) were more highly correlated with species abundance and occurrence, whereas micro- (vegetation characteristics) and macro-habitat (forest-patch characteristics) variables were of secondary importance. To my knowledge, Rodewald and Yahner (2001a) have conducted the only multi-scale study that simultaneously investigated the relative influence of variables at three spatial scales on avian nesting success. They examined habitat characteristics of the nest-patch (0.04 ha; macro-scale), the forest stand (25 ha; local plot-scale, including distance to edges), and the surrounding non-forest land (disturbance type (314 ha) and extent (1-km radius); landscape-scale) on the composite nesting success of ground-, understory-, mid-canopy-, and canopy-nesting songbirds. They found that daily nest survival was not associated with nest-patch or stand-level habitat characteristics, distance of nests from edges, or extent of non-forest disturbance at the landscape-scale; rather, daily nest survival was associated with the type of non-forest land-use surrounding the forest stand. The findings of this study suggest that landscape composition is the driving force in avian nesting success, whereas habitat variables at finer spatial scales are of lesser importance.

Landscape-level characteristics, such as the types of land uses within fragmented landscapes (Andren 1992) and the extent of habitat disturbances (Donovan et al. 1997), affect avian nesting success and have been argued to determine the expression of local-scale effects and dictate local patterns of nest predation and parasitism (e.g., Robinson et al. 1995, Donovan et al. 1997, Thompson et al. 2002). Although some studies have found that the expression of local-scale edge effects is dependent upon landscape-level characteristics such as the type of surrounding non-forest land use and the extent of forest cover (Donovan et al. 1997, Rodewald 2002), others have documented that landscape-level features alone do not determine nesting success, even in highly fragmented landscapes (Morse and Robinson 1999). Many ecological processes that might affect nest predation such as the dispersal and habitat selection of predators operate at multiple spatial scales (Bergin et al. 2000). Chalfoun et al. (2002b) documented that predator response (functional, numerical, or species richness) varied according to geographic region, landscape type, and spatial scale (landscape, patch, edge) and that these responses were taxon-specific, with different predator species having distinct responses. For example, several studies have found that corvids respond to both landscape-scale and local-scale habitat features (Yahner and Scott 1988, Robinson and Robinson 1999). Small-mammal populations are often variable spatially and temporally (Heske 1995) and may depend on local and annual food availability or on micro-habitat characteristics such as amount of coarse woody debris (Bayne and Hobson 1997). Medium-sized mammalian predators may be more tied to landscape-scale than to local-scale features (Dijak and Thompson 2000). Patterns of nest predation are complex and several interactions probably occur between different biogeographic regions, patterns of land use and land cover, habitat types, spatial scales, and predator species (Chalfoun et al. 2002b). Because local-scale processes like edge effects may be driven by habitat patterns at larger spatial scales, conservation plans should utilize a top-down regional approach where coarse-grain objectives are developed at a regional or landscape scale and local-scale decisions are made in light of the regional or landscape context (Freemark et al. 1993, Thompson et al. 1995, Donovan et al. 1997). Accurate interpretation of the mechanisms driving rates of nest predation and parasitism will require viewing these ecological processes at multiple scales (Donovan et al.

1997). Habitats do not exist in isolation, but in relation to other habitats within a hierarchy of spatial scales; thus, to properly manage for the conservation of songbird populations more studies need to use a multi-scale approach to investigate patterns of nest predation and brood parasitism and the mechanisms behind the patterns.

TABLES

Table 1.1: Review of studies that investigated nest predation and brood parasitism relative to habitat features of the nest site. For nest type, A=artificial and N=natural. For nest location, G=ground, S=shrub, C=canopy, and A=above ground.

Study	Location	Habitat	Nest Type	Nest Location	Habitat Feature	Scale	Predator/ Parasite	Predation/ Parasitism Affected
Angelstam (1986)	Sweden	coniferous	A	G	Concealment	micro, macro (5-m radius)	All[a]	↓ macro-scale concealment ↑ predation
Banks and Martin (2001)	Montana	riparian cottonwood-aspen	N DUFL WAVI YEWA AMRE	S, C	Nest Height, Concealment	micro	BHCO	no effect
Bayne and Hobson (1997)	Saskatchewan, Canada	boreal mixed	A	G, S	Concealment, % Cover of deciduous trees, coniferous trees, shrubs, dead/down woody material (heights <0.25, 0.25-1, 1-3, >3m)	micro (2 m, 1 m^2)	small mammals	↑ downed woody material ↑ predation (along clearcut edges)
Bowman and Harris (1980)	Florida	mature slash pine/ water oak	A	G	Concealment, Spatial Heterogeneity	micro, macro	Raccoon	↑ heterogeneity ↓ predation
Brittingham and Temple (1996)	Wisconsin	deciduous woods	N Mixed	G, S, C	% Cover: herbs/low shrubs, shrubs/saplings, sub-canopy, canopy (0-0.5 m, 0.5-3 m, 3-10 m, >10 m). # Stems (0.5-1 m, 1-3 m, 3-5 m, >5 m). # Trees (DBH: 7-14.5 cm, 14.5-22 cm, 23-37 cm, 37-52 cm, >52 cm). Distance to and # of Snags	macro (0.04 ha)	BHCO	↓ % sub-canopy (3-10 m), ↓ % canopy (>10 m), ↑ ground cover (0-0.5 m), ↑ density small shrubs (0.5-1 m), ↓ density tall shrubs (>5 m), ↓ density small trees (< 14 cm DBH) ↑ parasitism. Proximity to snags no effect.

Study	Location	Habitat	Nest Type	Nest Location	Habitat Feature	Scale	Predator/ Parasite	Predation/ Parasitism Affected
Budnick (2002)	Missouri	grassland-shrub	N BEVI	S	Nest Height, Side Concealment, Presence/Absence of Perch, Shrub Cover	micro, macro (10-m radius; perch), habitat-patch/territory (shrub cover)	BHCO	no effect of nest height, ↑ side concealment ↓ parasitism, presence of perch ↑ parasitism, ↑ shrub cover ↓ parasitism
Chasko and Gates (1982)	Maryland	oak-hickory	N Mixed	G, S, C	Concealment, Height of: Nest, Nest-Plant, Understory and Overstory Canopy. Density of: Stems, Dead Woody Plants, Grass, Greenbrier, and Grapevine. % Cover of: Ground-layer, Understory Canopy, and Overstory Canopy. Distance to: Ground-layer Patches, and Nearest Understory and Overstory Tree. Vegetation Heterogeneity of: Ground-layer, Understory, and Overstory. Soil Moisture. # Trees (DBH: 0-5 cm, 5-15 cm, 15-30 cm, > 30 cm).	micro, macro (0.04 ha)	na[b]	Utility Corridor: ↑ heterogeneity/patchiness, ↑ % canopy closure, ↑ density of shrub patches, ↓ grass density, ↓ distance to nearest tree ↑ nest success Forest Interior: ↑ concealment, ↑ % canopy closure, ↑ ground density of grapevine, ↑ diversity of understory, ↑ distance to nearest tree, ↓ shrubs, ↓ # dead woody plants ↑ nest success
Clotfelter (1998)	Wisconsin	prairie	N RWBL	S	Nest Height, Lateral and Overhead Nest Cover, Proximity to Perches	micro, macro	BHCO	no effect of nest height or cover, ↓ distance to nearest perch ↑ parasitism
DeGraaf (1995)	New Hampshire	northern hardwood	A	G, S	Stem Density (<0.5, 0.5-1.0 , 1-2, >2 m), % Ground Cover, Basal Area, Tree Spp, Tree Height	micro (0.001 ha) macro (0.02 ha)	All[a]	↑ stem density > 1 m ↓ predation of ground nests
Donovan et al. (1997)	Midwestern US Illinois, Indiana, Missouri	oak-hickory, mixed hardwood	A	G	Concealment	micro	All[a]	No

Study	Location	Habitat	Nest Type	Nest Location	Habitat Feature	Scale	Predator/ Parasite	Predation/ Parasitism Affected
Evans and Gates (1997)	Maryland	northern hardwood	BHCO	relative abundance	Total Vegetation Volume (TVV), Forest Height Density (FHD; 1-2 m), Snag Basal Area (SBA)	macro	BHCO	areas with ↑ TVV, FHD, and SBA had ↑ cowbird abundance
Filliater et al. (1994)	Ohio	mature woodlands, croplands, secondary growth, pasture	N NOCA	S	Concealment Nest Height Plant Species	micro	All[a]	No
Flaspohler et al. (2000)	Wisconsin Michigan	mixed hardwoods	N HETH	G	Concealment	micro	All[a]	↑ side concealment ↓ predation
Flaspohler et al. (2000)	Wisconsin Michigan	mixed hardwoods	N OVEN	G	Concealment	micro	All[a]	No
Hahn and Hatfield (1995)	New York	oak-maple-hemlock forest	N Mixed	G, S, C	Nest Height	micro	BHCO	ground and < 1 m greater parasitism than > 1m
Hanski et al. (1996)	Minnesota	northern hardwood	N Mixed	G, S, C	Canopy Cover, Nest Height, Concealment	micro	All[a]	↑ canopy cover ↑ predation
Hauber and Russo (2000)	New York	field	N SOSP	G	Concealment (overhead), Perch Proximity	micro, macro	BHCO	no effect of concealment, ↑ perch proximity ↑ parasitism
Howlett and Stutchbury (1996)	Pennsylvania	beech-maple-hemlock	N HOWA	G	Concealment, Vegetation Density, Nest Height, Plant Species	micro	All[a]	No
Huhta et al. (1996)	Finland	boreal coniferous	A	G	Horizontal Visibility Shrub Layer (cover, count, type) Tree Layer (cover, count, type)	macro (5-m radius, 10-m radius)	All[a]	↑ count of pine and spruce ↑ predation

Study	Location	Habitat	Nest Type	Nest Location	Habitat Feature	Scale	Predator/ Parasite	Predation/ Parasitism Affected
Huhta et al. (1998a)	Finland	boreal coniferous	A	A (1.5 m)	nest type: open vs box	micro	All[a]	open nests ↑ predation
Huhta et al. (1998a)	Finland	boreal coniferous	A	A (1.5 m)	Stem and Shrub Count, Shrub and Canopy Cover, Concealment	micro (3-m radius)	All[a]	↑ horizontal visibility due to more open vegetation structure ↑ predation (along clearcut edges)
King et al. (1996)	New Hampshire	northern hardwood	N OVEN	G	Canopy Cover, Canopy Height, Herb Cover, Stem Density, Litter Depth	macro (0.04 ha)	All[a]	No
King et al. (1998a)	New Hampshire	northern hardwood	A	S	Concealment, Nest Height	micro	All[a]	No
Larison et al. (1998)	California	riparian willow-cottonwood	N SOSP	S	Nest Height, Substrate, Concealment, # Saplings, Foliage Cover (<1, 1-2, 2-3 m), Canopy Cover, Ground Cover, Foliage Height Lateral Cover (<1, 1-2, 2-3 m), # Trees, Understory Cover	micro, macro: local (5-m radius), broad (11.3-m radius)	BHCO	local: ↑ foliage cover 2-3 m ↑ parasitism broad: ↑ lateral coverage < 1 m ↓ parasitism
Manolis et al. (2000)	Minnesota	northern hardwood	N Mixed (80% OVEN)	G	# Trees, # Shrubs, Canopy Height, % Canopy Cover, % Ground Cover, Litter Depth, Concealment	macro (5-m radius, 11.3-m radius)	All[a]	No
Manolis et al. (2000)	Minnesota	northern hardwood	A	G	# Trees, # Shrubs, Canopy Height, % Canopy Cover, % Ground Cover, Litter Depth, Concealment	macro (5-m radius, 11.3-m radius)	All[a]	↑ concealment ↓ predation
Martin (1992) Literature Review	Various (35 Locations within Continental US and Canada)	Various (deciduous, coniferous, and riparian forests, forest edge, shrublands, desert, grasslands, marsh)	N Mixed (32 spp)	G, S, C	Foliage Density	micro	All[a]	↑ foliage density ↑ concealment ↓ predation

Study	Location	Habitat	Nest Type	Nest Location	Habitat Feature	Scale	Predator/ Parasite	Predation/ Parasitism Affected
Martin (1992) Literature Review	Various (35 Locations within Continental US and Canada)	Various (deciduous, coniferous, and riparian forests, forest edge, shrublands, desert, grasslands, marsh)	N Mixed (32 spp)	G, S, C	Foliage Density	macro	All[a]	↑ foliage density ↓ predator search efficiency (more potential nest sites to search and hindered mobility) and ↓ predation
Martin (1992) Literature Review	Various (35 Locations within Continental US and Canada)	Various (deciduous, coniferous, and riparian forests, forest edge, shrublands, desert, grasslands, marsh)	N Mixed (32 spp)	G, S, C	nest-patch density	territory	All[a]	more patches within a territory ↓ predator search efficiency and ↓ predation
Martin (1993a)	Arizona, Arkansas	mixed-conifer and deciduous forest	A	G , S, C	Nest Height	micro	All[a]	shrub > canopy > ground
Martin (1993a)	Various (Literature Review)	shrubland/ grassland	A	G , S, C	Nest Height	micro	All[a]	ground > shrub ~ canopy
Martin (1993a)	Arizona and Arkansas, Various	mixed-conifer and deciduous forest, shrubland/grassland	A	G , S, C	Nest Height	micro	All[a]	ground > shrub > canopy
Martin (1993b)	Arizona	pine-fir-aspen-oak-maple	N MCWA HETH	G, S	Vegetation Density (stems), Potential Nest Sites	macro (5-m radius)	All[a]	↑ # nest sites ↓ predation
Martin (1995) Literature Review	Various (Literature Review)	Various (Literature Review)	N Mixed	G , S, C	Nest Height Nest Type (open, cavity: excavator, non-excavator)	micro	All[a]	shrub > canopy > NonExCav ~ ground >> ExCav

Study	Location	Habitat	Nest Type	Nest Location	Habitat Feature	Scale	Predator/ Parasite	Predation/ Parasitism Affected
Martin (1998)	Arizona	pine-fir-aspen-oak-maple	N Mixed	G, S	Use vs Non-Use/Random Sites: # Stems of Understory Woody Plants (dbh: <2.5 cm, 2.5-8 cm, 8-23 cm), # Understory Conifers (height: <1 m, 1-3 m, 3-5 m), # Canopy Trees (dbh: 8-23 cm, 23-38 cm, > 38 cm), % Ground Cover	macro (5-m radius, 11-m radius)	na[b]	Nest sites were chosen non-randomly (preference) and adaptively (greater success). Differences in macrohabitat vegetation between successful nest-sites and random non-use sites was species-specific (i.e., no general trend among all 7 bird species).
Martin and Roper (1988)	Arizona	pine-fir-aspen-oak-maple	N HETH	G	Concealment, Nest Height, Stems, Plant Species	micro	All[a]	↑ concealment ↓ predation, ↑ height and more white firs (potential nest sites) ↓ predation
Martin et al. (2000)	Arizona	mixed-conifer and deciduous forest	N Mixed	G, S, C	Nest Site and Parental Activity (incubation vs nestling stages)	micro, macro, territory	All[a]	When held parental activity constant, poor nest sites suffered increased predation. Parental activity increased predation during nestling stage.
Moorman et al. (2002)	South Carolina	bottomland hardwood	N HOWA	S	Substrate Spp, Substrate Height, Nest Height, Concealment, Canopy Cover, Stem Density (<3 m, ≥ 3m), % Ground Cover, # Trees, Vegetation Profile	micro, macro (5-m radius)	na[b] BHCO	↑ concealment from below ↑ success, ↑ stem density (≥3m) ↑ success, ↓ ground cover ↑ parasitism
Ortega and Capen (2001)	Vermont	northern hardwood	A	G, A (1-2 m)	Nest Height, Concealment; Canopy Cover, Ground Cover, Shrub Density, # Stems, Tree Species, Tree DBH, Litter Depth, Shrub Height, Canopy Height, Slope; Forest Cover, Development	micro, macro (0.04 ha), landscape (2-km and 5-km radius)	All[a]	↑ height ↑ predation

Study	Location	Habitat	Nest Type	Nest Location	Habitat Feature	Scale	Predator/ Parasite	Predation/ Parasitism Affected
Rangen et al. (1999)	Alberta, Canada	mixed-wood	A	G, A	Nest Height Concealment	micro	mice, voles, squirrels, birds	mice and voles depredated well concealed ground nests. Squirrels and birds depredated poorly concealed above ground nests. Higher nests were more likely depredated by birds.
Ratti and Reese (1988)	Idaho	coniferous	A	G, S	Nest Height	micro	All[a]	No
Ricketts and Richison (2000)	Kentucky	deciduous woods, fields, fencerows	N YBCH	S	Concealment Vegetation Structure	micro, macro, territory	na[b]	nest-sites had more foliage and lateral cover, but no difference in nest success
Robinson et al. (2000)	Illinois Ozarks, Cache River, central, northwestern	oak-hickory, bottomland hardwoods	N Mixed	G, S, C	Nest Height	micro	BHCO	canopy > shrub ~ ground
Rudnicky and Hunter (1993)	Maine	coniferous	A	G, S	% Cover (heights <0.25, 0.25-1, 1-3, >3m), Slash, Nest Height	micro (1-m^2)	All[a]	↑ cover ↓ predation ↑ slash ↑ predation
Rudnicky and Hunter (1993)	Maine	forest vs clearcut	A	G	% Cover (heights <0.25, 0.25-1, 1-3, >3m) Nest Height	micro (1-m^2)	All[a]	forest: ↑ cover ↓ predation clearcut: ↑ cover ↑ predation ↑ height ↑ predation
Soderstrom (1999) Literature Review	Various (US, Canada, Costa Rica, Panama, Amazon, Andes)	temperate forest (deciduous, coniferous, mixed), tropical forest (montane and lowland)	A	G, S	Nest Height	micro	All[a]	temperate: shrub > ground tropical: ground > shrub
Storch (1991)	Germany	coniferous	A	G	% Ground Cover	macro	All[a]	No

Study	Location	Habitat	Nest Type	Nest Location	Habitat Feature	Scale	Predator/ Parasite	Predation/ Parasitism Affected
Tittler and Hannon (2000)	Alberta, Canada	boreal mixed	A	G, S	Nest Height, % Lateral and Overhead Cover, % Canopy Cover, Basal Area, % Ground Cover, Litter Depth, Stem Density	micro ($1 m^2$), macro (5-m radius, 11.3-m radius)	All[a] (murid, avian, squirrel)	↑ nest height ↓ predation, ↑ % conifer and ↑ nest height ↓ murid predation, ↑ litter depth ↓ avian predation, no effect for squirrel predation, ↑ # shrubs ↑ avian predation within clearcut
Uyehara and Whitefield (2000)	California	riparian forest (willow-cottonwood)	N SWFL	S	Concealment	micro, macro-nest patch (0.04 ha), random macro-territory patch (0.04 ha)	BHCO	↑ cover in macro-nest patches and macro-territory patches ↓ parasitism, larger patches of dense understory within macro-territory patches ↓ parasitism
Vander Lee et al. (1999)	Texas	agricultural/ range CRP grasslands	A	G	Vegetation Density	micro	All[a]	↑ vegetation density ↓ predation
Weidinger (2002)	Eastern Bohemia, Czech Republic	deciduous woods within farmland	A, N Song Thrush, Blackbird, Blackcap, Yellowhammer	G, S	Concealment	micro	mice, corvids	↑ concealment ↓ predation. Corvids depredated poorly concealed nests, while mice depredated well-concealed nests
Wilson (1997)	Arkansas	bottomland hardwoods	N ACFL	C	Plant Species, Nest Height, Concealment, Bole/Edge Distance	micro	All[a]	No
Yahner and Cypher (1987)	Pennsylvania	aspen	A	A (0.5, 1.5 m)	Nest Height, Vegetation Structure[c]	micro, macro	All[a] (AMCR)	↑ height ↑ predation, ↓ vertical complexity and ↑ shrub density ↓ predation
Yahner et al. (1989)	Pennsylvania	aspen	A	G, A (1.5 m)	Nest Height	micro	All[a]	↑ height ↑ predation (along clearcut edge)

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a=refers to all predators; study not include brood parasitism

b=refers to nest success, not predation per se

c=vegetation structure based on forest age; 4 year-old clearcut=simple vertical structure with dense shrub layer, 8 year-old clearcut and mature (60 year-old) forest=complex vertical structure and less dense shrub layer

Table 1.2: Review of forest fragmentation studies, including fragmentation caused by silvicultural practices, agriculture, fields, water, and other non-forested land. Unless otherwise noted, a positive fragmentation effect refers to an increase in nest predation with increased forest fragmentation. In addition to nest-centered studies, some studies focused on the relative abundance of brood parasites and potential predators. In these studies, a positive fragmentation effect refers to an increase in relative abundance with increased forest fragmentation. Gray areas represent data that were not available. For nest type, A=artificial and N=natural. For nest location, G=ground, S=shrub, C=canopy, and A=above ground.

Study	Location	Habitat	Nest Type	Nest Location	Fragment Type	Fragment Age	Forest Cover	Scale	Fragmentation Effect
Annand and Thompson (1997)	Missouri	mixed oak, oak-pine	BLJA AMCR BHCO	relative abundance	clearcuts (< 16 ha), shelterwood, group-cuts (0.2-0.4 ha), single tree, uncut	3-6 yrs	60% (site) 85% (region)	260 ha (site) landscape	No (BLJA, AMCR) Yes (BHCO)
Bayne and Hobson (1997)	Saskatchewan, Canada	boreal mixedwood	A	G, S	agriculture vs clearcuts (25%)				Yes (agriculture) No (clearcuts)
Bourque and Villard (2001)	New Brunswick, Canada	deciduous, coniferous	N BTBW	S	selection cuts, clearcuts, spruce plantations, roads	< 5 yrs (selection cuts)	45% vs >70%	49 km^2	No (site) No (landscape)
Bourque and Villard (2001)	New Brunswick, Canada	deciduous, coniferous	N OVEN	G	selection cuts, clearcuts, spruce plantations, roads	< 5 yrs (selection cuts)	45% vs >70%	49 km^2	No (site) Yes (landscape)
DeGraaf (1995)	New Hampshire	northern hardwood	A	G, S	clearcuts	10 yrs	65% sawtimber, 17% poletimber, 18% sapling vs 96% sawtimber, 4% poletimber	64-ha plot	No
DeGraaf and Angelstam (1993)	New Hampshire	northern hardwood	A	G, S	clearcuts	sapling, pole, mature	87% mature, 5% poletimber, 8% sapling	64-ha plot	No

Study	Location	Habitat	Nest Type	Nest Location	Fragment Type	Fragment Age	Forest Cover	Scale	Fragmentation Effect
Donovan et al. (1995)	Midwestern US Missouri, Wisconsin/Minnesota	oak-hickory, maple-basswood-birch	N OVEN, REVI, WOTH	G, S, C	agriculture		fragmented (<25%) vs contiguous (>90%)	10-km radius	Yes[a]
Donovan et al. (1997)	Midwestern US Illinois, Indiana, Missouri	oak-hickory, mixed hardwood	A	G	agriculture, fields, wildlife openings		highly fragmented (<15%), moderately fragmented (45-55%), unfragmented (>90%)	864 km^2	Yes (mammal, BHCO[b]) No (avian)
Linder and Bollinger (1995)	Illinois	oak	A	G	agriculture, selective logging		32%	5, 10, 25 km radius	Yes
Marini et al. (1995)	Illinois	oak-hickory, tulip-maple-beech	A	G, S, C	agriculture (crops)		50-68%	5, 10, 25 km radius	Yes
Morse and Robinson (1999)	Illinois (southern)	tulip, beech, maple	N KEWA	G	clearcuts, wildlife openings, pine plantation	6-22 yrs (clearcuts)	53%	10-km radius	Yes
Ratti and Reese (1998)	Idaho	coniferous	A	G, S	clearcuts	4 yrs, 6yrs	47-76%	5, 10, 25 km radius	No
Robinson et al. (1995)	Midwestern US Illinois, Indiana, Minnesota, Missouri, Wisconsin		N Mixed	G, S, C	agriculture		6-95%	10-km radius	Yes[a]
Robinson and Robinson (1999)	Illinois (southern)	upland deciduous	BLJA BHCO	relative abundance	group-cuts, single-tree cuts, (0.02-0.4 ha)	uncut, 1-5 yrs, 10-15 yrs	53%	10-km radius	Yes (BLJA) No (BHCO)

Study	Location	Habitat	Nest Type	Nest Location	Fragment Type	Fragment Age	Forest Cover	Scale	Fragment-ation Effect
Robinson and Robinson (2001)	Illinois (southern)	upland deciduous	N ACFL, WOTH, NOCA, KEWA	G, S, C	group-cuts (0.1-0.6 ha)	1-6 yrs, 10-15 yrs	53%	10-km radius	No[c]
Rodewald (2002), Rodewald and Yahner (2001a)	Pennsylvania	aspen	N Mixed	G, S, C	forested landscape disturbed by agriculture vs silviculture	≤ 15 yrs (clearcuts)	45-79% (agriculture) 49-82% (silviculture)	1-km radius	agriculture < silviculture[c]
Rodewald and Yahner (2001a)	Pennsylvania	aspen	N Mixed	G, S, C	agriculture, silviculture	≤ 15 yrs (clearcuts)	45-82%	1-km radius	No[c]
Rodewald and Yahner (2001b)	Pennsylvania	aspen	AMCR BLJA BHCO	relative abundance	forested landscape disturbed by agriculture vs silviculture	≤ 15 yrs (clearcuts)	45-79% (agriculture) 49-82% (silviculture)	1-km radius	AMCR, BHCO > in landscape disturbed by agriculture than by silviculture
Rudnicky and Hunter (1993)	Maine	coniferous	A	G	clearcuts	3-10 yrs	46-68%	5, 10, 25 km radius	No
Small and Hunter (1988)	Maine	oak-pine	A	G	fields, roads, powerlines, water bodies		27-66%	5, 10, 25 km radius	No
Steventon et al. (1999)	British Columbia, Canada	Coastal Western Hemlock and Sub-boreal Spruce Zones	A	G	partial cuts, clearcuts, uncut	1 yr	70%, 40% 0% 100%	20-ha plot	No
Steventon et al. (1999)	British Columbia, Canada	Coastal Western Hemlock and Sub-boreal Spruce Zones	A	S	partial cuts, clearcuts, uncut	6 yrs	70%, 40% 0% 100%	20-ha plot	No

Study	Location	Habitat	Nest Type	Nest Location	Fragment Type	Fragment Age	Forest Cover	Scale	Fragment-ation Effect
Thompson et al. (1992)	Missouri (Ozarks)	oak-hickory-pine	BLJA AMCR BHCO	relative abundance	clearcuts	0-10, 11-20, >20 yrs	10% regenerating, 10% sapling, 80% pole-sawtimber vs 100% mature	200 ha	No
Twedt et al. (2001)	Louisiana	bottomland hardwoods	N Mixed	G, S, C	group cuts	1-2 yrs	86%	1-km radius	No
Wilcove et al. (1986)	Maryland	deciduous	A	G, A	agriculture		50-63%	5, 10, 25 km radius	Yes
Wood (1999)	Arkansas	bottomland hardwood	N PROW	S, C	clearcuts, thinnings	1-3 yrs	78%, 99%	50-ha plot	No
Yahner and Mahan (1996)	Pennsylvania	aspen	A	G	clearcuts	5-16 yrs	100%, 50%, 25%	270 ha	No 25% > 100% >50%
Yahner et al. (1993)	Pennsylvania	aspen	A	G	clearcuts, uncut	6-14 yrs	75%	128 ha	No
Yahner and Scott (1988)	Pennsylvania	aspen	A	G, A (1.5 m)	clearcuts	5-6 yrs, 5-10 yrs	100%, 75%, 50%	270 ha	Yes 50% > 75% >100%
Yahner and Wright (1985)	Pennsylvania	aspen	A	G	clearcuts	2 yrs, 6 yrs	55-62%	5, 10, 25 km radius	No

a=applies to parasitism as well as predation

b=refers to BHCO abundance, not parasitism

c=refers to nest success, not predation

Table 1.3: Review of edge effects at external edges created between the forest and the non-forest land that envelops the forest fragment. Unless otherwise noted, a positive edge effect refers to an increase in nest predation near the edge compared to within the forest interior. In addition to nest-centered studies, one study focused on the relative abundance of brood parasites and potential predators. In these studies, a positive edge effect refers to an increase in relative abundance near the edge compared to within the forest interior. Gray areas represent data that were not available. For nest type, A=artificial and N=natural. For nest location, G=ground, S=shrub, C=canopy, and A=above ground.

Study	**Location**	**Habitat**	**Nest Type**	**Nest Location**	**Edge Type**	**Dominant Habitat**	**Distance (m)**	**Edge Effect**
Andren and Angelstam (1988)	Sweden	coniferous	A	G	Agriculture	Agriculture (58%)	0, 50, 100, >300	Yes
Angelstam (1986)	Sweden	coniferous	A	G	Agriculture	Forest (87%)	0 - >1500	No
Arango-Velez and Kattan (1997)	Columbia	cloud forest	A	G, S	Agriculture	Agriculture	0-10, 200	No (opposite), Yes[a]
Bayne and Hobson (1997)	Saskatchewan, Canada	boreal mixedwood	A	G, S	Agriculture	Agriculture (70%)	1-5, 100-200	No/Yes[b] (edge) Yes (landscape)
Bjorklund (1990)	Sweden	deciduous	N Scarlet Rosefinch	S	Agriculture		0-100	Yes
Brittingham and Temple (1983)	Wisconsin	deciduous	N	A	Open (>0.2 ha) (agriculture, clearcuts, regenerating)	Forest	0 - >300 (100-m intervals)	Yes[c]
Burkey (1993)	Belize	rainforest	A	G	Field and Road	Forest	30-500	Yes

Study	Location	Habitat	Nest Type	Nest Location	Edge Type	Dominant Habitat	Distance (m)	Edge Effect
Chalfoun et al. (2002a)	Missouri	deciduous	BHCO Predators: avian (BLJA, AMCR), small mammals, medium mammals, snakes	relative abundance	Agriculture	Agriculture (62%)	0-50 vs 200+	Yes (BHCO, BLJA, AMCR, snakes) No (mammals)
Danielson et al. (1997)	Massachusetts	deciduous	A	G, S	Agriculture	Forest	20-420 (100-m intervals)	No
Donovan et al. (1997)	Midwestern US Illinois, Indiana, Missouri	oak-hickory, mixed hardwood	A	G	Agriculture/ Grassland	Agriculture (85%)	0-50, >250	No (mammals, BHCO[d]) Yes (avian)
Donovan et al. (1997)	Midwestern US Illinois, Indiana, Missouri	oak-hickory, mixed hardwood	A	G	Agriculture/ Grassland	Forest (45-55%)	0-50, >250	No (BHCO[d]) Yes (mammals, avian)
Donovan et al. (1997)	Midwestern US Illinois, Indiana, Missouri	oak-hickory, mixed hardwood	A	G	Agriculture/ Grassland	Forest (>90%)	0-50, >250	No (mammals) Yes (avian, BHCO[d])
Gates and Gysel (1978)	Michigan	deciduous	N	A	Agriculture	Agriculture	0-123	Yes
Gibbs (1991)	Costa Rica	tropical	A	G, A (1-3 m)	Agriculture/ Pasture		5, >500	No opposite

Study	Location	Habitat	Nest Type	Nest Location	Edge Type	Dominant Habitat	Distance (m)	Edge Effect
Huhta et al. (1996)	Finland	coniferous	A	G	Agriculture	Agriculture	0-5, 150-200	Yes (corvids)
Kuitunen and Helle (1988)	Finland	coniferous	N Treecreeper	A Nest Box	Open (Lake, Field, Bog)	Forest (65%)	0 - >200	Yes
Linder and Bollinger (1995)	Illinois	oak	A	G	Agriculture	Agriculture	20, 200, 400	Yes
Marini et al. (1995)	Illinois	oak-hickory, tulip-maple-beech	A	G, S, C	Agriculture	Agriculture (60%)	10-15, >300	Yes
Moller (1989)	Denmark	deciduous	A	G	Agriculture	Agriculture (98%)	0, 25, 100	Yes
Morse and Robinson (1999)	Illinois	tulip, beech, maple	N KEWA	G	Agriculture	mix (forest, regenerating, plantation, opening)	all	Yes[c]
Nour et al. (1993)	Belgium	deciduous	A	A	Agriculture		1-125	No
Rodewald (2002)	Pennsylvania	aspen	N Mixed	G, S, C	Agriculture	Forest (45-82%)	0-200+	No
Rodewald and Yahner (2001a)	Pennsylvania	aspen	N Mixed	G, S, C	Agriculture	Forest (45-79%)	0-200+	No
Sandstrom (1991)	Sweden	deciduous	A Natural Cavities	A	Agriculture		0 - >20	Yes
Santos and Telleria (1992)	Spain	deciduous	A	G, A	Agriculture	Forest	0-100	No

Study	Location	Habitat	Nest Type	Nest Location	Edge Type	Dominant Habitat	Distance (m)	Edge Effect
Suarez et al. (1997)	Illinois (southern)	deciduous	N INBU	S	Agriculture, Field	mix (forest, regenerating, plantation, wildlife opening)	na[e]	Yes[f]
Temple and Cary (1988)	Wisconsin	deciduous	N	A	Agriculture	Agriculture /Forest 50/50	0 - >200 (100-m intervals)	Yes
Wilcove et al. (1986)	Maryland Tennessee	deciduous	A	G, A	Agriculture	Agriculture	0-1000	Yes

a=study had two forest fragments (300 and 75 ha). The 300 ha fragment had higher nest predation in the interior than the edge. The 75 ha fragment had higher nest predation at the edge than the interior during the non-rainy season, but not during the rainy season.

b=no increase in predation rate, but increase in diversity of predators

c=refers to brood parasitism, not predation

d=refers to BHCO abundance, not parasitism rate

e=not a study of distance from edge; comparison among different types of edges: abrupt, permanent edges (agriculture, wildlife openings, old fields) versus gradual, temporary edges where plant succession occurred (treefall gaps, streamsides, groupcut silvicultural gaps). Nests located within the edges.

f=predation twice as great at abrupt, permanent exterior edges than at gradual, temporary, interior edges

Table 1.4a: Review of edge effect studies at internal forest edges created by silvicultural practices. Unless otherwise noted, a positive edge effect refers to an increase in nest predation near the forest-cut edge compared to within the forest interior. In addition to nest-centered studies, some studies focused on the relative abundance of potential nest predators and brood parasites. In these studies, a positive edge effect refers to an increase in relative abundance near the forest-cut edge compared to within the forest interior. In addition to studies of distance from silvicultural edges, also included are studies that compare nest predation, brood parasitism, and relative abundance of predators and brood parasites among silviculturally treated stands of different timber size/class (na[j] within distance column). In these studies, the experimental unit is the stand, not the nest. Nests were located within the stands of different age. For these studies, an edge effect equals an increase in predation, parasitism, or relative abundance of predators/parasites within the younger stands. Additionally, included are studies that compare nest predation, brood parasitism, and relative abundance of predators/parasites among plots with different silvicultural treatments (na[m] within distance column). For these studies, the experimental unit is the plot, not the nest. Nests were placed in the mature forest of the treatment plot. For these studies, an edge effect equals an increase in predation, parasitism, or relative abundance of predators/parasites within treated plots as opposed to uncut plots. For nest type, A=artificial and N=natural. For nest location, G=ground, S=shrub, C=canopy, and A=above ground. Gray areas represent data that were not available. All studies were conducted within forest-dominated landscapes with the exception of Morse and Robinson (1999), Robinson and Robinson (1999, 2001), and Suarez et al (1997).

Study	**Location**	**Habitat**	**Nest Type**	**Nest Location**	**Cut Size**	**Cut Age**	**Distance (m)**	**Edge Effect**
Bayne and Hobson (1997)	Saskatchewan, Canada	boreal mixedwood	A	G, S		1-10 yrs	1-5, 200-300	No (sm mammals) Yes (avian)
Cotterill and Hannon (1999)	Alberta, Canada	boreal mixedwood	A	G, S	10-60 ha (40 ha)	pre-harvest, 1 yr, 5 yrs	0-200[a] (20 m)	No
Evans and Gates (1997)	Maryland	northern hardwood	BHCO	relative abundance	2.1-23.2 ha	1-10 yrs	0, 250	Yes
Fenske-Crawford and Niemi (1997)	Minnesota	northern hardwood	A	G	2-42 ha	2-4 yrs	0, 50, 100	Yes
Flaspholer et al. (2001a)	Wisconsin	northern hardwood	N OVEN	G	8-48 ha (22 ha)	1-6 yrs (4 yrs)	0-950 (<300 vs >300)	Yes
Flaspholer et al. (2001b)	Wisconsin	northern hardwood	N OVEN, HETH	G	8-48 ha (22 ha)	1-6 yrs (4 yrs)	0-950 (<300 vs >300)	Yes

Study	Location	Habitat	Nest Type	Nest Location	Cut Size	Cut Age	Distance (m)	Edge Effect
Flaspholer et al. (2001b)	Wisconsin	northern hardwood	N Mixed	C	8-48 ha (22 ha)	1-6 yrs (4 yrs)	0-950 (<300 vs >300)	No
Gibbs (1991)	Costa Rica	deciduous	A	A		tree plantation	5 to > 500	Yes
Hanski et al. (1996)	Minnesota	northern hardwood	N Mixed	G, S, C		<2 m, 2-8 m, >8 m[b]	0-25, 25-50, >50	No
Huhta and Jokimaki (2001)	Finland	boreal	N[c] PIFL, Redstart	A (1.5 m)	1-50 ha (20 ha)		0-250 (50 m)	Yes
Huhta et al. (1996)	Finland	coniferous	A	G			0-5, 150-200	No
Huhta et al. (1998a)	Finland	coniferous	A (open,box)	A (1.5 m)	≥ 10 ha	2-10 yrs	0-1, 100	No
King et al. (1996)	New Hampshire	northern hardwood	N OVEN	G	2-5 ha	≤ 6 yrs	0-200, 200-400	Yes
King et al. (1998a)	New Hampshire	northern hardwood	A	S	0.5-1.0 ha, 10 ha	4-5 yrs	0-5, 45-50	Yes
King et al. (1998b)	New Hampshire	northern hardwood	Eastern chipmunk, Red squirrel, BLJA	relative abundance	2-5 ha	≤ 6 yrs	100 within clearcut to 300 within adjacent forest (50-m intervals)	Yes (chipmunk, squirrel) No (BLJA)
Manolis (1999)	Minnesota	northern hardwood	A	G	5-40 ha (16 ha)	3-18 yrs (11 yrs)	0-300 (50 m)	Yes
Manolis (1999)	Minnesota	northern hardwood	N Mixed (OVEN)	G	5-40 ha (16 ha)	3-18 yrs (11 yrs)	0-1500	Yes
Manolis et al. (2000)	Minnesota	northern hardwood	N REVI	S, C	5-40 ha (16 ha)	3-18 yrs (11 yrs)	0-1500	No

Study	Location	Habitat	Nest Type	Nest Location	Cut Size	Cut Age	Distance (m)	Edge Effect
Manolis et al. (2000)	Minnesota	northern hardwood	N LEFL	C	5-40 ha (16 ha)	3-18 yrs (11 yrs)	0-1500	No
Manolis et al. (2000)	Minnesota	northern hardwood	A	G	5-40 ha (16 ha)	3-18 yrs (11 yrs)	0-300 (50 m)	Yes
Manolis et al. (2000)	Minnesota	northern hardwood	N Mixed (80% OVEN)	G	5-40 ha (16 ha)	3-18 yrs (11 yrs)	0-300	Yes
Manolis et al. (2002)	Minnesota	northern hardwood	N Mixed	G	5-40 ha (16 ha)	3-18 yrs (11 yrs)	0-1000	Yes
Moorman et al. (2002)	South Carolina	bottomland hardwood	N HOWA	S	0.06-0.5 ha, 25-32 ha	2-4 yrs, 10-12 yrs	0-50, 50-100, >100	No[d] Yes[e,f]
Morse and Robinson (1999)	Illinois (southern)	tulip, beech, maple	N KEWA	G	14.6 ha, 3.6-9.5 ha	6-9 yrs, 13-22yrs	all	No[g]
Ratti and Reese (1988)	Idaho	coniferous	A	G, S	11 ha, 18 ha	6 yrs, 4 yrs	0-160[h] (20 m)	No opposite
Rodewald (2002)	Pennsylvania	aspen	N Mixed	G, S, C	7-38 ha	≤ 15 yrs	0-200+	No
Rodewald and Yahner (2001a)	Pennsylvania	aspen	N Mixed	G, S, C	7-38 ha	≤ 15 yrs	0-200+	No
Rudnicky and Hunter (1993)	Maine	coniferous	A	G	2-107 ha	3-10 yrs	-300 to 300 (15 m)	No
Rudnicky and Hunter (1993)	Maine	coniferous	A	S	2-107 ha	3-10 yrs	0-300 (15 m)	Yes
Song and Hannon (1999)	Alberta, Canada	boreal mixedwood (aspen)	A	G, S	25 ha	1-3 yrs	0-60	No

Study	Location	Habitat	Nest Type	Nest Location	Cut Size	Cut Age	Distance (m)	Edge Effect
Storch (1991)	Germany	coniferous	A	G	5-25 ha	2 m[b]	0-100 (50 m)	No opposite
Strelke and Dickson (1980)	Texas	pine-hardwood	BLJA, BHCO	relative abundance	mature forest edge vs interior, clearcut edge vs interior	<3 yrs	150 within clearcut to 150 within forest (50-m intervals)	No[i] (BLJA) Yes[i] (BHCO)
Tittler and Hannon (2000)	Alberta, Canada	boreal mixed	A	G, S	10-60 ha	3 yrs	0, 50	No
Vander Haegen and DeGraaf (1996)	Maine	sub-boreal Acadian	A	G	27 ha (avg)	8-10 yrs	0-195 (15 m) (<75 vs >75)	No
Vander Haegen and DeGraaf (1996)	Maine	sub-boreal Acadian	A	S	27 ha (avg)	8-10 yrs	0-195 (15 m) (<75 vs >75)	Yes
Yahner (1991)	Pennsylvania	aspen	N Mixed	G, S	1 ha	4-7 yrs, 8-10 yrs	0-10, 10-25, 25-50	No
Yahner and Mahan (1996)	Pennsylvania	aspen	A	G	1 ha	5-16 yrs	50, >50	No
Yahner and Mahan (1997)	Pennsylvania	aspen, oak, maple, pine	A	G	1 ha	7-9 yrs	≤ 1, >50	Yes
Yahner et al. (1993)	Pennsylvania	aspen	A	G	1 ha	6-14 yrs	5, 50	No
Yahner et al. (2001)	Pennsylvania	oak-hickory	A	G	28-38 ha	3-5 yrs	-50, 0, 50, 150	No
Yahner and Wright (1985)	Pennsylvania	aspen	A	G	1 ha	2 yrs, 6 yrs	5-10, 50	No

Study	Location	Habitat	Nest Type	Nest Location	Cut Size	Cut Age	Distance (m)	Edge Effect
DeGraaf and Angelstam (1993)	New Hampshire	northern hardwood	A	G, S	< 16 ha	sapling, pole, mature	na[j]	No
Hanski et al. (1996)	Minnesota	northern hardwood	N Mixed	G, S, C		clearcuts (<2m), regenerating (2-8m), mature (>8m)	na[j]	No (mature >> regenerating ~ clearcut)
King and DeGraaf (2000)	New Hampshire	northern hardwood	Eastern chipmunk, Red squirrel, BLJA, COGR	relative abundance	mature forest, shelterwood forest, clearcuts	3-5 yrs	na[j]	No (mature ~ shelterwood >> clearcut)
Moorman and Guynn (2001)	South Carolina	bottomland hardwoods	BLJA, AMCR, BHCO	relative abundance	0.06, 0.13, 0.26, 0.5 ha	2-4 yrs, uncut	na[j]	No (BLJA, AMCR) Yes (BHCO)
Morse and Robinson (1999)	Illinois (southern)	tulip, beech, maple	N KEWA	G	3.6-14.6 ha	6-9 yrs, 13-16 yrs, 19-22 yrs, mature (70-120 yrs)	na[j]	Yes[k]
Ratti and Reese (1988)	Idaho	coniferous	A	G, S	11 ha, 18 ha	4 yrs, 6 yrs, mature	na[j]	No (mature > clearcuts)
Rudnicky and Hunter (1993)	Maine	coniferous	A	G	2-107 ha	clearcut (3-10 yrs), mature	na[j]	No (mature > clearcuts)

Study	Location	Habitat	Nest Type	Nest Location	Cut Size	Cut Age	Distance (m)	Edge Effect
Thompson et al. (1992)	Missouri (Ozarks)	oak-hickory-pine	BLJA, AMCR, BHCO	relative abundance	200 ha managed site:10% regenerating, 10% sapling, 80% pole-sawtimber	0-10 yrs (regenerating), 11-20 yrs (sapling), >20 yrs (pole-sawtimber)	na[j]	No (BLJA, AMCR) Yes[l] (BHCO)
Yahner and Cypher (1987)	Pennsylvania	aspen	A	G, S	1 ha	4 yrs, 8 yrs, mature (60 yrs)	na[j]	No (mature ~ 8 yrs > 4 yrs)
Yahner and Wright (1985)	Pennsylvania	aspen	A	G	1 ha	2 yrs, 6 yrs, mature (55 yrs)	na[j]	No (mature > clearcuts)
Annand and Thompson (1997)	Missouri	mixed oak, oak-pine	BLJA, AMCR, BHCO	relative abundance	clearcuts <16 ha, shelterwood, groupcuts 0.2-0.4 ha, single-tree, uncut	3-6 yrs	na[m]	No (BLJA, AMCR) Yes[n] (BHCO)
Bourque and Villard (2001)	New Brunswick, Canada	deciduous, coniferous	N OVEN, BTBW	G, S	uncut, selection cuts (30% removal)	< 5 yrs	na[m]	Yes[d] (OVEN) No[d] (BTBW)
DeGraaf (1995)	New Hampshire	northern hardwood	A	G, S	< 16 ha vs uncut	10 yrs	na[m]	No
King and DeGraaf (2000)	New Hampshire	northern hardwood	A, N	S	mature forest, shelterwood forest, clearcuts	3-5 yrs	na[m]	No
Robinson and Robinson (1999)	Illinois (southern)	deciduous	BLJA, BHCO	relative abundance	0.02-0.4 ha	uncut, 1-5 yrs, 10-15 yrs	na[m]	Yes (BLJA) No (BHCO)

Study	Location	Habitat	Nest Type	Nest Location	Cut Size	Cut Age	Distance (m)	Edge Effect
Robinson and Robinson (2001)	Illinois (southern)	deciduous	N ACFL, WOTH, NOCA, KEWA	G, S, C	0.1-0.6 ha	uncut, 1-6 yrs, 10-15 yrs	na[m]	Yes[e] (ACFL, KEWA) No[e] (WOTH, NOCA) No[d] (All)
Steventon et al. (1999)	British Columbia, Canada	transitional b/t Coastal Western Hemlock and Sub-Boreal Spruce zones	A	G, S	mature forest, clearcuts, partial cuts (30% & 60% removal)	1, 6 yrs	na[m]	No
Thompson et al. (1992)	Missouri (Ozarks)	oak-hickory-pine	BLJA, AMCR, BHCO	relative abundance	200 ha managed site:10% regenerating, 10% sapling, 80% pole-sawtimber	pole-sawtimber of managed vs unmanaged site	na[m]	No
Twedt et al. (2001)	Louisiana	bottomland hardwood	N Mixed	G, S, C	group cuts (<1 ha), uncut	1-2 yrs	na[m]	No[g] Yes[d] (ACFL) No[d] (NOCA)
Wood (1999)	Arkansas	bottomland hardwoods	N PROW	S, C	clearcuts (<3.5 ha), uncut	1-3 yrs	na[m]	No[d,e]
Yahner and Mahan (1996)	Pennsylvania	aspen	A	G	1 ha	5-16 yrs, uncut	na[m]	No
Suarez et al. (1997)	Illinois (southern)	deciduous	N INBU	S	0.1-0.4 ha	0-6 yrs	na[o]	No[p]

Study	Location	Habitat	Nest Type	Nest Location	Cut Size	Cut Age	Distance (m)	Edge Effect
Winslow et al. (2000)	Indiana	maple-beech-oak-hickory	BHCO N Mixed	Relative Abundance G, S, C	6.6-11.1 ha, 0.3-1.0 ha	7 yrs, 0-3 yrs	na[q]	No Yes[e,r]
Yahner et al. (1989)	Pennsylvania	aspen	A	G, A (1.5 m)	1 ha	2 yrs vs 12 yrs	na[s]	No

a=additional transects added to examine greater than 200 m: 0-340 m and 0-620 m (20 m intervals)

b=age not provided, just height of regenerated vegetation

c=secondary cavity nesters; used nest boxes for study

d=applies to nest success, not predation per se

e=applies to parasitism only

f=parasitism higher near clear cut edge, up to 100 m into adjacent forest. Parasitism not higher near group cut edges, but greatest adjacent to edge of 0.5 ha group cut openings.

g=applies to predation and parasitism

h=edge ranged from clearcut to 70 meters of feathered edge to mature forest

i=BLJA more abundant within wood interior than wood edge, and not present within clearcut edge or clearcut interior. BHCO abundant at wood edge and not present at wood interior. BHCO more abundant at clearcut interior than clearcut edge.

j=not a study of distance from silvicultural edge; comparison among treated stands of different timber size/class. The experimental unit is the stand, not the nest. Nest is located within stands of different age. An edge effect equals an increase in predation or parasitism within the younger stands.

k=daily predation rate was twice as high in all young forests combined than in mature forest. Daily predation rate was higher in the more recent clearcuts than in the older clearcuts, the tree plantation, and the mature forest; increased forest age, decreased predation. Hypothesized that predators can more easily search and find nests in a more homogenous environment (such as those of young clearcuts or tree plantations) with less structural complexity, than a more heterogeneous environment (such as that of mature forest).

l=increased abundance of BHCO within the regenerating areas compared to the sapling or pole-timber areas.

m=not a study of distance from silvicultural edge; comparison among plots with different silvicultural treatments. The experimental unit is the plot, not the nest. Nests placed in mature forest. Edge effect equals an increase in predation or parasitism within treated plots as opposed to uncut plots.

n=BHCO abundance greatest within clearcut treatments, followed by shelterwood treated sites, and much less common in groupcut, single-tree, and mature sites

o=not a study of distance from silvicultural edge; comparison among different types of edges: abrupt, permanent edges (agriculture, wildlife openings, old fields) versus gradual, temporary edges where plant succession occurred (treefall gaps, streamsides, groupcut silvicultural gaps). Agricultural and field edges were large (> 10 ha) and exterior to the forest, whereas other edges were small (0.1-0.4 ha) and interior. Nests located within the edges.

p=predation twice as high at abrupt, permanent exterior and interior edges than at gradual, temporary interior edges. No difference in parasitism among edge types.

q=not a study of distance from silvicultural edge; comparison among forest interior, external forest-agriculture edge, internal forest-clearcut edge, and internal forest-managed opening edge (cut or burned).

r=over all forest-breeding species, levels of parasitism were higher at sites adjacent to both exterior and interior edges than in the forest interior. Different host species experienced different frequencies of parasitism, as well as different patterns of parasitism within landscapes. e.g., ACFL: interior(I)=1.5%, exterior(E)=5.4%, clearcut(C)=15.7%, opening(O)=2.8%; REVI: I=9.6%, E=60.7%, C=54.8%, O=20%; WOTH: I=7.7%, E=16.2%, C=20.7%, O=50%; WEWA: I=12%, E=43.3%, C=25%, O=33.3%

s=not a study of distance from silvicultural edge; comparison of abrupt and gradual edges. Nests were placed 5 m from abrupt edges (those created by 2 year-old clearcuts) and 5 m of gradual edges (those created by 12 year-old clearcuts)

Table 1.4b: Summary results of silvicultural edge, timber size/class (na^{j}), and silvicultural treatment (na^{m}) studies with respect to increased predation, parasitism, or relative abundance of predators and Brown-headed Cowbirds (BHCO). Where appropriate, studies are broken down by nest type and vertical placement.

Edge, Distance, and Predation

Nest Type	Artificial		Natural	
Increased Predation	Yes	No	Yes	No
Total	8	13	7	8
Ground	4	8	6	0
Above	4	1	1	4
Ground and Above	0	4	0	4

Edge, Distance, and Parasitism

Increased Parasitism	Yes	No
Total	1	1

Edge, Distance, and Relative Abundance

Nest Type	Predators		BHCO	
Increased Abundance	Yes	No	Yes	No
Total	0	1	2	0

Timber Size/Class (na^{j}) and Predation

Nest Type	Artificial		Natural	
Increased Predation	Yes	No	Yes	No
Total	0	6	1	0
Ground	0	2	1	0
Above	0	0	0	0
Ground and Above	0	4	0	0

Timber Size/Class (na^{j}) and Relative Abundance

Nest Type	Predators		BHCO	
Increased Abundance	Yes	No	Yes	No
Total	0	3	2	0

Silvicultural Treatment (na^{m}) and Predation

Nest Type	Artificial		Natural	
Increased Predation	Yes	No	Yes	No
Total	1	4	0	0
Ground	0	1	0	0
Above	1	1	0	0
Ground and Above	0	2	0	0

Silvicultural Treatment (na^{m}) and Parasitism

Increased Parasitism	Yes	No
Total	1	1

Silvicultural Treatment (na^{m}) and Relative Abundance

Nest Type	Predators		BHCO	
Increased Abundance	Yes	No	Yes	No
Total	1	2	1	2

Table 1.5: Review of studies that investigated edge effects at internal edges caused by narrow forest-dividing corridors such as trails, roads, utility rights-of-way, and streams. Unless otherwise noted, a positive edge effect refers to an increase in nest predation near the edge compared to within the forest interior. In addition to nest-centered studies, some studies focused on the relative abundance of brood parasites and potential predators. In these studies, a positive edge effect refers to an increase in relative abundance near the edge compared to within the forest interior. Gray areas represent data that were not available. For nest type, A=artificial and N=natural. For nest location, G=ground, S=shrub, C=canopy, and A=above ground. All studies were conducted within forest-dominated landscapes, except Bergin et al. (1997), Marini et al. (1995), and Miller and Hobbs (2000).

Study	**Location**	**Habitat**	**Nest Type**	**Nest Location**	**Edge Type**	**Corridor Width**	**Distance (m)**	**Edge Effect**
Bergin et al. (1997)	Iowa	row crops (63%), pasture, CRP land, woodland (18%)	A	G	roads (gravel)	8.2 m	2, 10	No
Boag et al. (1984)	Alberta, Canada	deciduous	A	G	trails		0-50	No
Boulet and Darveau (2000)	Quebec, Canada	alder, fir, spruce, birch	A	G, C	highway, logging road, river	38 m, 13 m, 5-15 m	na[a]	highway > logging road > river
Burkey (1993)	Belize	rainforest	A	G	roads		30-500	Yes
Chasko and Gates (1982)	Maryland	oak-hickory	N Mixed[b]	G, S, C	utility right-of-way (grassy, maintained by mowing)	48 m	0-90 (30-m intervals)	Yes[c]
Chasko and Gates (1982)	Maryland	oak-hickory	N Mixed[b]	G, S, C	utility right-of-way (shrubby, maintained by herbicides)	52 m	0-90 (30-m intervals)	Yes[c]

Study	Location	Habitat	Nest Type	Nest Location	Edge Type	Corridor Width	Distance (m)	Edge Effect
Chasko and Gates (1982)	Maryland	oak-hickory	N Mixed[b]	G, S, C	utility right-of-way (grassy vs shrubby)	48 m, 52 m	na[a]	grassy > shrubby
King and DeGraaf (2002)	New England	northern hardwood	N OVEN	G	roads[d] (unsurfaced)	8 m	0-75 vs 75-150, 0-150 vs > 150	No[e]
Latta et al. (1995)	Puerto Rico	subtropical/ montane wet forest	A	G, A (1.5-2 m)	highway	20 m	5, 25, 50, 100, 150, 250 (5-50, 100-250)	No
Lindenmayer et al. (1999)	New South Wales	pine plantation	A	A (1.5-2 m)	roads (gravel logging)		0-200 (50 m intervals)	No
Manolis et al. (2000)	Minnesota	northern hardwood	N Mixed (80% OVEN)	G, S, C	roads (unsurfaced logging)		All	No
Marini et al. (1995)	Illinois	oak-hickory, tulip-maple-beech[f]	A	G	road, ravine		1-20 (5-m intervals) (1-10, 15-20)	Yes (15-20 m)
Marini et al. (1995)	Illinois	oak-hickory, tulip-maple-beech[f]	A	G	road		1-20 (5-m intervals) (1-15, 20)	Yes (20 m)
Marini et al. (1995)	Illinois	oak-hickory, tulip-maple-beech[f]	A	G	ravine		1-20 (5-m intervals) (1-10, 15-20)	No
Marini et al. (1995)	Illinois	oak-hickory, tulip-maple-beech[f]	A	C	road, ravine		1-20 (5-m intervals) (1-10, 15-20)	No

Study	Location	Habitat	Nest Type	Nest Location	Edge Type	Corridor Width	Distance (m)	Edge Effect
Marini et al. (1995)	Illinois	oak-hickory, tulip-maple-beech[f]	A	C	ravine		1-20 (5-m intervals) (1-5, 10-20)	Yes (10-20 m)
Miller et al. (1998)	Colorado	pine	N	G, S, C	recreation trails	1.17 m	0, 50, 100	Yes[e] No[g]
Miller and Hobbs (2000)	Colorado	riparian[h] (cottonwood)	A	A (0.5-2 m)	recreation trails (paved)	2.5 m	Trail side/ Non-trail side[i]	No (overall) Yes (corvids) No (mice)
Ortega and Capen (2001)	Vermont	northern hardwood	A	G, A (1-2 m)	roads[j] (unsurfaced)	9.6 m	10, 300	No
Rodewald (2002)	Pennsylvania	aspen	N Mixed	G, S, C	roads (unimproved)	10-15 m	0-200+	No
Yahner and Mahan (1997)	Pennsylvania	aspen, oak, maple, pine	A	G	roads (unsurfaced logging)	6-20 m	1, >50	No[k] opposite
Evans and Gates (1997)	Maryland	northern hardwood	BHCO	relative abundance	interior vs. forest-edge: -powerline, -stream, -open canopy road, -closed canopy road	45.9 m, 5.5 m, 6.0 m, 3.7 m	na[l]	stream > powerline >> open road > closed road > interior
Gates and Giffen (1991)	Maryland	northern hardwood	BHCO	relative abundance	stream	3.4 m	0-60, 60-120, 120-360, 360-690	Yes[m]

Study	Location	Habitat	Nest Type	Nest Location	Edge Type	Corridor Width	Distance (m)	Edge Effect
Hickman (1990)	Illinois	sugar maple bottomlands, oak-hickory uplands	BLJA BHCO	relative abundance	trails	2-3 m	0-120	Yes
Ortega and Capen (2001)	Vermont	northern hardwood	BLJA red squirrel chipmunk	relative abundance	roads[j] (unsurfaced)	9.6 m	10, 300	No
Rich et al. (1994)	New Jersey	oak-pine, hardwood swamp	Avian Predators (BLJA, AMCR, FICR, COGR) BHCO	relative abundance	roads (unsurfaced)	8 m	0, 100, 300	No
Rich et al. (1994)	New Jersey	oak-pine, hardwood swamp	Avian Predators (BLJA, AMCR, FICR, COGR) BHCO	relative abundance	roads[n] (paved)	16 m	0, 100, 300	No (predators) Yes (BHCO)
Rich et al. (1994)	New Jersey	oak-pine, hardwood swamp	Avian Predators (BLJA, AMCR, FICR, COGR) BHCO	relative abundance	utility right-of-way	23 m	0, 100, 300	Yes[o]

Study	Location	Habitat	Nest Type	Nest Location	Edge Type	Corridor Width	Distance (m)	Edge Effect
Rich et al. (1994)	New Jersey	oak-pine, hardwood swamp	Avian Predators (BLJA, AMCR, FICR, COGR) BHCO	relative abundance	unsurfaced roads, paved roads, utility right-of-way	8 m, 16 m, 23 m	na[p]	Predators no difference BHCO paved > unpaved ~ utility

a=not a comparison of distances from internal edge to forest interior; comparison of predation among different types of internal forest edges

b=mostly mixed-habitat species that nest in openings and shrubs, rather than forest-interior birds

c=applies to nest predation and brood parasitism

d=density of roads 1.7 km/km^2

e=refers to nest success, not predation per se

f=landscape 40% forested. Nests located within the forest interior >500 m from forest-farm edge.

g=refers to brood parasitism only, not nest predation

h=60-m wide riparian woodland with recreational trails within the riparian zone. Riparian woodlots surrounded by mosaic of mixed-grass prairie, agricultural land, and low-density rural housing.

i=three transects with nests: two paired, one on riparian side of stream with the trail and one on riparian side of the stream without the trail; third transect away from trail on random side of river as a reference transect.

j=road density 700m/km^2

k=study design confounded by proximity to clearcut edges.

l=not a comparison of distances from internal edge; comparison of relative abundance of brood parasites among four types of internal edges and interior forest.

m=increased abundance of BHCO near forest-stream ecotone. Most BHCO within 0-60 m: 1.27 times more within 0-60 m than within 60-120 m, 4.14 times more within 0-60 m than within 120-240 m, absent > 240 m from stream.

n=paved roads had maintained mowed grass on either side, which is attractive to BHCO for feeding.

o=increased avian predators (crows) along shrubby rights-of-way. Increased BHCO along grassy rights-of-way, but not shrubby rights-of-way.

p=not a comparison of distances from internal edge; comparison of relative abundance of predators and brood parasites at the three types of internal edges.

Table 1.6: Review of studies that investigated edge effects at internal edges created by water bodies other than streams and rivers. All studies were conducted within forest-dominated landscapes. For nest type, A=artificial and N=natural. For nest location, G=ground, S=shrub, C=canopy, and A=above ground.

Study	**Location**	**Habitat**	**Nest Type**	**Nest Location**	**Edge Type**	**Distance (m)**	**Increased Predation**
Bollinger and Peak (1995)	Illinois	deciduous	A	G	forest-lake vs forest-field	na[a]	lake ~ field
Boulet and Darveau (2000)	Quebec, Canada	alder, fir, spruce, birch	A	G, C	highway, logging road, river, lake	na[b]	highway > logging road ~ lake > river
Huhta et al. (1998a)	Finland	coniferous	A open, nest boxes	S	marsh	0, 100	No
Huhta et al. (1998a)	Finland	coniferous	A open, nest boxes	S	forest-clearcut (man-made) vs forest-marsh (natural)	na[c]	clearcut ~ marsh
Manolis et al. (2000)	Minnesota	northern hardwood	N Mixed (80% OVEN)	G, S, C	swamp (0.5-10 ha)	All	No
Pierre et al. (2001)	western Canada	boreal mixed-wood	A duck cavity	A (2m)	lake	50, 150	No
Small and Hunter (1988)	Maine	oak-pine	A	G	forest fragment surrounded entirely by non-forest land vs forest fragment bordered on one side by a large body of water	0-360 (15-m intervals)	Nests within forest fragments bordered on one side by a large water body had lower predation rates. No distance effect.

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a=Not a comparison of distances from internal lake edge to forest interior; comparison of predation between nests located at forest-field edge and forest-lake edge. Nests placed 20 m from edges. Predation rates did not differ between edge types and was high for both.

b=Not a comparison of distances from internal edge to forest interior; comparison of predation among four types of edges (highway, logging road, lake, river). Nests placed 10 m from edges. Found predation high near highways, intermediate near logging roads and lake edge, and low near river edges.

c=Not a comparison of distances from internal edge to forest interior. Comparison of predation between two types of edges; man-made forest-clearcut edge and natural forest-marsh edge. Nests placed 0-1 m from edges. Nest predation was not statistically different.

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CHAPTER 2

BACKGROUND

INTRODUCTION

Populations of many neotropical migratory songbirds have declined in recent decades (Robbins et al. 1989, Askins et al. 1990). Although the declines in many forest-dwelling neotropical migrant birds can be linked to a reduction in breeding and wintering habitats, the high degree of forest fragmentation and habitat loss in the eastern United States suggests that factors on the breeding grounds are the primary cause of migrant declines, presumably through decreased reproductive success (Robinson et al. 1995). Increased rates of nest predation (Wilcove 1985) and brood parasitism (Brittingham and Temple 1983) suffered by forest-interior songbirds in these fragmented landscapes may be a cause of their decline in North America (Robbins et al. 1989, Askins et al. 1990).

A drastic example of forest habitat loss in the southeastern United States has been in bottomland hardwood forests (MacDonald et al. 1979, Mitsch and Gosselink 1986). It is estimated that 55% of the existing bottomland hardwoods are found in the Mississippi Alluvial Valley (MAV; Mitsch and Gosselink 1986), however, only about 20% of the original 9 to 10 million hectares of bottomland hardwood forests in the MAV remain (Yin et al. 1997). In addition to actual losses of bottomland hardwood forests, much of the remaining bottomland hardwoods are in an ecologically degraded condition due to severe fragmentation, hydrologic alterations, and poor timber management practices (Allen 1997). Because bottomland hardwood forests are of hemispheric importance to neotropical migratory birds as prime breeding habitat (Hunter et al. 1993), the loss and reduced quality of the remaining bottomland hardwood forests could negatively impact regional populations of neotropical migrants that depend on functioning bottomland forest ecosystems; this is especially true for those birds that reach their highest breeding densities within bottomland hardwood forests.

Despite the importance and the imperiled state of bottomland hardwood forests, long-term data sets that investigate the reproductive success of birds breeding within bottomland hardwood forests are lacking. The White River National Wildlife Refuge, located in the MAV of southeast Arkansas, is one of the largest remaining contiguous tracts of bottomland hardwood forest within the US. Previous research within the Refuge has focused on the reproductive success of two neotropical migrants, the Acadian Flycatcher (*Empidonax virescens*; Wilson 1997) and the Prothonotary Warbler (*Protonotaria citrea*; Wood 1999). Both of these species are declining within the Mississippi Alluvial Plain and, as a result of area sensitivity (Acadian Flycatcher and Prothonotary Warbler) and extreme habitat specificity (Prothonotary Warbler), have been listed by Partners in Flight as species of concern. Research on Acadian Flycatchers within the Refuge has investigated the relationship between micro- and macro-habitat characteristics of nest sites and nest success and parasitism (Wilson 1997). Research on Prothonotary Warblers focused on nest success and parasitism status in relation to internal fragmentation by patch and group cuts (Wood 1999). Although studies within forested wetlands suggest that breeding bird communities are related to both vegetation structure and hydrology (Smith 1977, Swift et al. 1984, Wakeley and Roberts 1996), information on the reproductive success of birds in relation to hydrology is virtually nonexistent. Within the Refuge, as well as elsewhere within bottomland hardwood forests, research investigating the effects of internal edges and hydrology on the reproductive success of forest-interior songbirds is lacking and research that simultaneously investigates the relative importance of habitat characteristics at multiple spatial scales to the nesting success of birds is needed.

This study initiates filling the gap in knowledge concerning the reproductive success of neotropical migrant songbirds breeding within bottomland hardwood forests of the MAV. The study was conducted within the White River National Wildlife Refuge during the breeding seasons of 1996-2000. We focus on the nests of two common bottomland forest songbirds, the Acadian Flycatcher and Prothonotary Warbler, to examine nest predation and brood parasitism in relation to the physical characteristics of the nesting habitat at multiple spatial scales (micro, macro, and landscape). These physical characteristics include descriptions of nest placement, vegetation structure, proximity and exposure to various internal edges such as trails, roads, sloughs, and patchcuts, and proximity to external forest edges. Additionally, we investigate how characteristics of the water that describe the timing, duration, magnitude, and spatial extent of the seasonal flooding are related to nest predation. This chapter contains accounts of the focal bird species, a description of the study area, methods, as well as background information on the number of and the success of nests within the study area, the habitat variables measured on the study plots and at each nest, the hydrological characteristics of the study area, and the water variables measured for each nest. This background information is valuable as a basis for understanding the characteristics particular to this study area as well as the specific habitat and water variables used to investigate patterns of nest predation and brood parasitism.

SPECIES ACCOUNTS

ACADIAN FLYCATCHER

The following information is based on the Birds of North America account for the Acadian Flycatcher and the references therein (Whitehead and Taylor 2002), unless otherwise noted. The Acadian Flycatcher is a small (13 g) neotropical migrant that breeds in the eastern United States and winters in Central and South America (Ehrlich et al. 1988). It is widely distributed in the forested landscape of the eastern United States (Figure 2.1a). The northern limit of the breeding range extends from southeast Minnesota, southern portions of Wisconsin, Michigan, and Ontario, southeast New York, Connecticut, Rhode Island, and Massachusetts. The southern extent of the breeding range includes southern portions of Louisiana, Mississippi and Alabama, and northern Florida. The western extent of the breeding range includes the eastern portions of Iowa, Missouri, Kansas, Nebraska, Oklahoma, and Texas. Wintering grounds include the Caribbean slope of Nicaragua, the Caribbean and Pacific slopes of Costa Rica and Panama, northern and western Columbia, northwestern Venezuela, and western Ecuador. Within its breeding range, the Acadian Flycatcher is generally found in habitats with mature deciduous forests and is associated with water, often found in bottomland forests, swamps, wooded ravines, riparian thickets, and along streams. Though information on the wintering grounds of the Acadian Flycatcher is sparse, they are found in primary and secondary growth lowland forests that are structurally similar to the breeding habitat.

The Acadian Flycatcher nests and forages in the mid-canopy. Nests are open cup and are built in a fork of a small horizontal or slightly drooping branch away from the bole and close to the branch edge. Nests are often associated with water and are usually over an open area, such as a stream, trail, or other clearing. This species forages for insects, including insect larvae and other arthropods. Foraging techniques are predominantly short flights directed at insects on leaves. It will also hawk insects from the air, glean some prey from branches and boles, and occasionally forage on the ground.

The Acadian Flycatcher breeds from early May to late August, with the peak time between late May and the end of July. The female selects the nest site within the male's territory and does all of the nest building, incubating, and brooding, while both sexes feed the nestlings and fledglings. Clutch size is usually 3 eggs (2-4). Incubation lasts 14 days (13-15). Hatchlings are altricial. Nestlings fledge in 14 days, but they can prematurely jump from the nest as early as day 8 and survive until able to fly if provisioned by the adults. Young are fed for at least 14 days post fledging. This species is often single brooded, but many individuals are double brooded, especially in the southern portion of its range.

The Acadian Flycatcher is a common host for the brood parasitic Brown-headed Cowbird (*Molothrus ater*), although the frequency of parasitism (14-50%; Trine et al. 1998) is usually lower than for most other songbird species within the same forest habitats. Multiple parasitism events (i.e., when more than one female cowbird lays an egg in the same host nest) are low, except in areas with high rates of parasitism. Acadian Flycatchers will rarely abandon a parasitized nest and may occasionally build over a parasitized clutch and lay a new clutch. Once parasitic eggs have hatched, Acadian Flycatchers treat the parasitic nestlings as their own. The reproductive success of parasitized nests is significantly lower than non-parasitized nests, with reported reductions in expected output ranging from 77% to 90% (Walkinshaw 1961, Robinson unpublished data, Whitehead and Taylor 2002; but see Trine et al. 1998).

Nest mortality is predominantly due to predation (often 50-85%). Predation is higher during the nestling than the egg stage. It is generally assumed that most nests are taken by avian predators (Hazler et al. 2004) or snakes (Wilson and Cooper 1998), but there are few direct observations of actual predation events. Acadian Flycatchers aggressively defend their nests from female cowbirds and predators by way of threatening displays and vocalizations, chasing, and attacking.

Data from the Breeding Bird Survey for 1966-2004 revealed no significant population trends for the Acadian Flycatcher across its breeding range in the United States (annual decline of –0.1%, p=0.61; Sauer et al. 2005). However, within different physiographic regions of its breeding range, the Acadian Flycatcher exhibited a mosaic of increases and decreases. In particular, the Acadian Flycatcher showed a non-significant (p=0.92) decline of –0.3% per year within the Mississippi Alluvial Plain and a significant (p=0.02) decline of –2.6% per year within Arkansas (Sauer et al. 2005; Figure 2.2a). The species has received a high-priority ranking for management and monitoring in the Southeast by Partners in Flight (Hunter et al. 1993, Rich et al. 2004). The high ranking reflects perceived threats on both wintering and breeding grounds, including the steady decrease in bottomland hardwood forests in the lower Mississippi Alluvial Valley. In addition, this species is considered to be area-sensitive and negatively impacted by habitat fragmentation, requiring >24 ha of contiguous forest for successful reproduction (Wilson 1997).

PROTHONOTARY WARBLER

The following information is based on the Birds of North America account for the Prothonotary Warbler and the references therein (Petit 1999), unless otherwise noted. The Prothonotary Warbler is a small (15 g) neotropical migrant that breeds in the eastern United States (Figure 2.1b) and winters in Central and South America. It is patchily abundant in forested wetlands throughout most of the southeast United States. It breeds along the eastern coastal plain from southern New Jersey to north-central Florida, west to east-central Texas, central Oklahoma, and eastern Kansas, and north to northern Missouri, southern Illinois, and southern Indiana. There are small populations scattered throughout Ohio, Pennsylvania, eastern Kentucky, and north-central Tennessee. This species is restricted to the Mississippi River floodplain in western Illinois, eastern Iowa, east-central Minnesota, and western Wisconsin. They reach their highest breeding densities in the remaining bottomland hardwood forest tracts of the Mississippi Alluvial Valley (Figure 2.1b), the panhandle of Florida, and eastern North Carolina. Wintering grounds in Central America include the Caribbean coast of southern Veracruz, Mexico, and Honduras; the Caribbean and Pacific slopes of Nicaragua and Panama; and the Pacific slope of Costa Rica. In South America, wintering grounds include lowlands of northern Colombia and Venezuela. This species will rarely winter in the Caribbean in Puerto Rico, Bermuda, and the Virgin Islands and Lesser Antilles.

Within its breeding range, the Prothonotary Warbler inhabits swampy lowland forests and river bottom woodlands that are subject to flooding. Suitable breeding habitats include a wooded area with water and available cavities. Breeding grounds are usually low elevation, flat terrain, shaded forest habitats with sparse understory. Prothonotary Warblers are moderately area sensitive and avoid forests < 100 ha in area and waterways with wooded borders < 30 m wide. On the wintering grounds, this warbler inhabits mangrove swamps.

The Prothonotary Warbler is a secondary cavity nester that nests in low-lying natural and excavated cavities of decaying snags or branches of live trees. Cypress knees with cavities are frequently used where available. Nests are often near or over standing or slow-moving water. The warbler fills the cavity to within 10 cm of the entrance with moss and then forms an open cup nest. The average height of nests is 2 m, but it ranges from 0.5 m to 10 m above ground. They will readily nest in nest boxes.

Prothonotary Warblers are primarily insectivorous, with the major food items including caterpillars, flies, midges, mayflies, and spiders. It will also take mollusks and isopods. Foraging usually takes place below 7 m in height. Prey are taken from fallen logs, tree trunks and branches, and foliage. Most foraging maneuvers are gleans from leaves, twigs, and branches, but this species will also hover and fly-catch.

The Prothonotary Warbler breeds from early April to the end of July, with the peak from late April to mid-July. The male designates a territory around one or more cavities, fills several cavities with a small amount of moss, and then displays the cavities to the female. Upon selecting a cavity, the female builds the nests, and does all of the incubating and brooding. Males will provision the incubating and brooding female. Both sexes feed nestlings and fledglings; however, only the male will feed fledglings if the female is starting a second brood. Clutch size ranges from 3-7 eggs. Incubation starts with the penultimate egg and lasts 12-14 days. Hatchlings are altricial. Fledging occurs at day 10-11. Adults will continue to feed young up to 35 days post fledging. This species is frequently double brooded in its southern range.

The Prothonotary Warbler is a common host of the brood parasitic Brown-headed Cowbird, with reported frequencies of 10.7% to 26.9%. The incidence of parasitism for this species is much higher than for other cavity-nesting species. Female cowbirds usually lay a parasitic egg during the egg-laying period of the warbler, before clutch completion, but may lay an egg before the first host egg to several days after incubation begins. Prothonotary Warblers do not eject cowbird eggs, but may respond by abandoning parasitized nests. Adults that tend parasitized nests and successfully fledge young exhibit greatly reduced per nest productivity, with 25% (Petit 1991) to 53% (Hoover 2001) lower reproductive output resulting from cowbird removal of host eggs, reduced hatching success, and reduced survival of hatchlings due to starvation or trampling. Prothonotary Warblers are considered a high quality cowbird host because on average they fledge 56% of cowbird eggs.

Nest mortality is primarily due to predation. Common nest predators of the Prothonotary Warbler are raccoons (*Procyon lotor*), rat snakes (*Elaphe obsoleta*), and squirrels. Other predators include Red-bellied Woodpeckers (*Melanerpes carolinus*; Hazler et al. 2004), Blue Jays (*Cyanocitta cristata*), House Wrens (*Troglodytes aedon*), weasels, and mice. Nest predation is higher during the nestling stage when adults are active at the nest. Other common causes of nest mortality include inundation due to floods and the loss of decayed nest trees.

Nest defense includes alarm calls and possible attack of predators. During the nestling stage, females may perform the Broken-Wing Distraction Display in an attempt to draw potential predators away from the nest. Both adults are aggressive toward Red-Bellied Woodpeckers and female Brown-headed Cowbirds.

Breeding Bird Survey data from 1966-2004 indicate a significant (p=0.01) overall decrease of –1.5% annually for the Prothonotary Warbler (Sauer et al. 2005). Populations in the Mississippi Alluvial Plain have shown declines of –2.2% annually (p=0.08), with a significant (p=0.01) annual decline of –4.6% reported for Arkansas (Sauer et al. 2005; Figure 2.2b). Extreme habitat specificity makes this species highly susceptible to loss of habitat throughout its breeding range. Forest area sensitivity adds to its vulnerability. The Prothonotary Warbler is listed on the Partners in Flight watch list as a species of high conservation priority throughout its breeding range (Hunter et al. 1993). Additionally, the bottomland hardwood forests on which they depend for breeding have been listed by Partners in Flight as a habitat of regional concern (Hunter et al. 1993).

BROWN-HEADED COWBIRD

The Brown-headed Cowbird is a small (40-50 g) brood parasitic blackbird that breeds (Figure 2.3) and winters across much of North America (Lowther 1993). Originally limited to open grasslands of central North America, they greatly expanded their range with the clearing and opening of forests and transformation to agricultural and suburban landscapes that occurred upon European settlement. They occupy virtually all habitat of North America except areas above treeline and some treeless deserts (Lowther 1993). Within its breeding range, the Brown-headed cowbird prefers habitats with low or scattered trees among grassland vegetation – woodland edges, brushy thickets, prairies, fields, pastures, orchards, and residential. They show a preference for wood-field ecotones, often favoring forest-edge or secondary growth over either extensive woods or extensive field, and are associated with agricultural areas and human-modified habitats (Lowther 1993).

Cowbirds are brood parasites; females select nests of other bird species in which to lay their eggs and depend upon these host species to rear their young. They are generalist brood parasites, reportedly parasitizing the nests of over 220 host species (Friedmann 1963, Friedmann et al. 1977, Friedmann and Kiff 1985). Selected hosts range in size from 10 g gnatchcatchers to 150 g meadowlarks, but are usually smaller (<40 g) than cowbirds (Rothstein and Robinson 1998). It is generally accepted that female cowbirds locate host nests by observing host activities; they may do so from prominent perches or by walking along the ground (Norman and Robertson 1975). In some cases, they may also actively search vegetation for host nests. Female cowbirds need not only locate nests, but also select nests that are at the appropriate nest stage. Host activity about the nest – when building, laying, and incubating – serve as cues to cowbirds for identifying nest location and assessing nest stage (Lowther 1979). Cowbirds lay eggs from the beginning of April through the beginning of August, with most eggs deposited during May and June. Throughout the breeding season, a single female will lay an average of 40 eggs, with a laying rate of about 0.7-0.8 eggs/day (Rothstein and Robinson 1998). Female cowbirds are territorial on their breeding grounds (Darley 1983, Rothstein et al. 1986), but find it difficult to exclude all other females from their large breeding ranges (Rothstein et al. 1984, Thompson 1994). Thus, while a female will lay only one egg per host nest, overlap of laying areas among females is common in areas with high local densities of cowbirds and results in more than one female laying in the same host nest (multiple parasitism; Rothstein et al. 1984). Cowbirds lay most of their eggs during the egg-laying period of their selected host (Friedmann 1929). They lay their eggs in host nests before sunrise (Scott 1991), often removing a host egg from the nest prior to laying their own egg (Sealy 1992). Eggs require 10-12 days of incubation to hatch and 8-13 days to fledge. The short incubation period means that cowbird eggs laid synchronously with egg laying of their host usually hatch first, giving them a developmental head start and a competitive advantage against their host nest mates. In addition to hatching earlier than their nest mates, cowbird nestlings have large mouths and intense begging behavior allowing them to garner a disproportionate share of host feedings and develop more quickly, often to the detriment of their host nest mates. Cowbird parasitism usually causes a marked decrease in host reproductive output, but hosts vary enormously in the cost of parasitism; some raise mixed broods of cowbirds and host young, whereas others raise only the cowbird young. In general, smaller (< 15 g) hosts and those with longer incubation and nestling periods suffer higher reductions in reproductive output as a result of parasitism (Rothstein 1975, Pease and Grzybowski 1995).

Survival of cowbird eggs from laying to fledging averages 0.13, with a reported range of 0.05-0.34 (Lowther 1993). Eggs may fail to hatch because they are either rejected by the host species (ejected, buried, or abandoned) or because they are laid during an inappropriate nest stage and therefore receive inadequate incubation. Outside of hatching failure, failure of eggs to fledge is contingent on the success of the host nest and is subject to the same threats of predation, food limitation, and weather. Overall survival from egg to adulthood is 0.03 (Lowther 1993). This estimate is consistent with a 0.025 survival rate and lifetime fecundity of 80 eggs/female necessary to maintain a stable population (Lowther 1993).

As brood parasites, cowbirds are free from the responsibility of rearing young and are not spatially limited to fulfilling all of their needs within a confined nesting area. As such, cowbirds are extremely mobile, often maintaining distinct breeding, foraging, and roosting sites at different times of the day (Rothstein et al. 1980, 1984), and have large home ranges (405-1592 ha; Rothstein et al. 1984, Gates and Evans 1998). Although their home ranges are large, they utilize only a small percentage of it for different activities: for example, 9.5 ha, 16.5 ha, and 1.8 ha for breeding, foraging, and roosting, respectively (Evans and Gates 1997). Cowbirds will routinely commute > 7 km daily between morning breeding sites and afternoon feeding sites (Rothstein and Robinson 1998). They feed in large flocks within open areas containing short grass where they forage on the ground for seeds and arthropods, frequently in association with grazing ungulates that flush insect prey. The cowbirds ability to feed and breed in separate areas, and the large distances between such areas, allows them great flexibility in breeding habitat selection and enables them to exploit hosts in many habitats while remaining specialized in their foraging behavior (Rothstein et al. 1984). Cowbirds show a preference for breeding within forests (Hahn and Hatfield 1995), but are limited by feeding opportunities and thus flourish in fragmented landscapes that offer a mixture of feeding (agriculture) and breeding (forest) habitat (Donovan et al. 1997).

As a generalist brood parasite, cowbird numbers are not limited by the population densities of any single host species. Fragmentation of eastern deciduous forests and conversion of landscapes to agriculture has permitted range expansion by cowbirds from the central Great Plains to virtually all parts of North America. Their abundances are greatest within the Great Plains and expand outward from there, with high breeding densities within the Mississippi Alluvial Valley (Figure 2.3). Year after year, the Brown-headed Cowbird appears on more Breeding Bird Census plots than any other species (Rothstein 1994). Fragmentation of forests has increased edge and provided access to forest-interior species that were previously isolated from the effects of parasitism. The range expansion of the cowbird and the exposure of naïve hosts is a major management concern, with many believing that cowbirds are contributing to the declines of many forest-breeding neotropical migrants (Mayfield 1977, Brittingham and Temple 1983, Bohning-Gaese et al. 1993). Cowbird management to date entails trapping and removing cowbirds from host breeding ranges. This technique is effective in reducing the effect of parasitism on threatened/endangered host species that have small populations and restricted distributions (Lowther 1993). However, effective control for widespread and common host species may require large-scale planning to maintain contiguous forests and decrease feeding opportunities within forested areas.

STUDY AREA

The White River National Wildlife Refuge (NWR) is located in the southeast Arkansas portion of the Mississippi Alluvial Valley (Figure 2.4) and spans Phillips, Desha, Monroe, and Arkansas counties. It is located within the Lower White Basin, within the flood plain of the lower White River, approximately 12 km above its confluence with the Mississippi River. The refuge is a 65,000-ha managed, seasonally flooded, bottomland hardwood forest that extends approximately 104 km along the White River.

The White River NWR was established in 1935 for the protection of migratory birds and is managed by the USFWS for multiple uses, including wildlife diversity, waterfowl habitat, public recreational activities such as hunting and fishing, and timber. Prior to the establishment of the refuge, the area had been logged and run with cattle and hogs since the early 1900s (Denman 2002). Since 1950, the refuge has been under three different Forest Management Plans (FMPs; Denman 2002). The dominant (~ 70%) timber harvest method has been uneven-aged selective thinning of sawtimber-sized trees (> 40 cm DBH) on a 15-year entry cycle. Additionally, a few areas have been selectively cut for trees > 20 cm DBH, while a small percentage (< 1%) of the refuge has undergone even-aged patch clearcutting, where cuts are less than 3-ha in size. About 3% of the refuge has been under protective management with no tree cutting (Denman 2002). Silvicultural methods serve several management objectives including the reduction of canopy cover to increase growth of shade-intolerant bottomland oaks, the creation of a diverse plant community with a multi-layered canopy, the maintenance of early successional habitat, and the enhancement of habitat for wildlife (game and non-game; Denman 2002).

The White River NWR is one of the largest contiguous bottomland hardwood forests remaining in the United States (Harris and Gosselink 1990). Although large, the refuge is narrow (4.8-15.5 km-wide) in shape and is surrounded by agricultural fields of rice and soybean, and small rural towns; as such, it contains generalist predators and cowbirds that prey upon and parasitize the nests of songbirds breeding within the forest. A grassy levee, on which cattle graze, runs parallel to the east side of the refuge and serves as a foraging ground for large flocks of Brown-headed Cowbirds.

Topography on the refuge is typical of naturally flooded bottomland forest, with wide flats broken by low ridges and swales (Wilson 1997). Of the total refuge area, about 91% is forested, 8% is in waterways and lakes, and less than 2% is grassland and cropland. Elevations in the refuge range from 41-70 m above Mean Sea Level (Denman 2002); however, elevation within the study plots (see below) ranges from approximately 44-46 m above Mean Sea Level. Bayous, oxbow-lakes, and sloughs are common throughout the refuge. Annual flooding occurs due to stacking from northern Arkansas waters flowing down the White River and backup of waters from the Mississippi River and inundates much of the refuge under the 48.8 m contour (Denman 2002). Flooding can occur at any time but is most prevalent during late winter and spring. From 1996-1999, the study plots averaged about eight weeks of partial and/or complete inundation during the spring and summer breeding season, but the timing, duration, and maximum depth of floods varied from year to year.

In 1993, six 50-ha (500 m x 1000 m) plots were established within a single management compartment (Number 8) of the refuge (Figure 2.5). The compartment was 1,376 ha in size and consisted of contiguous homogenous habitat. The dominant overstory tree species were overcup oak (*Quercus lyrata*), Nuttall oak (*Quercus nuttallii*), green ash (*Fraxinus pennsylvanica*), bitter pecan (*Carya aquatica*), American elm (*Ulmus americana*), cedar elm (*Ulmus crassifolia*), waterlocust (*Gleditsia aquatica*), sugarberry (*Celtis laevigata*), and cypress (*Taxodium distichum*). Understory vegetation was predominantly comprised of possumhaw (*Ilex decidua*), swamp privet (*Forestiera acuminata*), hawthorn (*Crataegus spp.*), and water elm (*Planera aquatica*), as well as seedlings and saplings of overstory tree species. For further description of this area, see Wilson and Cooper (1998a,b).

METHODS

PLOTS

In 1993, six 50-ha (500 m x 1000 m) plots were established (Figure 2.5). In the fall of 1995, three silvicultural treatments (no cut, selective cut, and patch cut) were randomly allocated to two plots each. The selective cut plots had 300 m^2 basal area of timber removed. Each of the two patch cut plots had four blocks (averaging 2.8 ha/block) of timber completely removed or felled (Figure 2.6). A 25-m grid system (21 columns x 41 rows) was established and maintained on each plot for use in navigation and nest location. Because of our interest in definable internal edges, this study focused solely on the no cut and patch cut plots; thus, all subsequent information applies only to these four plots.

NESTS

NEST SEARCHING

Intensive nest searches were conducted on all plots during the breeding seasons of 1996-1998 and 2000. Nest searching for Acadian Flycatchers started upon the arrival of the females and continued through the end of July or early August (Figure 2.7a). For Prothonotary Warblers, nest searching began upon the arrival of the females and continued through the breeding season until the males began to abandon territories (Figure 2.7b). Nest searching efforts varied between years and between species (Table 2.1). Nest searching methods varied from systematically searching the plot grid, to observing adult behavior such as nest building. The tendency for Acadian Flycatchers to nest over open air space, such as trails that nest searchers may use for travel, made it essential to incorporate systematic searches to prevent bias in the location of nests. Additional search tactics for the Prothonotary Warbler included systematically checking all potential nest cavities and plotting territories of banded individual males and searching for respective nests. Once a nest was found, a nest card was created that included detailed directions to the nest based on the plot grid system. Flagging tape was used to facilitate the re-location of the nest. Tape was placed more than 5 meters from the nest and care was taken to approach the nest from different pathways on subsequent nest checks.

NEST MONITORING

Once a nest was located, its contents were noted. Mirror poles were used to examine nests when contents could not be seen from the ground. If nest height was too high for mirror poles (about 9 m for Acadian Flycatchers and 5 m for Prothonotary Warblers), the nest was observed from a distance using binoculars, and contents of the nest or nest stage were determined by observing the behavior of the adult birds (e.g., incubating or brooding females indicated that the nest was still active, frequent visits by the adults carrying food or disposing of fecal sacs indicated that the nest contained nestlings). In addition, the architectural structure of Acadian Flycatcher nests often made it possible to determine the status, if not stage, of the nests by looking through the bottom of nests while standing directly beneath it. Nests were visited every two to four days following Breeding Bird Inventory and Research Database (BBIRD) protocol (Martin et al. 1997) to determine clutch size, number of nestlings, number of fledglings, and fate of the nest as accurately as possible.

NEST FATE

Fates were recorded for the host species, for cowbirds if parasitized, and for the overall nest. Fates fell within three categories: successful, failed, or uncertain. A host was considered successful if one or more host young fledged. A cowbird was successful if one or more cowbird young fledged. A nest was considered successful if one or more young fledged, regardless of the species. Evidence for success included hearing or observing fledglings outside of the nest, observing chicks ready to fledge at last active visit, or flattened nest rim and/or feces on rim and outside of nest. In the absence of the above nest fate cues, the following criteria was used: if the median date between the last active nest check and the final nest check was within two days of predicted fledging date, and if on the final nest check the nest was empty without signs of predation, the nest was considered successful (Martin et al. 1997). For Acadian Flycatchers and Prothonotary Warblers, using a three-day nest check, this criterion translates into a last active nestling age of 10 and 7 days, respectively. The failed category was broken down into the following classifications: predation, parasitism, abandonment, adult mortality, flooding, physical causes such as weather or tree fall, and unknown. Nests were considered depredated if entire nest contents disappeared between nest checks during the egg laying, incubation, or early nestling stage when insufficient time had expired between checks for young to have fledged. Partial predation was not considered a failure unless it resulted in the adults abandoning the nest. Host failure due to parasitism occurred when host eggs did not hatch in the presence of hatched parasitic eggs or when host nestlings died when parasitic nestlings remained (e.g., starvation or trampling). Nest failure due to parasitism only occurred when a nest was abandoned due to the parasitic event. Uncertain fates occurred when there was insufficient information to determine success or failure. Nests were excluded from analysis if the nest failed prior to laying of the first egg or if observers caused mortalities.

NEST TERMINATION

If a nest failed or fledged between nest checks, the midpoint of the check was used as the termination date. If the fate of the nest was uncertain, the last active nest check was used as the termination date. Exposure days were determined by subtracting the date found, or the date initiated if the nest was found prior to the first egg, from the date terminated. Therefore, exposure days only included days that the nest was active and under observation.

NEST SUCCESS

Nesting success was calculated by the methods of Mayfield (1961, 1975), which estimates the probability of nest survival based on nest exposure days. Exposure days from nests with uncertain fates were included in the calculations. Nesting success was calculated for each species, using exposure days for only the host species. Nest success was plotted by year and plot.

A daily probability of nest survival and its standard error was calculated for each stage of the nesting period: the egg stage (from first egg to hatching) and the nestling stage (hatching to fledging). Nest-stage survival estimates were obtained by raising the daily survival probability of a given stage to the number of days in the respective stage. For Acadian Flycatchers, the egg stage is 15 days and the nestling stage is 14 days. For Prothonotary Warblers, the egg stage is 16 days (based on an average clutch size of five) and the nestling stage is 11 days. The overall probability of nest success was calculated as the product of the two stage survival probabilities. Calculating overall nest success in this manner assumes that mortality is constant within, but not necessarily across, the different nest stages. The standard error for overall nest success was calculated by the method of Hensler (1985). The daily probability of nest survival for the entire nesting period was calculated by raising the overall nest survival to the inverse of the number of days in the full nesting period (*n*), which for Acadian Flycatchers and Prothonotary Warblers is 29 days and 27 days, respectively. The standard error of the daily probability was approximated by dividing the standard error for overall nest success by [*n**((daily survival probability)^(*n*-1))].

HABITAT MEASUREMENTS

MICRO-SCALE

At the end of the breeding season, when nests were no longer active, habitat characteristics were measured at the micro-scale, right at the nest site (Table 2.2, Figure 2.8). The measurements included characteristics of the nest substrate and nest placement. These measurements were based on Breeding Biology Research and Monitoring Database (BBIRD) protocol (Martin et al. 1997).

ACADIAN FLYCATCHER – For each nest, we measured nest tree height and height of the canopy base, defined as the lowest part of the canopy. Clinometers were used to measure heights unless it was reachable with a measuring pole. Nest tree diameter at breast height (DBH) was measured with a DBH-tape. We used a densiometer to measure the percentage of canopy cover in the four cardinal directions and then averaged the measurements to obtain an overall percent canopy cover. Measurements of nest placement included nest tree species, nest height, nest distance from the edge of the branch, and nest distance from the nest tree bole. In 2000, we measured nest concealment and the number of vines. Concealment was measured in each of the cardinal directions, as well as above and below the nest, by estimating the percentage of the nest that was concealed by vegetation located within 1 m of the nest. Percentages of concealment were recorded as one of five categories: 0, 0-25%, 25-50%, 50-75%, and 75-100%. The six measurements were then averaged for an overall measure of concealment. Vines located on the bole of the nest tree were counted if they reached from the ground up to the first branch and were > 1 cm in diameter. The location of the nest was recorded as the distance and direction from the closest grid point with the use of a SONIN electronic distance estimator and a compass.

PROTHONOTARY WARBLER – For each nest, we measured nest tree height, nest tree diameter at breast height (DBH), canopy cover, and nest location relative to the plot grid in the same manner as for Acadian Flycatcher nests. Characteristics of nest placement included nest tree status (live/dead) and nest height above ground. We measured width and height of the cavity entrance. Based on histograms of the two cavity entrance dimensions, we grouped width and height into four and five size categories, respectively (Figure 2.9). The product of a cavity's width and height was used to assign it one of five codes that described its overall cavity entrance size (Figure 2.9). The cavity code was treated as a continuous variable, where cavities of code 1 were smaller than average, cavities of code 2 were average size, and cavities of code 3 and 4 were incrementally larger than average. Cavities that were open in height (i.e., had no top), regardless of width, were assigned a cavity code of 5; these cavities were considered to represent the upper extreme of the size continuum. We also recorded cavity type (split or hole). Splits were natural openings created by injury/decay of the tree with an entrance greater in height than width. Holes were natural or excavated cavities with a circular shape.

MACRO-SCALE

At the end of the breeding season, habitat characteristics were measured at the macro-scale, within an 11.3 m-radius circle (0.04 ha) centered at each nest (Table 2.2, Figure 2.8). Our measurements were modified from the methods developed by James and Shugart (1970). We established 0.04-ha circular plots centered around each nest. Within each of these nest plots we recorded the species and diameter at breast height (DBH) for all trees with a DBH ≥ 10 cm, thus obtaining the number of trees and the average DBH for the nest plot. Estimates of percent canopy cover and canopy height were obtained using a densiometer and a clinometer, respectively. These measurements were taken in the four cardinal directions while standing at the nest plot perimeter. The four measurements were averaged to obtain an overall percent canopy cover and canopy height for the nest plot. The nest plot was divided into four quadrants based on the four cardinal directions. Within each 0.01-ha quadrant we measured the distance from the nest to the closest tree ≥ 10 cm DBH; if no tree ≥ 10 cm DBH was present within the quadrant, we measured the distance to the nearest tree beyond the 11.3-m radius circle. The four distances were averaged to provide an indicator of openness around the nest site. Within a 5 m-radius circle around each nest, we recorded the number of woody stems (trees and saplings < 10 cm DBH). The same macro-scale measurements were taken at 15 recurring grid points per plot each year; these grid points were systematically selected within the plot core (i.e., the interior area at least 100 meters from the plot boundary).

LANDSCAPE SCALE

PLOT GRID **–** During the spring and summer of 2000, a Trimble GeoExplorer II Geographic Positioning System (GPS) was used to obtain the location of the four corner grid points of each plot. The positional dilution of precision (PDOP) and the signal to noise ratio

(SNR) were set to 6, and a minimum of 700 points were collected at each location. The projection, coordinate system, zone, datum, and units were as follows: Transverse Mercator, Universal Transverse Mercator (UTM), UTM zone 15 North, North American Datum 1927 (NAD27), and meters. The GPS unit received non-differentially corrected positions. The positions were differentially corrected post collection with the use of GPS Pathfinder Office Software Version 7.0 and data from the University of Arkansas at Monticello base station located less than 100 km from our study plots. The GPS positions were then converted into ArcView shapefiles and exported to ArcView (ESRI 1999).

Starting from the northwest corner of each plot, we measured the distance and azimuth from one grid point to the next grid point in a leapfrog method. Distance and direction were measured with a SONIN electronic distance estimator and hand held compass, set to the appropriate declination. Slope was ignored due to the flat terrain, but care was taken to measure distance in a level position. An x and y UTM location for each grid point was calculated based on the above measurements, the UTM location of the northwest grid point that had previously been obtained with a GPS unit, and basic principles of geometry.

ROADS – During the summer of 2001, all roads running through or near the study plots were located by a similar method as the grid points (see *PLOT GRID* above). The beginning point of a road was referenced to the closest grid point. We then proceeded to walk down the middle of road in a leapfrog manner, taking the distance and direction from one point to the next. Distances between points depended on the curvature of the road, but averaged 14.6 meters with a range of 3.1 - 67.4 m. When possible, points along the road were referenced to the plot grid system every fifth segment. At every fifth segment, or fewer if there were significant changes, the width of the road was measured; width included the travel area and half of the shoulder. Basic principles of geometry were used to calculate an x and y location for each road point. These points were imported as a shapefile into ArcView. In ArcView, the road points were connected with a line and the line was buffered to the measured widths (Figure 2.6).

Roads that were greater than 200 meters from the study plot perimeters and that were visible on a 1:24,000 scale digital raster graphic (DRG) were digitized in ArcView directly off the DRG at a 1:2,000 scale (Figure 2.6). The full extent of the study area spanned four quadrangle maps, Henrico_ne, Indianbay_se, Weber, and Ethel. The DRGs were created from aerial photographs flown in 1964 and field checked in 1967.

We classified roads into six categories, depending upon the type and frequency of use. The categories were ranked from light and infrequent use to heavy and frequent use and are as follows: minor all terrain vehicle (ATV), logging, major ATV, unimproved dirt, improved dirt, and gravel. For each study plot, the length and area of roads and the area of each type of road were determined in ArcView.

PATCH CUTS – During the summer of 2000 and 2001, we spatially located the eight patch cuts within two of the study plots. The patch cuts were located in a similar manner as the roads and were referenced to the plot grid. Starting at one corner of a patch cut, we measured the distance and direction from a grid point with a known UTM location to the corner point. From that point, we walked along the edge of the cut measuring distance and direction from point to point using a SONIN and a hand held compass. Distances between points depended on the pattern of the patch cut edge; however, the points matched the edge curvature in detail. When possible, we referenced the patch cut points back to grid points. The distances and directions between points were entered into a spreadsheet and the x and y UTM locations for each point were calculated. The point locations were added to ArcView as a shapefile. Points were connected to create a polygon for each patch cut (Figure 2.6). Area and perimeter of each cut were calculated in ArcView and summarized by plot.

SLOUGHS AND PONDS – During the summer of 2001, all sloughs that ran through or near the study plots were located in the same manner as the roads. The first slough point was referenced to the nearest grid point by measuring the distance and direction from the grid point to the slough point. We walked down the middle of the slough taking distance and direction from one slough point to the next. The distances between points varied and depended on the curvature of the slough; each segment averaged 16.8 meters in length with a range of 3.4 - 56.9 m. When possible, points along the slough were referenced to the plot grid. At every fifth segment, or fewer if there were substantial changes, the width of the slough was measured. In addition, we took measures of slough depth (see HYDROLOGY for details). The measured distances and directions were used to calculate an x and y UTM for each point. These points were imported as a shapefile into ArcView. In ArcView, the slough points were connected with a line and the line was buffered to the measured widths (Figure 2.6). The area of sloughs per plot was determined.

There was one small pond located within one of the study plots. We set up points along the pond edge and referenced them by distance and direction from fixed grid points with known UTM locations. The points were imported into ArcView as a shapefile and connected to create a polygon (Figure 2.6). Area and perimeter of the pond were determined in ArcView.

FOREST EDGE, LEVEE, AND OTHER WATER BODIES – The exterior forest/agriculture edge was digitized on-screen at a 1:4,000 scale from a 1:40,000 scale color infrared digital orthophoto quarter-quadrangle (DOQQ; Figure 2.5). The DOQQ was created from aerial photographs taken in February 2000 and in January 2002. The levee and water bodies such as major bayous, lakes, and the White River were digitized on-screen at a 1:2,000 scale directly off a 1:24,000 scale DRG. The DRGs were created from aerial photographs flown in 1964 and field checked in 1967. All of these features were located greater than 200 meters from the study plots. Distances from nests to the forest/agricultural edge and the levee, as well as area of sloughs, ponds and other water bodies, were summarized for each plot.

LANDSCAPE MEASUREMENTS FOR EACH NEST – Habitat characteristics were measured at the landscape scale (Table 2.3, Figure 2.8). Distances from each nest to the exterior forest edge and to the levee were measured in ArcView GIS 3.2. The distance from each nest to the closest road, slough, and patch cut was recorded. The type of road closest to each nest was also documented. Circular buffers were created around each nest at 25-m intervals (i.e., 0-25 m, 0-50 m, 0-75 m, 0-100 m, etc.; Figure 2.10). The buffers were used to calculate the area (m^2) of roads and sloughs within 0-100 m of each nest, and the area of patch cuts within 0-300 m of each nest. In addition to area, the length (m) of road, slough, and patch cut edge was measured within each distance interval. Distance intervals of 25 meters followed Paton's (1994) suggestion for studies of edge effects and avian nest success.

In an attempt to target landscape features relevant to parasitism, canopy openings within the study area were mapped. Roads, sloughs, and other water bodies greater than 5 meters wide were combined with patch cuts to create an ArcView shapefile of canopy openings (Figure 2.11). The area of open canopy was summarized for each plot. The closest distance from each nest to a canopy opening was determined. In addition, the percent of open canopy within 200 meters of each nest was calculated. A 200 m-radius buffer is equivalent to 12.5 ha and was chosen for two reasons: 1) to correspond with the breeding home range of a female cowbird (average 9.7 ha, range 4.7-16 ha; McGeen and McGeen 1968) and 2) to provide an adequate range of values for the percent of open canopy.

HYDROLOGY

MICRO- AND MACRO-SCALE

Water was monitored on both a spatial and temporal scale (Table 2.4). During each nest check, the depth of water directly under the nest was measured to the closest centimeter. The percent water coverage within an 11.3 m-radius circle around each nest was also estimated during each nest check. In addition, during the 2000 breeding season, one to four grid points per plot were monitored for water depth and percent coverage every three days. The chosen grid points were in low elevation areas that were wet at the beginning of the season. The grid points served as benchmarks for water activity during the dry breeding season of 2000.

LANDSCAPE SCALE

Direct measures of water at the plot scale could not be made during nest checks, so a different technique was required to obtain measures of water at the plot scale. During March 4 to

March 10, 2001, when the study plots were completely inundated by floodwater, we measured water depth to the closest centimeter at each grid point from canoe. We attempted to obtain a measurement at each grid point, every 25 meters. Due to the water, not all grid points were visible and we estimated their positions based on distance and direction from the surrounding grid points that were visible. Out of 2,346 measurements, 12.2% were made at estimated grid point locations. For three of the plots, measurements were made over two days. For the fourth plot, measurements were gathered over a three-day period. Actions were taken to adjust for varying water levels within and between days. We recorded the day and the hour of all measurements. For each plot visited, the first grid point measured for the day was re-measured at the end of data collection for that day. This allowed us to check and, if necessary, adjust for varying water levels within the day. The water varied negligible amounts within a day and adjustments were not necessary. The same calibration grid point was measured on the subsequent measuring day(s). Based on these measurements, we adjusted measurements taken on separate days to make them comparable to each other. Changes between days ranged from 0 - 14 cm and the appropriate adjustments were made.

The grid point-depth measurements did not sample the sloughs that run through each of the plots. For this reason, slough depths had to be measured in a different manner and then incorporated into the existing depth data. During the summer of 2001, sloughs within the plots were located (see <u>HABITAT MEASUREMENTS</u>→LANDSCAPE→*SLOUGHS AND PONDS* above). Some sloughs contained water, some were dry, and some were a mixture of wet and dry. Slough depth was measured by a combination of methods (Figure 2.12). While one person stood in the middle of the slough and another stood at a grid point with known depth, we ran a level string from the base of the grid point to directly above the slough point. We then measured the height of the string above ground at the slough point to the closest centimeter. The height of the string, added to the known depth of the grid point, provided the depth of the slough had it been measured on the same day as the grid point. If water was present at the slough point, the depth of the water was measured. Thus, the depth at subsequent slough points could be measured and compared to the point that was referenced to the grid point. Slough depth was measured every three segments if depth was constant, but more often if depth was variable. Depth was measured on average every 2.1 segments (range of 1-12 segments), or every 35.3 meters.

The grid point water depths were used to create a digital elevation model for each plot. The elevation models were created per plot; plots were not relative to each other. For a given plot, the point (grid or slough) with the largest water depth was identified. This point was the lowest elevation point on the plot and was set to an elevation of 0 cm. The elevations of all other points within the plot were referenced to the lowest point by subtracting the depth of the deepest point from the depth measurement of each point and taking its negative (Figure 2.13). The grid point locations, along with their elevation attributes, were imported into ArcView as a point shapefile. For each plot, elevation was interpolated by the inverse distance weighted (IDW) method, using 5-m cells and all points within a 40-m radius.

The slough points, containing their width and elevation attributes, also were imported into ArcView as a point shapefile. As previously mentioned, the points were connected with a line and the line was buffered by the measured widths. For each plot, slough elevation was interpolated by the IDW method; we used 5-m cells and the two closest neighboring slough points, one on each side. The slough polygons were converted to grid, using 5-m cells. The grid format of the slough locations was used to clip the interpolated slough elevation coverage. The clipped slough elevation coverage was then merged with the existing plot elevation coverage to create the final plot level digital elevation model (Figure 2.14). Slough points were interpolated separately from grid points, creating two coverages that were then merged, to restrict the influence of the slough points to the width of the slough.

The plot level digital elevation models (DEM) were used to create snapshots of water coverage at the plot scale every three days throughout the breeding seasons of 1996-1998 and 2000 (Figure 2.15). To create snapshots, ground elevations for all nests were extracted from the elevation model. On a given day and on a single plot, all nests with elevations and water depths greater than zero were used to calculate an average elevation and an average water depth. A new raster coverage of the water depth across the plot on that given day was created by using Map Calculator (ArcView GIS 3.2; ESRI 1999) and subtracting the DEM from the average elevation and then adding the average water depth. Grid values that were less than zero were set equal to zero. The percent water coverage at the plot scale was then calculated for each snapshot by dividing the number of cells with depth greater than zero by the total number of cells on the plot with a value (i.e., cells with no data were not included) and multiplying by 100. This information was used to calculate the percent water coverage at the plot scale for each nest during each nest check.

In addition to gathering the depth and plot scale water coverage at each nest check, we calculated a 15-day trend in depth and plot scale water coverage at each nest check. Trends for both were calculated to investigate possible time lag effects of water on nest survival. We used the three-day snapshots to backdate the depth and plot coverage information at each nest site to the beginning of the breeding season. At each nest check of each nest, the water data for dates up to 15 days prior were used to fit a quadratic equation to the curve of the data. The result was four measurements that completely described the quadratic curve and its lack of fit to the data: intercept, slope, quadratic term, and the root mean square error (RMSE). A 15-day trend was chosen to capture the fluctuation in the water when floodwaters were advancing or receding. Because water data were not available until nests were being monitored, the trends could not be calculated for the first nests of the breeding season. A minimum of four data points was required to estimate parameters of the trend. The average number of points used to create the trend was 5.9. The average number of days that the trend covered was 13.8 (range of 9-15 days).

The timing, depth, duration, and extent of flooding varied between years. To depict the variable flooding patterns within the study plots, graphs of the water depth per plot and year were created for the breeding season. The depth plotted was the depth for the lowest elevation point per plot. When the depth exceeded the elevation of the highest point, the plot was completely inundated. Additionally, graphs portraying plot coverage per plot and year were created. Flood stage (before, during, or after 100% plot inundation) was determined for each nest check of each nest. The stage of flooding was ascertained by plot coverage data and was specific to plot and year.

The U.S. Army Corps of Engineers manage the Graham-Burke pumping station on the White River, 4.5 km south of the study plots. Daily records are taken at 8 a.m. of the depth of the White River to the closest tenth of a foot and are publicly available (USACE 2004a). The depths were graphed and compared to the water trends on the study plots for the same dates.

DATA ANALYSIS

NEST SUCCESS

We used the program CONTRAST (Hines and Sauer 1989) to compare nest survival probabilities among years grouping by plot and among plots grouping by year. This computer program implements the methods of Sauer and Williams (1989) to make multiple comparisons of rate estimates by way of matrix algebra and chi-square tests. The program allows both simple (contrast of 2 groups) and composite (contrast of > 2 groups) hypotheses to be tested.

VARIABLE TRANSFORMATIONS

A logit transformation was applied to percent macro-canopy cover and percent open canopy within 200 meters of a nest. A log transformation was used on the macro-habitat variable, tree distance. Transformations were applied to obtain a more balanced distribution of the data. More specifically, because the variables were to be used as predictors in linear models, transformations more clearly distinguished among values near support boundaries (e.g., proportions near 0/1) and reduced the influence of highly-skewed values (e.g., distances).

PRINCIPAL COMPONENTS ANALYSIS

Principal components analysis (PCA) was used to simplify the representation of information within several correlated variables by creating a reduced set of new, uncorrelated variables that could then be used as covariates in models. We performed the PCA using the procedure PRINCOMP in SAS Release 8.02 (SAS 2001). To standardize for different units of measure among the original variables, we used the correlation matrix. We maintained all principal components that explained at least 100/P percent of the total variance, where P is equal to the number of original variables (Afifi and Clark 1996). We calculated the correlation (r_{ij}) between the i^{th} principal component C_i and the j^{th} variable x_j by the equation $r_{ij} = a_{ij}(\mathrm{Var}\ C_i)^{1/2}$, where a_{ij} is the coefficient of the j^{th} variable for the i^{th} principal component; variables with a correlation of at least 0.5 were used to interpret the individual principal components (Afifi and Clark 1996).

MACRO-HABITAT VARIABLES – Principal components analysis was performed on a set of five interrelated macro-habitat variables. The original five variables included tree count, average DBH, average canopy height, and the transformed versions of tree distance and macro-canopy cover. Macro-habitat measurements taken at the nest sites of both bird species and at sampling grid points were combined for all years (n=1033) to run the PCA.

OPEN CANOPY – Principal components analysis was executed on two highly correlated variables describing nest exposure to open canopy at the landscape level: distance to open canopy and the transformed version of percent open canopy within 200 meters of a nest. Measures of openness taken from the nest locations of both bird species were combined for all years (n=1012) to run the PCA.

GIS EXTRACTION OF MACRO-HABITAT PRINCIPAL COMPONENTS

Macro-habitat features were not measured at Prothonotary Warbler nests in 1998 because of logistical constraints. The missing values prevented statistical analyses of data including both macro-habitat variables and 1998 nests; that is, we had to choose between using macro-habitat variables and dropping all nests from the year 1998 or dropping the macro-habitat variables and including nests from 1998. To remedy this situation, we created an interpolated coverage of the macro-habitat principal components to impute habitat values for Prothonotary Warbler nests monitored during the 1998-breeding season.

To create the interpolated coverage, we used the macro-habitat principal component values from all nests (Acadian Flycatcher and Prothonotary Warbler) and from sampled grid points over all years (n=1033). The principal components were interpolated separately for each plot by the inverse distance weighted method, with a 22-m cell, and all neighboring points within a 50-m, 75-m, 100-m, and 200-m radius. The radius used depended on the principal component being interpolated and was chosen post-hoc based upon performance during the validation process (see details in next paragraph). The mean (range) number of points within a 50-m, 75-m, 100-m, and 200-m radius of the 1998 Prothonotary Warbler nests was: 4 (0-17), 9 (0-33), 15 (0-49), and 51 (2-133), respectively. A value was extracted from the interpolated coverage and provided as an imputed value for a nest based on the following restrictions: 1) the nest had at least four points within a 50-m radius, six points within a 75-m radius, or nine points within a 100-m radius; and 2) the nest was not located on the outskirts of other points. Using these restrictions, out of 208 nests with missing macro-habitat data, principal component values were imputed for 134 of them.

To evaluate the accuracy of the imputed principal component values, we excluded Acadian Flycatcher nests from 1998 (n=42) and re-created the interpolated coverages with the remaining nests and grid points (n=992). For each principal component, four different interpolations were completed using all neighboring points within a 50-m, 75-m, 100-m, and 200-m radius. From these coverages, we extracted the principal component values for the 42 excluded nests, applying the same two data selection restrictions as above. To compare the interpolated values to the true values, we calculated the mean squared difference, the standard error, and the upper and lower 95% confidence intervals. We also ran a two-tailed two-sample paired t-test. Of the four interpolated coverages created for each principal component, we retained the one that performed the best. Lastly, we compared the performance of interpolated coverages created by the method of kriging to the ones created by the inverse distance weighted method.

RESULTS

NESTS

Totals of 441 Acadian Flycatcher and 579 Prothonotary Warbler nests were monitored on the four study plots during the breeding seasons of 1996-1998 and 2000 (Table 2.1). For both species, the majority of nests were found in the building and the laying stages (Table 2.5). Over all years and plots, apparent nest success (percentage of nests that fledged $\geq$1 young) for Acadian Flycatchers was 27%. The overall nest survival rate, based on Mayfield's exposure method, was 0.25 ± 0.02; however, success rates varied by year (χ^2_3=9.95, p=0.019; Figure 2.16a) where success was highest during the 1996-breeding season. When contrasting plots grouping years, nest survival was comparative among plots (χ^2_3=4.36, p=0.225). Overall, apparent nest success of Prothonotary Warblers was 21%, while Mayfield nest survival for Prothonotary Warblers was 0.17 ± 0.02. Nest success rates varied by year (χ^2_3=25.27, p<0.0001; Figure 2.16b); nest survival was highest in 1997 and lowest in 1998. Grouping by year, survival rates were comparable among plots (χ^2_3=2.26, p=0.520). Nest predation was the primary cause of nest failure for both species, consistently responsible for terminating over 70% of failed nests (Table 2.6). Over all years, 29% of Acadian Flycatcher nests and 35% of Prothonotary Warbler nests were parasitized by Brown-headed Cowbirds; however, complete failure to fledge host young, as a direct result of parasitism, was considerably lower (12% and 8%, respectively; Table 2.6).

HABITAT

Macro-scale habitat characteristics were similar among the four study plots, with the exception of the density of stems (Table 2.7). On average, the patch cut plots, D and E, had a higher count of stems per 0.04 ha than the no cut plots. The plots were spaced across the width of the narrow refuge. The no cut plots were closest to the forest/agriculture edge, where plot A was closest to the west edge and plot F was closest to the east edge, while the patch cut plots were in the middle, the furthest from either edge (Table 2.8, Figure 2.5). The plots were located at a linear distance gradient from the levee; no cut plots A and F were the furthest and closest, respectively, while patch cut plots D and E were at intermediate distances from the levee (Table 2.8, Figure 2.5). Plot A contained the most area and length of roads (Table 2.8, Figure 2.6). Across all plots, all terrain vehicle (ATV) trails were the dominant road type (Table 2.8). The patch cuts on plot D were greater in area and edge than on plot E and were located more within the plot core than on plot E (Table 2.8, Figure 2.6). Mean micro-, macro-, and landscape scale habitat characteristic are summarized for each species over all years and plots (Tables 2.9, 2.10, and 2.11).

HYDROLOGY

During all years, except 2000, the study plots flooded and were completely inundated during some part of the breeding season; however, the timing, depth, spatial extent, and duration of the flooding were variable from year to year (Figures 2.17 and 2.18). Floodwaters rose and receded quickly. During the breeding season of 1996, the study plots started out dry, flooded mid-season for about five weeks of complete inundation, and then dried out. During 1997, the study plots flooded early, prior to nest initiation, and the floodwaters were in the process of receding by the beginning of the breeding season. At the beginning of the 1998-breeding season, the floodwaters were high and continued to rise, with 100% inundation for four weeks. The maximum depth reached during the breeding seasons of 1996, 1997, and 1998 was equivalent. The year 2000 was dry; the water on the plots consisted of wet pockets remaining from previous flooding, and past and present rainwater. The variable water trends in timing, depth, spatial extent, and duration are reflected in the mean water characteristics measured at the nest sites of Acadian Flycatchers and Prothonotary Warblers (Table 2.12).

The water trends observed on the study plots are similar to those recorded at the Graham-Burke pumping station for the same dates (USACE 2004a; Figure 2.19). In general, when depth at the pumping station exceeds 24 ft, the study plots begin to flood with overflow from the White River and its tributaries. When the depth at the pumping station exceeds 30 ft, all four study plots are completely inundated.

PRINCIPAL COMPONENTS ANALYSIS

The principal components analysis (PCA) of the five interrelated macro-scale habitat variables produced three orthogonal principal components that accounted for 78% of the variance (Table 2.13a). The first principal component (PC) had high loadings on three of the original macro-scale variables: number of trees, average tree DBH, and average distance between trees. Based on the signs of these loadings, we interpreted the first PC to represent forest age/disturbance (Table 2.14). Large PC values are associated with few, large trees that are spread out, such as an area with little disturbance and older trees. Small PC values are associated with many, small trees that are located close together, such as an area with frequent disturbance and younger trees. The second PC had a high positive loading on macro-scale canopy cover; thus, high values represent areas with high canopy cover, and small values represent areas with low canopy cover. The third PC had a high positive loading on macro-scale canopy height; thus, high values represent areas with tall canopy and small values represent areas with short canopy. The PCA of the two highly correlated variables describing exposure to open canopy produced one principal component that accounted for 90% of the variance (Table 2.13b). Based on the signs of the loadings on the original variables, large values of the PC represent close proximity to large openings and small values represent greater distance from small canopy openings (Table 2.14). Mean PC values are summarized for each plot over all years (Table 2.15) and for each species over all years and all plots (Table 2.16).

GIS EXTRACTION OF MACRO-HABITAT PRINCIPAL COMPONENTS

Extraction of macro-scale principal component values from an interpolated GIS coverage had mixed results. For each PC, the interpolated coverages created from neighboring points within a 50-m, 75-m, 100-m, and 200-m radius were comparable; however, the coverage resulting from a radius of 100 m performed best for the first PC, while a radius of 200 m was best for the second and third PC (Appendix 2A). Based on the comparison between the known PC scores and the extracted PC values for 42 Acadian Flycatcher nests, the extracted values of the first and third PC were unbiased and were not significantly different than the observed PC scores (Table 2.17). However, the mean absolute differences between the actual and extracted values were large relative to the ranges of the PC values, averaging 17-18% of the range. The extracted values of the second PC consistently over predicted, leading to extracted values that were biased high and significantly different than the actual PC scores (Table 2.17). Based on the same comparison between the actual and the predicted PC values, the inverse distance weighted method of interpolation performed better than did the kriging method.

DISCUSSION

NESTS

SUCCESS, PREDATION, AND PARASITISM

Nest success of Acadian Flycatchers within the study area was comparable to that reported by Wilson (1997) during 1993-1995 within the same study area. Nest success of the Acadian Flycatcher within our study area of eastern Arkansas is lower than reported within breeding sites of Michigan (64.6%; Walkinshaw 1966) and Indiana (34.8%; Whitehead and Taylor 2002). The high number of failed nesting attempts resulting from depredated nests has been found in other studies of Acadian Flycatchers (Whitehead and Taylor 2002) and is a general phenomenon found among neotropical migrant songbirds (Ricklefs 1969, Martin 1992). While parasitism rates are known to vary by region, degree of forest fragmentation, and host species (Robinson et al. 1995, Thompson et al. 1996, Winslow et al. 2000), the extent of brood parasitism on Acadian Flycatcher nests within our study area is within the large range of parasitism rates reported for the species in different regions containing varying amounts of forest cover. For example, parasitism rates varied from 3%-7.5% within highly forested areas of Missouri and central Indiana to 20%-50% in highly fragmented portions of Illinois and central Missouri (Whitehead and Taylor 2002). Although the rate of parasitism of Acadian Flycatcher nests is not exceedingly high, and a parasitism event does not destine a nest to failure, the reproductive success of parasitized nests is drastically lowered; compared to non-parasitized nests, parasitized Acadian Flycatcher nests may suffer up to a 90% reduction in expected reproductive output (Whitehead and Taylor 2002). In general, decreased reproductive output is a result of female cowbird removal of host eggs, hatching failure of remaining host eggs due to interrupted/improper incubation, and trampling or starvation of host nestlings by larger parasitic nestlings that hatch earlier and consume parental resources to the detriment of host young.

Prothonotary Warbler nest success within our study area was comparable to historical values reported by Walkinshaw (1941) in Michigan (23%), but low compared to values he reported for Prothonotary Warbler nests in Tennessee (63%). Success was also low relative to Prothonotary Warbler nests studied more recently in Tennessee (Petit 1989); however, the high success rate of nests within Petit's study may have been an artifact of the study design that utilized nest boxes. Nests located within nest boxes may have enjoyed a lower risk of nest predation, causing artificially elevated survival rates of these nests. As with Acadian Flycatchers and most passerine species, nest predation was the primary factor affecting nest success. The high percentage of depredated nests is consistent with percentages reported for other studies of Prothonotary Warblers nesting in natural cavities (Hoover 2001). Relative to other passerines, the Prothonotary Warbler is listed as a frequent host of Brown-headed Cowbirds (Friedmann 1963, Friedmann et al. 1977); their frequency as a host is exceptionally high when compared to other cavity-nesting species (Petit 1999). Brood parasitism within our study area is on the high end of the range reported for other studies; reported parasitism rates for the species range from 0% in Michigan and Tennessee (Walkinshaw 1941), 20% in Tennessee (Petit 1989), 27% in Wisconsin (Flaspohler 1996), and 41-50% in Illinois (Hoover 2001). The ever-expanding range of the cowbird as a result of increased forest fragmentation and agriculture is undoubtedly responsible for the increase in parasitism observed since the day of Walkinshaw's study. Parasitism frequency is highly variable among study sites and may be related to variation in landscape features and local cowbird abundance (Petit 1999). Additionally, variation in parasitism rates within study sites may be related to variation in size of cavity entrance (Petit 1991, Flaspohler 1996), which may limit access to female cowbirds. Although parasitism rates within our study area are not exceptionally high, and complete nest failure due to parasitism is low, successful parasitized Prothonotary Warbler nests suffer reduced reproductive success (22% to 53%; Petit 1999, Hoover 2001) by way of a reduction in the number of host young fledged (Petit 1989, 1991, Wood 1999, Hoover 2001).

Decreased success of Acadian Flycatcher and Prothonotary Warbler nests as a result of high nest predation and brood parasitism rates was not unexpected within our study area. Although the Refuge in which our study was conducted is a large, contiguous tract of forest, it is narrow (only 6.5-km wide at the study location) and surrounded by agriculture. These characteristics of the Refuge make it attractive to generalist predators, such as raccoons, and brood parasitic cowbirds, both of which abound within the study area. Generalist predators and cowbirds can infiltrate the forest from the surrounding agricultural matrix resulting in elevated rates of nest predation (Hanski et al. 1996) and brood parasitism (Donovan et al. 1997). Although foraging opportunities for cowbirds are infrequent within the Refuge, because cowbirds routinely travel up to 7 km between foraging and breeding sites (Thompson 1994), all nests within our study area are within the range of breeding cowbirds.

Nest predation was the main factor causing failure of Acadian Flycatcher and Prothonotary Warbler nests within our study area, and brood parasitism significantly reduces reproductive success of both species; thus, effective management and conservation of these bird populations depends on reducing the limiting nature of nest predation and parasitism. Knowledge of the birds' breeding biology, understanding their habitat requirements, and identifying and preserving the habitat features that positively affect their breeding productivity and survival can aid in accomplishing this goal (Martin 1992). Analyses of nest predation and parasitism patterns relative to habitat features within our study area are needed.

ANNUAL VARIATION

Variation in nest success by year suggests that annual variability is especially important in this system. When investigating patterns of nest predation and brood parasitism, reasons for this variability will need to be modeled. Annual variation in nest success also highlights the need for long-term studies in order to capture the extent of the variability and address potential mechanisms. As a seasonally flooded bottomland hardwood forest, water is a prominent feature of our study area and is an obvious feature that varies from year to year; fluctuations in annual flooding patterns include variability in the timing, duration, depth, and spatial extent of the flooding. Characteristics of the annual flooding patterns need to be investigated and potential links between flooding and variation in nest success need to be addressed. We address the relationship between hydrology and nest predation in Chapter 3 of this thesis.

HABITAT

Means and ranges of habitat features within study plots and at nest sites are presented simply to provide background on the habitat characteristics particular to our study area as well as introduce the micro-, macro-, and landscape scale habitat features whose relationships with nest predation and brood parasitism we will investigate in Chapters 3 and 4 of this thesis. There is ample variability for each habitat characteristic measured, lending them to investigation of potential relationships with nest survival from predation and parasitism status.

HYDROLOGY

Our study area was located within a seasonally flooded bottomland hardwood forest, and as such, hydrology is a prominent feature of the habitat. We measured water on the study plots in an attempt to describe the annual variation in the timing, duration, depth, and spatial extent of the flooding. As with other habitat features, we introduced this information to provide background on the hydrological characteristics of the study area. Past researchers of Prothonotary Warbler nest success in the same study area speculated that annual variation in nest success might be tied to the hydrology of the area (Wood 1999); this supposition, however, was not directly investigated. We measured water characteristics of the nesting habitat at three different spatial scales and over a temporal scale in an attempt to dissect the different components of the flooding patterns and to describe the variability of nest exposure to water. These measurements were taken in order to examine the potential relationship between nest predation and the flooding patterns of the study area; this relationship is explored in Chapter 3.

Depth measurements of the White River taken at the Graham-Burke pump station can be loosely related to the depth and extent of the flooding found on our study plots. This relationship can be of great value in providing a general idea of the flooding conditions on the study plots. Such information can be helpful for examining the variable flood patterns of this specific area of the Refuge, providing historical perspective as well as continued monitoring. Access to these types of information may be incredibly valuable in light of three US Army Corps of Engineer (USACE) projects currently underway or in planning (White River Navigation Project, Grand Prairie Irrigation Project, and Montgomery Point Lock and Dam; USACE 2004b,c,d) that may drastically alter the existing flooding regime of the White River.

PRINCIPAL COMPONENTS ANALYSIS

The principal components analyses (PCA) of the five interrelated macro-scale habitat variables and the two correlated variables describing canopy openness were successful in producing a reduced number of orthogonal variables to describe these characteristics of the habitat. The success of the extraction of macro-scale principal components (PC), however, is questionable. Extraction of Macro_PC2 was undeniably biased and unsound and it therefore would be inappropriate to use extracted values of this variable to investigate patterns of nest predation and parasitism. Extracted values of the first and third PC, although unbiased and statistically not different, contained substantial inaccuracies relative to the range of values for the variables. For this reason, these values should be used with caution and results derived from their use should be interpreted with prudence. Keeping this cautionary note in mind, we use the extracted Macro_PC1 and Macro_PC3 values when exploring patterns of nest predation and parasitism in Chapters 3 and 4. Their use allows us to include all years of study, greatly increasing our sample sizes, and all spatial scales; excluding these extracted values would either preclude the use of our 1998 data or the use of our macro-scale habitat features.

Why extraction of the second PC failed to sufficiently predict actual values is not clear. It is possible that macro-scale canopy cover, the characteristic that Macro_PC2 described, is too variable at nest sites to be predicted with accuracy; this may be especially true for Acadian Flycatchers that often select nest sites over openings in canopy (Whitehead and Taylor 2002) caused by roads or other disturbances. Canopy cover within our study area is relatively homogeneous and openings are caused only by infrequent disturbances such as roads and patch cuts or natural tree falls; however, selection of these intermittent canopy openings by nesting Acadian Flycatchers may circumvent accurate interpolation across the study plots and prediction.

TABLES

Table 2.1: The number of nests found and monitored per year and plot for (a) Acadian Flycatchers and (b) Prothonotary Warblers.

(a) Acadian Flycatcher

Year	Plot				Total
	A	D	E	F	
1996	42	28	25	45	140
1997	53	33	35	40	161
1998	13	10	10	12	45
2000	24	27	20	24	95
Total	132	98	90	121	441

(b) Prothonotary Warbler

Year	Plot				Total
	A	D	E	F	
1996	46	17	38	26	127
1997	51	28	40	38	157
1998	60	38	55	43	196
2000	28	19	22	30	99
Total	185	102	155	137	579

Table 2.2: Abbreviations and descriptions of micro-habitat and macro-habitat variables measured at Acadian Flycatcher and Prothonotary Warbler nests.

Abbreviation	**Variable Description**
Micro-habitat	**Acadian Flycatcher and Prothonotary Warbler**
Nest_Ht	Height of the nest above ground (m)
Tree_Ht	Height of the nest tree above ground (m)
Tree_DBH	Diameter at breast height of the nest tree (cm)
Can_Cov	Average percent canopy cover above the nest, measured in each of the 4 cardinal directions
	Acadian Flycatcher
Dist_Edge	Distance from the nest to the nest branch edge (cm)
Dist_Bole	Distance from the nest to the nest tree bole (m)
Can_Base	Height of the lowest part of the nest tree canopy (m)
Conceal	Average nest concealment within 1 m, measured in each of the 4 cardinal directions and above and below the nest. Measured in following units: 0=0%, 1=0-25%, 2=25-50%, 3=50-75%, 4=75-100%.
Vines	Number of vines > 1 cm diameter on the nest tree bole that reach from the ground to the first branch. Converted to a dichotomous variable: 0=no vines, 1=one or more vines.
	Prothonotary Warbler
Cav_Ht	Height of the cavity entrance (cm)
Cav_Wid	Width of the cavity entrance (cm)
Cav_Code	Index of cavity entrance size, combining cavity height and width. Measured in the following units: 1=smaller than average, 2=average, 3 and 4= larger than average, 5=open top or infinite height.
Cav_Split	Cavity type (split/hole). Dichotomous variable: 0=non-split, 1=split
Live	Nest tree status (live/dead). Dichotomous variable: 0=dead, 1=live
Macro-habitat	**Acadian Flycatcher and Prothonotary Warbler**
Macro_CanCov	Average percent canopy cover, measured 11.3 m from the nest in each of the 4 cardinal directions
Can_Ht	Average height of the canopy, measured 11.3 m from the nest in each of the 4 cardinal directions (m)
Trees	Number of trees > 10 cm DBH within an 11.3-m radius around the nest (trees/0.04 ha)
DBH	Average DBH of the trees > 10 cm DBH within an 11.3-m radius around the nest (cm)
Tree_Dist	Average distance from the nest to the closest tree > 10 cm DBH, measured in each of the 4 cardinal directions (m)
Stems	Number of woody stems < 10 cm DBH within a 5-m radius around the nest (stems/0.008 ha)

Table 2.3: Abbreviations and descriptions of landscape level variables measured for each nest. All measurements were made in ArcView GIS. Buffers around each nest were used to calculate area and edge length of roads, sloughs, and patch cuts. Buffers were created with radii increasing at increments of 25 m until a maximum of 300 m was reached (i.e., 0-25m, 0-50m, 0-75m, 0-100m, etc.). Canopy openings were defined as openings in the canopy > 5-m wide that resulted from roads, patch cuts, sloughs, or other water bodies. Measurements were made to the closest tenth of a meter.

Abbreviation	**Variable Description**
Forst_Dist	Distance from nest to closest forest/agricultural edge (m)
Levee_Dist	Distance from nest to the levee (m)
Road_Type	Type of road closest to the nest, based on frequency and type of use. Coded from light and infreqent use to heavy and frequent use: 1=minor atv, 2=logging, 3=major atv, 4=unimproved dirt, 5=improved dirt, 6=gravel
Road_Dist	Distance from nest to the closest road (m)
Rd_Area_25: Rd_Area_100	Area of road within 0-100 m of the nest, measured at 25-m intervals (m^2)
Rd_Edge_25: Rd_Edge_100	Length of road within 0-100 m of the nest, measured at 25-m intervals (m)
Slou_Dist	Distance from nest to the closest slough (m)
Sl_Area_25: Sl_Area_100	Area of slough within 0-100 m of the nest, measured at 25-m intervals (m^2)
Sl_Edge_25: Sl_Edge_100	Length of slough within 0-100 m of the nest, measured at 25-m intervals (m)
Cut_Dist	Distance from nest to the closest patch cut (m)
Cut_Area_25: Cut_Area_300	Area of patch cut within 0-300 m of the nest, measured at 25-m intervals (m^2)
Cut_Edge_25: Cut_Edge_300	Length of patch cut edge within 0-300 m of the nest, measured at 25-m intervals (m)
Open_Dist	Distance to closest canopy opening > 5 m in width (m)
Open_Percent	Percent of area within 200 m of the nest that contains a canopy opening > 5 m in width

Table 2.4: Description of water variables measured at three spatial scales: micro, macro, and landscape. All water variables were measured at each nest check and are time-dependent.

Abbreviation	Variable Description
Micro-Scale	
Depth	Depth of water directly under the nest to nearest centimeter
Wpresence	Dichotomous variable for presence/absence of water directly under the nest
Depth2	Quadratic form of depth: depth + depth^2
Depth Trend	Set of 4 variables describing the 15-day trend in depth of water directly under the nest
depth_int	intercept
depth_slope	slope
depth_quad	quadratic term
depth_rmse	root mean square error
Macro-Scale	
Nest_Cov	Percent water coverage within 11.3 m-radius circle around the nest
Nest_Cov2	Quadratic form of nest_cov: nest_cov + nest_cov^2
Landscape Scale	
Plot_Cov	Percent water coverage of the plot
Plot_Cov2	Quadratic form of plot_cov: plot_cov + plot_cov^2
Plot_Cov Trend	Set of 4 variables describing the 15-day trend in percent water coverage at the plot scale
pcov_int	intercept
pcov_slope	slope
pcov_quad	quadratic term
pcov_rmse	root mean square error
Plot_Cov Dummies	Set of 4 dummy variables describing water coverage at the plot scale compared to 100% coverage
pcov_1	0-25%
pcov_2	25-50%
pcov_3	50-75%
pcov_4	75-99%
Flood Stage	Set of two dummy variables describing stage of flooding; before and during flooding compared to after flooding
flood_b	before flooding
flood_d	during flooding

Table 2.5: Percent of nests found in the building, laying, incubating, and nestling stages for (a) Acadian Flycatchers and (b) Prothonotary Warblers. Nests were combined for all years and sample size (n) is noted. For both species, the majority of nests were found in the building and laying stages (57.82% and 68.05% respectively).

(a) Acadian Flycatcher

Stage Found	**Percent** (n=441)
Building/Laying	57.82
Incubating	35.83
Nestling	6.35

(b) Prothonotary Warbler

Stage Found	**Percent** (n=579)
Building	53.02
Laying	15.03
Incubating	30.22
Nestling	1.73

Table 2.6: Host and nest fates for (a) Acadian Flycatchers and (b) Prothonotary Warblers during 1996-1998, 2000, and all years combined. Sample size (n) is noted. Values are percentages. Failure is broken down into percentages of failure types.

(a) Acadian Flycatcher

Host Fate	**1996**	**1997**	**1998**	**2000**	**Total**
	(n=140)	(n=161)	(n=45)	(n=95)	(n=441)
Successful	34.29	20.50	22.22	29.47	26.98
Failure	62.14	74.53	68.89	64.21	67.80
Depredated	80.46	85.83	80.65	72.13	80.94
Parasitism[a]	9.20	10.00	16.13	19.67	12.37
Abandoned	5.75	0.83	0.0	4.92	3.01
Unknown	4.60	3.33	3.23	3.28	3.68
Uncertain[b]	3.57	4.97	8.89	6.32	5.22
Nest Fate					
Successful	35.71	27.33	24.44	36.84	31.75
Failure	59.29	68.32	64.44	56.84	62.59
Depredated	87.95	94.55	93.10	88.89	91.30
Abandoned[c]	6.02	1.82	3.45	5.56	3.99
Unknown	6.02	3.64	3.45	5.56	4.71
Uncertain[b]	5.00	4.35	11.11	6.32	5.67

(b) Prothonotary Warbler

Host Fate	**1996**	**1997**	**1998**	**2000**	**Total**
	(n=127)	(n=157)	(n=196)	(n=99)	(n=579)
Successful	21.26	31.85	11.22	22.22	20.90
Failure	77.17	62.42	84.18	72.73	74.78
Depredated	69.39	76.53	78.79	88.89	77.83
Parasitism[a]	4.08	18.37	6.67	1.39	7.85
Abandoned	0.0	3.06	3.03	5.56	2.77
Flooded	22.45	0.0	11.52	0.0	9.47
Weather	0.0	0.0	0.0	1.39	0.23
Unknown	4.08	2.04	0.0	2.78	1.85
Uncertain[b]	1.57	5.73	4.59	5.05	4.32
Nest Fate					
Successful	21.26	35.03	13.78	22.22	22.63
Failure	77.17	59.24	82.14	71.72	73.06
Depredated	71.43	87.10	82.61	90.14	82.27
Abandoned[c]	3.06	8.60	5.59	5.63	5.67
Flooded	22.45	0.0	11.80	0.0	9.69
Weather	0.0	0.0	0.0	1.41	0.24
Unknown	3.06	4.30	0.0	2.82	2.13
Uncertain[b]	1.57	5.73	4.08	6.06	4.32

[a] Includes abandonment due to parasitism and nests in which parasitic young lived longer than host young.

[b] Includes nests with insufficient information to determine fate and nests in which monitoring ceased due to end of field season.

[c] Includes abandonment of parasitized and non-parasitized nests; only applies to nest fates.

Table 2.7: Comparison of macro-habitat characteristics (Mean ± SE) of the four study plots at White River NWR, all years combined. Means were calculated from measurements taken at nest sites of both species and at designated plot grid points. Nest or grid sites in which the 0.04 ha macro-plot encompassed a pond (plot A) or a patch cut (plots D and E) were excluded. See Table 2.2 for variable descriptions.

Variable	**Plot**			
	A	**D**	**E**	**F**
	(n=314)	(n=195)	(n=236)	(n=272)
Macro_CanCov (%)	93 ± 0.28	94 ± 0.35	93 ± 0.38	94 ± 0.28
Can_Ht (m)	21.3 ± 0.18	21.4 ± 0.27	21.7 ± 0.23	21.6 ± 0.20
Trees (#)	25.5 ± 0.60	22.3 ± 0.59	25.0 ± 0.64	29.0 ± 0.55
DBH (cm)	21.3 ± 0.29	22.9 ± 0.41	22.8 ± 0.35	20.6 ± 0.29
Tree_Dist (m)	4.95 ± 0.08	5.08 ± 0.11	4.86 ± 0.09	4.51 ± 0.09
Stems (#)	23.3 ± 0.97	35.0 ± 2.77	39.3 ± 1.73	23.2 ± 1.22

Table 2.8: Summary of landscape features of the four study plots. Distances from forest/agricultural edge and levee are averages of nest distances for each plot (Mean ± SE). Values for roads, patch cuts, water bodies, and open canopy are calculated for features (and portions of features) contained within the plot and up to 50 m outside the plot boundaries. Road area is broken down into percentages by road type. The area and edge of patch cuts are totaled for the entire plot and means are provided per cut. Area of open canopy is separated into percentages by type of opening.

Variable	**Plot**			
	A	**D**	**E**	**F**
Forst_Dist (m)[a]	1264.4 ± 9.91	3242.5 ± 11.12	3433.4 ± 9.66	2707.5 ± 9.03
Levee_Dist (m)[a]	4557.4 ± 8.03	2203.8 ± 11.28	1564.9 ± 9.40	819.3 ± 9.96
Road_Area (ha)	1.05	0.62	0.82	0.74
unimproved_dirt (%)	27.62	0.0	0.0	18.87
major_atv (%)	48.42	54.91	23.64	45.25
logging (%)	0.0	45.09	67.22	0.0
minor_atv (%)	23.96	0.0	9.14	35.88
Road_Length (m)	2895.5	1278.8	1631.0	2268.6
Patch Cut_Area (ha)	-----	12.13	10.35	-----
mean ± se (ha/cut)	-----	3.03 ± 0.38	2.59 ± 0.27	-----
Patch Cut_Edge (m)	-----	3535.8	3166.3	-----
mean ± se (m/cut)	-----	883.9 ± 48.35	791.6 ± 53.67	-----
Patch Cut_Nearest Neighbor (m)[b]	-----	130.1 ± 19.02	179.9 ± 78.88	-----
Water Bodies_Area (ha)	1.14	1.60	0.65	1.43
Open Canopy_ Area (ha)[c]	1.59	13.67	11.05	0.94
Roads (%)	62.92	1.30	6.68	50.36
Patch Cuts (%)	0.0	88.37	91.46	0.0
Water (%)	37.08	10.33	1.85	49.64
Core_Area (ha)[d]	31.02	15.22	23.70	44.09

[a] See Table 2.3 for variable description.

[b] Nearest neighbor is the mean distance between a patch cut and its closest neighboring cut.

[c] Open canopy is defined as a canopy opening that is greater than 5-m wide and is created by a road, patch cut, or water body.

[d] Core area is the area greater than 50 m from any patch cut, road, slough, or other water body.

Table 2.9: Mean micro-habitat characteristics of (a) Acadian Flycatcher and (b) Prothonotary Warbler nest sites. Years and plots were combined to compute all means, with the exception of Conceal and Vines (data only from 2000). Sample size (n) is provided in parentheses. See Table 2.2 for variable descriptions.

(a) Acadian Flycather

Variable	**Mean ± SE**	**(n)**	**Min**	**Max**
Nest_Ht (m)	7.58 ± 0.16	(437)	1.50	20.57
Tree_Ht (m)	14.4 ± 0.36	(434)	3.0	39.1
Tree_DBH (cm)	24.4 ± 0.95	(434)	2.3	118.0
Can_Cov (%)	95 ± 0.39	(428)	0	100
Dist_Edge (cm)	68 ± 1.99	(420)	10	265
Dist_Bole (m)	3.71 ± 0.09	(432)	0.40	10.59
Can_Base (m)	5.5 ± 0.12	(435)	1.1	18.1
Conceal	1.9 ± 0.08	(94)	0.5	3.7
Vines (#)	0.9 ± 0.18	(95)	0	7

(b) Prothonotary Warbler

Variable	**Mean ± SE**	**(n)**	**Min**	**Max**
Nest_Ht (m)	2.44 ± 0.04	(550)	0.48	7.00
Tree_Ht (m)	3.66 ± 0.09	(542)	1.08	16.50
Tree_DBH (cm)	14.5 ± 0.29	(542)	2.5	55.3
Can_Cov (%)	90 ± 0.52	(550)	0	100
Cav_Ht (cm)	7.20 ± 0.32	(411)	2.50	50.00
Cav_Wid (cm)	4.72 ± 0.08	(436)	2.00	18.50
Cav_Code	2.3 ± 0.05	(448)	1	5

Table 2.10: Mean macro-habitat characteristics of (a) Acadian Flycatcher and (b) Prothonotary Warbler nest sites. Years and plots were combined to compute all means. Sample size (n) is provided in parentheses. See Table 2.2 for variable descriptions.

(a) Acadian Flycather

Variable	**Mean ± SE** (n=427)	**Min**	**Max**
Macro_CanCov (%)	95 ± 0.23	62	100
Can_Ht (m)	21.8 ± 0.17	12.3	34.6
Trees (#)	24.3 ± 0.45	4	57
DBH (cm)	21.4 ± 0.25	12.0	49.1
Tree_Dist (m)	5.25 ± 0.07	1.71	10.15
Stems (#)	31.4 ± 1.53	0	348

(b) Prothonotary Warbler

Variable	**Mean ± SE** (n=381)	**Min**	**Max**
Macro_CanCov (%)	90 ± 0.45	10	100
Can_Ht (m)	21.9 ± 0.17	4.3	32.4
Trees (#)	28.7 ± 0.50	3	65
DBH (cm)	21.1 ± 0.24	13.6	40.5
Tree_Dist (m)	5.27 ± 0.25	1.23	70.53
Stems (#)	29.0 ± 1.62	0	450

Table 2.11: Mean landscape distance (m) characteristics of (a) Acadian Flycatcher and (b) Prothonotary Warbler nest sites. Years and plots were combined to compute all means. Means for Cut_Dist were computed only for nests located on patch cut plots. Sample sizes (n) are provided in parentheses; the second number applies only to Cut_Dist. See Table 2.3 for variable descriptions.

(a) Acadian Flycather

Variable	**Mean ± SE** (n=441, 188)	**Min**	**Max**
Forst_Dist	2536.3 ± 42.64	922.8	3708.4
Levee_Dist	2400.3 ± 72.01	438.3	4777.8
Road_Dist	113.5 ± 4.07	0	584.6
Cut_Dist	59.5 ± 3.80	0	307.4
Slou_Dist	197.4 ± 6.71	0	599.3
Open_Dist	89.3 ± 3.06	0	284.4

(b) Prothonotary Warbler

Variable	**Mean ± SE** (n=579, 257)	**Min**	**Max**
Forst_Dist	2539.8 ± 38.27	867.8	3734.5
Levee_Dist	2455.4 ± 62.66	427.6	4827.5
Road_Dist	127.7 ± 4.02	0.2	538.6
Cut_Dist	96.3 ± 4.50	0	362.3
Slou_Dist	197.4 ± 6.35	0	647.8
Open_Dist	89.0 ± 2.67	0	271.9

Table 2.12: Mean water characteristics of nest sites at three spatial scales: micro, macro, and landscape. Means are provided for (a) Acadian Flycatcher and (b) Prothonotary Warbler nests by year. Plots were combined to compute all means. Sample size is provided in parentheses. See Table 2.4 for variable descriptions.

(a) Acadian Flycather

Year	**Variable**								
	Depth (cm)			**Nest_Cov (%)**			**Plot_Cov (%)**		
	Mean ± SE	Min	Max	Mean ± SE	Min	Max	Mean ± SE	Min	Max
1996 (140)	139 ± 7.32	0	265	85 ± 2.99	0	100	84 ± 2.66	1	100
1997 (161)	1 ± 0.37	0	40	10 ± 1.96	0	100	12 ± 0.40	0	35
1998 (45)	34 ± 8.97	0	225	38 ± 6.87	0	100	39 ± 5.64	0	100
2000 (95)	1 ± 0.58	0	48	3 ± 1.46	0	100	10 ± 0.83	1	35

(b) Prothonotary Warbler

Year	**Variable**								
	Depth (cm)			**Nest_Cov (%)**			**Plot_Cov (%)**		
	Mean ± SE	Min	Max	Mean ± SE	Min	Max	Mean ± SE	Min	Max
1996 (127)	97 ± 7.85	0	280	75 ± 3.54	0	100	68 ± 3.33	1	100
1997 (157)	41 ± 4.19	0	238	62 ± 3.60	0	100	48 ± 3.06	2	100
1998 (196)	123 ± 6.55	0	309	77 ± 2.89	0	100	71 ± 2.87	1	100
2000 (99)	4 ± 0.98	0	52	22 ± 3.66	0	100	13 ± 0.98	1	40

Table 2.13: (a) Principal components analysis for macro-habitat variables. Macro-habitat measurements from nests of both species and from plot grid points were used (n=1033). Transformed versions of Macro_CanCov (logit) and Tree_Dist (log) were used. The first three principal components were retained because they each explained at least 20% of the total variance (using the 100/P percent rule of thumb, where P is the number of original variables). Within the eigenvector of each principal component, bold and asterisked coefficients indicate the variables with a correlation greater than or equal to 0.5 that were used to interpret the principal component. (b) Principal components analysis for open canopy. Measurements from nests of both species were included (n=1012). The transformed version of Open_Percent (logit) was used. The first principal component was retained based on the proportion of variance explained.

(a) Macro-habitat

Variable	**Principal Component**		
	1	**2**	**3**
Macro_CanCov (%)	0.1109	**0.9664 ***	0.1584
Can_Ht (m)	0.2235	-0.1221	**0.9165 ***
Trees (#)	**-0.6236 ***	0.0640	0.1546
DBH (cm)	**0.5964 ***	-0.1681	0.0331
Tree_Dist (m)	**0.4395 ***	0.1373	-0.3315
Eigenvalue	1.9450	0.9962	0.9758
Cumulatiave Proportion Explained	0.3890	0.5882	0.7834

(b) Open Canopy

Variable	**Principal Component**
	1
Open_Dist (m)	-0.7071
Open_Percent (%)	0.7071
Eigenvalue	1.7903
Cumulatiave Proportion Explained	0.8951

Table 2.14: Abbreviations and interpretations of the macro-habitat and open canopy principal components.

Variable	Interpretation
Macro_PC1	Represents age/disturbance. Large values are associated with few trees, that have a large DBH and are spread far apart. This could be an area with little disturbance and older trees. Small values are associated with many, small trees that are close together. This could be an area with frequent disturbance and younger trees.
Macro_PC2	Represents macro-scale canopy cover. Large values represent a high percent canopy cover, while small values represent low percent canopy cover.
Macro_PC3	Represents macro-scale canopy height. Large values represent tall canopy and small values represent short canopy.
Open	Represents proximity and amount of open canopy. Large values represent close proximity to canopy openings and large amounts of open canopy. Small values represent long distances to canopy openings and small amounts of open canopy.

Table 2.15: Comparison of mean macro-habitat principal component values and open canopy principal component values of the four study plots at White River NWR. Variables in *italics* are the variables from which the principal component, Open, was derived. Means are calculated from values of nest sites of both species. Years were combined to compute means. Macro-habitat principal component values that were extracted from the GIS coverage were not included in the means. Sample sizes (n) are noted in parentheses; the first number applies to the macro-habitat principal components and the second number applies to the open canopy variables.

Variable	**Plot**			
	A	**D**	**E**	**F**
	(n=273 , 317)	(n=174 , 200)	(n=211 , 245)	(n=229 , 258)
Macro_PC1	-0.1050 ± 0.0869	0.4788 ± 0.1055	0.0560 ± 0.1020	-0.3215 ± 0.0947
Min	-5.0011	-2.4943	-3.4087	-3.7503
Max	5.8378	3.546	3.8684	4.7006
Macro_PC2	-0.0216 ± 0.0639	0.1956 ± 0.0921	-0.0663 ± 0.0757	0.2498 ± 0.0685
Min	-2.7797	-3.1197	-1.7986	-1.8419
Max	2.9627	2.4239	2.5527	2.4288
Macro_PC3	-0.1017 ± 0.0601	-0.0183 ± 0.0769	0.2067 ± 0.0760	0.1946 ± 0.0668
Min	-2.9120	-2.0092	-2.9431	-2.1947
Max	2.8223	3.1007	4.0339	3.0907
Open	-0.1664 ± 0.0530	1.1902 ± 0.0462	0.3854 ± 0.0768	-1.0682 ± 0.0864
Min	-3.6749	-3.9778	-3.8297	-3.9419
Max	1.2637	1.9282	1.8349	1.4808
Open_Dist	93.6 ± 2.99	42.1 ± 2.78	79.0 ± 3.87	128.9 ± 4.26
Min	0	0	0	0
Max	255.9	284.4	269.9	281.1
Open_Percent	2.78 ± 0.10	22.07 ± 0.69	11.85 ± 0.61	1.85 ± 0.17
Min	0	0	0	0
Max	8.45	41.75	33.52	11.24

Table 2.16: Means of the macro-habitat principal components and the open canopy principal component for (a) Acadian Flycatcher and (b) Prothonotary Warbler nest sites. Years and plots were combined to compute means. Macro-habitat principal component values that were extracted from the GIS coverage were not included in the means. Sample size is noted in parentheses; the first number applies to the macro-habitat principal components and the second number applies to the open canopy principal component.

(a) Acadian Flycatcher

Variable	Mean ± SE (n=427 , 441)	Min	Max
Macro_PC1	0.2465 ± 0.0660	-3.4193	5.8378
Macro_PC2	0.4185 ± 0.0492	-2.1862	2.9627
Macro_PC3	0.0091 ± 0.0498	-2.9121	4.0339
Open	0 ± 0.0640	-3.9778	1.8179

(b) Prothonotary Warbler

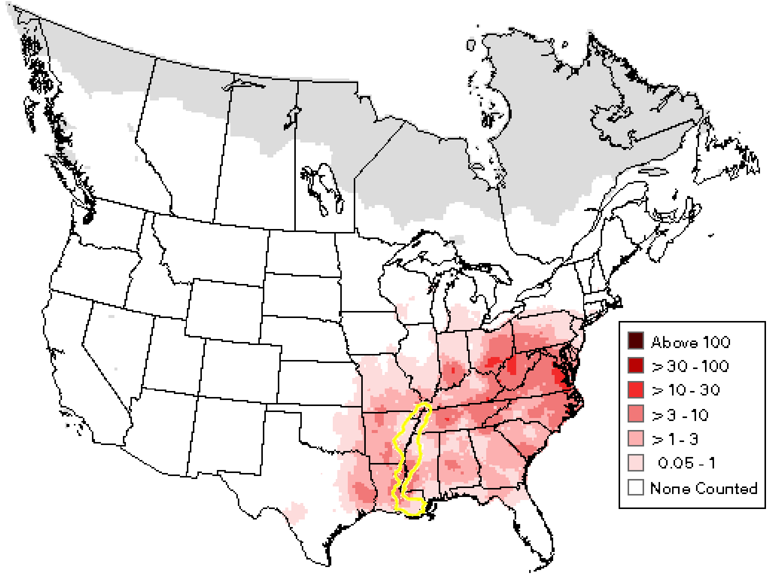
Variable	Mean ± SE (n=380 , 571)	Min	Max
Macro_PC1	-0.2986 ± 0.0706	-5.0011	3.5460
Macro_PC2	-0.2971 ± 0.0490	-3.1197	2.5967
Macro_PC3	0.1221 ± 0.0481	-2.9431	2.8223
Open	0 ± 0.0560	-3.8526	1.9282

Table 2.17: Performance of extracted macro-habitat principal component (PC) values. Values for PC 1 were extracted from an interpolated coverage created using a 100-m radius, while values for PC 2 and PC 3 were extracted from an interpolated coverage created using a 200-m radius. Assessment is based on 42 Acadian Flycatcher nests from 1998 with known scores compared to scores extracted from an interpolated grid coverage. The range reflects the span of the actual principal component scores for the 42 nests. Differences between values were calculated as (actual – extracted). A two-tailed two-sample paired t-test was used to compare the actual and the extracted values (df=41).

	Principal Component		
	1	**2**	**3**
N	42	42	42
Range	5.0965	2.1000	5.4240
Mean Absolute Difference	0.9045	0.7612	0.9350
Mean Difference	0.1868	-0.6975	-0.2040
Mean Squared Difference	1.3858	0.9053	1.3692
Standard Error	0.1816	0.1468	0.1806
95% Confidence Interval	{-0.1692, 0.5428}	{-0.9852, -0.4097}	{-0.5579, 0.1499}
t-statistic	1.042	-7.086	-1.148
p-value	0.3036	<0.0001	0.2576

FIGURES

(a) Acadian Flycatcher



(b) Prothonotary Warbler

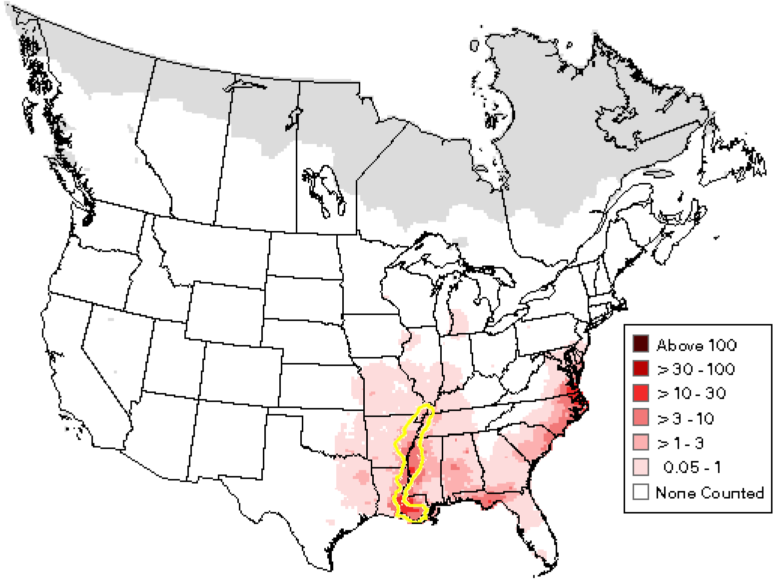
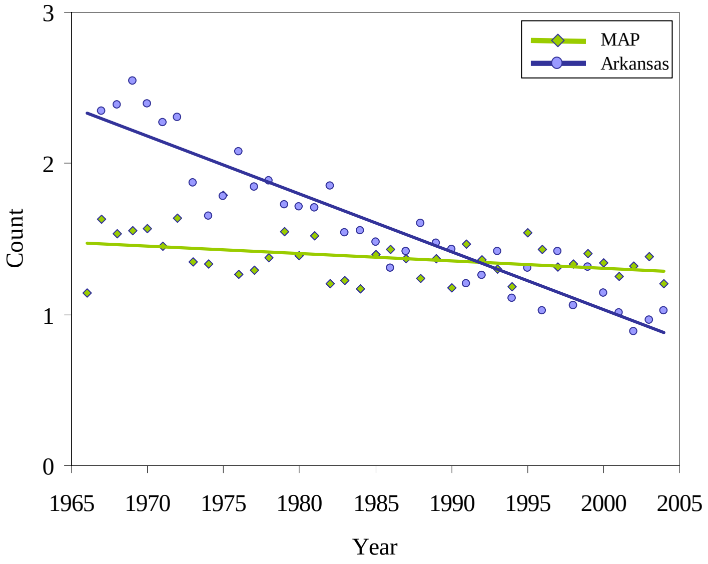


Figure 2.1: Summer distribution and abundance of (a) Acadian Flycatchers and (b) Prothonotary Warblers in North America based on the Breeding Bird Survey 1994-2003 (Sauer et al. 2005). Prothonotary Warblers reach one of their highest breeding densities in the remaining tracts of bottomland hardwood forests within the Mississippi Alluvial Valley, outlined here in yellow.

(a) Acadian Flycatcher



(b) Prothonotary Warbler

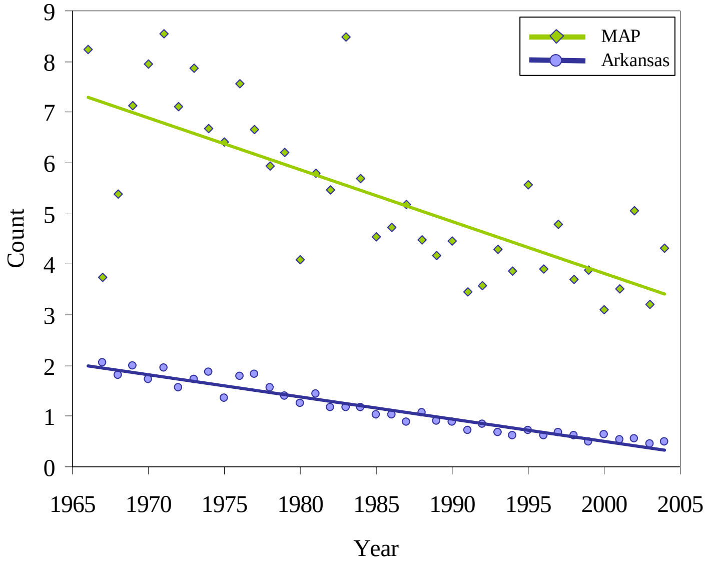


Figure 2.2: Population trends for (a) Acadian Flycatchers and (b) Prothonotary Warblers in the Mississippi Alluvial Plain (MAP) and in the state of Arkansas. For Acadian Flycatchers, a non-significant annual decline of –0.3% (p=0.92) is depicted within the MAP, while a significant annual decline of –2.6% (p=0.02) is depicted in Arkansas. For Prothonotary Warblers, an annual decline of –2.2% (p=0.08) is depicted in the MAP, while a significant annual decline of –4.6% (p=0.01) is depicted in Arkansas. Trends were based on the Breeding Bird Survey 1966-2004 (Sauer et al. 2005).

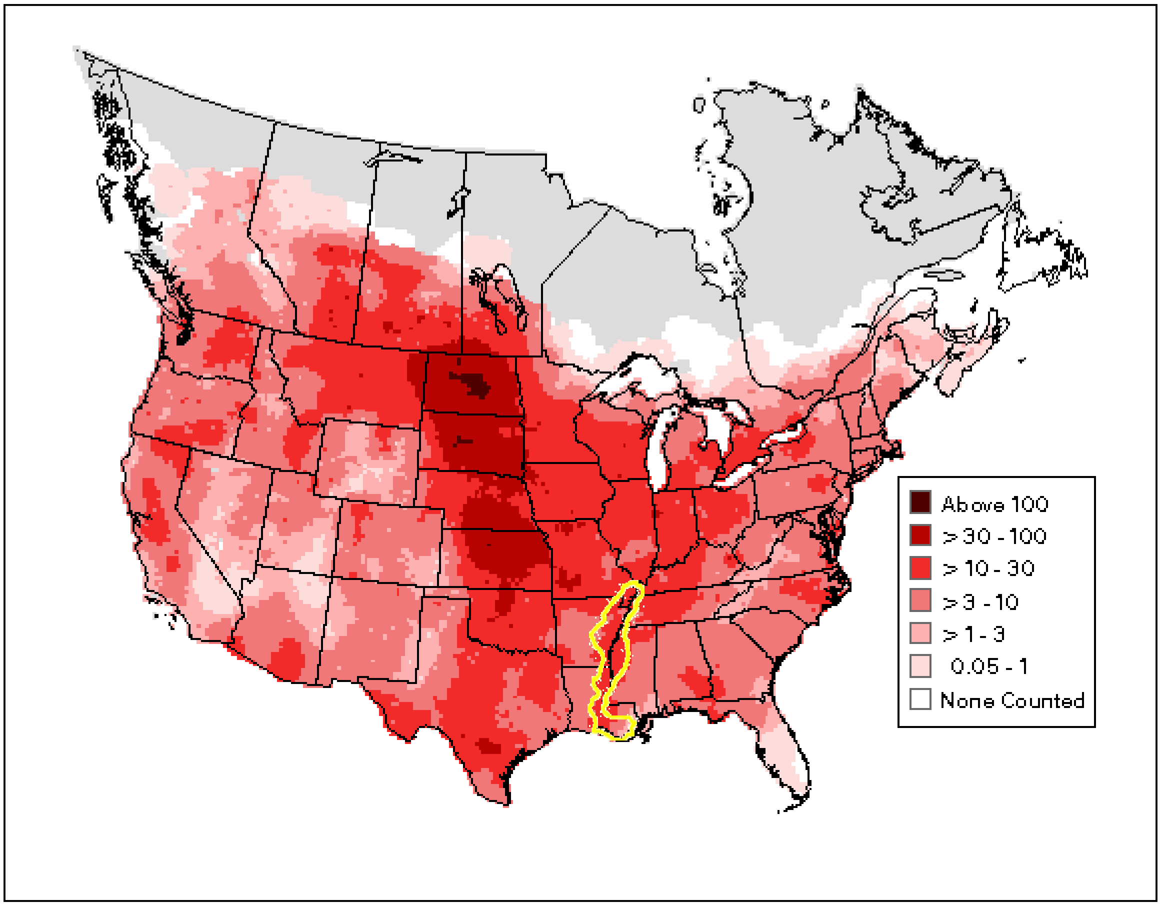


Figure 2.3: Summer distribution and relative abundance of the Brown-headed Cowbird in North America based on data from the Breeding Bird Survey 1994-2003 (Sauer et al. 2005). Abundance of breeding cowbirds within the Mississippi Alluvial Valley, outlined here in yellow, ranks among the third highest in relation to other portions of the cowbird's breeding range.

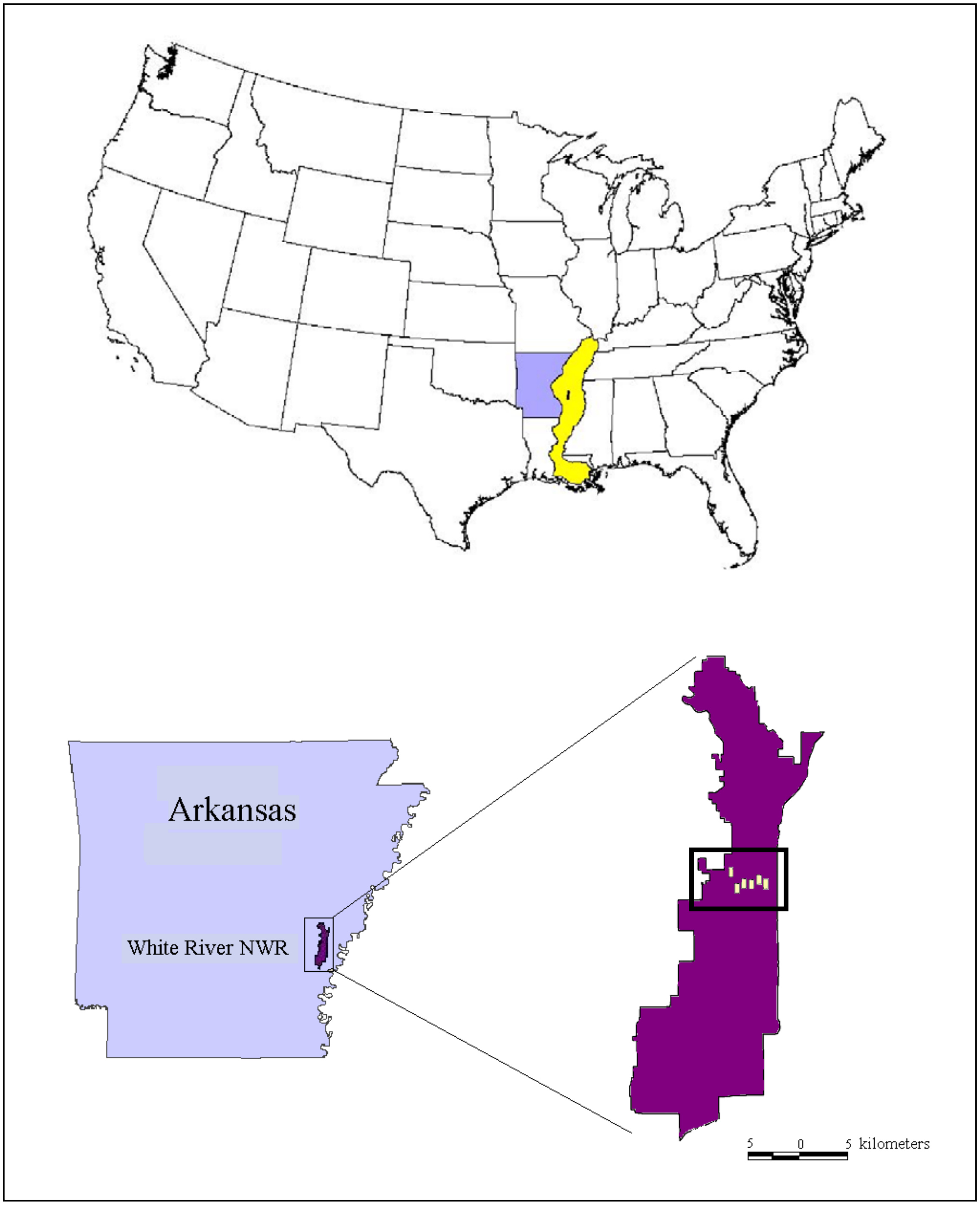
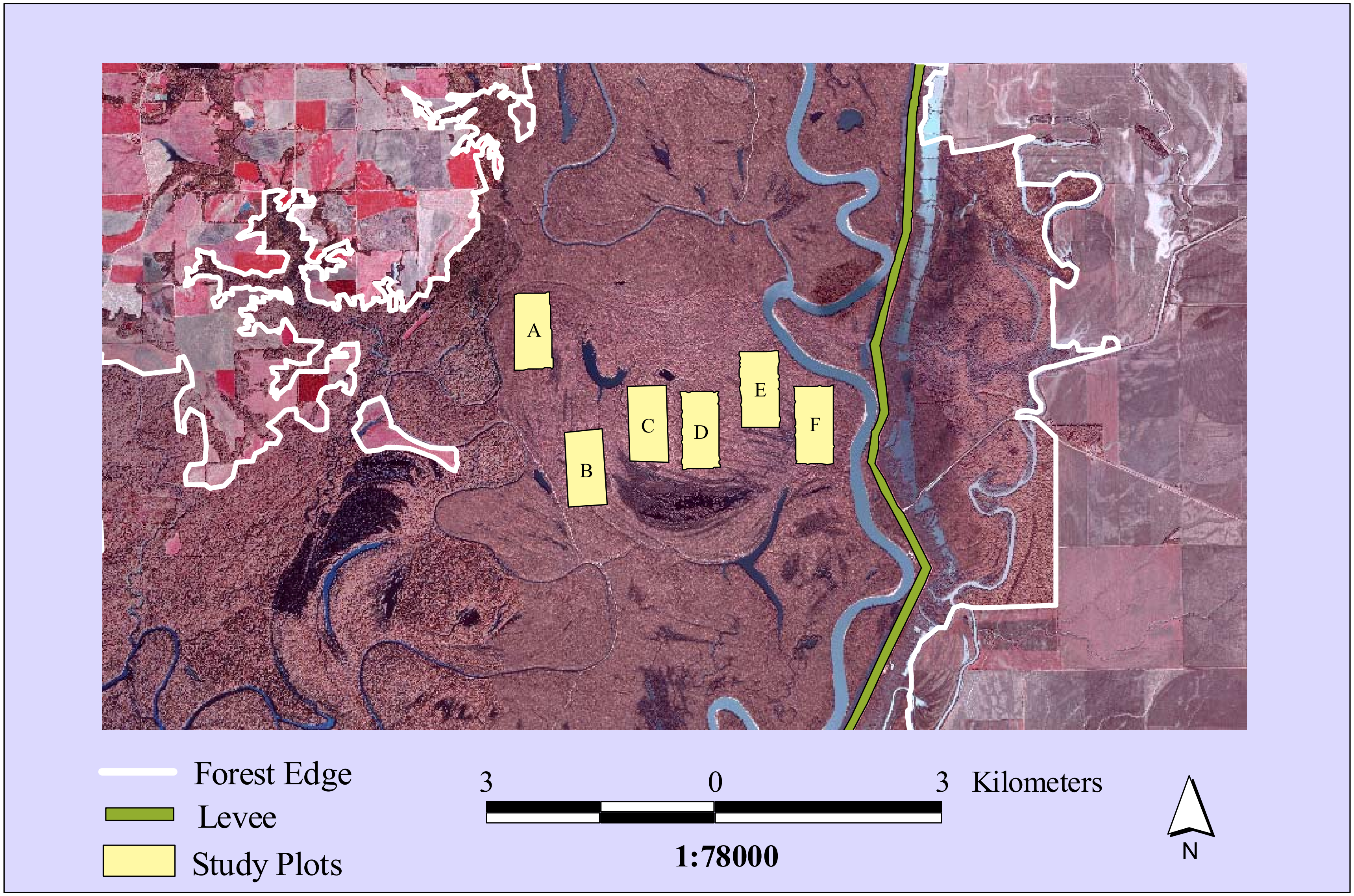


Figure 2.4: Location of the White River National Wildlife Refuge (NWR) within the Mississippi Alluvial Valley (yellow) and within the state of Arkansas, and the location of the six study plots within the Refuge.

Figure 2.5: Location of the six study plots and the surrounding area, including the forest/agricultural edge, the levee and the White River. Plots A and F are “no cut” plots, plots B and C are “selective cut” plots, and plots D and E are “patch cut” plots. This study focused solely on plots A, D, E, and F, the no cut and patch cut plots. The image is a color infrared digital ortho-quarter quad from 2001.


A
B
C
D
E
F
Forest Edge
Levee
Study Plots
3
0
3 Kilometers
1:78000
N

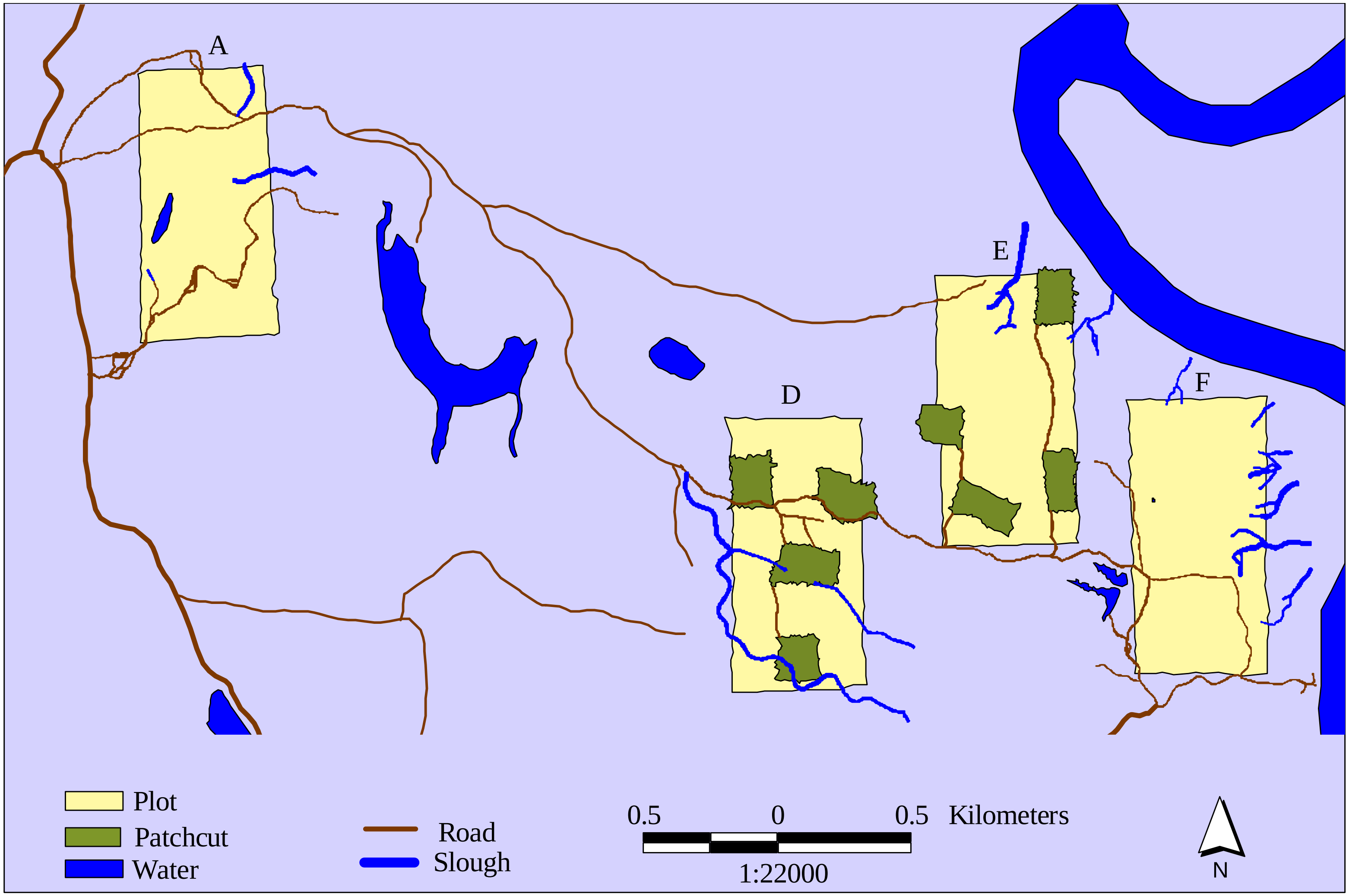
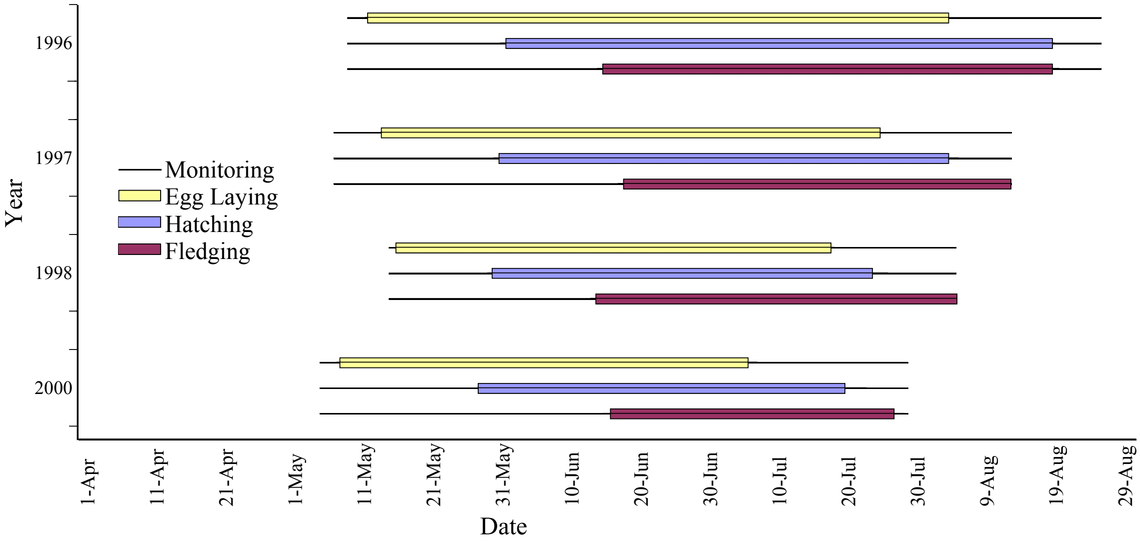


Figure 2.6: Close up view of the four focal study plots and the roads, sloughs, lakes, ponds, and river within the study area. Plots A and F are “no cut” plots. Plots D and E are “patch cut” plots.

(a) Acadian Flycatcher



(b) Prothonotary Warbler

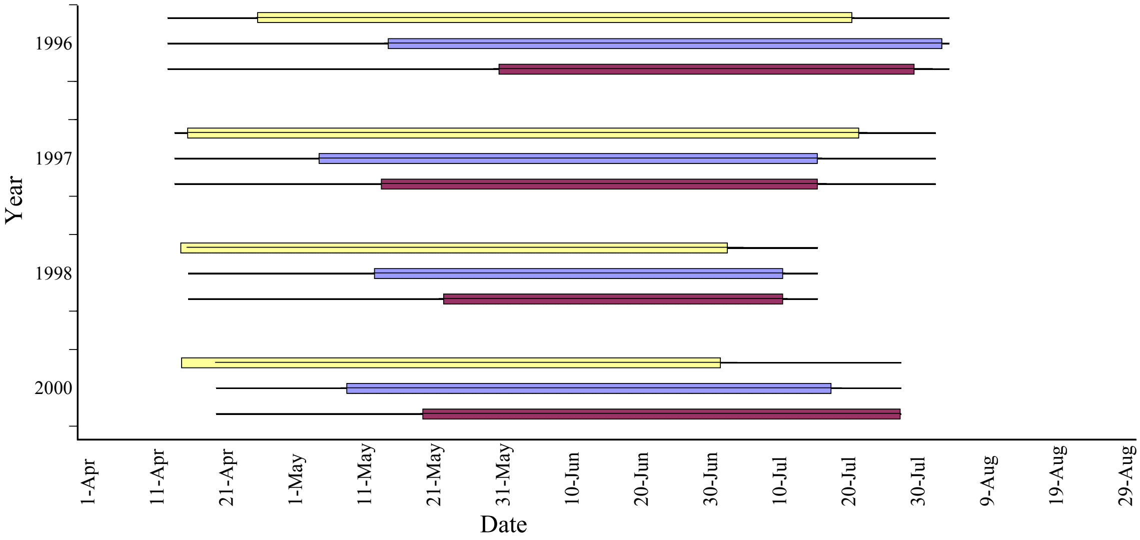


Figure 2.7: Dates of nest observation, egg laying, hatching, and fledging during each year for (a) Acadian Flycatchers and (b) Prothonotary Warblers. Nests for both species were found upon arrival of the females. The length of the field season limited the dates for the last Acadian Flycatcher nests. That is, nest searching ceased when the days left in the field season were too few for a nest to complete its cycle. For Prothonotary Warblers, nests were monitored during their entire breeding season.

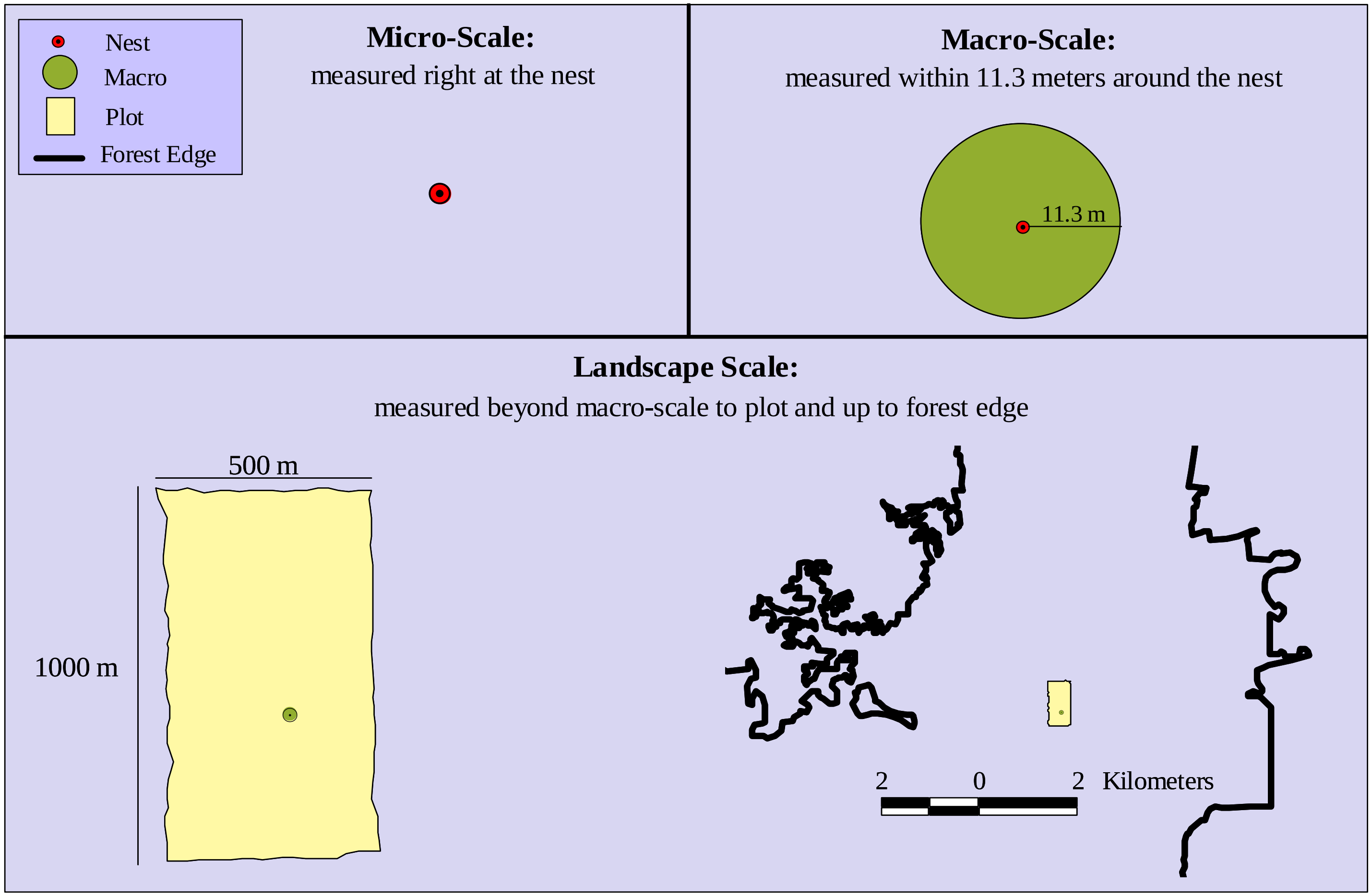
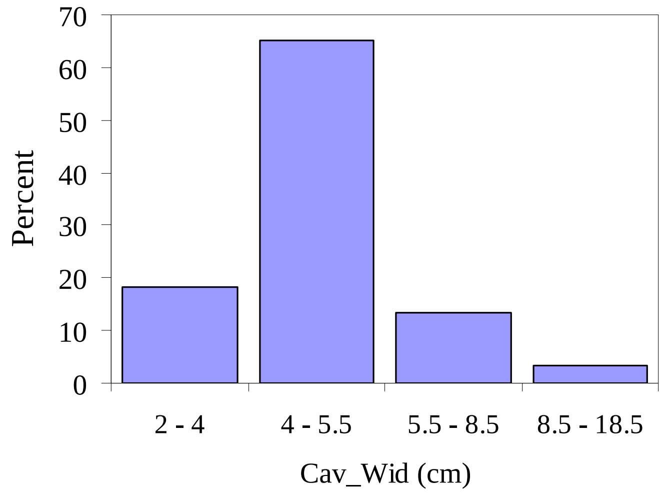
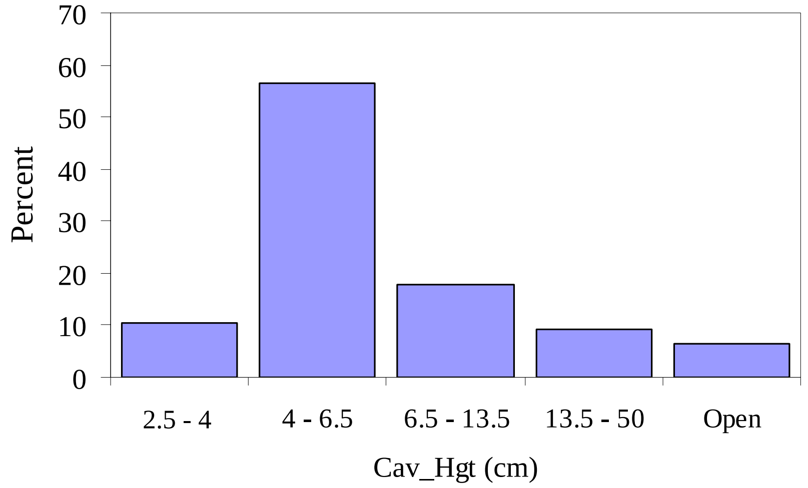
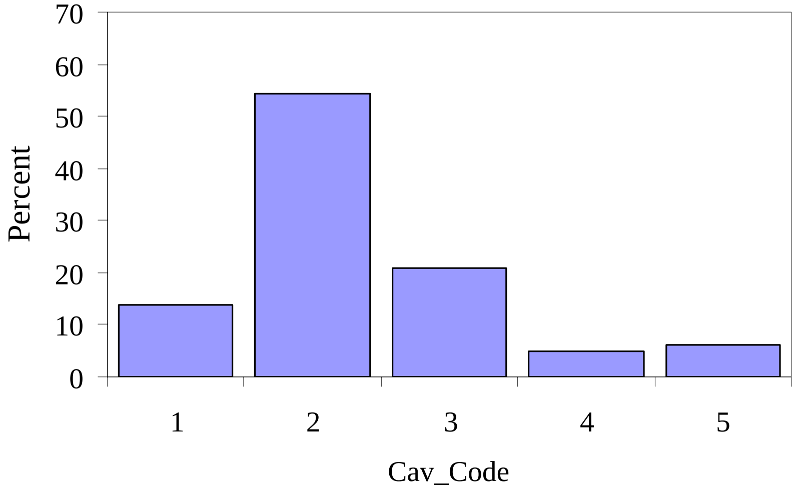


Figure 2.8: Depiction of the three spatial scales at which habitat characteristics were measured: micro, macro, and landscape. Micro-scale includes measurements taken right at the nest. Macro-scale includes variables measured within an 11.3 m-radius circle (0.04 ha) centered at each nest. Landscape scale includes characteristics measured beyond the macro-scale and up to the plot and forest/agriculture edge. Water variables span all three spatial scales.

Figure 2.9: Histograms of cavity entrance dimensions, width and height, and cavity entrance code (n=579). Cavity code is an index of overall cavity size based on a combination of cavity width and height. Cavity width and height were grouped into four and five categories, respectively, as depicted in their respective histograms. The product of a cavity's width and height were used to assign it one of five codes that described its overall cavity entrance size. Cavity codes were assigned to cavities with a width*height product as follows: Code 1 < 16 cm, 16 cm $\leq$ Code 2 < 35.75 cm, 35.75 cm $\leq$ Code 3 < 114.75, and 114.75 $\leq$ Code 4. Cavities that were open in height (i.e., had no top), regardless of width, were assigned a cavity code of 5. The cavity code was treated as a continuous variable for modeling purposes, where cavities of code 1 were smaller than average, cavities of code 2 were average size, and cavities of code 3 and 4 were incrementally larger than average. Cavities of code 5 were non-definable in size but considered to represent the upper extreme of this size continuum.


Percent
70
60
50
40
30
20
10
0
2 - 4
4 - 5.5
5.5 - 8.5
8.5 - 18.5
Cav_Wid (cm)


Percent
70
60
50
40
30
20
10
0
2.5 - 4
4 - 6.5
6.5 - 13.5
13.5 - 50
Open
Cav_Hgt (cm)


Percent
70
60
50
40
30
20
10
0
1
2
3
4
5
Cav_Code

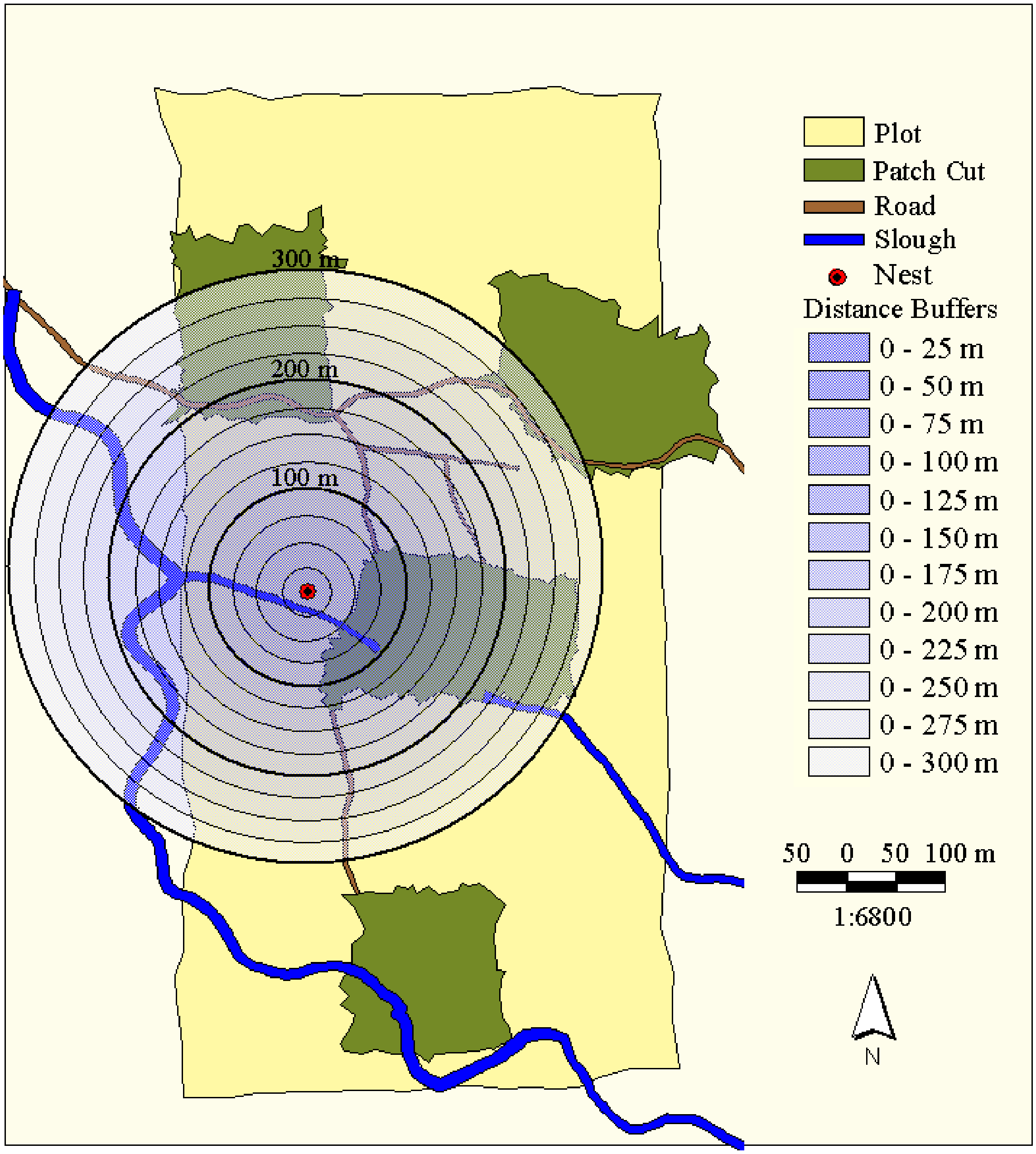


Figure 2.10: Landscape characteristics were measured around each nest within buffers that increased in radii by 25-m increments. Within each distance interval, the area (m^2) and edge length (m) of roads, sloughs, and patch cuts were measured. Roads and sloughs were measured at 25-m increments up to 100 meters. Patch cuts were measured at increments up to 300 meters.

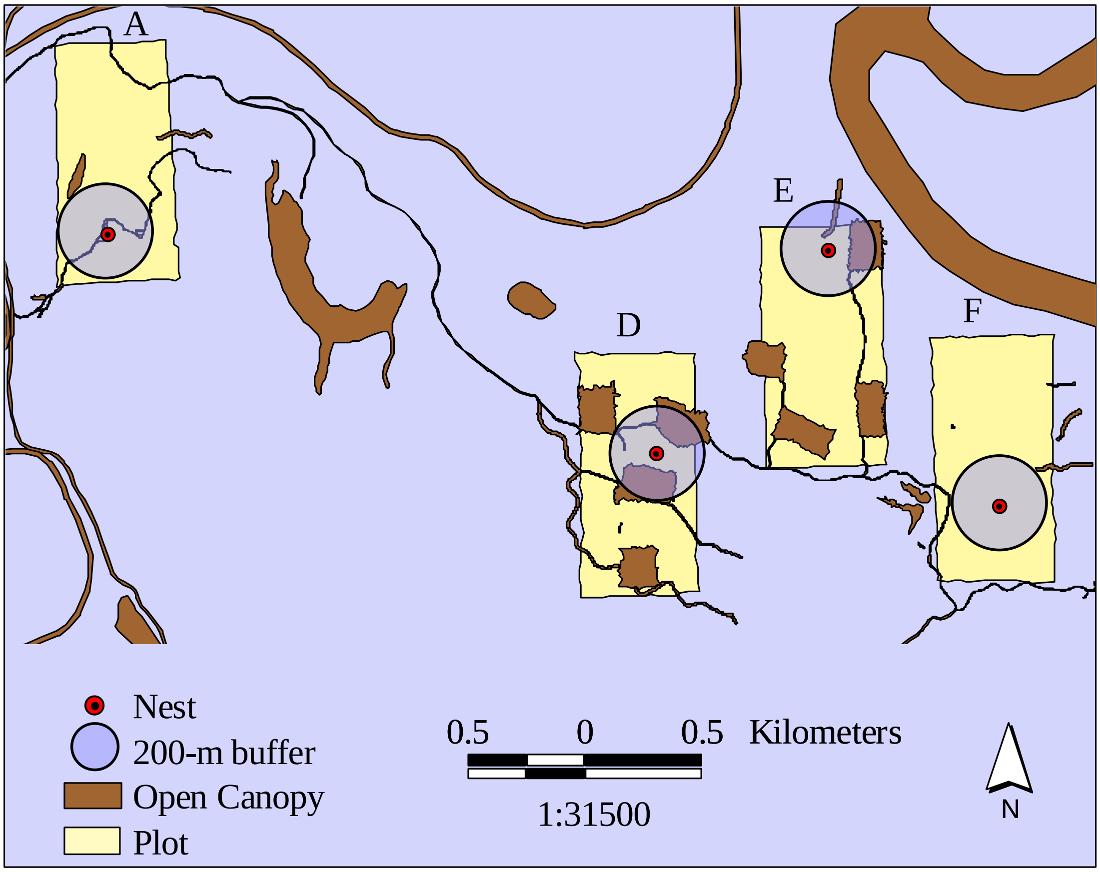
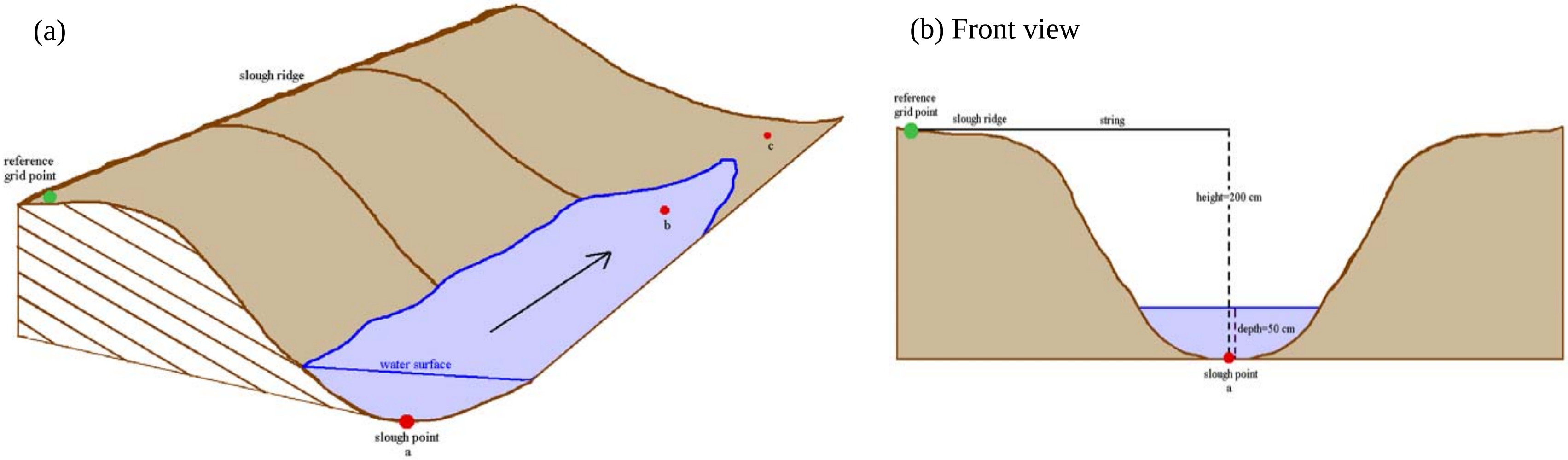


Figure 2.11: Depiction of the study plots and the open canopy within the study area. Canopy openings consist of roads, sloughs, and other water bodies greater than 5-meters wide and patch cuts. The amount of open canopy within 200 meters of each nest was calculated in ArcView GIS. Depicted here are four nests, one per plot (A, D, E, and F), surrounded by 200-m buffers. For these particular nests, the percent area within the buffer that consists of open canopy is 2.6%, 41.1%, 22.8%, and 0%, respectively.

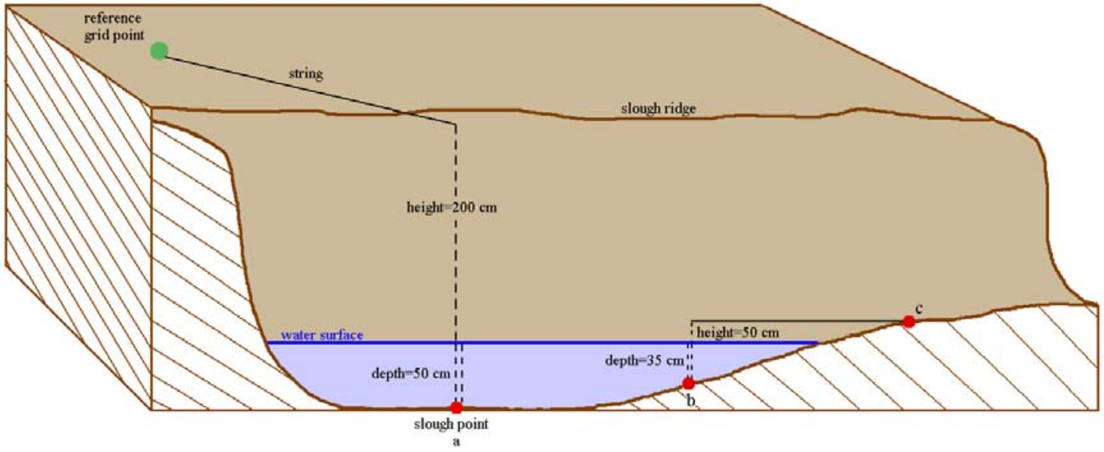
Figure 2.12: Depiction of methodology for obtaining depths of sloughs. Grid point depths were measured during the spring of 2001 when the plots were inundated with water. (a) During the summer of 2001, when plots were dry, slough points (labeled here as *a*, *b*, and *c*) were referenced to grid points. (b) A level string was run from the base of the grid point to above the slough point and the height of the string above ground was measured to the nearest centimeter. Assuming the depth of the grid point was previously measured as 100 cm, the depth of slough point *a*, if measured on the same day as the grid point, would equal [$\text{depth}_{\text{grid point}}$ + $\text{height}_{\text{string}}$] or [100 + 200] = 300 cm. (c) If the current depth of water at slough point *a* was 50 cm and the depth of water at slough point *b* was 35 cm, then the relative depth of slough point *b* would equal [relative depth_{a}+ (depth_{b} – depth_{a})] or [300 + (35-50)] = 285 cm. The relative depth of slough point *c* would be referenced to a grid point if available. If not available, then a level string would be run from point *c* to above point *b* and the height of the string above the ground measured. The relative depth of slough point *c* would equal [relative depth_{b} – $\text{height}_{\text{string}}$] or [285 – 50] = 235 cm.



(a)

(b) Front view

(c) Longitudinal cross-section



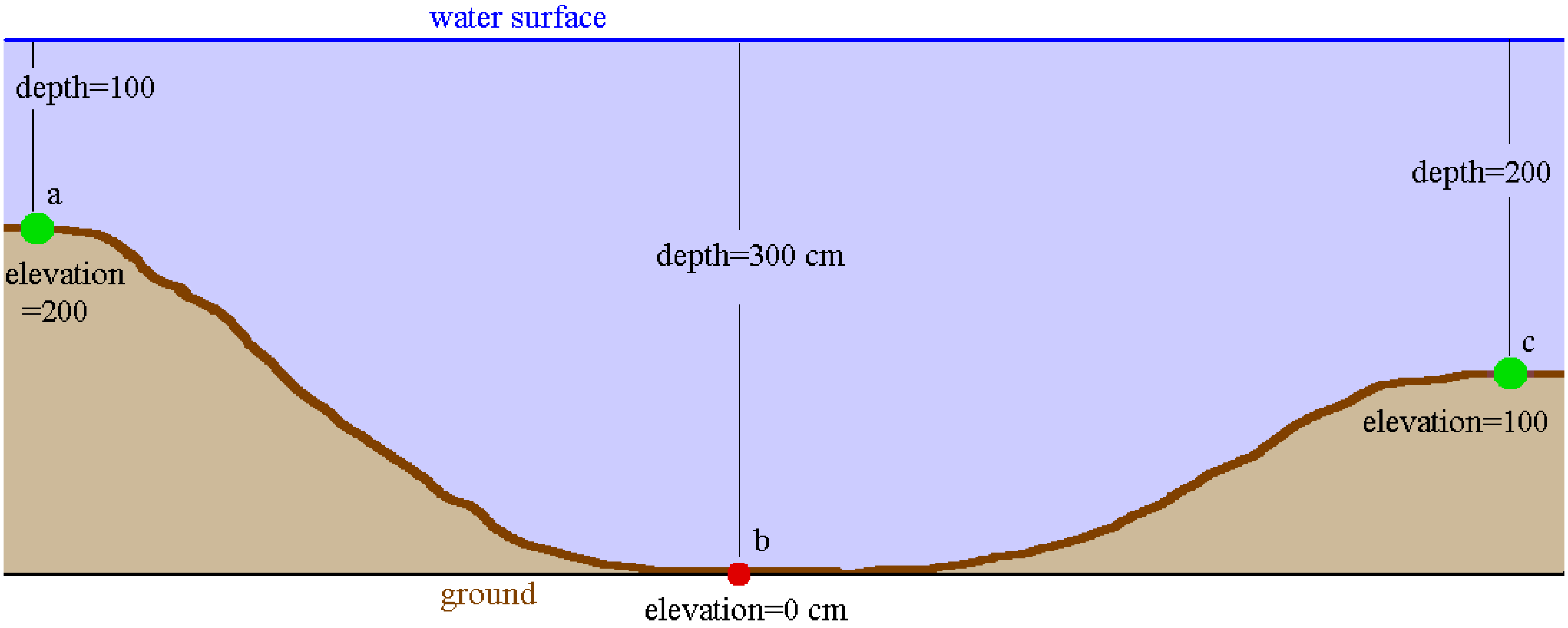


Figure 2.13: Depiction of methodology for obtaining relative elevation of grid and slough points within a plot. When the plot was completely inundated, water depth was measured to the closest centimeter at grid points (depicted here as green circles labeled *a* and *c*) located every 25 m. Depths of slough points (depicted here as a maroon circle labeled *b*) were referenced to grid points and were obtained when the plot was dry (Figure 2.12). The point (grid or slough) with the largest depth per plot (point *b*) was designated as the lowest elevation point on the plot and was set to an elevation of 0 cm. To obtain the relative elevation of all other points on the plot, the depth at point *b* was subtracted from each point and the total multiplied by –1. For example: elevation *a* = -1 * [depth *a* – depth *b*] = -1* [100-300] = 200 cm.

Figure 2.14: Example digital elevation model (DEM), depicting topography on plot A. The x and y axes, which depict the perimeter of the plot, are measured in meters. The z-axis, which represents elevation, is measured in centimeters. Black denotes areas with no elevation data.

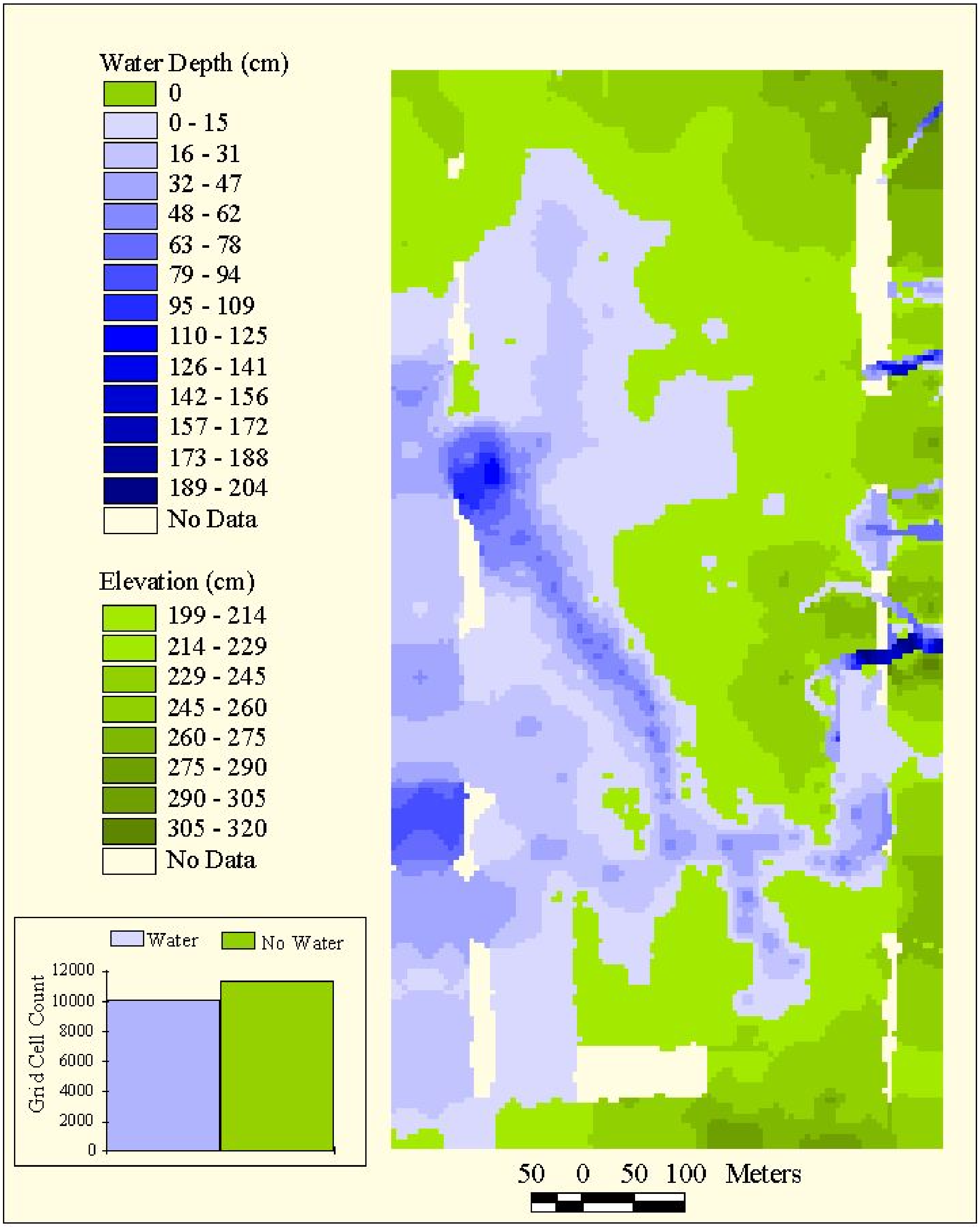
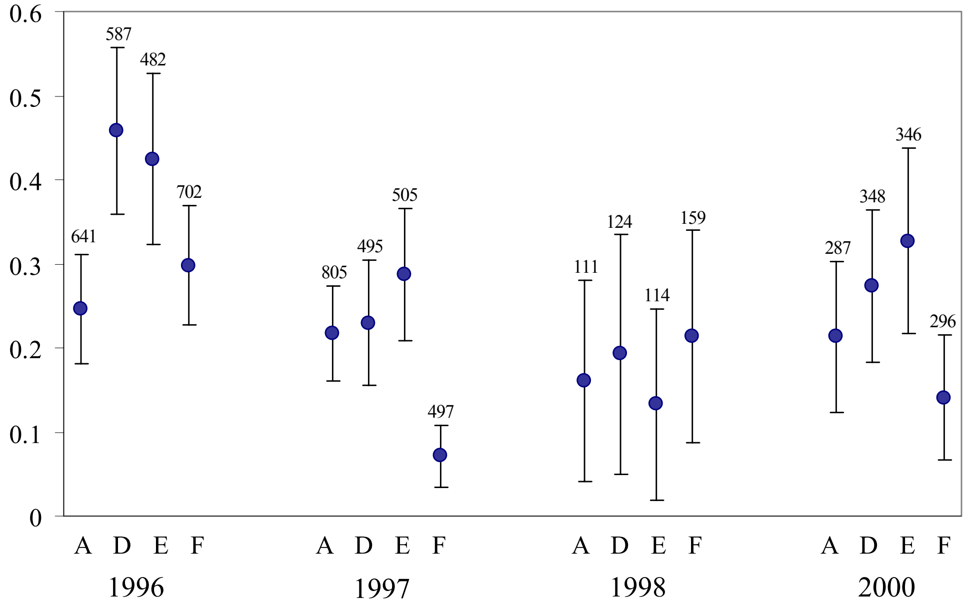


Figure 2.15: This is an example of a water coverage snapshot. This snapshot depicts plot F on May 13, 1997. On this particular day, the water coverage of the plot was 46.9%.

(a) Acadian Flycatcher



(b) Prothonotary Warbler

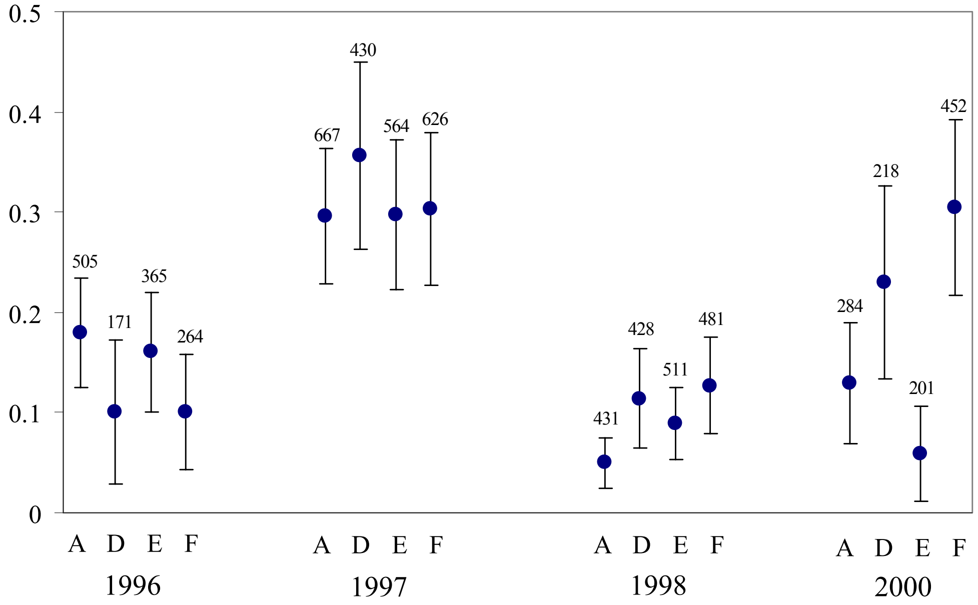
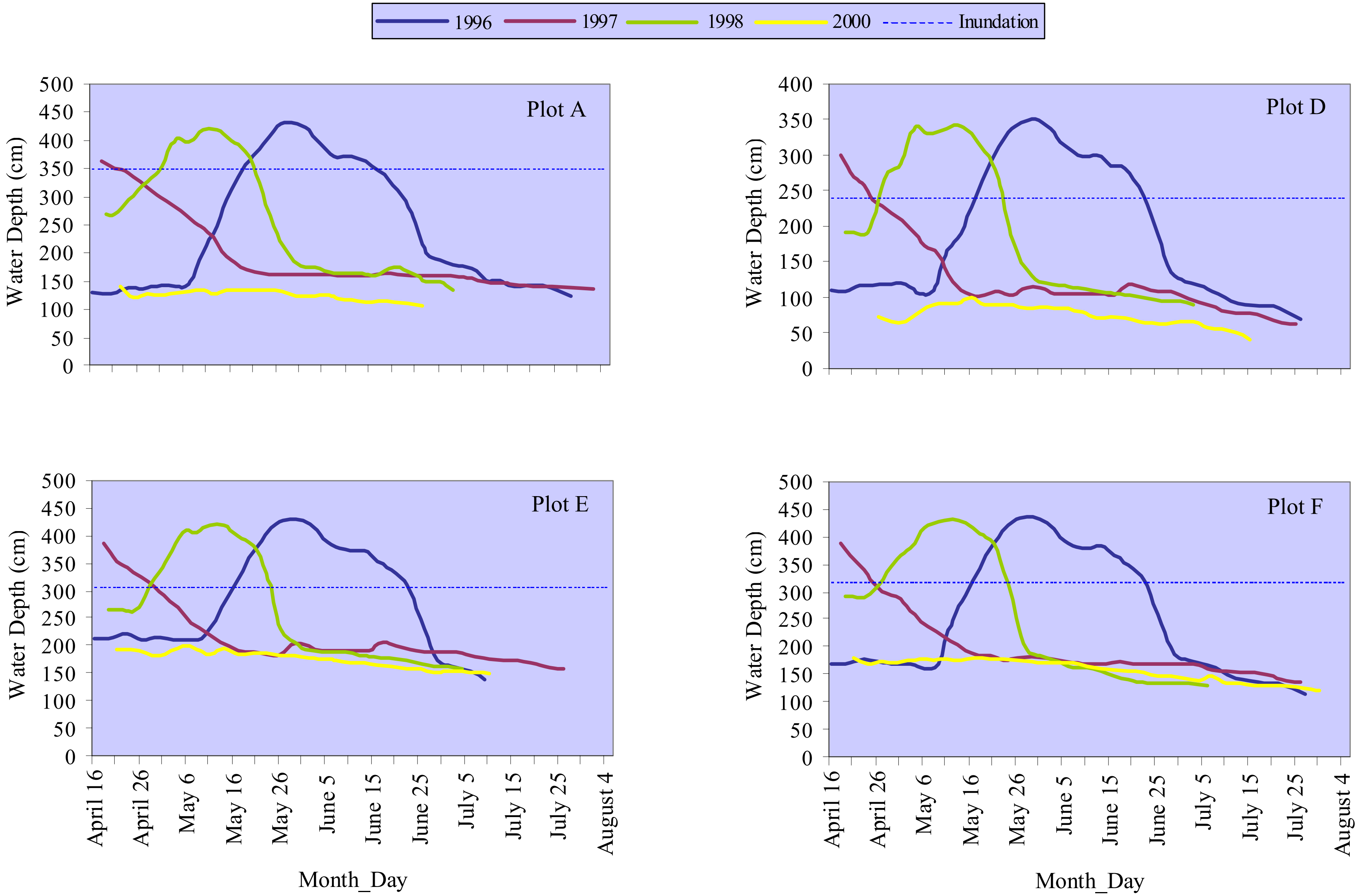


Figure 2.16: Mayfield estimates of survival for (a) Acadian Flycatcher and (b) Prothonotary Warbler nests by year and plot. Bars represent ± 1 SE. Numbers above bars indicate nest exposure days.

Figure 2.17: Water depths on each of the four study plots during the breeding seasons of 1996, 1997, 1998, and 2000. Depths depicted here are for the lowest elevation point on each plot. Depths are not relative among plots. On each plot, when the depth exceeds the dotted “Inundation” line, all areas of the plot are completely under water.


1996
1997
1998
2000
Inundation
Plot A
Plot D
Plot E
Plot F
Water Depth (cm)
0
50
100
150
200
250
300
350
400
450
500
April 16
April 26
May 6
May 16
May 26
June 5
June 15
June 25
July 5
July 15
July 25
August 4
Month_Day

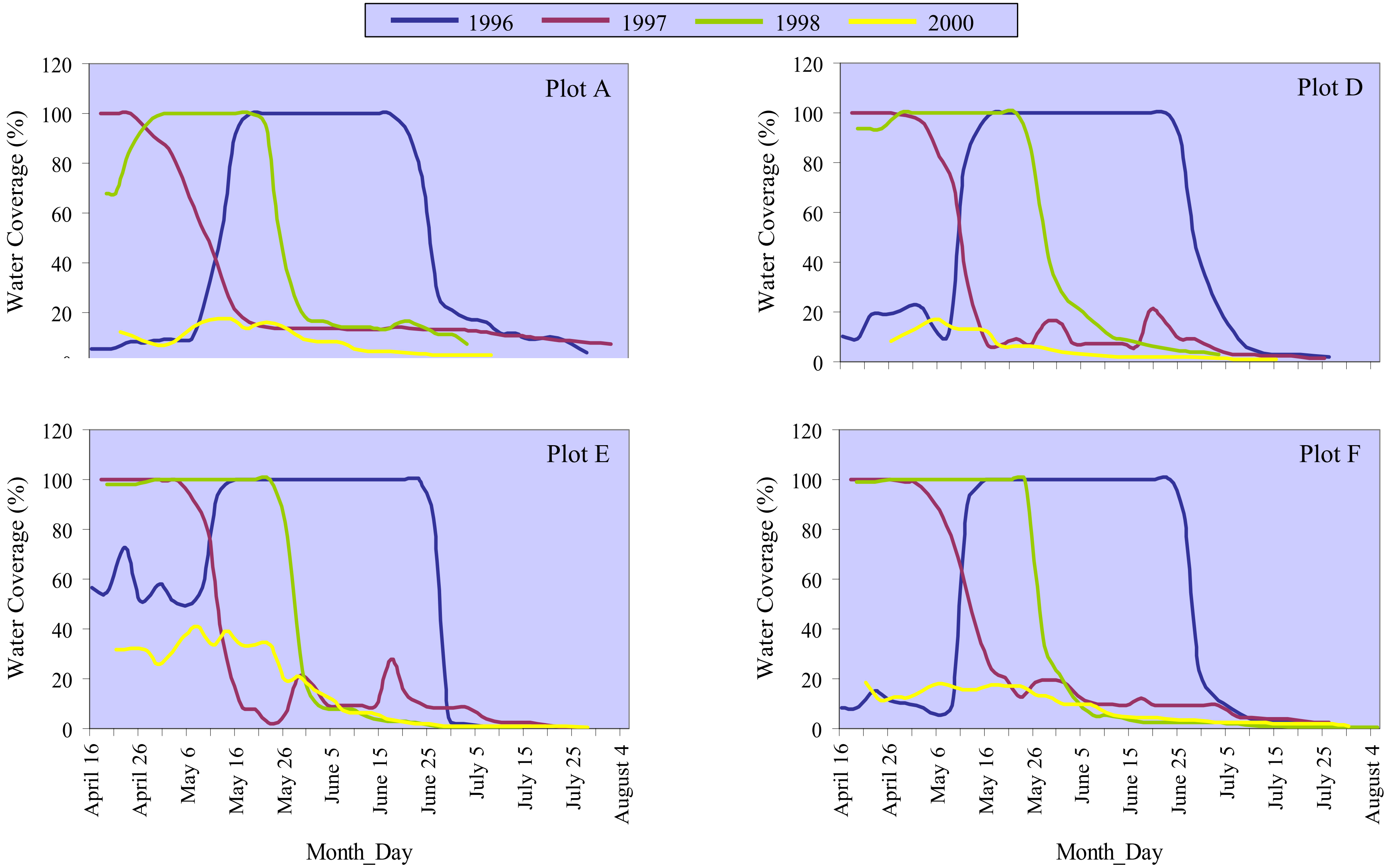


Figure 2.18: Percent water coverage of each of the four study plots during the breeding seasons of 1996, 1997, 1998, and 2000.

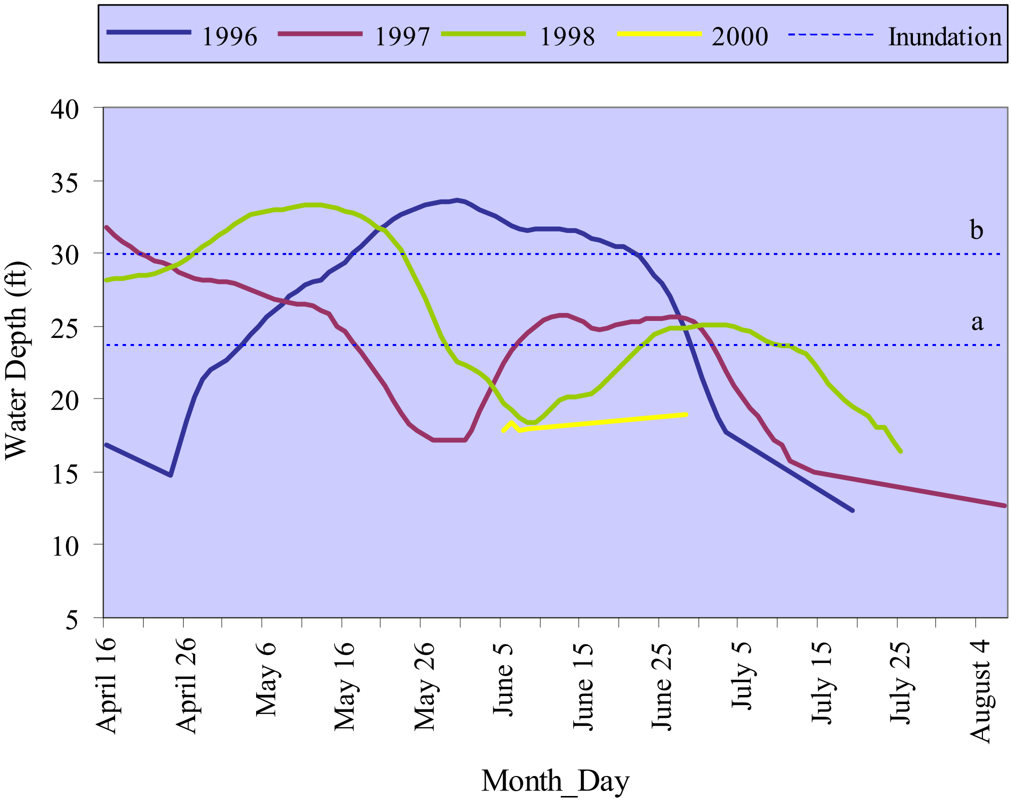


Figure 2.19: Water depth of the White River as measured at the Graham-Burke pumping station during the breeding seasons of 1996, 1997, 1998, and 2000 (USACE 2004a). Depths are measured every day at 8 AM. When the river depth drops below 16.8 ft, depth is not measured (year 2000). In general, when depth at the pumping station exceeds 24 ft, the study plots begin to flood (Inundation line "a") and when depth exceeds 30 ft, the study plots are completely inundated (Inundation line "b").

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APPENDICES

Appendix 2A: Performance of macro-habitat principal component values extracted from interpolated coverages created using all data points within a 50-m, 75-m, 100-m, and 200-m radius. Assessment is based on Acadian Flycatcher nests from 1998 with known principal component scores. Differences between values were calculated as (actual – extracted). A two-tailed two-sample paired t-test was used to compare the actual and the extracted values.

	Principal Component 1			
	Spatial Scale			
	50-m radius	75-m radius	100-m radius	200-m radius
N	34	41	42	42
Range	5.0965	5.0965	5.0965	5.0965
Mean Absolute Difference	1.0091	0.9072	0.9045	0.9261
Mean Differernce	0.0715	0.1275	0.1868	0.2324
Mean Squared Difference	1.5371	1.3632	1.3858	1.3794
Standard Error	0.2158	0.1846	0.1816	0.1834
95% Confidence Interval	{-0.3515 , 0.4945}	{-0.2343 , 0.4893}	{-0.1692 , 0.5428}	{-0.1271 , 0.5919}
t-statistic	0.332	0.695	1.042	1.292
p-value	0.7420	0.4912	0.3036	0.2035

	Principal Component 2			
	Spatial Scale			
	50-m radius	75-m radius	100-m radius	200-m radius
N	34	41	42	42
Range	2.1000	2.1000	2.1000	2.1000
Mean Absolute Difference	0.8183	0.7884	0.7725	0.7612
Mean Differernce	-0.7471	-0.7033	-0.6785	-0.6975
Mean Squared Difference	0.9873	0.9202	0.9102	0.9053
Standard Error	0.1730	0.1517	0.1490	0.1468
95% Confidence Interval	{-1.0861 , -0.4080}	{-1.0006 , -0.4060}	{-0.9705 , -0.3864}	{-0.9852 , -0.4097}
t-statistic	-6.550	-6.819	-6.477	-7.086
p-value	<0.0001	<0.0001	<0.0001	<0.0001

	Principal Component 3			
	Spatial Scale			
	50-m radius	75-m radius	100-m radius	200-m radius
N	34	41	42	42
Range	5.4240	5.4240	5.4240	5.4240
Mean Absolute Difference	1.0446	0.9575	0.9301	0.9350
Mean Differernce	-0.1058	-0.1709	-0.1763	-0.2040
Mean Squared Difference	1.6150	1.3778	1.3412	1.3692
Standard Error	0.2212	0.1856	0.1809	0.1806
95% Confidence Intervals	{-0.5394 , 0.3278}	{-0.5346 , 0.1929}	{-0.5308 , 0.1782}	{-0.5579 , 0.1499}
t-statistic	-0.480	-0.931	-0.986	-1.148
p-value	0.6344	0.3576	0.3298	0.2576

CHAPTER 3

THE IMPORTANCE OF MULTI-SCALE HABITAT CHARACTERISTICS TO NEST PREDATION OF TWO BOTTOMLAND HARDWOOD FOREST SONGBIRDS: A PROPORTIONAL HAZARDS MODEL[1]

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[1] Gannon, J., R.J. Cooper, and C.T. Moore. To be submitted to *Ecological Applications*.

ABSTRACT

Population declines of forest-interior songbirds may be linked to increased nest predation resulting from a reduction and degradation of breeding habitat; bottomland hardwood forests of the southeastern U.S. are an example of an important breeding habitat that has undergone severe reductions in both amount and quality. Given that nest predation is the main cause of reproductive failure in birds and that features of the nesting habitat may affect rates of nest predation, we developed species-specific, multi-scale Cox regression models to investigate the relative importance of habitat characteristics to nest predation of two neotropical migrant songbirds, the Acadian Flycatcher (*Empidonax virescens*) and the Prothonotary Warbler (*Protonotaria citrea*), breeding within the bottomland hardwood forests of the White River NWR. We demonstrated that risk of nest predation was influenced by habitat characteristics of the micro-scale nest site, the macro-scale nest patch, and the plot/landscape. Micro-scale nest height and macro-scale canopy height were negatively related with risk of nest predation, while landscape-scale nest exposure to forest-interior roads was associated with increased risk of nest predation. We did not observe a positive edge effect of patch cuts on nest predation risk. Water associated with seasonal flooding played a primary role in reducing the risk of nest predation at all spatial scales, while brood parasitism notably increased the risk of nest predation. We conclude that 1) landscape-level management efforts to reduce internal forest disturbances may be most successful in reducing nest predation within the Refuge and 2) anthropogenic disturbances with potential to alter the existing flooding pattern of the Refuge should be investigated for possible detrimental effects on the nesting success of bottomland forest songbirds. Management efforts within our study area would benefit from future research that focused on identifying responsible nest predators and studying their abundance, spatial distribution, and behavior relative to the habitat and their prey.

INDEX WORDS: Bottomland hardwoods, Acadian Flycatcher, Prothonotary Warbler, Nest predation, Habitat characteristics, Micro-Scale, Macro-Scale, Landscape Scale, Roads, Patch cuts, Flooding, Water, Cox regression

INTRODUCTION

Populations of many neotropical migratory songbirds have declined in recent decades (Robbins et al. 1989, Askins et al. 1990). Although the declines in many forest-dwelling neotropical migrant birds can be linked to a reduction in breeding and wintering habitats, the high degree of forest fragmentation and habitat loss in the eastern United States suggests that factors on the breeding grounds are the primary cause of migrant declines, presumably through decreased reproductive success (Robinson et al. 1995). Increased rates of nest predation (Wilcove 1985) experienced by forest-interior songbirds in these fragmented landscapes may have contributed to the population declines of neotropical migrants in North America (Robbins et al. 1989, Askins et al. 1990).

The pervasive nature of nest predation indicates that the nesting season is a critical period for maintenance of bird populations (Martin 1993b). Effective management for the conservation of songbird populations depends on reducing the limiting nature of nest predation through knowledge of the birds' breeding biology, understanding their habitat requirements, and identifying and preserving the specific habitat features that positively affect their breeding productivity and survival (Martin 1992). Physical features of the breeding habitat influence opportunities for nesting, foraging, and protection from enemies (Cody 1981) and may ultimately reflect the suitability of a site for the reproduction and survival of breeding birds (Hilden 1965). Given that nest predation is the main factor causing reproductive failure in passerine birds (Ricklefs 1969, Martin 1992), it is imperative to identify the physical features of the nesting habitat that influence rates of nest predation. Long-term solutions to maintaining populations of neotropical migrant birds includes the identification of habitat features that directly impede the effectiveness of predators at locating nests (Martin 1992). In addition, the identification and reduction of land use practices that augment nest predator populations are necessary. As a result of interest in the population dynamics of declining neotropical migrant songbird species, many recent studies have considered effects of nest-site habitat characteristics, habitat fragmentation, and external and internal forest edges on their reproductive success.

The structural characteristics of the habitat immediately surrounding nests may influence chances of nest success (Chasko and Gates 1982) and it has been documented that nest predation rates vary with attributes of nest sites (Nice 1957, Ricklefs 1969, Collias and Collias 1984, Martin and Roper 1988, Kulesza 1990, Martin and Li 1992, Martin 1993b). Studies have suggested that nest-site selection within bird species, as well as differences in nest types between species, are important determinants of variation in nest predation risk (Martin 1993b, 1995, 1996, 1998). Characteristics of the nesting micro-habitat (< 5-m radius) and macro-habitat (5-m to 11.3-m radius), such as nest concealment, nest height, percent canopy and ground cover, and vegetation density and heterogeneity, have been related to predation risk, although the evidence about their relative influence on predation likelihood is conflicting. In general, studies suggest that nests with greater concealment and located in areas of greater vegetative structural complexity are less likely to be depredated (Bowman and Harris 1980, Martin 1992).

At larger spatial scales, the adverse effects of habitat fragmentation and decreased proportion of forest cover on rates of nest predation are well documented (Faaborg et al. 1995, Robinson et al. 1995, Donovan et al. 1997, Hartley and Hunter 1998). Nest predation increases with fragmented forest habitat because many predators benefit from the increased ratio of edge to forest interior (Wilcove 1985, Temple and Cary 1988, Small and Hunter 1988). Increased nest predation rates often coincide with fragmentation of breeding habitats, and nest success often varies with fragmentation-related variables such as patch size, nature of the landscape matrix, and distance to habitat edges (Lariviere 2003). Increased nest predation on forest-interior birds within forests fragmented by agriculture is often explained by a higher density of generalist predators that are able to penetrate the forest and prey on nests (Hanski et al. 1996). However, fragmentation caused by silvicultural practices in forest-dominated landscapes may not have the same effect (Andren 1995, but see Manolis et al. 2000).

Studies examining the effect of forest fragmentation on rates of nest predation have predominantly been conducted in agricultural landscapes where many have documented elevated rates of predation in association with increased forest fragmentation and the creation of external edge (see Paton 1994 and Andren 1995 for reviews). Fewer studies have been conducted in forest-dominated landscapes fragmented by forestry practices, and evidence of increased predation within these landscapes and at the internal edges timber management creates has been equivocal. Several studies found edge-related increases in nest predation in areas fragmented by timber cuts (2-48 ha in size; King et al. 1996, 1998a, Fenske-Crawford and Niemi 1997, Manolis et al. 2000, 2002, Flaspohler et al. 2001a), while others found no edge effect (Ratti and Reese 1988, Hanski et al. 1996, Rodewald 2002). Differences in landscape structure, edge type, permanence of edge, and predator communities in agriculturally versus industrially fragmented forests may preclude generalization regarding nest predation within fragmented landscapes and at the external and internal edges they create (Cotterill and Hannon 1999).

Most studies examining effects of internal edge within forests have focused on the extensive openings created by silvicultural practices, disregarding narrow breaks in the forest canopy created by anthropogenic disturbance such as recreational trails, roads, and utility right-of-way corridors or natural forest openings created by streams. Although forest edges are frequently associated with increases in edge-related nest predation, it is unclear whether narrow internal edges, man-made or natural, create the same edge conditions that concentrate predators near edges adjacent to large, human-induced openings (King and DeGraaf 2002). Of the studies that examined the effects of trails on forest-nesting songbirds, some found decreased nest success (Miller et al. 1998), increased nest predation (Miller and Hobbs 2000), and increased abundance of nest predators (Hickman 1980) near trails, while others found no such effects (Boag et al. 1984). Potentially more harmful than recreational trails, is the creation of roads within the forest interior. Most studies that examined nest predation levels relative to road edges reported no difference in predation rates at varying distances from the edge (Lindenmayer et al. 1999, Ortega and Capen 2001, Rodewald 2002); however, results may depend upon size and use of roads. Nest predation rates and relative abundance of potential nest predators were reported to be higher along wide, high-use roads than along narrow and lower intensity-use roads (Rich et al. 1994, Boulet and Darveau 2000). Research to date suggests that small-width, forest-dividing corridors created by utility rights-of-way may also generate detrimental edge effects of increased nest predation and decreased nesting success (Chasko and Gates 1982). Few studies have investigated the potential detrimental effects of riparian ecotones on forest-interior breeding birds; however, research by Gates and Giffen (1991) suggests that conditions at forest-stream edges might be conducive to increased nest predation within forested landscapes.

A more complete understanding of the factors that control populations of forest-nesting songbirds on their breeding grounds will require information on responses to habitat features at multiple scales. Studies have documented that rates of nest predation respond to habitat variation at the nest-site (Martin 1993b) and the nest-patch scale (Bowman and Harris 1980), as well as to edge proximity (Gates and Gysel 1978) and the pattern of forest and interstitial land use in the surrounding landscape (Donovan et al. 1997). Although variables at several spatial scales have been investigated and show that both localized and landscape-level factors have profound effects on nest predation rates, further knowledge on the relative importance and the interaction of variables at multiple scales with respect to reproductive success is necessary for comprehensive management of songbird populations. Despite this need, few studies have simultaneously investigated the relative importance of habitat characteristics at more than one spatial scale to the reproductive success of birds. To our knowledge, Rodewald and Yahner (2001a) have conducted the only multi-scale study that simultaneously investigated the relative influence of variables at three spatial scales on avian nesting success; however, the study did not specifically address nest predation. Many ecological processes that might affect nest predation operate at multiple spatial scales and are complex, potentially involving several interactions between variables at different spatial and temporal scales (Bergin et al. 2000). Therefore, accurate interpretation of the mechanisms driving rates of nest predation will require viewing these ecological processes at multiple scales (Donovan et al. 1997) and proper management of songbird populations will require more studies to use a multi-scale approach.

A drastic example of forest habitat loss in the southeastern United States has been in bottomland hardwood forests of the Mississippi Alluvial Valley (MAV; MacDonald et al. 1979, Mitsch and Gosselink 1986); only about 20% of the original 9 to 10 million hectares of bottomland hardwood forests in the MAV remain (Yin et al. 1997). Conversion to agriculture, timber removal, and the construction of flood control and navigation structures have eliminated bottomland hardwood forests from much of the MAV and, as a result, agriculture has replaced forest as the dominant land cover within the MAV. Most of the remaining bottomland forest within the MAV exists as small patches surrounded by a sea of agriculture; within such a landscape, forest-nesting birds are exposed to an abundance of generalist predators. In addition to actual losses of bottomland hardwood forests, the remaining bottomland hardwoods are in an ecologically degraded condition due to severe fragmentation, hydrologic alterations, and poor timber management practices (Allen 1997). The ecosystem changes within remaining bottomland hardwood forests of the MAV could negatively impact regional populations of neotropical migrant songbirds that depend on functioning bottomland forest ecosystems; this is especially true for those birds that reach their highest breeding densities within bottomland hardwood forests. For the above reasons, as well as continued timber removal, Partners in Flight has identified bottomland hardwood forests as a habitat of regional concern (Hunter et al. 1993). Despite the importance and imperiled state of bottomland hardwood forests, there is a lack of long-term data sets on the nesting success of songbirds breeding within these forests, indicating that research within bottomland hardwood forests is needed.

The White River National Wildlife Refuge, located in the MAV of southeast Arkansas, is one of the largest remaining tracts of bottomland hardwood forest within the US. Although large (65,000 ha), the Refuge is narrow (4.5-15.5 km-wide) in shape and is surrounded by agricultural fields; as such, it contains generalist predators that prey upon the nests of forest-interior songbirds breeding within the forest. The Refuge is managed by the USFWS for multiple uses, including wildlife diversity, waterfowl habitat, public recreational activities such as hunting and fishing, and timber. Consequently, logged areas, logging roads, and public access roads exist throughout the Refuge. It is unknown whether these features of the internal forest landscape exacerbate the already high rates of nest predation to which the breeding birds are exposed. Additionally, as a floodplain forest, hydrology is a dominant feature of the Refuge and potentially influences plant and animal communities within the Refuge, including breeding birds and their predators. Hydrology may affect the nest predation of bottomland forest birds at several spatial and temporal scales. For example, at a fine scale, protection from predators may be afforded to nests placed over water compared with nests over land (Petit 1989, Picman et al. 1993, Jobin and Picman 1997, Hoover 2001). At a larger scale, long-term flooding may force potential nest predators out of the area or into the forest canopy (e.g., Gehrt et al. 1993), with unknown effects on nest predation. Although studies within forested wetlands suggest that breeding bird communities are related to both vegetation structure and hydrology (Smith 1977, Swift et al. 1984, Wakeley and Roberts 1996), information on the reproductive success of forest-wetland birds in relation to hydrology is virtually nonexistent.

Previous research within the White River National Wildlife Refuge has focused on the reproductive success of two neotropical migrants, the Acadian Flycatcher (*Empidonax virescens*; Wilson 1997) and the Prothonotary Warbler (*Protonotaria citrea*; Wood 1999). Both of these species are declining within the Mississippi Alluvial Plain (Sauer et al. 2003) and, as a result of area sensitivity (Acadian Flycatcher and Prothonotary Warbler) and extreme habitat specificity (Prothonotary Warbler), the bird conservation group Partners in Flight has given the Acadian Flycatcher a high-priority ranking for monitoring and management in the Southeast and has listed the Prothonotary Warbler as a species of high conservation priority throughout its breeding range (Hunter et al. 1993, Rich et al. 2004). Research on the micro- and macro-habitat characteristics of Acadian Flycatcher nests revealed no relationship with nest success (Wilson 1997). Research on Prothonotary Warblers reported that the success of their nests was not related to plot-scale forest fragmentation caused by logging (patch and group cuts; Wood 1999). Wood (1999) documented that nest success of Prothonotary Warblers varied annually and speculated that variable flooding patterns, most likely through their influence on nest predators, may be a cause of the variable nest success. Within the Refuge, as well as elsewhere within bottomland hardwood forests, research investigating the effects of internal edges and hydrology on the reproductive success of forest-interior songbirds is lacking. Additionally, research that simultaneously investigates the relative importance of habitat characteristics at multiple spatial scales to the nesting success of birds is needed.

This study addresses the gap in knowledge concerning the reproductive success of neotropical migratory songbirds nesting within bottomland hardwood forests of the MAV. The study was conducted within the White River National Wildlife Refuge during the breeding seasons of 1996-2000. We examine nest predation of two common bottomland hardwood forest bird species, the Acadian Flycatcher and Prothonotary Warbler, in relation to physical characteristics of the nesting habitat at the micro-, macro-, and landscape scale. These physical characteristics include descriptions of nest placement, vegetation structure, proximity and exposure to internal edges created by patch cuts, trails, roads, and sloughs, as well as descriptions of water that represent the timing, duration, magnitude, and spatial extent of the seasonal flooding. Results are discussed in a management context for bottomland forest ecosystems in general and riparian birds in particular.

STUDY AREA

The White River National Wildlife Refuge (NWR) is located in the southeast Arkansas portion of the Mississippi Alluvial Valley (Figure 2.4). It is located within the Lower White River Basin, within the flood plain of the lower White River, approximately 12 km above its confluence with the Mississippi River. The Refuge is a 65,000-ha managed, seasonally flooded, bottomland hardwood forest that extends approximately 104 km along the White River. It is one of the largest remaining contiguous bottomland hardwood forests in the United States (Harris and Gosselink 1990). Although large, the Refuge is narrow in shape (4.8-15.5 km-wide) and is surrounded by agricultural fields; as such, it contains generalist predators and cowbirds that prey upon and parasitize the nests of songbirds breeding within the forest. A grassy levee, on which cattle graze, runs parallel to the east side of the Refuge and serves as a foraging ground for large flocks of Brown-headed Cowbirds (*Molothrus ater*). Of the total Refuge area, about 91% is forested, 8% is in waterways and lakes, and less than 2% is grassland and cropland.

Topography on the Refuge is typical of naturally flooded bottomland forest, with wide flats broken by low ridges and swales (Wilson 1997). Bayous, oxbow-lakes, and sloughs are common throughout the Refuge. Annual flooding occurs due to stacking from northern Arkansas waters flowing down the White River and backup of waters from the Mississippi River and inundates much of the Refuge. Flooding can occur at any time but is most prevalent during late winter and spring; however, the timing, duration, and magnitude of floods vary annually.

Within the Refuge, the dominant overstory tree species are overcup oak (*Quercus lyrata*), Nuttall oak (*Quercus nuttallii*), green ash (*Fraxinus pennsylvanica*), bitter pecan (*Carya aquatica*), American elm (*Ulmus americana*), cedar elm (*Ulmus crassifolia*), waterlocust (*Gleditsia aquatica*), sugarberry (*Celtis laevigata*), and cypress (*Taxodium distichum*). Understory vegetation is predominantly comprised of possumhaw (*Ilex decidua*), swamp privet (*Forestiera acuminata*), hawthorn (*Crataegus spp.*), and water elm (*Planera aquatica*), as well as seedlings and saplings of overstory tree species. For further description of this area, see Wilson and Cooper (1998a,b).

METHODS

PLOTS

In 1993, six 50-ha (500 m x 1000 m) plots were established within a single management compartment (Number 8) of the Refuge (Figure 2.5). The compartment was 1,376 ha in size and consisted of contiguous homogenous habitat. In the fall of 1995, three silvicultural treatments (no cut, selective cut, and patch cut) were randomly allocated to two plots each (Figure 2.5). The selective cut plots had 300.9 m^2 and 311.6 m^2 basal area of timber removed. Each of the two patch cut plots had four blocks (averaging 2.8 ha/block) of timber completely removed or felled (Figure 2.6). A 25-m grid system (21 columns x 41 rows) was established and maintained on each plot for use in navigation and nest location. Because of our interest in definable internal edges, this study focused solely on the no cut and patch cut plots; thus, all subsequent information applies only to these four plots.

NESTS

NEST SEARCHING

Intensive nest searches were conducted on all plots during the breeding seasons of 1996-1998 and 2000. Nest searching for Acadian Flycatchers started upon the arrival of the females in late April and continued through the end of July or early August (Figure 2.7a). For Prothonotary Warblers, nest searching began upon the arrival of the females in early April and continued through the breeding season until the males began to abandon territories (Figure 2.7b). Nest searching efforts varied between years and between species (Table 2.1). Once a nest was found, flagging tape was placed more than 5 meters from the nest and care was taken to approach the nest from different pathways on subsequent nest checks. The location of the nest was recorded as the distance and direction from the closest grid point with the use of a SONIN electronic distance estimator and a compass.

NEST MONITORING

Once a nest was located, its contents were noted. Mirror poles were used to examine nests when contents could not be seen from the ground. If nest height was too high for mirror poles (about 9 m for Acadian Flycatchers and 5 m for Prothonotary Warblers), the nest was observed from a distance using binoculars, and contents of the nest or nest stage were determined by observing the behavior of the adult birds; for example, brooding females indicated that the nest was still active, while delivering of food or disposing of fecal sacs indicated that the nest contained nestlings. In addition, the architectural structure of Acadian Flycatcher nests often made it possible to determine the status, if not stage, of the nests by looking through the bottom of nests while standing directly beneath it. Nests were visited every two to four days following Breeding Bird Inventory and Research Database (BBIRD) protocol (Martin et al. 1997) to determine clutch size, number of nestlings, number of fledglings, and fate of the nest as accurately as possible.

NEST FATE

Nest fates were recorded for the host species, for cowbirds if the nest was parasitized, and for the overall nest. Fates fell within three categories: successful, failed, or uncertain. A host was considered successful if one or more host young fledged. A cowbird was successful if one or more cowbird young fledged. A nest was considered successful if one or more young fledged, regardless of the species. Evidence for nest success followed BBIRD protocols (Martin et al. 1997). Nest failures were broken down into the following classifications: predation, parasitism, abandonment, adult mortality, flooding, physical causes such as weather or tree fall, and unknown. Nests were considered depredated if entire nest contents disappeared between nest checks during the egg laying, incubation, or early nestling stage when insufficient time had expired between checks for young to have fledged. Partial predation was not considered a failure unless it resulted in the adults abandoning the nest. Uncertain fates occurred when there was insufficient information to determine success or failure. Nests were excluded from analysis if the nest failed prior to laying of the first egg or if observers caused mortalities.

NEST INITIATION AND AGE

Nest initiation date (date when first host egg was laid) was determined in order to ascertain nest age, which was required to run the Cox regression analysis (see DATA ANALYSIS). Nest age was counted as days since the first host egg was laid. The majority of nests were found in the building and laying stages (Table 2.5); thus, nest age was apparent. When nests were found after egg laying commenced, nest initiation date was determined by backdating to the day that the first host egg was laid based upon the average length of the species' laying, incubating, and nestling periods. If the nest was found during the egg laying stage, because only one egg is laid per day, nest age was equal to the number of eggs present. If the nest was found during the incubation stage and continued to the nestling stage, age was backdated based on the hatching date. If the nest was found and terminated during the incubation stage, and it was observed for less than half of the average incubation period, it was assumed that the nest was found at the midpoint of incubation. If the nest was found and terminated during the incubation stage, and it was observed for more than half of the average incubation period, the number of observation days (o) was subtracted from the average number of incubation days (i) and it was assumed that the nest was found at the (i - o) or n^{th} day of the incubation stage. If the nest was found in the nestling stage, nestlings were aged and the age of the nest was backdated to the initiation date based on the average incubation period and average clutch size of the species.

NEST TERMINATION

If a nest failed or fledged between nest checks, the midpoint of the check was used as the termination date. If the fate of the nest was uncertain, the last active nest check was used as the termination date. Exposure days were determined by subtracting the date found, or the date initiated if the nest was found prior to the first egg, from the date terminated. Therefore, exposure days only included days that the nest was active and under observation.

NEST PREDATION

Nest survival from predation was calculated by the methods of Mayfield (1961, 1975), which estimates the probability of nest survival based on nest exposure days. The only mortality event of interest was predation; that is, all nests were used to count exposure days, but only depredated nests were regarded as failures. Exposure days included all days when the nest was active and under observation, regardless of the species (i.e., host or cowbird). Exposure days from nests with uncertain fates were included in the calculations. The resulting values represent the daily probability of not being depredated (rather than survival) and the daily probability of predation (rather than mortality).

A daily probability of nest survival from predation (here on referred to as simply nest survival) and its standard error were calculated for each stage of the nesting period: the egg stage (from first egg to hatching) and the nestling stage (hatching to fledging). Nest-stage survival estimates were obtained by raising the daily survival probability of a given stage to the number of days in the respective stage. For Acadian Flycatchers, the egg stage is 15 days and the nestling stage is 14 days. For Prothonotary Warblers, the egg stage is 16 days (based on an average clutch size of five) and the nestling stage is 11 days. The overall probability of nest survival was calculated as the product of the two stage survival probabilities. Calculating overall nest survival in this manner assumes that mortality is constant within but not necessarily across the different nest stages. The standard error for overall nest success was calculated by the method of Hensler (1985). The daily probability of nest survival for the entire nesting period was calculated by raising the overall nest survival to the inverse of the number of days in the full nesting period (n), which for Acadian Flycatchers and Prothonotary Warblers is 29 days and 27 days, respectively. The standard error of the daily probability was approximated by dividing the standard error for overall nest success by [n*((daily survival probability)^(n-1))]. The daily probability of predation was calculated as [1- (daily survival probability)].

HABITAT MEASUREMENTS

MICRO-SCALE

At the end of the breeding season, when nests were no longer active, habitat characteristics were measured at the micro-scale, right at the nest (Table 2.2, Figure 2.8); these measurements included characteristics of the nest substrate and nest placement and were based on BBIRD protocol (Martin et al. 1997). For each nest, we used a densiometer to measure the percentage of canopy cover in the four cardinal directions; the four measurements were then averaged to obtain an overall percent canopy cover. Nest heights of both species were measured with the use of a clinometer unless the nest was within reach of a measuring pole (< 5 m). For Acadian Flycatchers, additional measurements of nest placement included the distance of the nest from the edge of the nest branch and from the nest tree bole. During the 2000-breeding season, for Acadian Flycatchers, we measured nest concealment and counted the number of vines on the nest tree bole. Concealment was measured in each of the four cardinal directions, as well as above and below the nest, by estimating the percentage of the nest concealed by vegetation within 1 m of the nest. Percentages of concealment were recorded as one of five categories: 0, 0-25%, 25-50%, 50-75%, and 75-100%. The six measurements were then averaged for an overall measure of concealment. Vines located on the bole of the nest tree were counted if they reached from the ground up to the first branch and were > 1 cm in diameter. For Prothonotary Warblers, we measured nest tree diameter at breast height (DBH) with a DBH tape. Additionally, we measured width and height of the nest cavity entrance. Based on histograms of the two cavity entrance dimensions, we grouped width and height into four and five size categories, respectively (Figure 2.9). The product of a cavity's width and height was used to assign it one of five codes that described its overall cavity entrance size (Figure 2.9). The cavity code was treated as a continuous variable for modeling purposes, where cavities of code 1 were smaller than average, cavities of code 2 were average size, and cavities of code 3 and 4 were incrementally larger than average. Cavities that were open in height (i.e., had no top), regardless of width, were assigned a cavity code of 5; these cavities were considered to represent the upper extreme of the size continuum.

MACRO-SCALE

At the end of the breeding season, habitat characteristics were measured at the macro-scale, within an 11.3 m-radius circular plot (0.04 ha) centered at each nest (Table 2.2, Figure 2.8). Our measurements were modified from the methods developed by James and Shugart (1970). Within each 0.04-ha plot, we recorded the species and diameter at breast height (DBH) for all trees with a DBH ≥ 10 cm, thus obtaining the number of trees and the average DBH for the nest plot. Estimates of percent canopy cover and canopy height were obtained using a densiometer and a clinometer, respectively. These measurements were taken in the four cardinal directions and then averaged to obtain an overall percent canopy cover and canopy height for the nest plot. The nest plot was divided into four quadrants and within each 0.01-ha quadrant we measured the distance from the nest to the closest tree ≥ 10 cm DBH; if no tree ≥ 10 cm DBH was present within the quadrant, we measured the distance to the nearest tree beyond the 11.3-m radius circle. The four distances were averaged to provide an indicator of openness around the nest site. We recorded the number of woody stems (trees and saplings < 10 cm DBH) within a 5 m-radius circle around each nest. The same macro-scale measurements were taken at 15 recurring, systematically selected grid points per 50-ha plot each year.

LANDSCAPE SCALE

Habitat characteristics were measured at the landscape scale (Table 2.3, Figure 2.8). Distances from each nest to the exterior forest edge were measured in ArcView GIS 3.2 (ESRI 1999). The distances from each nest to the closest road, slough, and patch cut were recorded. The type of road closest to each nest was also documented. Circular buffers were created around each nest at 25-m intervals (i.e., 0-25 m, 0-50 m, 0-75 m, 0-100 m, up to 0-300 m; Figure 2.10). The buffers were used to calculate the area (m^2) and the edge length (m) of roads and sloughs within each distance interval up to 100 m, and patch cuts within each distance interval up to 300

m. Distance intervals of 25 meters followed Paton's (1994) suggestion for studies of edge effects and avian nest success.

HYDROLOGY

The timing, depth, duration, and extent of flooding varied between years. To depict the variable flooding patterns within the 50-ha study plots, we created graphs of the water depth per plot and year over the length of the breeding season (Figure 2.17). The depth plotted was the depth for the lowest elevation point per plot. When water depth exceeded the elevation of the highest point, the plot was completely inundated. Additionally, graphs portraying percent water coverage of each 50-ha plot were created for each year of the study (Figure 2.18).

MEASUREMENTS AT THE MICRO-, MACRO-, AND LANDSCAPE SCALE

Water was monitored on both a spatial and temporal scale (Table 2.4). During each nest check, the depth of water directly under the nest was measured to the closest centimeter. The percent water coverage within an 11.3 m-radius circle around each nest was also estimated during each nest check. In addition, during the 2000-breeding season, one to four grid points per plot were monitored for water depth and percent coverage every three days. The chosen grid points were in low elevation areas that were wet at the beginning of the season. The grid points served as benchmarks for water activity during the dry breeding season of 2000.

Direct measurements of water at the plot-scale could not be made during nest checks, so a different technique was used to obtain these measurements during each nest check of every nest. Using a GIS, we created plot-specific digital elevation models. Combined with locations, elevations, water depths, and dates of each nest, we used the digital elevation models to interpolate water coverage of each plot every three days during the breeding seasons of each year (see Chapter 2 for details). Using plot-scale water coverage, we determined the stage of flooding (before, during, or after 100% plot inundation) for each nest during each nest check. The stage of flooding was specific to plot and year.

MEASUREMENTS AT THE TEMPORAL SCALE

In addition to gathering the micro-scale water depth and plot-scale water coverage for all nests at each nest check, we calculated a 15-day trend in depth and water coverage for every nest at each nest check. Trends for both were calculated to investigate possible time lag effects of water on nest survival. We backdated the depth and plot coverage information at each nest site to the beginning of the breeding season. For each nest check of each nest, the water data for dates up to 15 days prior were used to fit a quadratic equation to the curve of the data. The result was four measurements that completely described the quadratic curve and its lack of fit to the data: intercept, slope, quadratic term, and the root mean square error (RMSE). A 15-day trend was chosen to capture the fluctuation in the water when floodwaters were advancing or receding. Because water data were not available until nests were being monitored, the trends could not be calculated for the first nests of the breeding season.

DATA ANALYSIS

VARIABLE TRANSFORMATIONS

A logit transformation was applied to percent micro-canopy cover and percent macro-canopy cover. A log transformation was used on the macro-habitat variables tree distance and stem count. Square root transformations were applied to the Acadian Flycatcher micro-habitat variables branch edge distance and bole distance. Transformations were applied to obtain a more balanced distribution of the data. More specifically, because the variables were to be used as predictors in linear models, transformations more clearly distinguished among values near support boundaries (e.g., proportions near 0/1) and reduced the influence of highly-skewed values (e.g., distances).

PRINCIPAL COMPONENTS ANALYSIS

Principal components analysis (PCA) was performed on a set of five interrelated macro-habitat variables. The PCA procedure was used to simplify the representation of the information by creating a reduced set of new, uncorrelated variables which could then be used as covariates in models. The original five variables included tree count, average DBH, average canopy height, and the transformed versions of tree distance and macro-canopy cover. Macro-habitat measurements taken at the nest sites of both bird species and at sampling grid points were combined for all years (n=1033) to run the PCA.

GIS EXTRACTION OF MACRO-HABITAT PRINCIPAL COMPONENTS

Macro-habitat features were not measured at Prothonotary Warbler nests in 1998 because of logistical constraints. The missing values prevented statistical analyses of data including both macro-habitat variables and 1998 nests; that is, we had to choose between using macro-habitat variables and dropping all nests from the year 1998 or dropping the macro-habitat variables and including nests from 1998. To remedy this situation, we created an interpolated coverage of the macro-habitat principal components, which were created using data from all years, to impute habitat values for Prothonotary Warbler nests monitored during the 1998-breeding season (see Chapter 2 for details).

MAYFIELD ESTIMATES OF PREDATION RATES

The program CONTRAST (Hines and Sauer 1989), which performs chi-square tests for comparisons among rate estimates, was used to compare daily rates of predation among groups of nests. We compared daily predation rates between nests grouped by year, plot, and nest stage (egg vs. nestling). We also used CONTRAST to compare the daily rates of predation among parasitized and non-parasitized Prothonotary Warbler nests.

COX REGRESSION MODELS

All analyses were performed using SAS Release 8.02 (SAS 2001). We developed exploratory Cox regression models using PHREG to evaluate the effects of habitat characteristics at multiple spatial and temporal scales on the hazard of nest predation for each species (Tables 3.1 and 3.9). Cox regression, also known as proportional hazards regression, models the effects of predictor variables on survival times (Cox 1972, Allison 1995). Survival time may be a more appropriate dependent variable than nest fate. Analyses, such as logistic regression, that use nest fate as the dependent variable ignore the length of time nests are observed; nests observed for short periods receive the same weight as those observed for long periods. Cox regression uses observation length for each nest, so nests observed briefly receive less weight and give less information about the contribution of covariates to survival than do nests observed at length (Manolis et al. 2000b). Because Cox regression models survival times, not nest fates, nests with uncertain fates are easily incorporated as censored observations (Manolis et al. 2000b). The model estimates rates of death or hazard, and can incorporate both categorical and continuous variables, as well as static and time-dependent variables. When incorporating one static (x_1) and one time-dependent (x_2) covariate, the model is expressed as follows:

$$\log h_i(t) = \alpha(t) + \beta_1 x_{i1} + \beta_2 x_{i2}(t)$$

where the hazard (*h*) of the event occurring for individual *i* at time *t* depends on the baseline hazard function (α) at time *t*, the value of x_1, and the value of x_2 at time *t*. The PHREG procedure estimates the baseline hazard function, an unstructured, nonparametric function of time, and it can be regarded as the hazard function for an individual whose covariates all have values of 0. A basic assumption of Cox regression is proportionality of hazard functions; hazard functions for individual nests in the study should be parallel to each other, although they can take any shape reflecting variable mortality over time (Manolis et al. 2000b). PHREG calculates a hazard ratio for each covariate in the model, which is the proportionate increase or decrease in the rate of death corresponding to a one-unit increase in x, holding all other variables constant.

Nest predation was the event of interest. Nests that fledged successfully, had uncertain fates, or failed due to reasons other than predation were considered censored. Survival times for each nest were measured from the day it was first active and under observation to the day it was terminated. Because nests were found at different stages of the nesting cycle, we had to account for late entry into the risk set (i.e., left censoring; Allison 1995). Nests that were active and technically at risk of predation, but not yet under observation and thus not observationally at risk, had to be removed from the risk set. If nest days prior to observation were included, it would cause an upward bias in the survival estimate because nests that terminated prior to being found are not included. The age of each nest, as counted from the day of the first egg, when found and when terminated was used to create an interval of time during which each nest was continuously at risk of predation.

Both static and time-dependent covariates were included in the model. Time-dependent variables, variables that change over time, were measured at each nest check (irregular intervals, about every three days) and included water variables and parasitism status. If a nest was parasitized between nest checks, the nest was coded as parasitized on the previous interval. The maximum number of time intervals for Acadian Flycatcher and Prothonotary Warbler nests was 13 and 12, respectively. For all nests, time intervals (as indexed 1, 2, …, 12 (or 13)) started with the day of the first egg, regardless of whether or not the nest was under observation, and continued with each nest check until the nest was terminated. However, data for only those intervals when the nest was observationally at risk were included in the analysis. We stratified the model by year and plot and used the EXACT option for ties in the data (Allison 1995).

Static variables were screened for problematic multicollinearity using the variance inflation factor, tolerance, and condition index diagnostics. We performed a regression analysis with PROC REG to derive these diagnostics. Correlations between the time-dependent water variables measured at the three spatial scales were obtained by performing two-way Pearson correlation coefficients on each time interval. If like time intervals of two water variables exhibited a correlation coefficient > 0.7, both water variables could not be included in the same candidate model. The data were examined for influential observations using diagnostic statistics derived from PROC PHREG (Allison 1995). In addition to using box plots to look for obvious outliers, we used the likelihood displacement statistics (LD and LMAX) to assess the impact of each observation on the overall fit of the model. Score residuals and DFBETAs were used to identify observations with excessive influence on individual parameter estimates. Each statistic was plotted against the nest observations to visually identify problematic observations.

Landscape variables pertaining to roads, sloughs, and patch cuts were measured by three different approaches: 1) the distance from the nest to the feature, 2) the area of the feature, and 3) the length of edge of the feature. In addition, several measurements were obtained for each of the latter two approaches because they were collected at multiple distances from the nest (Table 2.3, Figure 2.10). Only one measurement for each feature was included in the global model of static covariates. We chose the edge length of each feature for two reasons: 1) it provided the most detailed spatial description of the features' presence and pattern and 2) it was thought to be the characteristic to which predators were responsive. Lacking better biological or statistical rationale for choice of spatial scale, we chose the 75-m distance interval to quantify edge for three reasons: 1) it was the largest distance interval without spatial overlap between nesting pairs within breeding seasons, 2) it encompassed the average territory size of each nesting species, and 3) it expressed optimal variability in the response and thus provided greatest information content. Hence, the variables we used in analysis included the amount of road, slough, and patch cut edge within 75 meters of each nest.

A limited number of interactions between explanatory variables were created based on knowledge of the system. PROC PHREG was used to screen the interactions by adding them one at a time to a model containing the main effects and excluding those with a p-value greater than 0.2 from further consideration. In addition, parameters for the time-dependent variables, water and parasitism, were examined for evidence of temporal variability (as indicated by an interaction with time) to test for, and if necessary correct for, violations of the proportional hazards assumption. For interactions with time, a p-value of 0.10 was used as the cutoff for inclusion in candidate models.

We created candidate models from the explanatory variables within the global model. All one-, two-, three-, and four-variable combinations were created from the set of explanatory variables within the global model (SAS macro, APLR; C.T. Moore, USGS Patuxent Wildlife Research Center, unpublished software). The list of all possible models was filtered to exclude models that contained unacceptable water variable combinations (Table 3.2) and interaction terms without both main effects. We used a SAS macro (C.T. Moore, USGS Patuxent Wildlife Research Center, unpublished software) to run PROC PHREG on each candidate model. We used the information-theoretic approach described by Burnham and Anderson (1998) to compare models; this approach uses AIC as the basis for comparison. Models were ranked by AIC, corrected for small sample size (AICc), from smallest to largest. For each spatial scale, the water variable that was consistently present in the lowest ranked models was retained and a new abridged global model was formed. The fit of the global model was tested with the likelihood-ratio chi-square statistic provided by the PHREG output (Allison 1995).

From the restructured global model, now including only the chosen water variables, we re-created all possible one- to three-variable candidate models, re-ran PROC PHREG on each candidate model, and re-ranked the candidate models by their corrected AIC value. We used the Δ AICc values (AICc – minimum AICc) and the Akaike model weights (w_i) to determine if there was one “best” model among our set of candidate models. Akaike model weights indicate the relative likelihood of the model, given the data and the set of candidate models (Burnham and Anderson 1998). A given w_i is considered to be the weight of evidence in favor of model *i* being the actual best model; the weights are normalized so that the relative likelihoods sum to 1 (Burnham and Anderson 1998). We considered a top-ranked model to be “best” if the ratio of the top-ranked model to the second-ranked model was at least 10 (i.e, $w_1/w_2 \geq 10$). When we did not find one best model, we followed the recommendation of Burnham and Anderson (1998) and performed model averaging. Model averaging incorporates model selection uncertainty into estimates of parameters and estimates of their precision to produce unconditional parameter estimates, standard errors, and confidence intervals (Burnham and Anderson 1998). All candidate models were included in the scope of the averaged model and inferences were made from the resulting averaged model. To quantify the relative evidence of importance for each predictor variable (x_j) included in the averaged model, we summed the Akaike model weights (w_i) across all of the candidate models where variable *j* occurred (Burnham and Anderson 1998). To provide an idea of how the Akaike model weights were distributed among the candidate models, we calculated the 95% confidence set of candidate models. To do so, we summed the Akaike model weights of the ranked models from largest to smallest until that sum reached 0.95; the corresponding subset of models is a type of confidence set on the best model (Burnham and Anderson 1998). Despite steps we took to reduce the size of the candidate model set (a priori construction of candidate variable set, enforcement of upper size limit for any model, and specification of inclusion criteria for specific variables), the resulting set of candidate models was large, but within reason for the exploratory nature of our analysis (Burnham and Anderson 1998).

Using a global model with all static covariates of interest, we graphed the smoothed baseline hazard function with respect to nest age; baseline hazard functions cannot be produced when time-dependent covariates are included (SMOOTH macro; Allison 1995). The baseline hazard function was used to investigate whether the hazard of predation was constant, increasing, or decreasing through the nesting cycle.

Plots of standardized parameter estimates and their 90% confidence intervals were created to facilitate comparisons of relative effect sizes among the covariates included in the top-selected or the averaged models. Standardized parameter estimates are the quotient of the model coefficients and their standard errors (that is, *b/se(b)*). In addition to effect sizes, the plots indicate whether estimates were precise enough, relative to effect size, to conclude if and how the variables affect the hazard of nest predation. We used 90%, as opposed to 95%, confidence intervals to reduce the probability of committing a Type II error; in ecological situations, an incorrect conclusion that a variable is not important (Type II error) may be more detrimental to the resource than incorrectly concluding that a variable is important (Type I error; Johnson 1999). The marginal (i.e., all other variables held fixed) hazard of nest predation was plotted against the values of each variable whose 90% confidence interval did not span 0 and that had large Akaike weights relative to the other variables included in the model.

ACADIAN FLYCATCHER – As a result of yearly differences in hydro-pattern and availability of habitat data, we fit Cox regression models to three different data sets (Appendix 3A). The first regression was run on the complete data set, including static variables, water variables, and parasitism over all years (n=339; Model A). A second model was run using data from 1996 to investigate the effect that flood stage had on nest predation hazard (n=117; Model B). It was only during 1996 that the flooding pattern allowed this analysis. We created a time-dependent dichotomous variable for flood stage (during or after 100% plot inundation) and added it to the existing set of candidate models. The models were run and averaged as described above. We also ran a reduced set of candidate models, using flood stage as the only water variable. A third model was run on data from 2000 to investigate the effects of two additional micro-habitat characteristics that were not measured in previous years, nest concealment and the presence/absence of vines on the nest tree bole, on the hazard of nest predation (n=71; Model C). The two variables were added to the existing list of static variables and a new set of static candidate models was created by the methods described above. The full list of candidate models, including static variables and parasitism but excluding water variables, were run and averaged. Water variables were excluded from the 2000 analysis because it was a dry breeding season.

PROTHONOTARY WARBLER – The data set for Prothonotary Warblers had a large number of missing values. In particular, macro-scale habitat features were not measured in 1998. Additionally, many nests lacked cavity dimension measurements (23% across all years, 63% of which were from 1998). Because of this limitation, we used three different data sets to run Cox regression in an attempt to maximize sample size without losing information (Appendix 3B). The first data set included all variables of interest that were measured during all years (n=314; Model A). This data set included macro-scale variables and thus excluded all nests from 1998. The second data set included all years and variables at all spatial scales, including the GIS extracted macro-habitat variables from 1998, but excluded the cavity dimension variable (n=461; Model B). To satisfy skepticism concerning the inclusion of GIS extracted macro-habitat values, the third data set included all years, but excluded macro-scale variables and the cavity dimension variable (n=515; Model C). The third data set was reduced to a fourth data set that included only years 1996 and 1998 (n=280; Model D). The fourth data set was used to investigate the effect of the stage of flooding on the hazard of nest predation. Two time-dependent dummy variables for flood stage, representing before, during, and after flooding, were created. The flood stage water variables were added to the set of existing candidate models and run in competition with the other water variables; flood stage variables were either both included or both excluded in a given model, but were not included in the same candidate model with any other water variable. This allowed us to compare relative weights of each of the water variables. In addition, a reduced set of candidate models including flood stage as the only water variable was averaged to reveal the weight of flood stage in the absence of other water variables. It was only during 1996 and 1998 that the flooding pattern allowed this analysis.

SPATIAL AUTOCORRELATION

We tested for positive spatial autocorrelation among neighboring nests of the same species with respect to predation fate. We used two different programs, ROOKSCASE (Sawanda 1999) and GeoDa (Anselin 2003), specifying an irregular lattice and five cumulative 100-m lags to calculate Moran's I (Moran 1950). The index was compared to the z-score for the null hypothesis of a random spatial distribution to determine whether the nests in our sample dataset exhibited a spatially correlated pattern of nest predation within a breeding season. Moran's I ranges in value from –1 to 1; a positive value indicates a clustering of nest fates, where nests within the given distance interval are more similar to each other than expected by random, whereas a negative value indicates that nests are more dissimilar to each other than expected by random. Although Moran's I detects clustering, it does not convey the nature of the spatial clustering; that is, it does not distinguish whether the cluster is of depredated nests or of non-depredated nests. We considered spatial correlation among nests pre- and post-modeling, using raw nest fates (i.e., depredated/not depredated) and Cox regression residuals from the global model, respectively. If the raw fates of nests were spatially correlated, we expected that the inclusion of spatially explicit independent variables in the Cox regression model would account for the correlation, as would be manifested by spatial independence of the residuals.

RESULTS

NEST PREDATION

Totals of 441 Acadian Flycatcher and 579 Prothonotary Warbler nests were monitored on the four study plots during the breeding seasons of 1996-1998 and 2000 (Table 2.1). For both species, the majority of nests were found in the building and laying stages (Table 2.5). The percent of Acadian Flycatcher nests that were known to be depredated, by year and plot, ranged from 39% to 70%, with an overall percent predation of 57% (Figure 3.1a). The percent of Prothonotary Warbler nests that were known to be depredated, by year and plot, ranged from 47% to 77%, with an overall percent predation of 60% (Figure 3.1b). Nest predation was the leading cause of nest failure for both species, responsible for more than 80% of nest failures over all years (Table 2.6). The overall daily predation rate for Acadian Flycatchers was 0.039 ± 0.003. Daily rates of predation varied by year (χ^2=8.34, df=3, p=0.039; Figure 3.2a); daily predation rates were lowest during the 1996-breeding season (0.032 ± 0.004) and highest during the 1998-breeding season (0.055 ± 0.011). Daily rates of predation were significantly lower during 1996 than during 1997 or 1998 (χ^2=5.68, df=1, p=0.017 and χ^2=4.09, df=1, p=0.043, respectively). Over all years, nest predation rates did not vary among plots (χ^2=4.52, df=3, p=0.211). The overall daily predation rate for Prothonotary Warblers was 0.051 ± 0.003. Daily rates of predation varied by year (χ^2=22.72, df=3, p<0.0001; Figure 3.2b); predation rates were lowest during 1997 (0.035 ± 0.004) and highest during 1998 (0.069 ± 0.006). Daily rates of nest predation were significantly lower during the 1997-breeding season than during all other years (χ^2=4.31, df=1, p=0.038,

χ^2=20.92, df=1, p<0.0001, and χ^2=5.68, df=1, p=0.017, respectively). Predation rates were significantly higher during 1998 than during 1996 (χ^2=4.53, df=1, p=0.033) and 1997. Over all years, nest predation rates did not vary among plots (χ^2=4.09, df=3, p=0.251). For both species, predation rates were comparable during the 1996 and 2000 breeding seasons.

HYDROLOGY

During all years, except 2000, the study plots flooded and were completely inundated during some part of the breeding season; however, the timing, depth, duration, and spatial extent of the flooding were variable from year to year (Figures 2.17 and 2.18). Flooding patterns not only varied from year to year within the general breeding season, but due to disparate breeding dates of Acadian Flycatchers and Prothonotary Warblers, the flooding patterns also varied relative to species within years (Figure 3.3).

Acadian Flycatchers initiated nests around May 13 of each year (Figure 2.7a). During the 1996-breeding season, when predation rates were lowest for Acadian Flycatchers, plots were beginning to flood when Acadian Flycatchers initiated nests (Figure 3.3). After the first nests were initiated, the floodwaters continued to rise until the plots became completely inundated for about five weeks and then dried out. During the 1997-breeding season, floodwaters had almost completely receded upon nest initiation and plots were dry for the remainder of the season. During the 1998-breeding season, when predation rates were highest for Acadian Flycatchers, plots had already been 100% inundated for about 2.5 weeks upon nest initiation. After the first nests were initiated, the plots remained inundated for about 1.5 weeks before the floodwaters receded. Prothonotary Warblers initiated nests around April 19, about one month earlier than did Acadian Flycatchers (Figure 2.7b). During the 1996-breeding season, the plots were dry upon nest initiation and did not flood until mid-season. During the 1997-breeding season, when predation rates were lowest for Prothonotary Warblers, the study plots flooded early; they were 100% inundated upon nest initiation and floodwaters were already receding. Comparisons between the water patterns on the plots and at the Graham-Burke pumping station suggest that the plots had been inundated for six weeks prior to nest initiation and floodwaters had been declining for 3.5 weeks. During the 1998-breeding season, when predation rates were highest for Prothonotary Warblers, floodwaters were high upon nest initiation, quickly rose to 100% inundation, and maintained inundation for about four weeks before receding. For both bird species, the plots were relatively dry during the entire breeding season of 2000, with only pockets of water present within sloughs, ponds, and low spots where rainwater collected.

PREDATION MODELS

ACADIAN FLYCATCHER

The Cox regression global model contained both static and time-dependent variables measured at three different spatial scales: micro, macro, and landscape (Table 3.1). Due to yearly differences in hydro-pattern and availability of habitat data, Cox regression models were fit to three separate data sets (Models A, B, and C; Appendix 3A). Model A included all variables of interest from all years. Model B was restricted to nests from the 1996-breeding season and included all variables of interest, in addition to a variable (flood occurrence indicator) available only in 1996; this model was created to investigate the effects of flood stage on the hazard of nest predation. Model C included all variables of interest, except water, in addition to two new habitat variables (nest concealment and presence of vines) only measured during the 2000-breeding season, and was thus restricted to data from the year 2000.

MODEL A – The global model of Model A included ten static covariates (Table 3.1; Appendix 3A), ten time-dependent water variable combinations and variable groups (Table 3.2), and one time-dependent variable for parasitism status (Table 3.1; Appendix 3A). There was no evidence of interactions between covariates or of interactions between covariates and time. Water variables at the three spatial scales were highly correlated with each other. Thus, each candidate model contained only single-scale water variable combinations; variable combinations that included multiple scales were not allowed (Table 3.2). The ten possible water variable combinations included redundant measurements within the three spatial scales; four at the micro-scale, two at the macro-scale, and four at the landscape scale (Table 3.2). However, only one variable combination per scale was retained for analysis. For the micro-, macro-, and landscape scale, the variables Wpresence, Nest_Cov, and Plot_Cov dominated the highest weighted models; thus, the global model was recast in a smaller form by discarding the other water variables.

The restructured global model contained 14 covariates: 10 static continuous variables, two time-dependent continuous variables, and two time-dependent dichotomous variables (Table 3.3). The overall fit of the global model was significant, allowing us to conclude that the coefficient for at least one of the covariates in the model was not 0 (Likelihood Ratio; χ^2=32.58, df=14, p=0.003). We had 339 nests, including 200 predation events and 139 censored nests, with a complete set of data for all variables. Candidate models contained up to three variables from the global model, resulting in a total of 432 candidate models. Based on the ΔAICc values and the Akaike model weights, there was not one model among our set of candidate models that best explained the survival of nests from predation. The 95% confidence set of candidate models included 106 models. Model selection uncertainty was incorporated into estimates of parameters and estimates of their precision by averaging all candidate models to obtain unconditional parameter estimates and unconditional estimates of their standard errors and confidence intervals (Table 3.3). All inferences were based on the averaged model.

The baseline hazard function of the Cox regression Model A, including only static covariates, revealed that the hazard of nest predation was constant during the egg stage and then dramatically increased when the nest was around 14 days old, the time at which the nest transforms from the egg to the nestling stage (Figure 3.4). A comparison of the daily predation rates between the egg and nestling stage showed that nests in the nestling stage were subjected to a significantly greater rate of predation (χ^2=7.89, df=1, p=0.005; Figure 3.5).

The relative effects of the variables in the averaged model are shown as standardized coefficient estimates in Figure 3.6. This figure depicts how strongly and in what direction each of the covariates in the model affect the risk of nest predation. The 90% confidence intervals for the standardized parameter estimates of Can_Cov, Dist_Edge, Dist_Bole, Macro_PC1, Rd_Edge_75, Sl_Edge_75, Cut_Edge_75, Wpresence, and Parasitism all spanned 0, indicating that these variables were either unimportant or that our estimates were too imprecise, relative to effect size, to conclude whether or how these variables affect the hazard of nest predation. However, the predictor variables we considered spanned fairly wide ranges (Table 3.4), such that we expected to be able to detect biologically meaningful effects. Though the 90% confidence intervals of the covariates Stems and Plot_Cov slightly crossed 0, we determined that the hazard of nest predation was negatively related to the covariates Nest_Ht, Macro_PC3, Nest_Cov, and Plot_Cov and positively related to the covariate Stems.

We individually examined the relationship between the risk of nest predation and the variables Nest_Ht, Stems, Macro_PC3, Nest_Cov, and Plot_Cov. To do so, we held all continuous variables within the averaged model constant at their mean values and set class variables to 0, while varying only the value for the variable of interest. Under these conditions, we determined the estimated percent change in the hazard of nest predation that was associated with a one-unit increase in the variable of interest.

The hazard of nest predation was negatively related to nest height (Table 3.3, Figure 3.6). Of all the covariates, Nest_Ht had the largest relative effect on the hazard of predation and was the most important covariate considered, as was demonstrated by its presence in candidate models containing 92% of the weight (i.e., the sum of the Akaike model weights of all candidate models containing the covariate Nest_Ht equaled 0.92; Akaike weight, Table 3.3). Our model predicted that for every one-meter increase in nest height, the hazard of predation decreased by an estimated 10% (Table 3.3, Figure 3.7). The mean nest height of depredated nests was lower than that of non-depredated nests (Table 3.5).

The 90% confidence interval of Stems slightly spanned 0 (Figure 3.6) and its Akaike weight was relatively low (Table 3.3); however, the hazard of nest predation was positively related to the number of stems at the macro-scale. Our model predicted that for every one-unit increase in the log number of stems, the hazard of predation increased by an estimated 17.7% (Table 3.3, Figure 3.8). On average, depredated nests were in areas with denser stems than were non-depredated nests (Table 3.5).

The hazard of nest predation was negatively related to Macro_PC3, the principal component describing macro-scale canopy height (Table 3.3, Figure 3.6). Within the full set of candidate models, macro-scale canopy height was present in candidate models containing 43% of the weight. Our model predicted that for every one-unit increase in Macro_PC3, the hazard of predation decreased by an estimated 16.3% (Table 3.3, Figure 3.9). On average, depredated nests were in areas with shorter canopy than were non-depredated nests (Table 3.5).

The hazard of nest predation was negatively related to all three water variables: the presence of water at the micro-scale, the percent of water at the macro-scale, and the water coverage at the plot-scale (Table 3.3, Figure 3.6). Although each candidate model contained a maximum of one water variable, we derived parameter estimates for all three water variables because we averaged over all candidate models. Nest_Cov was the only water variable whose 90% confidence interval did not span 0. Additionally, Nest_Cov was more prevalent in the top ranked models than the other water variables (Akaike weights; Table 3.3). Thus, macro-scale water coverage had the largest effect on nest predation relative to micro-scale and plot-scale water measurements.

We individually examined the relationship between the risk of nest predation and macro- and plot-scale water. Our model predicted that for every one-percent increase in water coverage at the macro-scale, the hazard of predation decreased by an estimated 0.5% (Table 3.3, Figure 3.10). We ran an alternate model to examine Nest_Cov as a categorical, rather than continuous, variable. The model included all non-water variables, but excluded all water variables with the exception of dummy variables describing water at the macro-scale. The alternate model revealed that nests located in wet macro-habitats experienced significantly reduced risk of predation compared with nests located in dry macro-habitats (Figure 3.11a); however, at closer examination, we found this reduction in nest predation risk was restricted to nests that were either less than 50% surrounded by water or completely enveloped with water at the macro-scale (Figure 3.11b). For Plot_Cov, our model predicted that for every one-percent increase in water coverage at the plot-scale, the hazard of predation decreased by an estimated 0.46% (Table 3.3, Figure 3.12). Running an alternate global model to investigate plot-scale water coverage as a categorical variable, we found that nests experienced reduced risk of predation when plots were partially or completely inundated, where risk was lowest when plots were greater than 50% but less than 100% inundated with water (Figure 3.13a,b). On average, non-depredated nests did not have more water at the micro-, macro-, or plot-scale (Table 3.6).

MODEL B – We fit a second model (Model B; Appendix 3A) to a reduced data set to examine the effect of flood stage (during/after) on the hazard of nest predation. The analysis limited us to using nests from the 1996-breeding season. The global model contained the same covariates as Model A (Table 3.3), plus the time-dependent dichotomous flood variable, for a total of 15 covariates: ten static continuous variables, two time-dependent continuous variables, and three time-dependent dichotomous variables (Table 3.7). The overall fit of the global model was not significant, thus we could not conclude that the coefficient for at least one of the covariates in the model was not 0 (Likelihood Ratio; χ^2=17.26, df=15, p=0.304). There were 115 nests, including 62 predation events and 53 censored nests, with a complete set of data for all variables. Candidate models contained up to three variables from the global model, resulting in a total of 499 candidate models. Although the fit of the global model was non-significant, we continue to impart the results of this model with regards to the variable “Flood”, the variable of interest for which this model was created. Based on the ΔAICc values and the Akaike model weights, there was not one model among our set of candidate models that best explained nest survival from predation. The 95% confidence set of candidate models included 196 models. All candidate models were averaged to obtain unconditional parameter estimates and unconditional estimates of their standard errors and confidence intervals (Table 3.7). All inferences were based on the averaged model.

The relative effects of the variables in Model B are shown as standardized coefficient estimates in Figure 3.14. The 90% confidence intervals for the standardized parameters estimates of all four water covariates spanned 0, indicating water at all scales was either unimportant or our sample size was too small to conclude whether or how water affected the hazard of nest predation. Although the 90% confidence interval of "Flood" spanned 0, the hazard of nest predation tended to be higher after flooding, when the floodwaters were receding, than when plots were completely flooded.

MODEL C – We fit a third model (Model C; Appendix 3A) to a reduced data set to examine the effect of two additional micro-habitat characteristics that were not measured in previous years, nest concealment and presence of vines on the nest tree bole (Table 3.1), on the hazard of nest predation. The analysis limited us to using nests from the 2000-breeding season. The global model contained the same covariates as Model A (Table 3.3), with the exception of the water variables, in addition to Conceal and Vines, for a total of 13 covariates: 11 continuous variables, one dichotomous variable, and one time-dependent dichotomous variable (Table 3.8). The overall fit of the global model was significant, allowing us to conclude that the coefficient for at least one of the covariates in the model was not 0 (Likelihood Ratio; χ^2=20.90, df=13, p=0.075). There were 71 nests, including 37 predation events and 34 censored nests, with a complete set of data for all variables. Candidate models contained up to three variables from the global model, resulting in a total of 377 candidate models. Based on the ΔAICc values and the Akaike model weights, there was not one model among our set of candidate models that best explained nest survival from predation. The 95% confidence set of candidate models included 232 models. All candidate models were averaged to obtain unconditional parameter estimates and unconditional estimates of their standard errors and confidence intervals (Table 3.8). All inferences were based on the averaged model.

The relative effects of the variables in Model C are shown as standardized coefficient estimates in Figure 3.15. The 90% confidence intervals for the standardized parameters estimates of both Conceal and Vines spanned 0, indicating that these variables were either unimportant or our sample size was too small to conclude whether, or how, these variables affected the hazard of nest predation.

PROTHONOTARY WARBLER

The Cox regression global model contained both continuous and categorical variables as well as static and time-dependent variables measured at three different spatial scales: micro, macro, and landscape (Table 3.9). Yearly differences in data availability, specifically macro-scale measurements and cavity dimensions, made it necessary to fit Cox regression models to three separate data sets (Models A, B, and C; Appendix 3B) so that hypotheses could be fully (albeit separately) investigated with as much information as available. Model A included all measured variables of interest from all three spatial scales. As such, Model A excluded nests from the 1998-breeding season because they lacked macro-scale habitat measurements. Model B used all variables at all spatial scales from all years, except micro-scale cavity size and macro-scale stem count, but included the GIS extracted macro-habitat variables for the nests of the 1998-breeding season. Model C excluded all variables from the macro-scale, as well as cavity size, and included all years. A fourth model, Model D, was fit to data from 1996 and 1998 to investigate effects of flood stage on nest predation.

MODEL A – The global model of Model A included ten static covariates (Table 3.9; Appendix 3B), fourteen time-dependent water variable combinations (Table 3.2), one time-dependent variable for parasitism status, and one interaction term between parasitism and time (Table 3.9; Appendix 3B). The fourteen possible water variable combinations included redundant measurements within the three spatial scales: four at the micro-scale, two at the macro-scale, and four at the landscape scale (Table 3.2). However, only one variable combination per scale was retained for analysis. For the micro-, macro-, and landscape scale, the variables Wpresence, Nest_Cov, and Plot_Cov, respectively, dominated the highest weighted models; thus, the global model was recast in a smaller form by discarding the other water variables.

After filtering out redundant-scale water variables, the restructured global model contained 15 covariates: 10 static continuous variables, two time-dependent continuous variables, two time-dependent dichotomous variables, and one time-dependent interaction term (Table 3.10). The overall fit of the global model was significant, allowing us to conclude that the coefficient for at least one of the covariates in the model was not 0 (Likelihood Ratio; χ^2=34.08, df=15, p=0.0033). We had 314 nests, including 173 predation events and 141 censored nests, with a complete set of data for all variables. Candidate models contained up to three variables from the global model, resulting in a total of 470 candidate models. Based on the ΔAICc values and the Akaike model weights, there was not one model among our set of candidate models that best explained the survival of nests from predation. The 95% confidence set of candidate models included 229 models. Model selection uncertainty was incorporated into estimates of parameters and estimates of their precision by averaging all candidate models to obtain unconditional parameter estimates and unconditional estimates of their standard errors and confidence intervals (Table 3.10). All inferences were based on the averaged model.

The relative effects of the variables included in Model A are shown as standardized coefficient estimates in Figure 3.16. The 90% confidence intervals of the micro-scale variable Cav_Code and the macro-scale variable Stems, spanned 0 (Table 3.10 and Figure 3.16). Additionally, these two variables had relatively low Akaike weights (Table 3.10). Thus, we concluded that Cav_Code and Stems were not important factors for nest predation. We decided to drop the variables Cav_Code and Stems and to fit a second model (Model B) to an augmented data set, using the GIS extracted values for Macro_PC1 and Macro_PC3 and the nests from 1998, for the following three reasons: (1) the little evidence for Cav_Code and Stems effects in Model A, (2) the substantial reductions in sample size caused by missing data for cavity dimensions in all years and for macro-scale features in 1998, and (3) the acceptable performance of GIS extracted values for Macro_PC1 and Macro_PC3 (Table 2.17).

MODEL B – Cox regression Model B was fit to data that incorporated variables from all three spatial scales, including the GIS extracted macro-scale variables for 1998 nests, and thus included nests from all years. The variables for micro-scale cavity size and macro-scale stem count were excluded. The global model contained eight static covariates (Table 3.9; Appendix 3B), fourteen time-dependent water variable combinations (Table 3.2), one time-dependent variable for parasitism status, and one interaction term between parasitism and time (Table 3.9; Appendix 3B). As with Model A, only one water variable combination per spatial scale was retained. The variables Wpresence, Nest_Cov, and Plot_cov dominated the highest ranked candidate models for the micro-, macro-, and landscape scale, respectively. Thus, the global model was recast in a smaller form by discarding the other water variables.

After filtering out redundant-scale water variables, the restructured global model contained 13 covariates: eight static continuous variables, two time-dependent continuous variables, two time-dependent dichotomous variables, and one time-dependent interaction term (Table 3.11). The overall fit of the global model was significant, allowing us to conclude that the coefficient for at least one of the covariates in the model was not 0 (Likelihood Ratio; χ^2=58.36, df=13, p<0.0001). We had 461 nests, including 272 predation events and 189 censored nests, with a complete set of data for all variables. Candidate models contained up to three variables from the global model, resulting in a total of 299 candidate models. Based on the ΔAICc values and the Akaike model weights, there was not one model among our set of candidate models that best explained the survival of nests from predation; however, the 95% confidence set of models included only 11 candidate models (Table 3.12). All candidate models were averaged to obtain unconditional parameter estimates and unconditional estimates of their standard errors and confidence intervals (Table 3.11). Inferences were based on the averaged model.

The baseline hazard function of the Cox regression Model B, including only static covariates, revealed that the hazard of nest predation was relatively constant throughout the nest cycle, with a moderate increase around day 16, the time when the nest changed from the egg to the nestling stage (Figure 3.17). A comparison of the daily predation rates between nests in the egg and nestling stages showed no significant differences between the two stages (χ^2=0.80, df=1, p=0.370; Figure 3.18).

The effects of Macro_PC1 and Macro_PC3 on the hazard of nest predation were consistent in Model A and Model B (Tables 3.10 and 3.11); the parameter estimates, standard errors, and weights were comparable. The similar estimates for Macro_PC1 and Macro_PC3, in addition to the finding that the GIS extracted values of Macro_PC1 and Macro_PC3 were unbiased and not significantly different from the actual values (Table 2.17), gave us little reason to conclude that the use of extracted values in Model B was inappropriate. In addition to the effects of Macro_PC1 and Macro_PC3, the signs and magnitudes of the parameter estimates and the standard errors of the other covariates in Models A and B corresponded with each other (Tables 3.10 and 3.11).

The relative effects of the variables in Model B are shown as standardized coefficient estimates in Figure 3.19. The 90% confidence intervals for the standardized parameters estimates of Nest_Ht, Can_Cov, Macro_PC1, Macro_PC3, and Sl_Edge_75 all spanned 0, indicating that these variables were either unimportant or that our estimates were too imprecise, relative to effect size, to conclude whether or how these variables affect the hazard of nest predation. However, the predictor variables we considered spanned fairly wide ranges (Table 3.13), such that we expected to be able to detect biologically meaningful effects. The hazard of nest predation was related to the covariates Tree_DBH, Rd_Edge_75, Cut_Edge_75, water at all three spatial scales, and Parasitism.

We individually examined the relationship between the risk of nest predation and the variables Tree_DBH, Rd_Edge_75, Cut_Edge_75, Wpresence, Nest_Cov, Plot_Cov, and

Parasitism. To do so, we held all continuous variables within the averaged model constant at their mean values and set class variables to 0, while varying only the value for the variable of interest. Under these conditions, we determined the estimated percent change in the hazard of nest predation that was associated with a one-unit increase in the variable of interest.

The hazard of nest predation was positively related to the DBH of the nest tree (Table 3.11, Figure 3.19). Our model predicted that for every one-centimeter increase in the diameter of the nest tree at breast height, the hazard of predation increased by an estimated 2.5% (Table 3.11, Figure 3.20). Nests located in trees with greater than average DBH (> 14.5 cm; Table 3.13) suffered from a 44% greater risk of nest predation. On average, depredated nests were located in trees with larger DBH than were non-depredated nests (Table 3.14).

The hazard of nest predation was positively related to the amount of road within 75 meters of the nest (Table 3.11, Figure 3.19). Our model predicted that for every one-meter increase in the length of road within 75 meters of the nest, the hazard of predation increased by an estimated 0.12% (Table 3.11, Figure 3.21). On average, depredated nests had greater exposure to roads than did non-depredated nests (Table 3.14).

The hazard of nest predation was negatively related to the amount of patch cut edge within 75 meters of the nest (Table 3.11, Figure 3.19). Our model predicted that for every one-meter increase in patch cut edge within 75 meters of the nest, the hazard of predation decreased by an estimated 0.22% (Table 3.11, Figure 3.22). On average, depredated nests were less exposed to patch cut edge than were non-depredated nests (Table 3.14).

The hazard of nest predation was negatively related to all three water variables: the presence of water at the micro-scale, the percent of water coverage at the macro-scale, and the percent water coverage at the plot-scale (Table 3.11, Figure 3.19). Water measurements at the micro and macro spatial scales were highly correlated with each other; thus, models including water variables at both the micro- and macro-scales did not exist (Table 3.2). We derived estimates for all three water variables because we averaged over all candidate models. Micro-scale water presence/absence was more prevalent in the top-ranked models than were the broader-scale water variables (Akaike variable and model weights; Tables 3.11 and 3.12), especially than that of the plot-scale. While the relative effect of micro- and macro-scale water were similar in magnitude, both scales had a larger relative effect than did plot-scale water coverage (Figure 3.19). Water, at one or more spatial scale, was present in every candidate model of the 95% confidence set; thus, taken as a whole, water was the most important habitat characteristic included in the model (Table 3.12).

We individually examined the relationship between the risk of nest predation and micro-, macro-, and plot-scale water. Our model predicted that the hazard of predation for nests with water present directly under the nest was 50.8% lower than the hazard for nests without water present (Table 3.11, Figure 3.23). Examining categories of water depth, rather than simple presence/absence of water, revealed that risk of nest predation was significantly reduced in the presence of shallow water (< 35 cm); however, reduction of risk was even greater when nests were located over deep water (> 35 cm; Figure 3.24). Regarding Nest_Cov, our model predicted that for every one-percent increase in water coverage at the macro-scale, the hazard of predation decreased by an estimated 0.77% (Table 3.11, Figure 3.25). Nests experienced reduced risk of predation when their macro-habitat was partially or completely inundated, where risk was lowest when the macro-habitat was 100% inundated with water (Figure 3.26a,b). Considering Plot_Cov, our model predicted that for every one-percent increase in water coverage at the plot-scale, the hazard of predation decreased by an estimated 0.76% (Table 3.11, Figure 3.27). Examining categories of water coverage at the plot-scale demonstrated that the hazard of nest predation was significantly reduced when plots were at least 50% inundated with water, where the greatest reduction was achieved when plots were 100% inundated (Figure 3.28a,b). On average, during the relatively wet breeding seasons of 1996-1998, non-depredated nests had more water at the micro-, macro-, and plot-scale than did depredated nests (Table 3.15).

Parasitism interacted positively with time; that is, the effect of parasitism on the hazard of nest predation changed throughout the nesting cycle, growing stronger as the age of the nest increased (Table 3.11, Figure 3.19). After the combined water effects, parasitism status of the nest was the second most important nest/habitat characteristic that we considered; it was present in candidate models containing 92% of the weight (Table 3.11) and, along with water, comprised the covariates of the top three-ranked candidate models (Table 3.12). To examine the relationship between the hazard of nest predation and the parasitism status of the nest, we held all continuous covariates constant at their mean values and set all other class variables to 0 while varying time (the age of the nest) and varying Parasitism between its two dichotomous values (Figure 3.29). At time=0 (the day the first host egg was laid), the hazard of predation for a parasitized nest was 48.5% lower than the hazard for nests that were not parasitized. At time=14 (the first day that a cowbird nestling could emerge), the hazard of predation for a parasitized nest was 60.4% greater than the hazard for nests that were not parasitized. At time=27 (the average fledging day), the hazard of predation for a parasitized nest was 360.2% greater than the hazard for nests that were not parasitized.

Although Parasitism was treated as a time-dependent variable in the Cox regression model, for the purpose of obtaining the baseline hazard functions of nests by parasitism status, we treated Parasitism as a static variable. The baseline hazard functions for parasitized and non-parasitized nests were not parallel through time; thus, the assumption of proportional hazards was violated (Figure 3.30). The significant interaction term between Parasitism and time diagnosed the violation; however, the inclusion of the interaction term in the Cox regression model incorporated the non-proportionality, thus remedying the problem. The baseline hazards demonstrate that the hazard of nest predation for parasitized nests increased through time, with a striking increase at day 14, the time at which the first cowbird nestling could hatch (Figure 3.30).

A comparison of the daily predation rates between nests by parasitism status showed that parasitized nests were subjected to higher predation rates than were non-parasitized nests

(χ^2=11.89, df=1, p=0.0006; Figure 3.31). Because parasitism status interacted with nest age, we compared the predation rates between nests grouped by nest stage and by parasitism status (Figure 3.32a). Predation rates did not differ between the egg and nestling stage of non-parasitized nests (χ^2=0.06, df=1, p=0.807; Figure 3.32a). The comparison of daily predation rates between the egg and nestling stages of parasitized nests suggested higher predation rates during the nestling stage, however, did not show a statistically significant difference (χ^2=3.35, df=1, p=0.067; Figure 3.32a). Parasitized nests experienced higher rates of predation in both the egg stage (χ^2=4.39, df=1, p=0.036) and the nestling stage (χ^2=7.62, df=1, p=0.006), where the difference was more pronounced in the nestling stage (Figure 3.32a). It is not clear whether the increase in predation rates during the nestling stage of parasitized nests is due to the presence of cowbird nestlings or simply the presence of cowbird eggs during the nestling stage of the host (Figure 3.32b). Although nests can be, and were, parasitized multiple times, nests that were parasitized more than once did not demonstrate increased rates of predation (Figure 3.33). On average, a greater proportion of depredated nests were parasitized than were non-depredated nests (Table 3.14).

MODEL C – We fit a third model (Model C; Appendix 3B) to satisfy skepticism concerning the inclusion of the GIS extracted values of Macro_PC1 and Macro_PC3 in Model B. The data set for the third model excluded all macro-scale variables, as well as cavity dimensions, and included available nests from all years. The global model contained six static covariates (Table 3.9; Appendix 3B), fourteen time-dependent water variable combinations (Table 3.2), one time-dependent variable for parasitism status, and one interaction term between parasitism and time (Table 3.9; Appendix 3B). As with Models A and B, only one water variable combination per spatial scale was retained. The variables Wpresence, Nest_Cov, and Plot_Cov dominated the highest ranked candidate models for the micro, macro, and landscape scale, respectively. Thus, the global model was recast in a smaller form by eliminating the other water variables from further consideration.

After filtering out redundant-scale water variables, the abridged global model contained 11 covariates: six static continuous variables, two time-dependent continuous variables, two time-dependent dichotomous variables, and one time-dependent interaction term (Table 3.16). The overall fit of the global model was significant, allowing us to conclude that the coefficient for at least one of the covariates in the model was not 0 (Likelihood Ratio; χ^2=63.23, df=11, p<0.0001). We had 513 nests, including 306 predation events and 207 censored nests, with a complete set of data for all variables. Candidate models contained up to three variables from the global model, resulting in a total of 176 candidate models. Based on the ΔAICc values and the Akaike model weights, there was not one model among our set of candidate models that best explained the survival of nests from predation. The 95% confidence set of candidate models included 20 models. All candidate models were averaged to obtain unconditional parameter estimates and unconditional estimates of their standard errors and confidence intervals (Table 3.16). Inferences were based on the averaged model.

The signs and magnitudes of the parameter estimates, as well as the standard errors, of the covariates in Models B and C closely corresponded with each other (Tables 3.11 and 3.16). In addition, the relative effects of the variables in Models B and C were analogous to each other (Figures 3.19 and 3.34). The concordance of covariate estimates between Models A, B, and C led us to conclude that it was reasonable to use the GIS extracted macro-scale principal components in Model B. Thus, although the macro-scale variables were unrelated to the hazard of nest predation and dropping them provided a larger sample size, it was unnecessary to do so and we present Model B as our final model.

MODEL D – We fit a fourth model (Model D; Appendix 3B) to a reduced data set to examine the effect of plot-specific flood stage (before/during/after) on the hazard of nest predation. "During" applies to 100% plot inundation, where "Before" and "After" pertain to 0% up to, but not including, 100% plot inundation. Annual variability in hydro-patterns limited this analysis to the use of nests to the 1996 and 1998 breeding seasons. Because we were already working with a reduced data set, we dropped macro-scale variables and cavity dimensions from the analysis to retain the largest sample size possible. As with Models A, B, and C, the water variables Wpresence, Nest_Cov, and Plot_Cov were a better fit than the other water variables within the same spatial scales. Thus, the global model contained the same covariates as Model C (Table 3.16), plus two time-dependent dummy variables describing flood stage, for a total of 13 covariates: six static continuous variables, two time-dependent continuous variables, four time-dependent dichotomous variables, and one time-dependent interaction term (Table 3.17; Appendix 3B). In addition to the previously stated restrictions on combinations of water variables per candidate model (Table 3.2), the flood stage dummy variables were treated as a pair (i.e., they were either both included or both excluded) and could not be included in the same candidate model with any other water variable. The overall fit of the global model was significant, thus we concluded that the coefficient for at least one of the covariates in the model was not 0 (Likelihood Ratio; χ^2=46.36, df=13, p<0.0001). The data set contained 280 nests, including 174 predation events and 106 censored nests, with a complete set of data for all variables. Candidate models contained up to three variables from the global model, resulting in a total of 184 candidate models. Based on the ΔAICc values and the Akaike model weights, there was not one model among our set of candidate models that best explained nest survival from predation. The 95% confidence set of candidate models included 46 models. All candidate models were averaged to obtain unconditional parameter estimates and unconditional estimates of their standard errors and confidence intervals (Table 3.17). Inferences were based on the averaged model.

The relative effects of the variables in Model D are shown as standardized coefficient estimates in Figure 3.35. The hazard of nest predation was negatively associated with all water covariates, with the exception of Plot_Cov, which showed no relationship. Of all the water variables included in the model, micro-scale water presence/absence was the most strongly related to the risk of nest predation, whereas plot-level flood stage was the least associated

(Akaike weight; Table 3.17). When the flood stage variables were the only water variables considered, their Akaike weight increased from 0.0001 to 0.97. Thus, the stage of flooding was indeed an important factor affecting predation hazard, but only in the absence of the other water variables. The hazards of nest predation “Before” and “After” flooding were not significantly different from each other (Table 3.17, Figure 3.35). A re-parameterization of the dummy coding for flood stage (Figure 3.36) allowed us to directly compare "Before" and "After" flooding to "During" flooding. To examine the relationship between the hazard of nest predation and the plot-level flood stage, we held all continuous variables of the averaged model constant at their means values and set all other class variables to 0 while varying Flood_B and Flood_A between their two values. Under these conditions, our model predicted that the hazards of nest predation “Before” and “After” flooding were, on average, 63.9% and 98.1% higher than the hazard of predation “During” flooding, respectively (Figures 3.36 and 3.37).

SPATIAL AUTOCORRELATION

When we examined both the raw nest fates and the Cox regression residuals of Acadian Flycatcher global Model A, we did not find evidence for spatial autocorrelation among the Acadian Flycatcher nests (Table 3.18a). When we examined both the raw nest fates and the Cox regression residuals of Prothonotary Warbler global Model B, we did not find evidence for positive spatial autocorrelation among the Prothonotary Warbler nests (Table 3.18b).

DISCUSSION

NEST PREDATION

Acadian Flycatchers and Prothonotary Warblers breeding at our study site within the bottomland hardwoods of the White River NWR suffered from high rates of nest predation that accounted for over 80% of all nest failures. Nest predation is well known for its primary role in the nesting failure of neotropical migratory songbirds (Ricklefs 1969, Martin 1992). Nest predation rates, for both species, varied annually: a common finding among nest predation studies

(Martin 1992). There was also some disparity between species as to how the predation rates varied among years. Both species experienced the highest predation rates during the 1998-breeding season; however, Acadian Flycatchers encountered the lowest predation during the 1996-breeding season, while Prothonotary Warblers faced the least nest predation in 1997. Variability in annual predation could result from a variety of causes such as variation in the local predator assemblage, the local predator abundance, and the availability of alternative prey.

Changes in abiotic factors, or the environmental conditions, of the forest may have direct biological effects on the abundance and distribution of forest plant and animal species; the effects of which would be determined by the species-specific physiological tolerances to the environmental conditions (Murcia 1995). In return, changes in the abundance and distribution of plant and animal species can cause changes in species interactions, such as predation. As a seasonally flooded bottomland hardwood forest, water is a dominant feature characterizing the environment of our study site. Bottomland hardwood forests are complex mosaics of plant and animal associations, primarily due to spatial variations in the frequency, duration, and timing of flooding (Wakeley and Roberts 1996). Wetness gradients within bottomland hardwood forests are an important abiotic influence on the distribution and abundance of organisms. Responses of plant species to variation in the frequency, duration, and seasonality of flooding are determined by the species-specific physiological tolerances to flooding and result in the zonation of plant communities typical of bottomland hardwood forests. Animal species may respond indirectly to flooding-induced variation in vegetation structure/species composition and variation in alternative food resources, and/or they may respond directly to the presence of water (Wakeley and Roberts 1996). These responses will depend upon species-specific needs, tolerances, and behavior.
The timing, depth, duration, and spatial extent of flooding at our site is variable from year to year and has the potential to directly and indirectly influence the environment. As such, floodwater may be a key factor causing annual variation in nest predation rates.

Floodwater may indirectly and directly affect the local predator assemblage, predator abundance, and risk of nest predation. The presence of water may provide potential nest predators with alternative aquatic prey; for example, raccoons may benefit from abundant crayfish and frogs associated with water. Alternative prey may or may not change predation pressure on birds' nests; potential predators' food preferences and the spatial and/or temporal coexistence between alternative prey and bird nests may determine the impact that alternative prey have on the foraging strategies and the foraging-area use of potential nest predators (Schmidt 1999). In addition to alternative prey for potential nest predators, water associated with flooding may provide more abundant prey for our focal bird species, thus allowing them to spend less time foraging and more time being vigilant at the nest (Martin 1992). Water may also influence nest predation by directly affecting the behavior of potential nest predators; for example, some predators may avoid water or their movements and foraging techniques may be hindered or altered by the presence of water. Thus, water has the potential to influence nest predation, and the distinctive annual flooding patterns may be a main factor in the variable nest predation rates we observed among years. We discuss the specific effects of water on nest predation when we cover results of the species-specific predation models.

Variable pressure from different main predators may have contributed to the discrepant relative ranking of nest predation rates between species among years. Our study area contains a diverse predator community including potential nest predators such as raccoons (*Procyon lotor*), southern flying squirrels (*Glaucomys volans*), eastern fox squirrels (*Sciurus niger*), rat snakes (*Elaphe obsoleta*), and avian species including Red-bellied Woodpecker (*Melanerpes carolinus*), American Crow (*Corvus brachyrhynchos*), and Blue Jay (*Cyanocitta cristata*). Although we did not identify the responsible predators due to the difficulty and fallibility of doing so from nest remains (Lariviere 1999), based on the distinct nest-site characteristics of our two focal species, we believe that they are subjected to a different assemblage of predators. The location of Acadian Flycatcher nests on the ends of small diameter/frail branches, far from the nest-tree bole, most likely precludes predation from raccoons. These nests are presumably preyed upon by snakes, birds, and squirrels (Wilson and Cooper 1998a). In contrast, Prothonotary Warbler nests are located relatively low within cavities of snags and, as such, are accessible to most potential predators. Nest remains indicative of raccoon predation, torn open cavity, were common for Prothonotary Warblers (personal observation). Thus, discrepancies between annual levels of predation on Acadian Flycatcher and Prothonotary Warbler nests may reflect annual variation in the abundance and composition of their distinct groups of potential predators.

In addition to annual variation in predator abundance and assemblages, floodwater may differentially affect different nest predator species. Effects of water on predator behavior/foraging, if they occur, likely materialize in a species-specific manner. For example, flooding probably plays a more relevant role in the daily activities of terrestrial predators (raccoons) than it does to arboreal (birds) or semi-arboreal (snakes, squirrels) predators. Thus, differential effects of water on potential nest predators, along with distinctive predator groups of Acadian Flycatcher and Prothonotary Warbler nests, may explain disparate levels of nest predation that we observed for each species during the same years.

In addition to varying among years, due to different breeding dates of Acadian Flycatchers and Prothonotary Warblers, flooding patterns (timing, magnitude, duration, spatial extent) varied between bird species within years. When we looked at species-specific flooding patterns within breeding seasons, predictable relationships between flooding patterns and nest predation were non-existent. In fact, the flooding patterns present when Acadian Flycatchers experienced the lowest and highest rates of nest predation were equivalent to the patterns present when Prothonotary Warblers experienced the highest and lowest rates of nest predation, respectively. Specifically, Acadian Flycatchers suffered the least nest predation when, upon initiation of their nesting season, floodwaters were increasing, after which the plot was completely inundated, and then floodwaters receded. This same pattern upon initiation of the Prothonotary Warbler nesting season was present when they suffered their highest annual rates of nest predation. Similarly, while Acadian Flycatchers suffered their highest annual rates of nest predation when, upon initiation of their nesting season, the plot was already completely inundated and floodwaters were in recession, this same pattern was present when Prothonotary Warblers experienced their lowest annual rates of predation. Based on the above scenario, it seems unlikely that it is the pattern of flooding upon initiation of the nesting season that influences nest predation rates, but rather the overall seasonal pattern. These apparent divergent relationships between species-specific flood patterns and annual rates of nest predation, however, are based on arbitrary points of reference and potentially meaningless nest groupings. Because water is a prominent feature of our study site and has the potential to affect nest predation, a more detailed and objective look at the effect of water on each species is warranted to avoid making misleading conclusions.

We conducted such an investigation with species-specific predation models, using Cox regression for our analyses. These models allowed us to describe water characteristics on a daily basis for each individual nest during the time that it was active. Thus, we were able to capture the temporally variable nature of the flooding and to explicitly incorporate it into a model relating water characteristics to the risk of nest predation. Not only did we consider temporal effects of water, but by describing water at both local and landscape scales, we were able to explore the spatial scale at which water influences nest predation. By explicitly describing the temporal and spatial characteristics of the floodwater, we attempted to fully incorporate the pattern of flooding, its timing, magnitude, duration, and spatial extent, into our investigation of how water affects the risk of nest predation. We discuss results of these analyses in turn, as we cover the results of our predation models.

PREDATION MODELS

GENERAL

To account for the lack of macro-habitat measurements taken at Prothonotary Warbler nests during the 1998-breeding season, we created three different Cox regression models for this species. These three models differed in the variables and years included. Model A included all variables from all spatial scales, while excluding nests from the year 1998, and demonstrated that the micro-scale variable, Cav_Code, and the macro-scale variable, Stems, were not related to the risk of nest predation. Based on Model A, we concluded that further consideration of cavity size and stem count was not warranted. Model B included all variables and nests from all years, necessitating the inclusion of GIS extracted values for the macro-scale variables, Macro_PC1 and Macro_PC3. Model C included nests from all years while excluding all macro-scale variables. Comparison of Models A, B and C led us to conclude that use of the extracted values for Macro_PC1 and Macro_PC3 was reasonable. For this reason, we chose Model B as our final model; hence, the following discussion applies to the covariates of Model B and includes variables from the micro-, macro-, and landscape scale while incorporating data from all years of the study.

In addition to creating alternative models to manage missing data, we also constructed auxiliary models to investigate novel variables available only during restricted years of the study. For Acadian Flycatchers, Model A was our core model; however, creation of Models B and C let us explore potential relationships between flood stage and nest predation, as well as potential effects of nest concealment and vines. As stated above, Model B was our primary model for Prothonotary Warblers; however, we created Model D to examine the relationship between flood stage and the risk of nest predation.

For both Acadian Flycatchers and Prothonotary Warblers, each Model presented was originally comprised of a large number of candidate models. Burnham and Anderson (1998) suggest that this approach is justifiable for observational studies when inference is based on the Akaike weights of all models, rather than on one single best model. Accordingly, we followed the recommendation of Burnham and Anderson (1998) and implemented model averaging to incorporate model selection uncertainty into the parameter estimates, and estimates of their precision, of our final Model.

The risk of nest predation for both species was linked to local- and landscape-scale characteristics of the nest site and the surrounding habitat. Although Acadian Flycatchers and Prothonotary Warblers differ greatly in the characteristics of their nest sites and in their habitat selection, we investigated many of the same nest-site and habitat characteristics for both species because we anticipated they might be related to the presence, behavior, and foraging success of their shared predators. For this reason, we first simultaneously discuss the results of variables that are common to the models of both species. These variables include: micro-scale measurements of nest height and canopy cover, macro-scale descriptions of stem density, forest age/disturbance, and canopy height, landscape-scale exposure to roads, sloughs, and patch cuts, micro-, macro-, and plot-scale descriptions of water, and parasitism status of the nest. Variables that are unique to each species are discussed separately. For open-cup nesting Acadian Flycatchers, these include micro-scale nest-site characteristics of nest distance from branch edge, nest distance from tree bole, nest concealment, and presence/absence of vines on the nest-tree bole. For cavity nesting Prothonotary Warblers, these include micro-scale nest-site characteristics of nest-tree diameter and cavity entrance size.

NEST STAGE

The risk of nest predation was higher during the nestling stage for Acadian Flycatcher, but not for Prothonotary Warbler, nests. Nests are often more conspicuous during the nestling stage owing to vocalizations and scent of nestlings, as well as the increased activity of provisioning adults at the nest (e.g., Mullin and Cooper 2000). Assuming predators use various combinations of visual, auditory, and olfactory cues to locate and depredate nests, rather than simply happening upon them (i.e., incidental predation), it follows that nests in the nestling stage would be more heavily depredated than nests in the incubation stage. Parental activity is typically greater when feeding young than during the incubation period, yielding an expectation under Skutch's (1949) hypothesis of increased predation during the nestling period, providing nest-site effects are non-existent. Many investigators, however, have failed to find increased rates of nest predation during the nestling stage compared with the incubation stage (reviewed in Martin 1992). It is believed that selection of nest sites by birds is non-random and adaptive with regard to the risk of predation (Martin 1998). By selecting safe nest sites, birds can either decrease nest encounter rates by incidental nest predators (Vickery et al. 1992, Schmidt et al. 2001) or decrease nest detectability by actively searching predators (Weidinger 2002). Thus, variation in nest-site quality can often influence nest predation (Martin and Roper 1998) and such effects could mask effects of parental activity on nest predation (Martin et al. 2000). Specifically, if nests in poor sites are located and depredated the quickest (i.e., during the laying or incubation stage), such effects could increase predation rates during the incubation stage compared to the nestling stage. An innovative field experiment by Martin et al. (2000) demonstrated that, when controlling for nest-site effects, nest predation increased with increased parental activity during the nestling stage and that, for nests that survived the incubation stage, nest predation was higher during the nestling stage. With this in mind, the observation of higher predation during the nestling stage for Acadian Flycatchers suggests that sensory cues emitted during the nestling stage had a greater effect on nest predation than did the nest site. Whereas, the observation of no difference in nest predation between stages of Prothonotary Warbler nests suggests that nest predation did actually increase during the nestling stage, but was offset by antagonistic nest-site effects.

Nest Placement and Vegetation Structure

Micro-Scale – Nests of Acadian Flycatchers that were located higher in the canopy faced lower risk of nest predation than did nests located at lower heights. It has been suggested that flycatchers counteract high rates of nest predation by making nests less accessible to ground predators through increased nest height (Murphy 1983). Nest height is also positively correlated with nest concealment (Wilson and Cooper 1998a), another potential nesting characteristic that may serve to decrease nest predation. Previous analyses of Acadian Flycatcher data within the Refuge suggested that when the nests of individual females are depredated, their re-nesting attempt tends to be located higher in the canopy (Cooper, unpublished data), further supporting the notion that higher nests are an attempt to avoid nest predation. Not only may higher nests be more difficult for ground predators to access, but they may also be more difficult for them to detect. The relationship between nest height and susceptibility to nest predation, however, may vary with the type of predator. While canopy nests may be less conspicuous and less accessible to large mammalian predators, they may be easily detected and accessed by visually oriented avian predators flying overhead or scanning from nearby perches (Huhta et al. 1996, Yahner and Scott 1988).

While some studies have reported decreased nest predation with increasing nest height (Martin and Roper 1988, Martin 1993a), the majority of studies have found no relationship between nest height and predation (Ratti and Reese 1988, Filliater et al. 1994, Hanski et al. 1996, King et al. 1998a). Studies showing no relationship, however, focused on ground- and shrub-nesting species, where relatively little variation in nest height existed and "high" nests were still accessible to ground predators. This is likely the case with Prothonotary Warblers, which showed no relationship between nest height and risk of nest predation; a low mean nest height (< 2.5 m) implies that most nests were accessible to ground predators, while a small range of nest heights suggests that Prothonotary Warblers lack the elasticity in this nest-site trait to affect nest accessibility.

The risk of predation for Acadian Flycatcher and Prothonotary Warbler nests was not related to canopy cover of the micro-habitat. Increased canopy cover directly over open-cup nests could potentially provide overhead concealment from visually oriented avian predators. However, if avian predators forage below the canopy, rather than flying overhead, then canopy cover would not afford concealment to nests. Additionally, it is unlikely that canopy cover would affect discovery of cavity nests by avian or other predators. Other researchers also have not found a relationship between micro-scale canopy cover and nest predation (e.g., Hanski et al. 1996, Huhta et al. 1998a, Larison et al. 1998, Ortega and Capen 2001).

MACRO-SCALE – Contrary to our prediction, increased density of stems in the macro-habitat of Acadian Flycatcher nests was not associated with decreased risk of nest predation, but instead with increased risk of nest predation; however, stem density had no effect on predation of Prothonotary Warbler nests. Results of other studies have suggested that increased density, structural complexity, and heterogeneity/patchiness of vegetation in the surrounding nest-patch decrease predation rates (Bowman and Harris 1980, Chasko and Gates 1982, Martin and Roper 1988; reviewed in Martin 1992). The mechanism by which this relationship occurs, however, has been debated and several hypotheses have been suggested. Increased vegetation within the nest-patch may aid in concealing the nest (Howlett and Stutchbury 1996, Flaspohler et al. 2000), may reduce predator search efficiency (Bowman and Harris 1980, Martin and Roper 1988), or may provide alternative prey, in the form of other species' nests, insects, nuts, and berries, to generalist predators and divert attention from the nest. The above hypotheses were created with terrestrial predators in mind, especially raccoons. Assuming Acadian Flycatcher nests are depredated most heavily by arboreal and semi-arboreal predators, such as birds, squirrels, and snakes, vegetation density in the understory/mid-canopy may not hinder the movement and searching ability of these predator species. In fact, snakes (Mullin et al. 1998, Mullin and Cooper 2000) and squirrels may actually benefit from a more structurally complex understory/mid-canopy by way of increased cover from their own predators. For such species, foraging in intermediate levels of structural complexity may enhance predatory success as opposed to decreasing it (Mullin and Cooper 2000). While high vegetation density will not mask vomeronasal cues, it may obscure visual cues of prey from snakes (Mullin and Cooper 2000). The stem density within the nesting macro-habitats of Acadian Flycatchers may have been too low to thwart predatory activity, but high enough to facilitate it. In addition to the presence of stems possibly facilitating predation upon Acadian Flycatcher nests, increased stem density may simply be associated with disturbed habitats, such as along the edges of roads and patch cuts, which may themselves be associated with increased abundance/diversity of potential nest predators (Gates and Gysel 1978, Brittingham and Temple 1983).

The absence of an effect of stem density on nest predation risk, such as we found for Prothonotary Warblers, is also common in the literature (King et al. 1996, Tittler and Hannon 2000, Ortega and Capen 2001). Different predator groups may be partly responsible for the disparate results between our two focal species. Cavity nests, by their nature, may be more easily detected by visually oriented predators, especially those that develop search images. Thus, stem density may not affect the searching efficiency of these predators. The inconsistent relationship found between micro- and macro-habitat features of nest sites and the risk of nest predation is often attributed to spatial/temporal variation in the abundance and diversity of nest predators, as well as to interactions among the effects of nest sites and species-specific avian and predator behavior (Rangen et al. 1999, Schmidt 1999, Dion et al. 2000, Martin et al. 2000, Schmidt et al. 2001, Weidinger 2002). Factors influencing nest predation may vary according to whether predator communities are dominated by mammals or birds, or whether predators use visual or olfactory cues to locate nests (Whelan et al. 1994). Thus, interpretation of the observed patterns of predation is often limited by investigators' lack of knowledge concerning the identity of nest predators in their particular study system (Weidinger 2002). Additionally, an environment with a variety of predators, each using different nest-searching strategies, may eliminate the existence of predictably safe nest sites (Filliater et al. 1994). Because we did not attempt to identify responsible nest predators in our study, our interpretations our speculative; identification of the offending predators would greatly aid in elucidating the patterns we observed.

We found no evidence that the age/disturbance (based on the number, diameter, and dispersal of trees) of the nesting macro-habitat affected risk of nest predation for either focal species. Although it has been reported that generalist predators are attracted to disturbed habitat, these habitats are often associated with artificial edges and large, human-induced disturbances (Wilcove 1985). In contrast, our macro-habitat measurement reflects a natural range in the number, size, and dispersal of trees on a small scale and thus would not be expected to disproportionately attract predators. Similarly, other researchers have not found an effect of tree count or basal area on nest predation (Larison et al. 1998, Manolis et al. 2000a, Ortega and Capen 2001).

Nests of Acadian Flycatchers that were located in macro-habitats with taller trees had lower risk of nest predation. Taller trees may translate into more canopy and more total foliage, which suggest more micro-sites within the macro-habitat that potential predators need to search. It has been demonstrated that predator search efficiency decreases, with a concomitant decrease in nest predation, when the number of potential nest sites within a macro-habitat increases (Martin 1993b). Height of the trees within the nesting macro-habitat of Prothonotary Warblers did not affect their risk of nest predation. In contrast to fusing their nests into the canopy as do Acadian Flycatchers, Prothonotary Warblers nest in discrete cavities of snags, often devoid of foliage, in the understory. Consequently, more foliage in the upper canopy would not benefit them in the same way; their micro nest-site is distinct and uncommon.

LANDSCAPE-SCALE CHARACTERISTICS

ROADS – We predicted that exposure to roads within the forest interior would increase the risk of predation on Acadian Flycatcher and Prothonotary Warbler nests. We found that, whereas predation risk for Acadian Flycatchers was not related to road exposure, Prothonotary Warbler nests that were more exposed to roads suffered from increased risk of nest predation. Most studies that examined nest predation levels relative to roads reported no difference in predation rates at varying distances from road edge (Latta et al. 1995, Lindenmayer et al. 1999, Manolis et al. 2000a, Ortega and Capen 2001, Rodewald 2002). An increase in nest predation with close proximity to roads was reported in only two studies, both of which used artificial ground nests (Burkey 1993, Marini et al. 1995). Roads evaluated within the above studies varied in surface type, width, intensity of use, density, and changes in vegetative structure. Road width (Boulet and Darveau 2000, Haskell 2000), density (Forman 1998), and intensity of use (Boulet and

Darveau 2000), as well as other characteristics of the road, may influence the type and extent of the edge effects that occur. The roads that dissected our study plots were unsurfaced and varied in their width and intensity of use; however, in general they were relatively narrow (< 5 m) and low-intensity (often receiving < 1 ATV/truck visit per day). To incorporate details of road density, we described nest exposure to roads by measurements of road length, as opposed to using a rudimentary measurement of distance-to-closest-road. Furthermore, natural-nest studies do not lend themselves well to using distance categories, as investigators cannot ensure a certain number of nests per category.

Several hypotheses have been proposed to explain increased nest predation along narrow, forest-dividing internal edges, such as roads, within forested landscapes. The travel-lane hypothesis (Bider 1968; but see Lariviere 2003), which suggests that potential nest predators will incidentally take nests while traveling along linear corridors, is the most frequently invoked. Mammalian predators, such as canines, skunks, and raccoons are known or are suspected to have an affinity for linear habitat features and use of trails (Small and Hunter 1988, Miller and Hobbs 2000). Further, several authors have speculated that roads may provide a conduit for the movement of generalist predators, allowing them to invade forest interiors from surrounding non-forested habitats (Schonewald-Cox and Buechner 1992, Lindenmayer et al. 1999). Increased human activity within forested habitats is associated with the presence roads. Trash and road-kill associated with human activity may provide supplemental food for generalist mammalian and avian predators, which may increase their presence and influence their foraging behavior within the surrounding forest, thereby leading to elevated predation pressure on the nests located within these forested areas (Boulet and Darveau 2000). Lastly, it is proposed that increased structural complexity of the vegetation at road edges may attract a higher density of nesting birds (James 1971, Shugart 1984), resulting in increased nest predation (density-dependent predation; Fretwell 1972) as predators increase their search intensity in response to discovering occupied nests (Martin 1988).

Given the characteristics of the roads within our study site, as well as our finding that warbler nests encounter higher risks of predation when located in areas with more roads, we can deduce which, if any, of the above hypotheses apply to our study. Roads within our study plot were predominantly closed-canopy, and as such exhibited relatively little change in vegetation structure; thus excluding the density-dependent predation hypothesis. It is also unlikely that the low-intensity road use offered much in the way of human-generated supplementary food. While potential nest predators may use the roads as travel lanes, our model demonstrated that the amount of road within a 75-m radius of the nest influenced the risk of nest predation, suggesting that the increase was not simply due to incidental or opportunistic taking of nests while immediately traveling along roads. With the exception of the "road as a conduit" explanation, the above hypotheses predict increased levels of nest predation directly at the road edge, rather than further into the surrounding forest. It is possible that generalist mammalian predators (e.g., raccoons) in our study area use the roads to access the interior forest from the surrounding non-forest matrix. Even if already present within the interior, it is easy to foresee how a proclivity for moving along roads could increase predation pressure within the surrounding forest. We would expect, however, that the increase in predation would be stronger at closer proximity to the roads. Unfortunately, our natural setting was not conducive to teasing apart this type of relationship. The use of roads by terrestrial predators, such as raccoons, as opposed to squirrels, snakes, and avian predators, may explain the nonexistent relationship between road exposure and predation of Acadian Flycatcher nests in the presence of the positive relationship between roads and Prothonotary Warbler nest predation.

SLOUGHS – We had suspected that potential nest predators within our study site would be attracted to sloughs as sources of water and aquatic prey, as well as a paths of travel, and had predicted that nests located closer to sloughs would experience higher risks of predation. When standing water is limited, it has been documented that female raccoon home ranges are spatially aggregated around water (Gehrt and Fritzell 1998). Similarly, raccoon abundance has been related to stream density within forests (Dijak and Thompson 2000) and raccoons are known to show an affinity for foraging along streams and mud banks (Schoonover and Marshal 1951). Other researchers have found higher diversity of potential nest predators (Gates and Giffen 1991), as well as increased rates of nest predation (Marini et al. 1995), along forest-stream edges, suggesting that streams may concentrate predator activity and may be used as travel corridors by mammals (e.g., raccoon and mink; Harris 1984, Forman and Godron 1986). We did not, however, find an increased risk of predation for either Acadian Flycatcher or Prothonotary Warbler nests located in areas with greater exposure to sloughs. Our results suggest that nest predators do not aggregate at sloughs on our study plots. As a seasonally flooded bottomland hardwood forest, water was not a limiting resource; our study plots flooded during every breeding season of the study, with the exception of 2000. During the 2000-breeding season, however, rainwater was abundant and collected in low areas of the plot, remaining for much of the season and providing drinking water and aquatic prey, especially crayfish, to potential nest predators. Thus, water within sloughs may not have served as an attractant to predators. Additionally, sloughs within the study plots were relatively narrow, rarely creating breaks in the overhead canopy. Consequently, sloughs did not constitute "edge habitat" – where a higher diversity of animals congregated because of increased diversity and structural complexity of the vegetation. While potential predators were not attracted to sloughs, they may have avoided the area around sloughs during times of partial flooding. On our study plots, the land surrounding sloughs tended to be lower in elevation; these areas were the first to become submerged upon flooding and the last to dry out upon flood recession. When dry land is an option, water may act as a deterrent to some potential nest predators within our study area, thus affording protection to nests located over water (see HYDROLOGY below). Avoidance of inundated areas near sloughs may have contributed to the lack of pattern we observed for risk of nest predation relative to the presence of sloughs.

PATCH CUTS – Concerning nest predation and exposure to patch cuts, neither of our focal species demonstrated the predicted relationship of increased predation with greater exposure to patch cuts. The lack of relationship we observed between Acadian Flycatcher nest predation and exposure to patch cuts is in agreement with the findings of several researchers (Rudnicky and Hunter 1993, Hanski et al. 1996, Manolis et al. 2000a, Flaspohler et al. 2001b, Rodewald 2002), while incongruent with the findings of an equally abundant list of investigators who reported a positive relationship (Rudnicky and Hunter 1993, King et al. 1996, Fenske-Crawford and Niemi 1997, Manolis et al. 2000a, Flaspohler et al. 2001a,b). It is interesting to note that several of the above investigators demonstrated both positive and nonexistent relationships between nest predation and proximity to timber harvests. For example, Rudnicky and Hunter (1993) reported increased predation on artificial shrub nests, but not on artificial ground nests, near timber cuts. Results of artificial nest studies, however, must be interpreted with caution, as artificial nests may not accurately mimic natural nests (Major and Kendall 1996). In contrast, both Manolis et al. (2000a) and Flaspohler et al. (2001b) reported increased predation on natural ground nests, but not on natural canopy nests, near timber cuts. Hanski et al. (1996) and Rodewald (2002), both of which found no relationship between nest predation and proximity to forest cuts, used composite data from several ground-, shrub-, and canopy-nesting species. Incongruent results among these studies suggest differential predation pressure on nests located within different vertical strata, possibly owing to a different suite of predators foraging at the forest-cut edge than the forest interior. The results also suggest the potential for masking edge-related increases in predation when nests from many species are pooled and highlights the importance of examining species-specific patterns of nest predation at edges. Only a handful of studies have been conducted with natural nests of single species, most of which have been on ground-nesting Ovenbirds (*Seiurus aurocapillus*) and have found increased predation near clearcuts (King et al. 1996, Manolis et al. 2000a, Flaspohler et al. 2001a). To our knowledge, Manolis et al. (2000a) published the only single-species results of canopy-nesters (Least Flycatchers (*Empidonax minimus*) and Red-eyed

Vireos (*Vireo olivaceus*)); in their study, neither species showed a relationship between nest predation and proximity to clearcuts. The bottom line is that there is no general consensus as to whether or not timber cuts are associated with an increase in nest predation. Inconsistencies in study design and methods, as well as landscape-level or regional variations in vegetation structure, predator communities, and bird communities (Robinson et al. 1993, Donovan et al. 1997), likely contribute to the disparate results. Timber cut edge-associated increases in nest predation simply may not be a universal phenomenon. For this reason, and because biases may result when extrapolating findings from other studies, species-specific studies in various regions, landscapes, and habitats are needed to determine, on a case-by-case basis, whether timber cuts are detrimental to forest-interior nesting songbirds.

While neither of our focal species demonstrated the predicted positive relationship between nest predation and exposure to patch cuts, they showed disparate results. Whereas Acadian Flycatcher nests did not suffer increased risk of nest predation when exposed to greater amounts of patch cut edge, Prothonotary Warbler nests experienced decreased risk of predation when surrounded by more patch cut edge. We propose that this difference may be partly attributable to the distinct composition of the predator groups that prey upon these two songbirds: snakes, small mammals, and birds for Acadian Flycatcher nests versus raccoons, snakes, small mammals, and birds for Prothonotary Warbler nests. Levels of nest predation near forest edges will depend on the diversity of the predator community, as well as predator densities and habitat use (Cotterill and Hannon 1999). Because our focal bird species were located within the same habitat and exposed to the same predator community, we focus on how differences in predator habitat use at the fine-scale and location of the nest relative to predator distribution may explain patterns of nest predation in relation to patch cuts (Reitsma et al. 1990).

Although unsubstantiated, we believe that Acadian Flycatcher nests within our study site are most heavily preyed upon by snakes and birds (Wilson and Cooper 1998a). The climbing tendencies of rat snakes and their ability to prey upon the eggs, nestlings, and adults of arboreal nesting bird species are well documented (Durner and Gates 1993, Saenz et al. 1999). Nesting birds and small mammals are the main prey of rat snakes (Fitch 1963). Although uniform distribution of snakes (Cromer 1999, as cited in Moorman et al. 2002) and nest predation by snakes (Best 1978) in relation to timber cuts have previously been reported, Blouin-Demers and Weatherhead (2001a,b) documented with radio-telemetry that rat snakes prefer edge, corroborating the findings of studies by Weatherhead and Charland (1985) and Durner and Gates (1993). They suggest that snakes prefer edge because it offers both sunlight and shade, as well as structurally complex vegetation, allowing simultaneous access to habitat for thermoregulation and refuge from predators. The authors also demonstrated that rat snakes preferred to forage near (< 80 m) edge; this was presumably because they require a site that allows basking and safe retreat to properly digest, and have difficulty traveling far distances after consuming prey (Blouin-Demers and Weatherhead 2001a). Rat snakes may also prefer edge because of increased foraging opportunities associated with elevated prey at the cut edge; several studies have documented increased density of birds (Gates and Gysel 1978, Chasko and Gates 1982) and relative abundance of small mammals (e.g., eastern chipmunk and red squirrel (King et al. 1998b) and deer mice (Sekgororoane and Dilworth 1995)) at clearcut edges. Increased abundance of small mammals near cut edges could also contribute to an increased risk of nest predation for nests located proximal to cuts. It is not likely that predation by birds increased near cuts, as several studies have failed to document increases in the relative abundance of avian predators (corvids) adjacent to timber cuts or within young regenerating stands (Strelke and Dickson 1980, Thompson et al. 1992, King et al. 1998b, Moorman and Guynn 2001).

While the predator-edge relationships described above suggest that we may be justified in expecting to find increased predation on Acadian Flycatcher nests near patch cut edges, we did not find such a relationship. Inappropriate measurement techniques may be partly responsible for not observing a positive relationship. The amount of cut edge may not have been the most appropriate metric to describe nest exposure to patch cuts; for example, area of patch cuts or a strict distance-to-nearest patch cut may have been more suitable. Additionally, the spatial scale at which we quantified exposure to patch cuts, which was chosen based on Acadian Flycatcher territory size and spatial independence between neighboring nesting pairs, might have been inappropriate. A more fitting spatial scale may be one that targets the foraging-area use of the chief predators; however, to do so would require a detailed predator-centered nest study, which was not available. Alternatively, patch cuts simply may not influence nest predation on Acadian Flycatcher nests; aside from measurement deficiencies, biological explanations for a lack of increased nest predation near cuts abound.

Researchers who have not found elevated levels of nest predation with proximity to clearcuts have given a number of plausible explanations. In contrast to agricultural edges, openings created by timber harvesting within forest interiors do not produce isolation (King et al. 1996). Furthermore, timber cuts regenerate quickly and are relatively small, making them unsuitable to support resident predator populations that are specialized to living in logged openings (Suarez et al. 1997). Additionally, timber openings have more abrupt edge zones making them less attractive to nesting birds and subsequently to nest predators (Rudnicky and Hunter 1993). Lastly, timber cuts do not provide the habitat or food subsidy for generalist nest predators typically associated with more productive agricultural fields or suburban habitats; therefore, they lack the population augmentation of generalist predators (DeGraaf 1995, Hanski et al. 1996, Huhta et al. 1996, Huhta et al. 1998a).

Prothonotary Warbler nests located in areas with greater exposure to patch cuts not only did not show increased risk of predation, but demonstrated reduced risk of predation compared with those located further within the forest interior. For the reasons stated above, we would not expect raccoons, the supposed main predator of Prothonotary Warbler nests, to be attracted to patch cut edges. Furthermore, telemetry studies have documented that raccoons do not show an affinity for clearcut edges at any spatial scale (Oehler and Litvaitis 1996, Dijak and Thompson 2000). Moreover, raccoons may actually avoid traveling through or near patch cuts because of the thick understory vegetation that may hinder their movement (e.g., Bowman and Harris 1980). Concerning nest predators other than raccoons, researchers have documented that abundances of potential avian predators (Blue Jay, American Crow, and Common Grackle; King and DeGraaf 2000, Moorman and Guynn 2001, Thompson et al. 1992) and small mammalian predators (eastern chipmunk, red squirrel, and murids; Cotterill and Hannon 1999, King and DeGraaf 2000, Pierre et al. 2001; but see King et al. 1998b) are not relatively higher within regenerating clearcut stands than within mature forest. In fact, King and DeGraaf (2000) reported that the major nest predators of their study site (Blue Jay, eastern chipmunk, and red squirrel) were forest-associated and actually reached their greatest abundances within the interior of the mature forest. Ratti and Reese (1988), who also found decreased nest predation closer to timber cuts, similarly concluded that their main predators (jays) were associated with forest and avoided clearcuts.

To summarize, we suggest that the difference between Acadian Flycatcher and Prothonotary Warbler nest predation relative to patch cuts may be partly explained by fine-scale habitat use and distribution of their main predators relative to the location of the cuts. Again, this explanation relies on the supposition that Acadian Flycatchers are more heavily preyed upon by edge-associated snakes, while Prothonotary Warblers are predominantly depredated by raccoons and other forest-associated species. Actual identification of the responsible predators, in conjunction with studying their autecology, is essential to clarifying the relationship that we observed. Identification of nest predators and research on their behavioral ecology and foraging strategies are necessary to fully interpret the effects of forest habitat disturbances on avian nest predation and would alleviate the need to infer cause from correlation (Schmidt 1999, Chalfoun et al. 2002b).

It is noteworthy that identifying patterns of nest predation requires investigation of predator-prey interactions at the appropriate spatial scale. For example, a previous study within our same site, examining nest success at the plot-scale, reported no difference in nest success rates of Prothonotary Warblers nesting on patch-cut treated plots (Wood 1999). Our findings suggest that it is informative and necessary to consider different spatial scales and to investigate specific causes of nest failure. Chalfoun et al. (2002b) documented that predator response (functional, numerical, or species richness) varied according to spatial scale (landscape, patch, or local edge) and that these responses were taxon-specific, with different predator species having distinct responses. For example, several studies have found that corvids respond to both landscape-scale and local-scale habitat features (Yahner and Scott 1988, Robinson and Robinson 1999). Small-mammal populations are often variable spatially and temporally (Heske 1995) and may depend on local and annual food availability or on micro-habitat characteristics such as amount of coarse woody debris (Bayne and Hobson 1997). Medium-sized mammalian predators may be more tied to landscape-scale than to local-scale features (Dijak and Thompson 2000; but see Oehler and Litvaitis 1996). Patterns of nest predation are complex and several interactions probably occur between different regions, landscapes, habitats, spatial scales, and predator species (Chalfoun et al. 2002b). Accurate interpretation of the mechanisms driving rates of nest predation will require viewing these ecological processes at multiple scales (Donovan et al. 1997).

HYDROLOGY

The risk of nest predation for both focal species was negatively related to the presence of water at all spatial scales: directly under the nest, within 11.3 meters (0.04 ha) of the nest, and on the 50-hectare study plot. We propose that the mechanism by which water decreases nest predation may vary depending upon whether or not the study area is completely inundated with floodwater. When the study area is only partially flooded (i.e., < 100% inundated), and dry land is an option, water at the micro- and macro-scale may act as a deterrent to some predators, thus affording protection to nests that are located over water. In support of this idea, researchers have reported decreased predation rates, as well as decreased diversity of potential predators, with increasing water depth. Jobin and Picman (1997) found that water acted as a barrier to terrestrial mammals (especially raccoons), preventing foraging within flooded areas and depredation of nests located over deep water. They also linked nest predation rates with temporal fluctuations in water depth during the breeding season, showing that seasonal increases in predation pressure were associated with decreasing water levels. Picman et al. (1993) documented that nest predation by raccoons decreased from 64% to 4% when nests were located over water greater than 40 cm deep. They also reported a decrease in predator diversity with increasing water depth, concluding that lower nest predation within deeply inundated areas resulted from the exclusion of many predators that occur on dry land. A similar study of Prothonotary Warblers reported a decrease to 0% predation when nest boxes were placed over water that was 30-50 cm deep (Petit 1989). These studies, however, were conducted in marsh-like habitats and may not be representative of results found within forested wetlands. However, parallel results were described by Hoover (2001) within the seasonally flooded bottomland hardwood forest of the Cache River Watershed of southern Illinois. Hoover (2001) documented a decrease in daily predation rates on Prothonotary Warbler nests as water depth underneath the nest increased. He ascertained that nests located over shallow (0-20 cm) water suffered nearly 4.5 times greater rates of predation than did nests located over deep (>30 cm) water and identified differential rates of nest predation by raccoons as the cause. Rates of nest predation by other predators such as snakes, squirrels, and avian species were not associated with water depth and contributed little to the overall trend of increased nest predation with decreased water depth; the conclusion being that these predators were able to move throughout the canopy without touching the ground (water) and were thus less hindered by water (Hoover 2001).

While water at the micro- and macro-scale may have deterred predators and reduced risk of nest predation when the study plots were partially flooded, we believe a different mechanism decreased predation when the study plots were completely inundated with water. Compared with before (<100%) and after (<100%) complete inundation of the plots, the risk of nest predation was significantly less when the plots were entirely flooded. When the study area was completely inundated, and dry land was not an option, water presumably would no longer act as a physical barrier protecting nests. In fact, when plots were completely submerged with water, plot-scale water coverage was effectively the only scale at which water functioned to reduce nest predation. Based on observation, predators within our study area adapted to flooding by taking up an arboreal existence during periods when the study area was entirely covered with water. Gehrt et al. (1993) similarly documented raccoons switch to an arboreal lifestyle during annual flooding of a forest. Although rat snakes are known to cross bodies of water (Durner and Gates 1993, Weatherhead and Hoysak 1989), they do not make regular use of such habitats (McAllister 1995). Rather, rat snakes are capable of maintaining an arboreal lifestyle throughout the bird-breeding season, when possible moving within a continuous canopy (Mullin and Cooper 2000). During the time that our potential nest predators were primarily arboreal, we propose that their movement was limited; they most likely foraged over smaller areas, thereby decreasing the number of nests that they encountered and took incidentally. Changes in the physical condition of the environment, such as flooding, can directly affect the abundance and distribution of species (Wakeley and Roberts 1996), as well as their activity levels and behavior, thereby altering predator-prey interactions (Schmidt 1999). These changes may manifest as measurable differences in nest encounter rates and predators' search effort and strategy, ultimately affecting the rate of nest predation (Schmidt 1999). When flooding occurs, raccoons reportedly move from tree to tree above the water, as well as through the water, moving less and presumably using decreased home ranges (e.g., Gehrt et al. 1993). Even small changes in water levels have been documented to alter the activity patterns of raccoons (Ivey 1948, as cited in Gehrt et al. 1993). It is unlikely that floodwater directly affects avian predators; however, it may have an indirect influence through availability of alternative prey. Litter arthropods, for example, must escape to the canopy or perish during flooding and thus may become more available as prey items to avian predators. In summary, we propose that complete inundation and the subsequent arboreal lifestyle of potential nest predators within our study area may have created a change in the area over which they foraged, the foraging strategies that they employed, and the prey items that they exploited. While it is possible that some potential predators vacated the flooded study area for drier uplands, it is unlikely; when flooding occurs, it is widespread and the closest dry land is often beyond the traveling range of most of our predators. Moreover, raccoons have been documented to remain entirely within flooded forests during extended periods (69-78 days) of inundation when dry land was nearby ($\leq$ 1.5 km; Gehrt et al. 1993).

Although we found that water decreased nest predation for both of our focal songbird species, the effect was considerably larger for Prothonotary Warblers than for Acadian Flycatchers; water was the most important habitat characteristic that we considered for Prothonotary Warbler nests while only moderately important for Acadian Flycatcher nests. We suggest that this disparity is a reflection of the two species' micro-scale nest-site characteristics and ultimately their main predators. Snakes, squirrels, and birds, which prey upon the nests of Acadian Flycatchers, are (semi-)arboreal by nature; their arboreal tendencies probably tempered the direct influence that the floodwater had on their movement and area use compared to that of more terrestrial predators (i.e., raccoons). Additionally, the low/absent affect of micro-scale water on the risk of nest predation for Acadian Flycatchers may have been a consequence of inappropriately applied methods; we measured water directly under the nest, rather than at the nest-tree bole where access to the nest by terrestrial predators may have been limiting. While under-the-nest and nest-tree bole are spatially equivalent for Prothonotary Warblers, because Acadian Flycatchers nest on branch edges of the canopy, these two locations can be distant from each other. This may explain why macro-scale water coverage, which likely encompassed the nest-tree bole, had the largest influence on risk of Acadian Flycatcher nest predation. Lastly, because Acadian Flycatchers nest later in the season than do Prothonotary Warblers, their exposure to plot-scale fluctuating water levels associated with seasonal flooding was less extensive, possibly contributing to the comparatively lower effect of plot-scale water coverage on Acadian Flycatcher nest predation.

Although we used a simplified version of water presence/absence at the micro-scale, we found that nest predation decreased with increasing water depth under the nest. Based on the findings of Petit (1989), Picman et al. (1993), and Hoover (2001) we used the depth of 35 cm to look for a possible threshold effect of water depth. We did not find evidence of a threshold; the risk of nest predation was significantly reduced in the presence of shallow (< 35 cm) and deep (> 35 cm) water, though the reduction was more substantial in the presence of deeper water. Although we suspect distance to dry land may be important and show an interesting interaction with water depth, we were unable to look at this aspect and plan to do so in the future. This was likely not a critical oversight; while Picman et al. (1993) reported that the mean distance to dry land was greater for non-depredated nests, he found that relative to water depth, distance was unimportant.

BROOD PARASITISM

Brood parasitism by Brown-headed Cowbirds significantly increased the risk of nest predation for Prothonotary Warblers. Other researchers have also reported increased predation on parasitized versus non-parasitized nests (Payne and Payne 1998, Dearborn 1999, McLaren and Sealy 2000); however, the evidence does not consistently show that predation rates of parasitized nests are higher (e.g., Hauber 2000). Brood parasitism may facilitate nest predation by drawing predators' attention to the nest. Increased activity and noise that occurs during cowbird-egg deposit, if it elicits host defense, or during the nestling stage as a result of increased begging calls and/or increased food provisioning by adults, may increase the conspicuousness of nests to predators that use visual and auditory cues to locate nests. With an elegant field experiment, Dearborn (1999) demonstrated that the intense begging behavior of cowbird nestlings was indeed partly responsible for observed differences in predation risk during the nestling period at parasitized and non-parasitized Indigo Bunting (*Passerina cyanea*) nests. Most interesting, we found that the risk of nest predation increased as the nest progressed through time, where parasitized nests exhibited increasingly higher rates of nest predation during the nestling stage than during the egg stage. Additionally, while parasitized nests were preyed upon more heavily than non-parasitized nests during the egg and the nestling stages, the difference was increasingly pronounced during the nestling stage. Thus, something during the nestling stage, be it cowbird-nestling vocalizations, increased feeding trips by adults, or some other factor, disproportionately attracted predators to the nest. If the intense begging behavior of cowbird nestlings attracts predators to the nest, one might expect that nests with more cowbird nestlings would have higher rates of predation. Looking at number of cowbird eggs, rather than nestlings, we did not find a positive relationship with the rate of nest predation; however, number of cowbird eggs laid does not necessarily correlate with number of cowbird nestlings, as nests with multiple cowbird eggs often suffer from less efficient brooding and have decreased hatching success (Friedman 1963, Peer and Bollinger 2000).

As stated earlier, during the egg stage, increased predation of nests may have resulted if the actual parasitism event elicited host defense, thus calling attention to the nest. This scenario is unlikely given two pieces of information: (1) nests that suffered multiple parasitism events did not suffer a commensurate increase in nest predation, and (2) cowbirds lay their eggs before sunrise (Scott 1991), prior to arrival of Prothonotary Warblers at their nests (30.78 ± 2.45 minutes after sunrise; Hoover 2001). Thus, Prothonotary Warblers do not encounter cowbirds while in the parasitism act. An alternative explanation is that increased predation on parasitized nests may represent a coincidental preference by nest predators and brood parasites for particular habitat and nest-site features (Donovan et al. 1997, Tewksbury et al. 1998, McLaren and Sealy 2000). We did find some similarities between habitat features of parasitized and depredated nests, namely, they tended to be in younger, more disturbed macro-habitats. Alternatively, a nest that is parasitized may be located by a cowbird because it was conspicuous (i.e., visually obvious due to poor concealment or easily detected due to adult host behavior); predators using similar nest-searching strategies and sensory cues to cowbirds may locate the nest for the very same reasons. Simply put, a poor nest-site may just be a poor nest-site, regardless of the offending species.

While parasitism status had a considerable influence on the risk of Prothonotary Warbler nest predation, it did not appear to affect predation on Acadian Flycatcher nests. One possible explanation for this observation is that the main predators of Acadian Flycatcher nests may not be attracted to increased noise associated with parasitized nests. Snakes respond to vomernasal cues and visual stimuli (Mullin and Cooper 1998) and avian predators are known to detect nests visually (Schmidt 1999); however, neither potential predators use auditory cues to forage. Alternatively, while we did not find similarities between habitat features of parasitized and depredated nests, we observed that one nest-site characteristic, nest height, had distinctly opposite relationships to brood parasitism and nest predation. While higher nests benefited from decreased risks of nest predation, they suffered from increased parasitism. Assuming nest predation causes a greater reduction in reproductive output per female than does brood parasitism (Schmidt and Whelan 1999, Grzybowski and Pease 2000), this may be an evolutionary trade-off that Acadian Flycatchers must accept. Given that nest height is an important characteristic and opposing force affecting the outcome of both nest predation and brood parasitism, such that higher nests evade predation while encountering increased parasitism, even if parasitized nests at lower heights are depredated more heavily, the relationship between brood parasitism and nest predation would be obscured.

SPECIES-SPECIFIC MICRO-HABITAT CHARACTERISTICS

ACADIAN FLYCATCHER – Several of the micro-scale characteristics of Acadian Flycatcher nest sites that we investigated showed no relationship to nest predation. We had predicted that nest position relative to the branch edge and the tree bole would influence concealment and accessibility of the nest from/to potential predators. Specifically, we predicted that nests further from the branch edge would be more concealed from avian predators searching from overhead perches, while nests located further from the nest-tree bole would be less accessible to terrestrial predators climbing from below. Neither of these nest-site characteristics, however, were related to risk of nest predation. It is likely that the location of Acadian Flycatcher nests at the edges of small branches away from the bole precludes predation by raccoons altogether; furthermore, there is little variation in horizontal nest position along the branch, making differential predation by other predators unlikely. Additionally, in environments with many predator species, the high incidence of nest predation and diversity of nest-searching tactics used by those predators may preclude the existence of predictably safe nest sites (Filliater et al. 1994).

Micro-scale (1-m^2) nest concealment by foliage surrounding the nest did not have an influence on the risk of nest predation. The typical micro-site in which Acadian Flycatchers place their nests is by nature relatively exposed to the elements. Thus, nest concealment may be a characteristic of little consequence. Regardless, we had predicted that highly concealed nests would be preyed upon less by visually oriented predators that directly detect nests or that use adult activity to locate nests. Acadian Flycatchers are conspicuous at their nest sites; females often call while on the nest and males will frequently call from perches within close proximity of the nest (personal observation). As a result, even the most concealed nests may not go unnoticed by potential predators. Variation in nest-site quality has been shown to influence nest predation (Martin 1993a,b, 1995, 1996, 1998, Martin and Roper 1988); however, parental activity and nest sites exert antagonistic influences on rates of nest predation, such that beneficial effects of the nest site could be masked by the negative effects of parental activity (Martin et al. 2000). Specifically, increased adult activity at the nest site increases rates of nest predation; thus, high adult activity can offset the benefits of a well-concealed nest (Martin et al. 2000).

Nest concealment has received a lot of attention from investigators of nest predation; however, the relationship between concealment and nest predation has not been consistent. In his extensive review, Martin (1992) concluded that in the majority of passerines studied, dense foliage directly around the nest reduced the probability of predation through concealment of the nest. Researchers have reported negative relationships between nest concealment and nest predation (Martin and Roper 1988, Manolis et al. 2000a), as well as no relationship (Filliater et al. 1994, Hanski et al. 1996, Howlett and Stutchbury 1996, Donovan et al. 1997, King et al. 1998a, Ortega and Capen 2001). Rangen et al. (1999) and Weidinger (2002) documented an interaction between nest concealment and predator type, finding that mice and voles depredated well-concealed nests, while squirrels and birds depredated poorly concealed nests. Because many mammalian predators rely on both olfactory and visual cues while foraging, cover at the nest and surrounding vegetation may not be important unless it restricts movement, whereas, cover may decrease predation by avian predators that rely on visual cues (Cotterill and Hannon 1999). As a generalization, nests surrounded with more vegetative cover are less likely to be depredated (Martin 1992); however, predator diversity, distribution, and search tactics (Martin 1987, Moller 1989), as well as the behavior of the songbird (Martin et al. 2000), are all important factors that must be taken into account.

A previous study within our same study site found that Acadian Flycatchers nested preferentially in Nuttall oaks (*Quercus nuttallii*) and tended to be more successful in this species than in other tree species (Wilson and Cooper 1998a, Cooper et al. 1999). It was hypothesized that the smooth bark of mature Nuttall oaks prevented rat snakes from climbing them, thus providing nest locations that were safe from these predators. Snakes use substrate irregularities to facilitate movement, thus smooth tree bark may hinder climbing attempts (e.g., Saenz et al. 1999, Mullin and Cooper 2002). Mullin and Cooper (2002) found that in the absence of vines (e.g., poison ivy, trumpet creeper, grape) on the tree bole, rat snakes were incapable of ascending the trunks of mature Nuttall oaks. With vines present to provide purchase points, snakes could climb Nuttall oaks; however, climbing was encumbered, resulting in longer than average ascension times. Their results indicate that the presence of vines on the nest-tree bole may be an important variable affecting risk of nest predation for birds nesting in trees with smooth bark.

With the findings of Wilson and Cooper (1998a) and Mullin and Cooper (2002) in mind, we examined the potential effect of nest-tree bole vines on the risk of Acadian Flycatcher nest predation. However, we did not find a relationship between vine presence/absence and nest predation. In addition to our principal investigation of vines, we made *post-hoc* explorations of nest-tree species, nest-tree DBH, and two-way interactions among all three variables. With the exception of a significant relationship between DBH and predation risk, which was correlated with nest height and thus excluded from our original analyses, we did not find any evidence of decreased risk of predation for nests located in Nuttall oaks. Because bark surfaces of trees vary with species as well as age/size/height, without detailed descriptions of the actual bark surfaces of the nest-tree, it is impossible to effectively investigate the potential relationship among tree species, bark texture, vines, and the risk of nest predation.

Even if rat snakes were unsuccessful at reaching nests located in the canopy of trees with smooth bark and no attending vines, exclusion of these nests from snake predation is not the only conclusion. Climbing trees to access nest contents is a substantial energetic cost, even if it is offset by the pursuit of immobile prey (Mullin and Cooper 2000). Visual confirmation of prey (an active nest) may be a prerequisite before rat snakes attempt to climb a tree; thus, maximizing the energetic gain (Mullin and Cooper 1998). Rat snakes are sensitive to the visual stimulus of nest provisioning and reportedly direct their foraging maneuvers towards such movements; however, the extent of their visual perception has only been documented up to 2 meters (Mullin and Cooper 1998). Acadian Flycatchers within our study nested at heights far above 2 meters and thus may have gone undetected by snakes on the ground. It is more likely that once a snake climbs a tree, it reduces the repeated energetic cost of ascending trees by remaining arboreal throughout the bird-breeding season, moving through continuous canopy when possible (Mullin and Cooper 2000). If this were the case, the presence of vines and the texture of bark would be immaterial to the risk of nest predation.

PROTHONOTARY WARBLER – The risk of nest predation of Prothonotary Warblers was positively related to the girth of the nest tree/snag; nests located in cavities of large diameter trees experienced increased risk of nest predation. Large trees/snags may be easier for terrestrial predators to climb, especially if the nest tree is an unstable snag. Cavities located on the trunks of large trees may also be more conspicuous to visually oriented predators. Although not assessed, large diameter nest trees may have tended to be live and contain a canopy, as opposed to stark snags devoid of branches and foliage. If so, potential predators may have already been active within these trees and taken nests incidentally. In contrast, nests located within cavities of snags are depredated by deterministic behavior of predators; that is, the predator would have no other reason to access the snag except for the goal of preying upon the nest. Unlike Acadian Flycatchers, nest-tree DBH for Prothonotary Warblers was not correlated with nest height; thus, the positive relationship that we observed between DBH and nest predation was not spurious, being caused by higher, less accessible nests.

The size of the cavity entrance had no effect on nest predation risk. We had predicted that nests located in larger cavities would encounter higher risk of predation owing to increased conspicuousness to visually oriented predators and easier access to predators that do not physically enlarge the cavity entrance to obtain the nest contents. Raccoons frequently rip open cavities, while post-depredated condition of the cavity also indicates that squirrels and woodpeckers enlarge cavity entrances to gain access (personal observation). Predation by Red-bellied Woodpeckers on small cavity-nesting songbirds is well substantiated (Brackbill 1969, Conner 1974, Watt 1980, Nilsson 1984, Dunn 1984, Neil and Harper 1990), even in nest-boxes with small-diameter (3.2 cm) entrances (Brackbill 1969). Even if exclusion of some predators by small cavity entrances occurred, compensatory predation by the diverse community of potential predators within our study area no doubt would offset any benefits.

CONSERVATION AND MANAGEMENT IMPLICATIONS

GENERAL

Nest predation is the most important factor influencing breeding productivity of forest-interior songbirds (Ricklefs 1969). To effectively manage for the conservation of these birds, it is critical to identify the specific habitat features that influence rates of nest predation (Martin 1992). Our results, as well as the results of numerous other studies (Nice 1957, Ricklefs 1969, Collias and Collias 1984, Martin and Roper 1988, Kulesza 1990, Martin and Li 1992, Martin

1993b), indicate that nest predation rates vary with attributes of nest sites. However, in environments with abundant and diverse predators, the high incidence of nest predation and diversity of nest-searching tactics used by those predators may preclude the existence of predictably safe nest sites (Filliater et al. 1994). While studies at local scales confirm the importance of nest predation, many have suggested that predation is intensified within landscapes that are fragmented by human activity (Robinson 1992, Sherry and Holmes 1992). Although it is recognized that characteristics of the nesting habitat at multiple spatial scales affect the incidence of nest predation, it is generally argued that landscape-level management is the most vital and effective in controlling nest predation (Robinson et al. 1995, Thompson et al. 1995, Donovan et al. 1997). It is commonly accepted that the best defense against high rates of nest predation is the maintenance of large contiguous forested habitats that contain substantial core areas where internal disturbance is absent or at least kept to a minimum (Robinson et al. 1995, Donovan et al. 1997).

TIMBER MANAGEMENT

The White River NWR is a large contiguous tract of forested habitat, however, it is narrow in shape and embedded within an agricultural landscape. As such, generalist predators abound within our study area and songbirds nesting within our study area are subjected to high rates of nest predation. While reclaiming land to regenerate and connect isolated patches of bottomland hardwood forests is an on-going management objective within the MAV (Bonney et al. 2000), Refuge managers within the White River NWR are concerned with management of the forest and wildlife within the confines of the Refuge. Results of our study suggest that disturbances within the Refuge’s forest-interior, namely roads, may negatively affect the reproductive success of songbirds by increasing rates of nest predation. Accordingly, reducing these types of disturbances within the Refuge may help alleviate some predation pressure on nests. Although results of our study did not indicate that timber cuts (< 3.5 ha) increased rates of nest predation, further research is needed; meanwhile, it would be prudent to maintain low levels of timber harvest. Furthermore, reducing open-canopy within the Refuge may decrease brood parasitism by cowbirds, which we demonstrated to be associated with increased risk of nest predation. More research, however, is needed to ascertain how these disturbances affect other birds nesting within the Refuge. It is necessary to always keep in mind that while one management effort may benefit some species within the community, it may be detrimental to other species (Thompson et al. 1992).

Silvicultural management for bottomland oak species is an ever-present occurrence; however, the effects of timber harvesting on the nest predation of forest-interior bottomland hardwood songbirds remains virtually unknown due to the dearth of studies on the effects of timber cutting within bottomland hardwood forests. Existing studies within bottomland hardwood forests have been limited to comparing nest success (Moorman et al. 2002) or relative abundance of predators (Moorman and Guynn 2001) in relation to small group cuts (< 0.5 ha), or to grouping nests by plot and comparing nest success between treated an untreated plots (Wood 1999, Twedt et al. 2001). Ours is the first study to examine species-specific risk of nest predation in relation to exposure of individual nests to medium-sized (2.2-3.4 ha) timber cuts within bottomland hardwood forests. Thus, there is high demand for more research on the effects of alternative timber management techniques within bottomland hardwood forests on the reproductive success of forest-interior songbirds. At this time, suggestions for decreasing internal edge associated with timber harvesting activities include using fewer large cuts rather than several small cuts and making cuts circular rather than rectangular in shape. Additionally, uneven-aged single-tree selection, which creates small canopy openings, is an alternative technique which creates less edge and may not increase nest predation.

While we documented habitat features at local scales (nest-site and nest-patch) that influenced rates of nest predation, identification of responsible predators is crucial to determining how management efforts can most effectively be applied to reduce nest predation. Once predators are identified, information on their abundance, distribution, behavior, and foraging strategies will help clarify the predator-prey interactions at work, thus allowing the practical implementation of management efforts. Lastly, while nest predation within the Refuge is high, it may not be limiting to populations of songbirds that breed within the Refuge. Nest predation has a large influence on nest success; however, it is reproductive output per female that determines whether or not a population is successfully replacing itself or is functioning as a sink (Pulliam 1988). Thus, while nest predation studies are invaluable, data on demographic variables such as seasonal fecundity and survivorship are the parameters necessary to fully assess the impact of management practices on bird population health and persistence.

WATER MANAGEMENT

Our findings with regard to water may be the most pertinent to management of songbird populations within the Refuge. As forested wetlands, bottomland hardwood forests perform valuable services for human society by moderating severe floods, maintaining water quality, and protecting balanced, indigenous populations of biota (Harris and Gosselink 1990). Bottomlands act primarily as temporary reservoirs between the uplands and downstream areas during floods, storing water that would otherwise add to the peak flow. As the flood peak passes, this water is released back into the stream, so that the flood peak is lower and longer when there is a well-developed floodplain. Therefore, bottomlands influence the timing, magnitude of discharge, and stage of the stream (Harris and Gosselink 1990). However, the natural function of bottomland hardwoods has been radically compromised due to five major human activities: 1) draining, usually to enhance dry land agriculture and foresting; 2) clearing for crop production, including agricultural, forestry, and aquaculture crops; 3) impounding for flood control, reservoirs, and production of flooded crops (rice, catfish); 4) stream channelization for navigation; and 5) floodplain isolation with levees (Gosselink et al. 1990). Besides severely reducing the amount of bottomland hardwoods, these modifications have drastically altered the hydrological regime of the remaining bottomland hardwoods. In general, water levels are significantly higher in the present day hydrograph than in the pre-settlement hydrograph (Yin et al. 1997). More significant to our study, is that river and floodplain modifications designed for flood control and navigation alter the natural seasonality (timing) of floods. For example, the effect of impoundments is to "smooth out" the flow by reducing flood peaks and prolonging moderate flows. Consequently, changing the timing of natural flooding, reducing the magnitude of the flooding (depth and spatial extent), and increasing the duration of the flooding (Gosselink et al. 1990).

There are two US Army Corps of Engineer projects, the White River Navigation Project and the Grand Prairie Irrigation Project, currently underway that may affect the existing flooding regime of the White River. While the current flooding pattern of the White River is not its "natural" condition (i.e., pre-1824; Yin et al. 1997), it is the existing state and the only condition with which managers of present day have to work. Our findings demonstrated the importance of the timing, depth, duration, and spatial extent of the flooding to the risk of nest predation, and thus breeding success, on two songbirds within the Refuge. In light of our findings, we believe it is crucial to study the effects that these two new projects may have on the existing flooding regime of the White River. The cumulative impacts of several site modifications can be dramatic; thus, it will be imperative to assess the direction and intensity of these two projects within the context of their cumulative effects (Gosselink et al. 1990). In addition to determining the projected changes in the current flooding patterns, we need to investigate how these changes may affect the nest predation pressure felt by songbirds breeding within the floodplain of the White River, and ultimately, how these changes may affect their reproductive success and overall fitness.

SUMMARY/CONCLUSION

Conservation of bird species depends on reducing the limiting nature of nest predation through knowledge of the birds' breeding biology, understanding their habitat requirements, and identifying and preserving the habitat features that positively affect their breeding productivity and survival (Martin 1992). Given that features of the nesting habitat may affect the reproduction and survival of breeding birds (Hilden 1965) and that nest predation is the main factor causing reproductive failure in birds (Ricklefs 1969), we attempted to identify the physical features of the nesting habitat that influenced nest predation.

We developed species-specific Cox regression models to assess the importance of multi-scale characteristics of the nesting habitat on the risk of nest predation. We demonstrated that risk of nest predation was influenced by habitat characteristics of the micro-scale nest site, the macro-scale nest patch, and the plot/landscape. For Acadian Flycatchers, these characteristics included nest height, stem density and macro-scale canopy height, and the presence of water at the macro- and plot-scale. Nest height was the most important nest/habitat characteristic that we considered, whereas macro-scale canopy height and macro-scale water coverage were of secondary importance. Macro-scale features of Prothonotary Warbler nesting habitat were not related to the risk of nest predation; however, risk was related to micro-scale nest-tree diameter, landscape-scale exposure to roads and patch cuts, as well as to the presence of water at the micro-, macro-, and plot-scale. Additionally, brood parasitism of Prothonotary Warbler nests increased their risk of being preyed upon. Water, at all three spatial scales, and parasitism status were the two habitat/nest characteristics of primary importance that we considered for Prothonotary Warblers. For both species, there were many features of the nest site that were not associated with predation risk, suggesting that safe nest sites may not exist in an environment with an abundance and diversity of predators (Filliater et al. 1994).

Habitat characteristics that were important for both species showed similar relationships with the risk of nest predation. We explained the observed relationships with our existing knowledge of the potential predator species within our study area, where possible, using information about their behavior and foraging strategies. Our theories relied heavily on the supposition that Acadian Flycatcher nests are primarily preyed upon by rat snakes, squirrels, and avian species, whereas raccoons, squirrels, rat snakes, and birds are responsible for depredating the nests of Prothonotary Warblers. Our insight into the actual mechanisms that produced the patterns we observed was limited by our lack of predator identification. Future research within our study area would benefit immensely from a predator-focused nest study that identified predators responsible for depredations and studied their abundance, spatial distribution, and behavior relative to the habitat and their prey. This type of information would help clarify the intricacies of predator-prey interactions that are currently beyond our grasp and would help us understand how particular management practices might affect these interactions.

Our findings indicate that human-induced disturbances within the forest-interior, such as roads, may negatively affect songbirds by increasing their risk of nest predation. Additionally, brood parasitism, which may increase with internal forest disturbances that reduce canopy cover, may intensify nest predation pressure. Thus, management efforts to reduce internal forest disturbances may be beneficial to songbirds breeding within the Refuge. Our results also highlight the importance of water within this system, demonstrating its role in reducing predation pressure on nests. We strongly recommend that current and future projects that may affect the flooding patterns of the Refuge be thoroughly investigated before onset for their potential effects on the breeding success of songbirds nesting within the Refuge.

Bottomland hardwood forests are the most productive and ecologically important wetland ecosystems in the world today (Conner 1994), contain some of the richest and most diverse plant and animal life found in North America (Mitsch and Gosselink 1986), and are of hemispheric importance to neotropical migratory birds as prime breeding habitat (Hunter et al. 1993). Drastic loss of this habitat has occurred and what remains is in an ecologically degraded condition, making it a habitat of regional concern (Hunter et al. 1993). Conservation of this habitat, and the species that live within it, should be a priority. As a forested wetland, the importance of hydrology to this ecosystem cannot be stressed enough. As a species that is intimately tied to both the habitat and water, Prothonotary Warblers may make an ideal indicator species for future studies of ecosystem health.

TABLES

Table 3.1: Justification for inclusion of predictor variables and their expected relationship to the risk of nest predation for Acadian Flycatchers. See Tables 2.2, 2.3, 2.4, and 2.14 for variable descriptions.

Variable	**Justification and Expected Relationship**
Micro-Scale	
Nest_Ht	Higher nests may be more difficult for ground dwelling predators to reach. Expected relationship to predation risk: negative.
Can_Cov	More canopy cover may provide concealment from avian predators. Expected relationship to predation risk: negative.
Dist_Edge	Further distance from branch edge may provide concealment from avian predators. Expected relationship to predation: negative
Dist_Bole	Nests located further from the tree bole may be more difficult to reach. Expected relationship to predation risk: negative.
Conceal	More concealment may make nests more difficult to find by visually oriented predators. Expected relationship: negative.
Vines	Dichotomous variable: 0=no vines, 1= one or more vines. Vines on the nest tree bole may make it easier for snakes to climb trees. Expected relationship to predation risk: positive.
Macro-Scale	
Stems	An increased shrub layer may provide more alternative prey items (other species' nests, as well as fruits) to generalists predators. Expected relationship to predation risk: negative.
Macro_PC1	Few, large, spread out trees may reflect areas with less disturbance and may attract fewer predators. Expected relationship: negative.
Macro_PC3	Taller trees may provide more potential nest sites, creating more places for predators to search. Expected relationship: negative.
Landscape Scale	
Rd_Edge_75	Roads may be used by predators to travel and disturbance may attract predators. Expected relationship to predation risk: positive.
Sl_Edge_75	When plots are dry, sloughs may attract predators for water and may be used as paths of travel. Expected relationship: positive.
Cut_Edge_75	Patch cuts create edge and may attract predators. Expected relationship to predation risk: positive.
Time-Dependent	
Water	Functions at the micro-, macro-, and landscape scale. When dry land is accessible, water may deter ground dwelling predators and afford protection. Expected relationship to predation risk: negative. When study area completely inundated, predators may be forced into trees. Expected relationship: positive. In other words, expect a U-shaped response to increasing water coverage.
Parasitism	Dichotomous variable: 0=not parasitized, 1=parasitized. Parasitism may attract predators due to: host defense when parasitized, increased vocalizations of parasitic young, and increased activity at nest when feeding parasitic young. Also could be correlative relationship with predation (i.e., nests may be depredated and parasitized simply because they are identified by predators and parasites for the same reasons). Expected relationship to predation risk: positive.

Table 3.2: Water variable combinations included in candidate models for the Cox regression analysis of Acadian Flycatchers and Prothonotary Warblers. The number of variables in each combination is indicated by *k*. Multi-scale combinations were limited for each species by correlations between water measurements at more than one scale. An "x" denotes the combinations used for each species. See Table 2.4 for detailed descriptions of each variable.

Variable Combinations	**k**	**Species**	
		Acadian Flycatcher	**Prothonotary Warbler**
Micro-Scale			
Depth	1	x	x
Wpresence	1	x	x
Depth2	2	x	x
Depth Trend	4	x	x
Macro-Scale			
Nest_Cov	1	x	x
Nest_Cov2	2	x	x
Landscape Scale			
Plot_Cov	1	x	x
Plot_Cov2	2	x	x
Plot_Cov Trend	4	x	x
Plot_Cov Dummies	4	x	x
Multi-Scale			
Depth + Nest_Cov	2		x
Depth + Nest_Cov + Depth*Nest_Cov	3		x
Wpresence + Plot_Cov	2		x
Nest_Cov + Plot_Cov	2		x

Table 3.3: Model averaged results from the Cox regression analysis of Acadian Flycatcher nest predation risk (Model A). Sample size equaled 339 nests, including 200 predation events and 139 censored nests. There were 432 candidate models, where each model contained a maximum of three variables. All candidate models were averaged to obtain unconditional estimates of parameters and their standard errors and confidence intervals. Hazard Ratio is the estimated proportionate response to a one-unit increase in the independent variable (other variables held fixed), Akaike Weight is the sum of relative AIC weight (Burnham and Anderson 1998) for those models in which the variable appears, and # Models is the number of models in which the variable appears. A “t” denotes variables that were transformed prior to analysis. Models were stratified by year and plot.

Variable		Parameter Estimate	Standard Error	90% Confidence Interval	Hazard Ratio	Akaike Weight	# Models
Micro	Nest_Ht	-0.1008	0.0337	{-0.1560 , -0.0456}	0.9041	0.9189	89
	Can_Cov^{t}	-0.0751	0.0708	{-0.1913 , 0.0410}	0.9276	0.1110	89
	Dist_Edge^{t}	-0.0102	0.0347	{-0.0672 , 0.0467}	0.9898	0.0667	89
	Dist_Bole^{t}	-0.1691	0.2089	{-0.5117 , 0.1736}	0.8444	0.0950	89
Macro	Stems^{t}	0.1632	0.1080	{-0.0139 , 0.3403}	1.1773	0.1945	89
	Macro_PC1	0.0094	0.0574	{-0.0848 , 0.1035}	1.0094	0.0653	89
	Macro_PC3	-0.1780	0.0854	{-0.3180 , -0.0380}	0.8370	0.4266	89
Landscape	Rd_Edge_75	-0.0006	0.0010	{-0.0021 , 0.0010}	0.9994	0.0765	89
	Sl_Edge_75	0.0002	0.0014	{-0.0021 , 0.0025}	1.0002	0.0647	89
	Cut_Edge_75	0.0010	0.0009	{-0.0004 , 0.0024}	1.0010	0.1176	89
Water	Wpresence	-0.2424	0.2244	{-0.6104 , 0.1256}	0.7847	0.0746	67
	Nest_Cov	-0.0050	0.0024	{-0.0090 , -0.0011}	0.9950	0.3792	67
	Plot_Cov	-0.0046	0.0030	{-0.0096 , 0.0003}	0.9954	0.1326	67
Other	Parasitism	0.1228	0.1878	{-0.1852 , 0.4308}	1.1307	0.0791	89

Table 3.4: Mean micro, macro, and landscape characteristics of Acadian Flycatcher nest sites. Means were calculated for the nests and variables included in the Cox regression models. Variables in *italics* were not included the models, but were used to derive the principal component macro-scale variables. Years and plots were combined to compute all means. Vines, Wpresence, Flood, and Parasitism are dichotomous variables, thus the values represent the mean of the 0/1 values, or the proportion of nests with a value of 1. Sample size is provided in parentheses with the following exceptions: Conceal and Vines (measured in 2000 only; n=71), Cut_Edge_75 (provided for plots D and E only; n=149), and Flood (derived for 1996 only; n=115). See Tables 2.2, 2.3, 2.4, and 2.14 for variable descriptions.

Variable	**Mean ± SE** (n=339)	**Min**	**Max**
Nest_Ht (m)	6.64 ± 0.13	1.50	16.47
Can_Cov (%)	96 ± 0.36	0	100
Dist_Edge (cm)	69 ± 2.21	10	250
Dist_Bole (m)	3.48 ± 0.09	0.40	8.70
Conceal	1.7 ± 0.08	0.5	3.7
Vines	0.31	----	----
Stems (#)	31.9 ± 1.68	0	348
Macro_PC1	0.2282 ± 0.0729	-2.9797	5.8378
Macro_PC3	-0.0211 ± 0.0552	-2.9121	4.0339
Can_Ht (m)	21.7 ± 0.18	12.3	34.4
Trees (#)	24.4 ± 0.50	4	56
DBH (cm)	21.3 ± 0.28	12.0	49.1
Tree_Dist (m)	5.25 ± 0.08	1.71	10.15
Rd_Edge_75 (m)	52.19 ± 4.41	0	363.78
Sl_Edge_75 (m)	21.96 ± 3.15	0	419.39
Cut_Edge_75 (m)	130.31 ± 11.67	0	457.03
Wpresence	0.40	----	----
Nest_Cov (%)	39 ± 2.56	0	100
Plot_Cov (%)	41 ± 2.20	0	100
Flood	0.24	----	----
Parasitism	0.29	----	----

Table 3.5: Mean micro, macro, and landscape characteristics of Acadian Flycatcher nest sites by predation event. Means were calculated for the nests and non-water variables included in the Cox regression models. Means were computed post analyses and were not used to investigate potential variable effects. Means are presented simply for the purpose of documentation. Variables in *italics* were not included the model, but were used to derive the principal component macro-scale variables. Years and plots were combined to compute all means. Vines and Parasitism are dichotomous variables, thus the values represent the mean of the 0/1 values, or the proportion of nests with a value of 1. Sample size is provided in parentheses with the following exceptions: Conceal and Vines (measured in 2000 only; n=37 depredated and 34 not depredated) and Cut_Edge_75 (provided for plots D and E only; n=84 depredated and 65 not depredated). See Tables 2.2, 2.3, and 2.14 for variable descriptions.

Variable	**Predation**	
	Depredated	**Not Depredated**
	Mean ± SE (n=200)	Mean ± SE (n=139)
Nest_Ht (m)	6.33 ± 0.15	7.08 ± 0.23
Can_Cov (%)	96 ± 0.32	96 ± 0.76
Dist_Edge (cm)	67 ± 2.78	72 ± 3.60
Dist_Bole (m)	3.44 ± 0.11	3.54± 0.14
Conceal	1.7 ± 0.11	1.8 ± 0.12
Vines	0.27	0.35
Stems (#)	32.6 ± 2.32	30.9 ± 2.38
Macro_PC1	0.1998 ± 0.1002	0.2692 ±0.1043
Macro_PC3	-0.1390 ± 0.0697	0.1486 ± 0.0882
Can_Ht (m)	21.3 ± 0.23	22.2 ± 0.29
Trees (#)	24.5 ± 0.65	24.2 ± 0.78
DBH (cm)	21.3 ± 0.39	21.3 ± 0.39
Tree_Dist (m)	5.33 ± 0.11	5.14 ± 0.10
Rd_Edge_75 (m)	51.67 ± 5.90	52.94 ± 6.62
Sl_Edge_75 (m)	19.53 ± 3.61	25.44 ± 5.66
Cut_Edge_75 (m)	143.68 ± 16.59	113.04 ± 15.87
Parasitism	0.27	0.32

Table 3.6: Mean water characteristics of Acadian Flycatcher nest sites by year and by predation event. Means were calculated for the nests and variables included in the Cox regression Model A. Wpresence is a dichotomous variable; thus, the value represents the mean of the 0/1 values or the proportion of nests that had water present at the micro-scale. Average water values were calculated for each nest over all nest checks from nest initiation to nest termination and mean values were calculated over all nests. Means were computed post analyses and were not used to investigate potential variable effects. Means are presented simply for the purpose of documentation. Plots were combined to compute all means. Sample sizes are provided in parentheses; the first number applies to depredated nests and the second number applies to non-depredated nests. See Table 2.4 for variable descriptions.

	Variable					
Year	**Wpresence**		**Nest_Cov (%)**		**Plot_Cov (%)**	
	Depredated	**Not Depredated**	**Depredated**	**Not Depredated**	**Depredated**	**Not Depredated**
	Proportion	Proportion	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
1996 (62,53)	0.89	0.87	88 ± 4.07	87 ± 4.70	88 ± 3.23	85 ± 4.42
1997 (77,35)	0.08	0.20	8 ± 2.55	21 ± 6.29	12 ± 0.55	14 ± 1.00
1998 (24,17)	0.46	0.29	43 ± 9.71	32 ± 11.11	47 ± 8.22	33 ± 8.25
2000 (37,34)	0.03	0.09	2 ± 1.45	7 ± 3.72	10 ± 1.22	12 ± 1.64

Table 3.7: Model averaged results from the Cox regression analysis of Acadian Flycatcher nest predation risk (Model B). Analysis included flood stage as an additional water variable, and included only the year 1996. Flood is a dichotomous time-dependent variable, where 0=during flooding (100% plot inundation) and 1=after flooding (< 100% plot inundation). Sample size equaled 115 nests, including 62 predation events and 53 censored nests. There were 499 candidate models, where each model contained a maximum of three variables. All candidate models were averaged to obtain unconditional estimates of parameters and their standard errors and confidence intervals. Hazard Ratio is the estimated proportionate response to a one-unit increase in the independent variable (other variables held fixed), Akaike Weight is the sum of relative AIC weight (Burnham and Anderson 1998) for those models in which the variable appears, and # Models is the number of models in which the variable appears. A "t" denotes variables that were transformed prior to analysis. Models were stratified by year and plot.

Variable		Parameter Estimate	Standard Error	90% Confidence Interval	Hazard Ratio	Akaike Weight	# Models
Micro	Nest_Ht	-0.0455	0.0613	{-0.1460 , 0.0550}	0.9555	0.1390	100
	Can_Cov^t	0.0797	0.1245	{-0.1244 , 0.2838}	1.0830	0.1399	100
	Dist_Edge^t	-0.0407	0.0640	{-0.1456 , 0.0642}	0.9601	0.1313	100
	Dist_Bole^t	-0.0703	0.3186	{-0.5929 , 0.4523}	0.9321	0.1115	100
Macro	Stems^t	-0.1270	0.1967	{-0.4495 , 0.1956}	0.8808	0.1317	100
	Macro_PC1	-0.0242	0.1057	{-0.1976 , 0.1492}	0.9761	0.1095	100
	Macro_PC3	-0.4828	0.1736	{-0.7675 , -0.1981}	0.6171	0.9019	100
Landscape	Rd_Edge_75	-0.0008	0.0017	{-0.0036 , 0.0020}	0.9992	0.1180	100
	Sl_Edge_75	0.0033	0.0045	{-0.0040 , 0.0107}	1.0034	0.1360	100
	Cut_Edge_75	0.0000	0.0017	{-0.0028 , 0.0027}	1.0000	0.1063	100
Water	Wpresence	-0.2767	0.2825	{-0.7399 , 0.1866}	0.7583	0.1225	67
	Nest_Cov	-0.0032	0.0029	{-0.0079 , 0.0015}	0.9968	0.1422	67
	Plot_Cov	-0.0023	0.0031	{-0.0073 , 0.0028}	0.9977	0.0993	67
	Flood	0.2510	0.2753	{-0.2005 , 0.7026}	1.2854	0.1155	67
Other	Parasitism	0.0298	0.3759	{-0.5867 , 0.6463}	1.0303	0.1066	100

Table 3.8: Model averaged results from the Cox regression analysis of Acadian Flycatcher nest predation risk (Model C). Analysis used nests from year 2000 only and included two additional micro-habitat variables; conceal and vines. Water variables were not included in the analysis. Sample size equaled 71 nests, including 37 predation events and 34 censored nests. There were 377 candidate models, where each model contained a maximum of three variables. All candidate models were averaged to obtain unconditional estimates of parameters and their standard errors and confidence intervals. Hazard Ratio is the estimated proportionate response to a one-unit increase in the independent variable (other variables held fixed), Akaike Weight is the sum of relative AIC weight (Burnham and Anderson 1998) for those models in which the variable appears, and # Models is the number of models in which the variable appears. A “t” denotes variables that were transformed prior to analysis. Models were stratified by year and plot.

Variable		Parameter Estimate	Standard Error	90% Confidence Interval	Hazard Ratio	Akaike Weight	# Models
Micro	Nest_Ht	-0.0700	0.0747	{-0.1925 , 0.0526}	0.9324	0.1311	79
	Can_Cov^{t}	0.0783	0.1637	{-0.1902 , 0.3468}	1.0814	0.0957	79
	Dist_Edge^{t}	0.1246	0.0951	{-0.0314 , 0.2806}	1.1327	0.1955	79
	Dist_Bole^{t}	-0.5168	0.4561	{-1.2648 , 0.2312}	0.5964	0.1611	79
	Conceal	-0.2485	0.2715	{-0.6937 , 0.1967}	0.7800	0.1302	79
	Vines	-0.3728	0.3973	{-1.0243 , 0.2787}	0.6888	0.1333	79
Macro	Stems^{t}	0.4983	0.2375	{0.1088 , 0.8878}	1.6459	0.5502	79
	Macro_PC1	-0.2699	0.1562	{-0.5260 , -0.0138}	0.7635	0.3373	79
	Macro_PC3	-0.3099	0.1606	{-0.5733 , -0.0465}	0.7335	0.3862	79
Landscape	Rd_Edge_75	0.0012	0.0023	{-0.0025 , 0.0049}	1.0012	0.0993	79
	Sl_Edge_75	0.0000	0.0036	{-0.0059 , 0.0060}	1.0000	0.0890	79
	Cut_Edge_75	0.0031	0.0020	{-0.0001 , 0.0063}	1.0031	0.2724	79
Other	Parasitism	0.1129	0.4172	{-0.5714 , 0.7971}	1.1195	0.0894	79

Table 3.9: Justification for inclusion of predictor variables and their expected relationship to the risk of nest predation for Prothonotary Warblers. See Tables 2.2, 2.3, 2.4, and 2.14 for variable descriptions.

Variable	Justification and Expected Relationship
Micro-Scale	
Nest_Ht	Higher nests may be more difficult for ground dwelling predators to reach. Expected relationship to predation risk: negative.
Can_Cov	More canopy cover may provide concealment from avian predators. Expected relationship to predation risk: negative.
Tree_DBH	Smaller snags may wobble more when disturbed by a predator and allow nestlings close to fledging to escape (aka burglar alarm theory). Alternatively, larger trees may provide easier access for ground predators. Expected relationship to predation risk: positive.
Cav_Code	Larger cavities may be more obvious to visually oriented predators and may provide easier access for predators that do not rip the cavity open (e.g., squirrels, birds, and snakes). Expected relationship to predation risk: positive.
Macro-Scale	
Stems	An increased shrub layer may provide more alternative prey items (other species' nests, as well as fruits) to generalists predators. Expected relationship to predation risk: negative.
Macro_PC1	Few, large, spread out trees may reflect areas with less disturbance and may attract fewer predators. Expected relationship: negative.
Macro_PC3	Taller trees may provide more potential nest sites, creating more places for predators to search. Expected relationship: negative.
Landscape Scale	
Rd_Edge_75	Roads may be used by predators to travel and disturbance may attract predators. Expected relationship to predation risk: positive.
Sl_Edge_75	When plots are dry, sloughs may attract predators for water and may be used as paths of travel. Expected relationship: positive.
Cut_Edge_75	Patch cuts create edge and may attract predators. Expected relationship to predation risk: positive.
Time-Dependent	
Water	Functions at the micro-, macro-, and landscape scale. When dry land is accessible, water may deter ground dwelling predators and afford protection. Expected relationship to predation risk: negative. When study area completely inundated, predators may be forced into trees. Expected relationship: positive. In other words, expect a U-shaped response to water coverage.
Parasitism	Dichotomous variable: 0=not parasitized, 1=parasitized. Parasitism may attract predators due to: host defense when parasitized, increased vocalizations of parasitic young, and increased activity at nest when feeding parasitic young. Also could be correlative relationship with predation (i.e., nests may be depredated and parasitized simply because they are identified by predators and parasites for the same reasons). Expected relationship to predation risk: positive.

Table 3.10: Model averaged results from the Cox regression analysis of Prothonotary Warbler nest predation risk (Model A). Analysis included all variables of interest that were measured during each year at all spatial scales, and thus excluded data from 1998. Sample size equaled 314 nests, including 173 predation events and 141 censored nests. There were 470 candidate models, where each model contained a maximum of three variables. All candidate models were averaged to obtain unconditional estimates of parameters and their standard errors and confidence intervals. Hazard Ratio is the estimated proportionate response to a one-unit increase in the independent variable (other variables held fixed), Akaike Weight is the sum of relative AIC weight (Burnham and Anderson 1998) for those models in which the variable appears, and # Models is the number of models in which the variable appears. A "t" denotes variables that were transformed prior to analysis. An asterisk denotes an interaction. Models were stratified by year and plot.

Variable		Parameter Estimate	Standard Error	90% Confidence Interval	Hazard Ratio	Akaike Weight	# Models
Micro	Nest_Ht	0.0353	0.1028	{-0.1333 , 0.2038}	1.0359	0.0534	92
	Can_Cov^t	0.0035	0.0803	{-0.1282 , 0.1351}	1.0035	0.0497	92
	Tree_DBH	0.0253	0.0124	{0.0049 , 0.0458}	1.0257	0.2792	92
	Cav_Code	-0.0425	0.0993	{-0.2054 , 0.1204}	0.9584	0.0548	92
Macro	Stems^t	-0.0188	0.1050	{-0.1910 , 0.1534}	0.9814	0.0500	92
	Macro_PC1	-0.0695	0.0615	{-0.1704 , 0.0313}	0.9328	0.0913	92
	Macro_PC3	-0.0524	0.0919	{-0.2032 , 0.0983}	0.9489	0.0589	92
Landscape	Rd_Edge_75	0.0016	0.0011	{-0.0002 , 0.0034}	1.0016	0.1299	92
	Sl_Edge_75	-0.0012	0.0015	{-0.0037 , 0.0013}	0.9988	0.0694	92
	Cut_Edge_75	-0.0039	0.0018	{-0.0069 , -0.0008}	0.9962	0.3665	92
Water	Wpresence	-0.4483	0.1955	{-0.7690 , -0.1277}	0.6387	0.3260	80
	Nest_Cov	-0.0050	0.0023	{-0.0087 , -0.0013}	0.9950	0.2610	80
	Plot_Cov	-0.0069	0.0033	{-0.0124 , -0.0015}	0.9931	0.3010	92
Other	Parasitism	-0.6472	0.5497	{-1.5488 , 0.2544}	0.5235	0.4184	105
	Parasitism*time	0.0857	0.0287	{0.0386 , 0.1328}	1.0895	0.3338	14

Table 3.11: Model averaged results from the Cox regression analysis of Prothonotary Warbler nest predation risk (Model B). Analysis included variables at all spatial scales, including extracted macro-scale values for 1998, and included data from all years. Analysis excluded micro-scale cavity and macro-scale stem variables. Sample size equaled 461 nests, including 272 predation events and 189 censored nests. There were 299 candidate models, where each model contained a maximum of three variables. All candidate models were averaged to obtain unconditional estimates of parameters and their standard errors and confidence intervals. Hazard Ratio is the estimated proportionate response to a one-unit increase in the independent variable (other variables held fixed), Akaike Weight is the sum of relative AIC weight (Burnham and Anderson 1998) for those models in which the variable appears, and # Models is the number of models in which the variable appears. A "t" denotes variables that were transformed prior to analysis. An asterisk denotes an interaction. Models were stratified by year and plot.

Variable		Parameter Estimate	Standard Error	90% Confidence Interval	Hazard Ratio	Akaike Weight	# Models
Micro	Nest_Ht	0.0564	0.0702	{-0.0588 , 0.1715}	1.0580	0.0081	67
	Can_Cov^t	-0.0059	0.0689	{-0.1189 , 0.1071}	0.9941	0.0059	67
	Tree_DBH	0.0244	0.0095	{0.0088 , 0.0400}	1.0247	0.0625	67
Macro	Macro_PC1	-0.0573	0.0551	{-0.1477 , 0.0331}	0.9443	0.0102	67
	Macro_PC3	0.0075	0.0849	{-0.1317 , 0.1468}	1.0075	0.0061	67
Landscape	Rd_Edge_75	0.0012	0.0008	{-0.0002 , 0.0026}	1.0012	0.0158	67
	Sl_Edge_75	-0.0008	0.0013	{-0.0028 , 0.0013}	0.9992	0.0072	67
	Cut_Edge_75	-0.0022	0.0015	{-0.0046 , 0.0002}	0.9978	0.0188	67
Water	Wpresence	-0.7087	0.1487	{-0.9526 , -0.4648}	0.4923	0.5415	57
	Nest_Cov	-0.0077	0.0016	{-0.0104 , -0.0051}	0.9923	0.4114	57
	Plot_Cov	-0.0076	0.0029	{-0.0125 , -0.0028}	0.9924	0.0641	67
Other	Parasitism	-0.6628	0.2821	{-1.1254 , -0.2002}	0.5154	0.9217	78
	Parasitism*time	0.0811	0.0210	{0.0466 , 0.1155}	1.0845	0.9087	12

Table 3.12: List of the 11 top-ranked (out of 299) candidate models that comprised the 95% confidence set of models for the Model B Cox regression analysis of Prothonotary Warbler nest predation risk. The models are ranked from the highest weighted (smallest ΔAICc, largest AICc Weight) model to the lowest weighted (largest ΔAICc, smallest AICc Weight) model. The number of parameters per model is indicated by *k*. Although there was not one "best" model that explained nest survival from predation, models 1 and 2 combined accounted for 86% of the total Akaike weight shared among the 299 candidate models. The first-ranked model was only 1.2 times more likely than the second-ranked model to be the "best", but it was 10.8 times more likely than the third-ranked model and 66.6 times more likely than the fourth-ranked model. Based on these values, we can assume that the top three-ranked models are "best". The top three ranked models contained covariates describing two main habitat/nest characteristics involving water and parasitism status; water was expressed at each spatial scale, but the models were distinguished (in rank order) by increasing spatial scale of water. Water at one or more spatial scales was present in each model of the 95% confidence set.

Model	Covariates			k	ΔAICc	AICc_W
1	Wpresence	Parasitism	Parasitism*time	3	0	0.4795
2	Nest_Cov	Parasitism	Parasitism*time	3	0.4402	0.3848
3	Plot_Cov	Parasitism	Parasitism*time	3	4.7646	0.0443
4	Tree_DBH	Rd_Edge_75	Wpresence	3	8.4083	0.0072
5	Tree_DBH	Cut_Edge_75	Wpresence	3	8.4686	0.0069
6	Tree_DBH	Wpresence	Plot_Cov	3	8.7600	0.0060
7	Tree_DBH	Wpresence		2	8.8595	0.0057
8	Tree_DBH	Macro_PC1	Wpresence	3	9.4318	0.0043
9	Tree_DBH	Wpresence	Parasitism	3	9.8819	0.0034
10	Tree_DBH	Cut_Edge_75	Nest_Cov	3	10.1953	0.0029
11	Nest_Ht	Tree_DBH	Wpresence	3	10.3452	0.0027

Table 3.13: Mean micro, macro, and landscape characteristics of Prothonotary Warbler nest sites. Means were calculated for the nests and variables included in the Cox regression models. Variables in *italics* were not included the models, but were used to derive the index of Cav_Code and the principal component macro-scale variables. Years and plots were combined to compute all means. Wpresence, Flood, and Parasitism variables are dichotomous; thus, the values represent the mean of the 0/1 values, or the proportion of nests with a value of 1. Sample size is provided in parentheses with the following exceptions: Cav_Code (n=296), Stems and the original macro-scale variables (not measured in 1998; n=314), Cut_Edge_75 (provided for plots D and E only; n=207), and Flood (derived for 1996 and 1998 only; n=280). See Tables 2.2, 2.3, 2.4, and 2.14 for variable descriptions.

Variable	**Mean ± SE** (n=461)	**Min**	**Max**
Nest_Ht (m)	2.45 ± 0.04	0.48	6.70
Can_Cov (%)	91 ± 0.40	30	100
Tree_DBH (cm)	14.5 ± 0.30	2.5	55.3
Cav_Code	2.3 ± 0.05	1	5
Cav_Ht (cm)	7.16 ± 0.37	2.8	50
Cav_Wid (cm)	4.72 ± 0.10	2	18.5
Stems (#)	28.3 ± 1.35	1	142
Macro_PC1	-0.2417 ± 0.0595	-5.0011	3.5460
Macro_PC3	0.1151 ± 0.0386	-2.3843	2.8223
Can_Ht (m)	21.9 ± 0.18	11.2	32.4
Trees (#)	28.4 ± 0.54	5	65
DBH (cm)	21.1 ± 0.26	13.6	40.5
Tree_Dist (m)	4.71 ± 0.07	1.23	10.34
Rd_Edge_75 (m)	44.11 ± 3.36	0	361.86
Sl_Edge_75 (m)	21.51 ± 2.52	0	492.09
Cut_Edge_75 (m)	57.75 ± 5.06	0	227.65
Wpresence	0.62	----	----
Nest_Cov (%)	62 ± 2.12	0	100
Plot_Cov (%)	53 ± 1.90	1	100
Flood_B	0.22	----	----
Flood_D	0.53	----	----
Parasitism	0.35	----	----

Table 3.14: Mean micro, macro, and landscape characteristics of Prothonotary Warbler nest sites by predation event. Means were calculated for the nests and variables included in the Cox regression models. Means were computed post analyses and were not used to investigate potential variable effects. Means are presented simply for the purpose of documentation. Variables in *italics* were not included the model, but were used to derive the index of Cav_Code and the principal component macro-scale variables. Years and plots were combined to compute all means. Parasitism is a dichotomous variable; thus, the values represent the mean of the 0/1 values, or the proportion of nests that were parasitized. Sample size is provided in parentheses with the following exceptions: Cav_Code, Stems, and the original macro-scale variables (n=173 depredated and 141 not depredated) and Cut_Edge_75 (provided for plots D and E only; n= 127 depredated and 80 not depredated). See Tables 2.2, 2.3, and 2.14 for variable descriptions.

Variable	**Predation**	
	Depredated	**Not Depredated**
	Mean ± SE (n=272)	Mean ± SE (n=189)
Nest_Ht (m)	2.50 ± 0.06	2.36 ± 0.07
Can_Cov (%)	91 ± 0.53	90 ± 0.61
Tree_DBH (cm)	15.1 ± 0.43	13.5 ± 0.38
Cav_Code	2.3 ± 0.07	2.3 ± 0.07
Cav_Ht (cm)	6.38 ± 0.37	8.08 ± 0.67
Cav_Wid (cm)	4.91 ± 0.16	4.49 ± 0.10
Stems (#)	30.0 ± 2.04	26.2 ± 1.65
Macro_PC1	-0.2199 ± 0.0773	-0.2730 ± 0.0934
Macro_PC3	0.1211 ± 0.0513	0.1065 ± 0.0586
Can_Ht (m)	21.9 ± 0.26	22.0 ± 0.25
Trees (#)	28.7 ± 0.74	28.2 ± 0.79
DBH (cm)	21.2 ± 0.34	21.0 ± 0.42
Tree_Dist (m)	4.72 ± 0.11	4.69 ± 0.09
Rd_Edge_75 (m)	48.14 ± 4.57	38.32 ± 4.89
Sl_Edge_75 (m)	20.91 ± 3.07	22.37 ± 4.28
Cut_Edge_75 (m)	52.03 ± 6.37	66.82 ± 8.27
Parasitism	0.38	0.30

Table 3.15: Mean water characteristics of Prothonotary Warbler nest sites by year and by predation event. Means were calculated for the nests and variables included in the Cox regression Model B. Wpresence is a dichotomous variable; thus, the value represents the proportion of nests that had water present at the micro-scale. Average water values were calculated for each nest over all nest checks from nest initiation to nest termination and mean values were calculated over all nests. Means were computed post analyses and were not used to investigate potential variable effects. Means are presented simply for the purpose of documentation. Plots were combined to compute all means. Sample sizes are provided in parentheses; the first number applies to depredated nests and the second number applies to non-depredated nests. See Table 2.4 for variable descriptions.

Year	Variable					
	Wpresence		**Nest_Cov (%)**		**Plot_Cov (%)**	
	Depredated	**Not Depredated**	**Depredated**	**Not Depredated**	**Depredated**	**Not Depredated**
	Proportion	Proportion	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
1996 (62,54)	0.77	0.82	74 ± 5.15	79 ± 5.02	70 ± 4.56	71 ± 4.92
1997 (71,69)	0.58	0.65	59 ± 5.46	67 ± 5.24	49 ± 4.56	50 ± 4.62
1998 (78,34)	0.76	0.82	77 ± 4.66	84 ± 6.01	70 ± 4.64	81 ± 6.13
2000 (61,32)	0.28	0.09	26 ± 4.82	10 ± 5.14	13 ± 1.20	13 ± 1.85

Table 3.16: Model averaged results from the Cox regression analysis of Prothonotary Warbler nest predation risk (Model C). Analysis excluded micro-scale cavity and all macro-habitat variables, but included all years. Sample size equaled 513 nests, including 306 predation events and 207 censored nests. There were 176 candidate models, where each model contained a maximum of three variables. All candidate models were averaged to obtain unconditional estimates of parameters and their standard errors and confidence intervals. Hazard Ratio is the estimated proportionate response to a one-unit increase in the independent variable (other variables held fixed), Akaike Weight is the sum of relative AIC weight (Burnham and Anderson 1998) for those models in which the variable appears, and # Models is the number of models in which the variable appears. A "t" denotes variables that were transformed prior to analysis. An asterisk denotes an interaction. Models were stratified by year and plot.

Variable		Parameter Estimate	Standard Error	90% Confidence Interval	Hazard Ratio	Akaike Weight	# Models
Micro	Nest_Ht	0.0273	0.0659	{-0.0808 , 0.1354}	1.0277	0.0135	46
	Can_Cov^t	-0.0101	0.0677	{-0.1212 , 0.1010}	0.9899	0.0126	46
	Tree_DBH	0.0274	0.0093	{0.0122 , 0.0426}	1.0278	0.2739	46
Landscape	Rd_Edge_75	0.0020	0.0008	{0.0007 , 0.0033}	1.0020	0.1986	46
	Sl_Edge_75	-0.0014	0.0011	{-0.0031 , 0.0003}	0.9986	0.0314	46
	Cut_Edge_75	-0.0019	0.0013	{-0.0041 , 0.0002}	0.9981	0.0362	46
Water	Wpresence	-0.6857	0.1404	{-0.9160 , -0.4554}	0.5037	0.7708	38
	Nest_Cov	-0.0071	0.0015	{-0.0096 , -0.0046}	0.9929	0.1961	38
	Plot_Cov	-0.0059	0.0031	{-0.0110 , -0.0007}	0.9941	0.0686	46
Other	Parasitism	-0.5210	0.2823	{-0.9841 , -0.0580}	0.5939	0.6986	55
	Parasitism*time	0.0711	0.0196	{0.0390 , 0.1031}	1.0737	0.6638	10

Table 3.17: Model averaged results from the Cox regression analysis of Prothonotary Warbler nest predation risk (Model D). Analysis included flood stage as an additional water variable, and included only years 1996 and 1998. Analysis excluded micro-scale cavity and all macro-habitat variables. Sample size equaled 281 nests, including 175 predation events and 106 censored nests. There were 184 candidate models, where each model included a maximum of three variables. All candidate models were averaged to obtain unconditional estimates of parameters and their standard errors and confidence intervals. Hazard Ratio is the estimated proportionate response to a one-unit increase in the independent variable (other variables held fixed), Akaike Weight is the sum of relative AIC weight (Burnham and Anderson 1998) for those models in which the variable appears, and # Models is the number of models in which the variable appears. A "t" denotes variables that were transformed prior to analysis. An asterisk denotes an interaction. Models were stratified by year and plot.

Variable		Parameter Estimate	Standard Error	90% Confidence Interval	Hazard Ratio	Akaike Weight	# Models
Micro	Nest_Ht	0.0203	0.0796	{-0.1103 , 0.1509}	1.0205	0.0887	47
	Can_Cov^t	-0.0370	0.0980	{-0.1977 , 0.1238}	0.9637	0.0928	47
	Tree_DBH	0.0260	0.0119	{0.0065 , 0.0456}	1.0264	0.5303	47
Landscape	Rd_Edge_75	0.0020	0.0010	{0.0004 , 0.0037}	1.0020	0.4634	47
	Sl_Edge_75	-0.0014	0.0014	{-0.0037 , 0.0009}	0.9986	0.1444	47
	Cut_Edge_75	-0.0012	0.0017	{-0.0040 , 0.0016}	0.9988	0.1112	47
Water	Wpresence	-0.9168	0.1735	{-1.2014 , -0.6322}	0.3998	0.8726	38
	Nest_Cov	-0.0089	0.0018	{-0.0119 , -0.0059}	0.9911	0.1258	38
	Plot_Cov	0.0000	0.0034	{-0.0056 , 0.0056}	1.0000	0.0879	46
	Flood_B	-0.1892	0.3139	{-0.7040 , 0.3257}	0.8277	0.0001	8
	Flood_D	-0.6834	0.1800	{-0.9786 , -0.3882}	0.5049	0.0001	8
Other	Parasitism	-0.0100	0.2958	{-0.4952 , 0.4751}	0.9900	0.1595	56
	Parasitism*time	0.0517	0.0256	{0.0097 , 0.0938}	1.0531	0.0441	10

Table 3.18: Moran's I and values of significance for spatial autocorrelation among the nest fates of (a) Acadian Flycatcher nests and (b) Prothonotary Warbler nests located within a 100 meter distance interval. The # Pairs column indicates the number of neighboring nests used for the analysis within each breeding season. The analysis was conducted twice: once using the raw nest fates (depredated/not depredated) and once using the residuals from the Cox regression model. A p-value of 0.05 was considered significant; however, we were only concerned with positive spatial autocorrelation (which would be indicated by a significant positive value of the Moran's I).

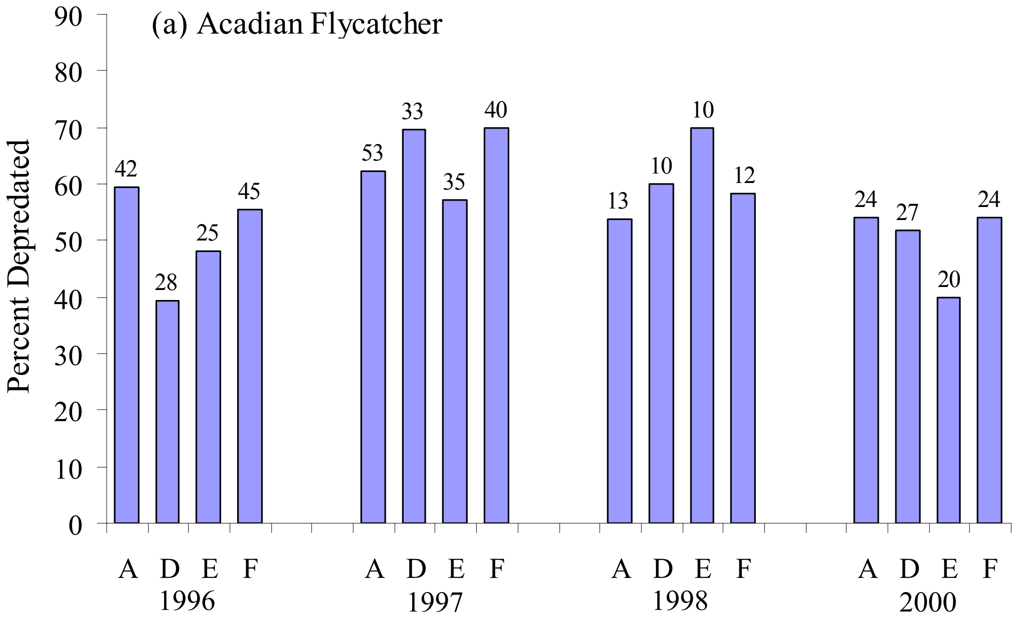
(a) Acadian Flycatcher

Year	# Pairs	Raw			Residual		
		Moran's I	z-score	p-value	Moran's I	z-score	p-value
1996	149	0.0656	0.9197	0.179	0.0110	0.2446	0.405
1997	119	-0.0026	0.0707	0.472	0.0597	0.7578	0.224
1998	19	0.0102	0.1560	0.436	0.0516	0.3419	0.367
2000	28	-0.2340	-1.1700	0.121	-0.2849	-1.4501	0.074

(b) Prothonotary Warbler

Year	# Pairs	Raw			Residual		
		Moran's I	z-score	p-value	Moran's I	z-score	p-value
1996	111	0.0011	0.1038	0.460	0.0282	0.3960	0.345
1997	104	-0.0443	-0.3816	0.352	-0.0139	-0.0688	0.472
1998	149	-0.1111	-1.2761	0.100	-0.1154	-1.3326	0.093
2000	55	-0.2229	-1.5991	0.055	-0.3189	-2.3299	0.010

FIGURES



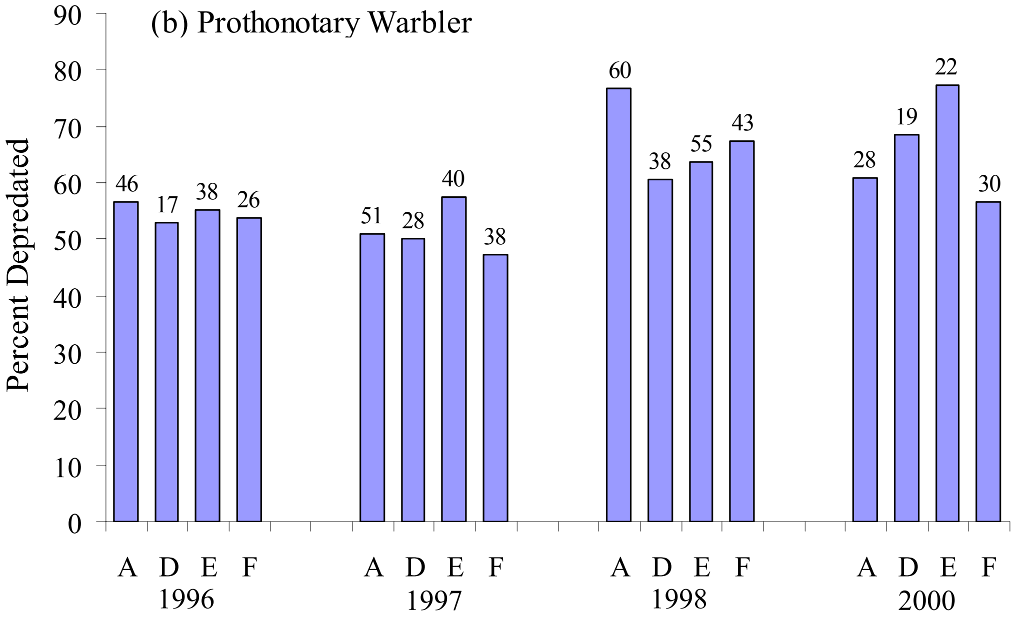
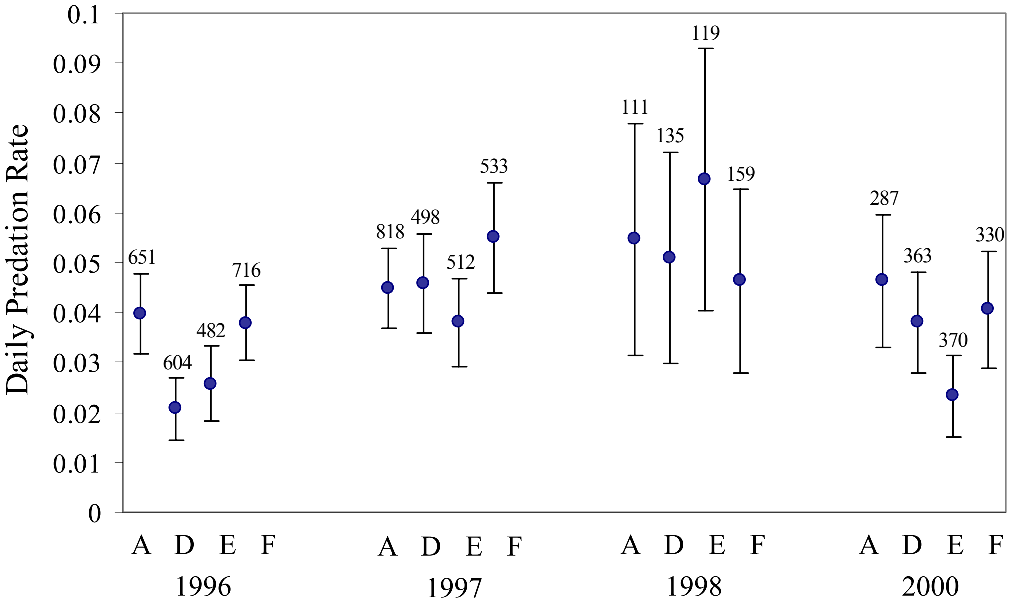


Figure 3.1: The percent of (a) Acadian Flycatcher and (b) Prothonotary Warbler nests that were depredated by year and plot. Numbers above columns indicate sample size.

(a) Acadian Flycatcher



(b) Prothonotary Warbler

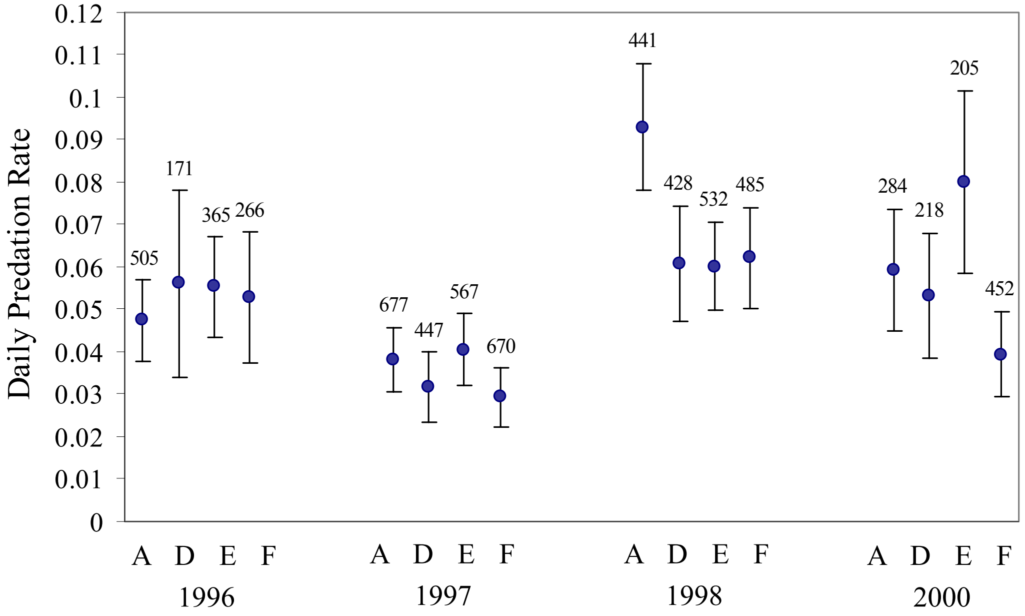


Figure 3.2: Daily predation rate of (a) Acadian Flycatcher nests by year and plot (n=436) and (b) Prothonotary Warbler nests by year and plot (n=574). Bars represent ± 1 SE. Numbers above bars indicate the number of nest exposure days.

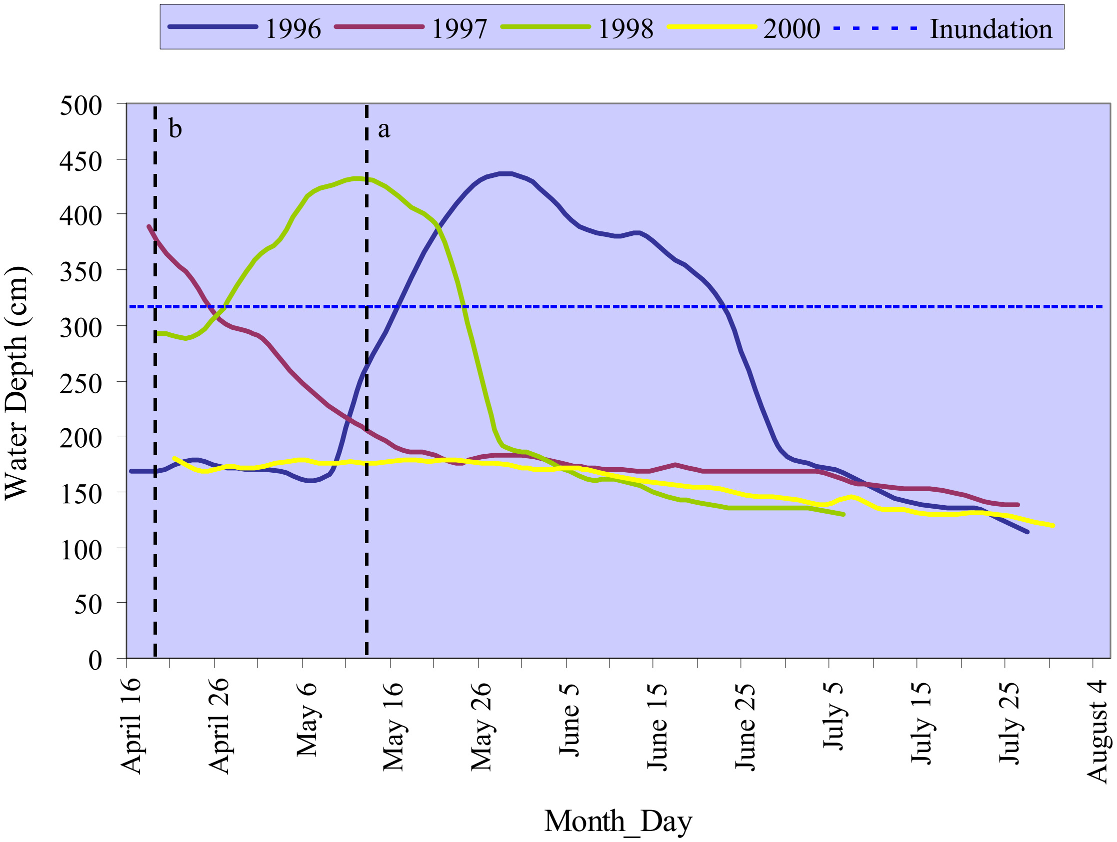


Figure 3.3: Water depths during the breeding seasons of 1996, 1997, 1998, and 2000. The depths depicted here represent depths at the lowest elevation point on plot F. When the depth exceeds the horizontal "Inundation" line, all areas of the plot are completely under water. The water pattern depicted here is representative of the pattern observed on all four study plots during the four years. The vertical line denoted as "a" indicates the average nest initiation date for Acadian Flycatchers during the four years. The line designated as "b" indicates the average nest initiation date for Prothonotary Warblers during the four years.

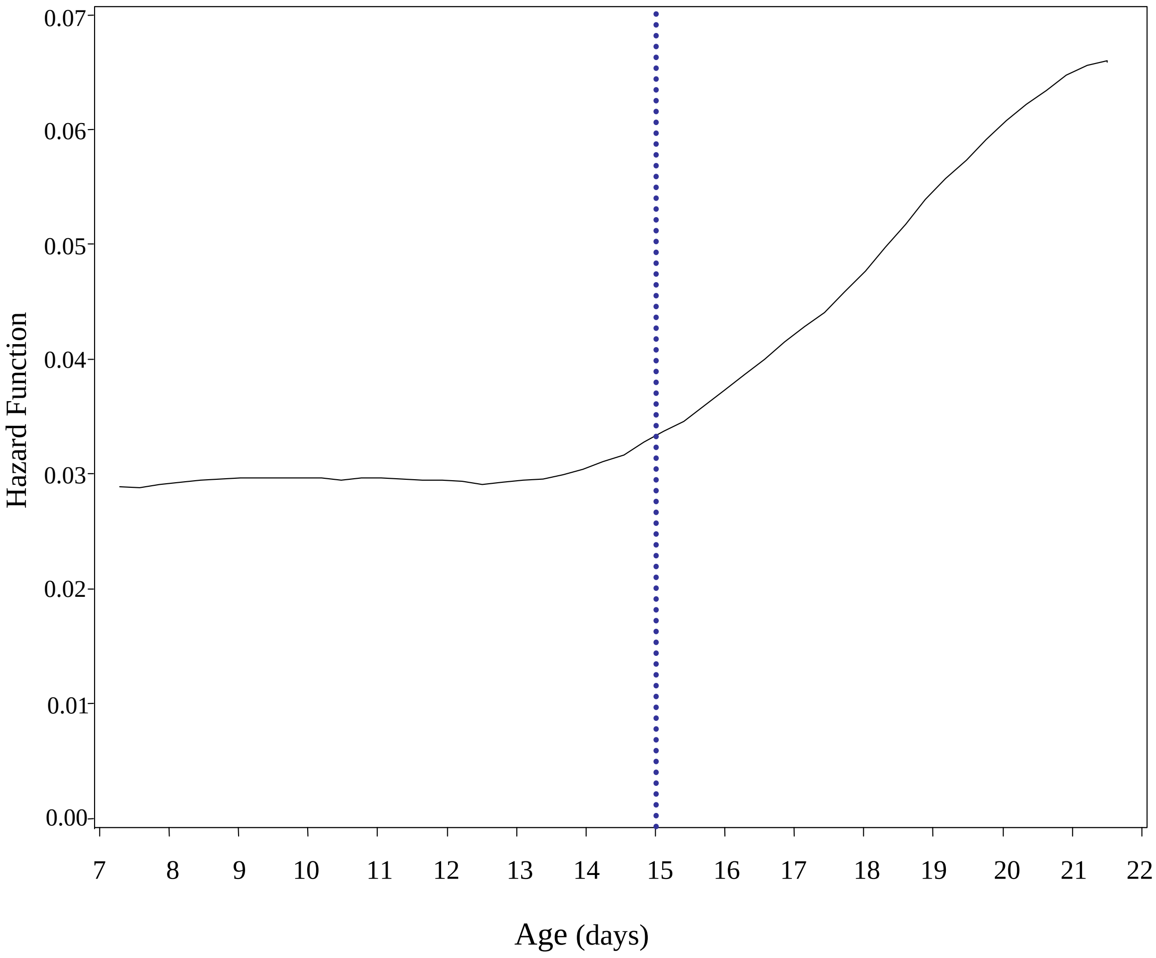


Figure 3.4: Baseline hazard function of the Acadian Flycatcher Cox regression Model A. By necessity, time-dependent covariates (water and parasitism variables) were excluded from the model to derive the baseline hazard function. Covariates were held constant at their mean values. The x-axis is age of the nest in days; the broken vertical line indicates the time at which the nest transitions from the egg stage to the nestling stage. A bandwidth of 6 days was used to create the smoothed hazard function.

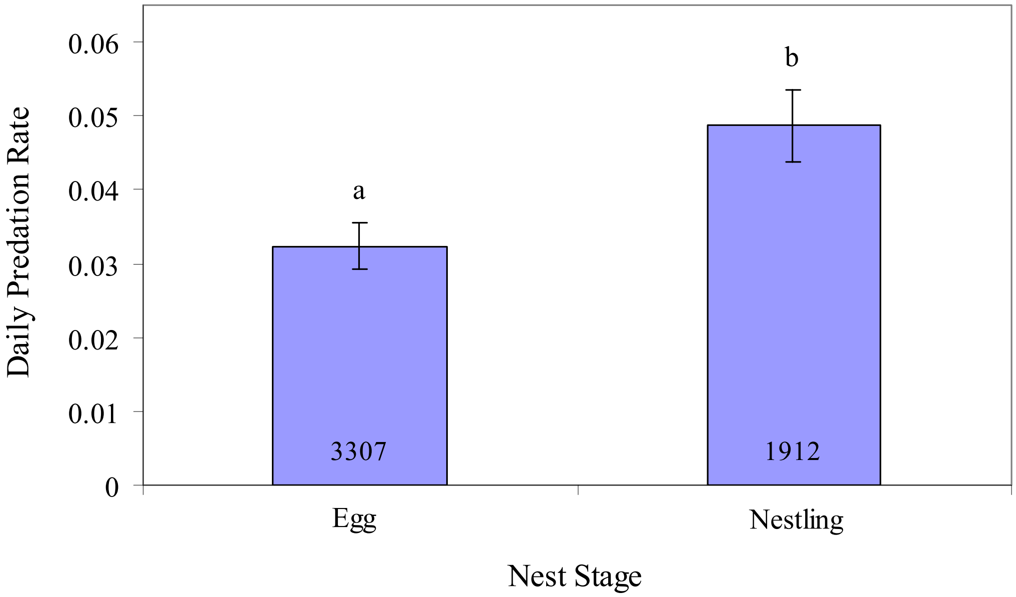


Figure 3.5: Comparison of daily predation rates during the egg stage and nestling stage of Acadian Flycatcher nests. Bars represent ± 1 SE. Letters above bars signify statistical differences between predation rates; unlike letters are statistically different. Numbers within columns indicate the number of nest exposure days. Nests from all plots and years were combined (n=339).

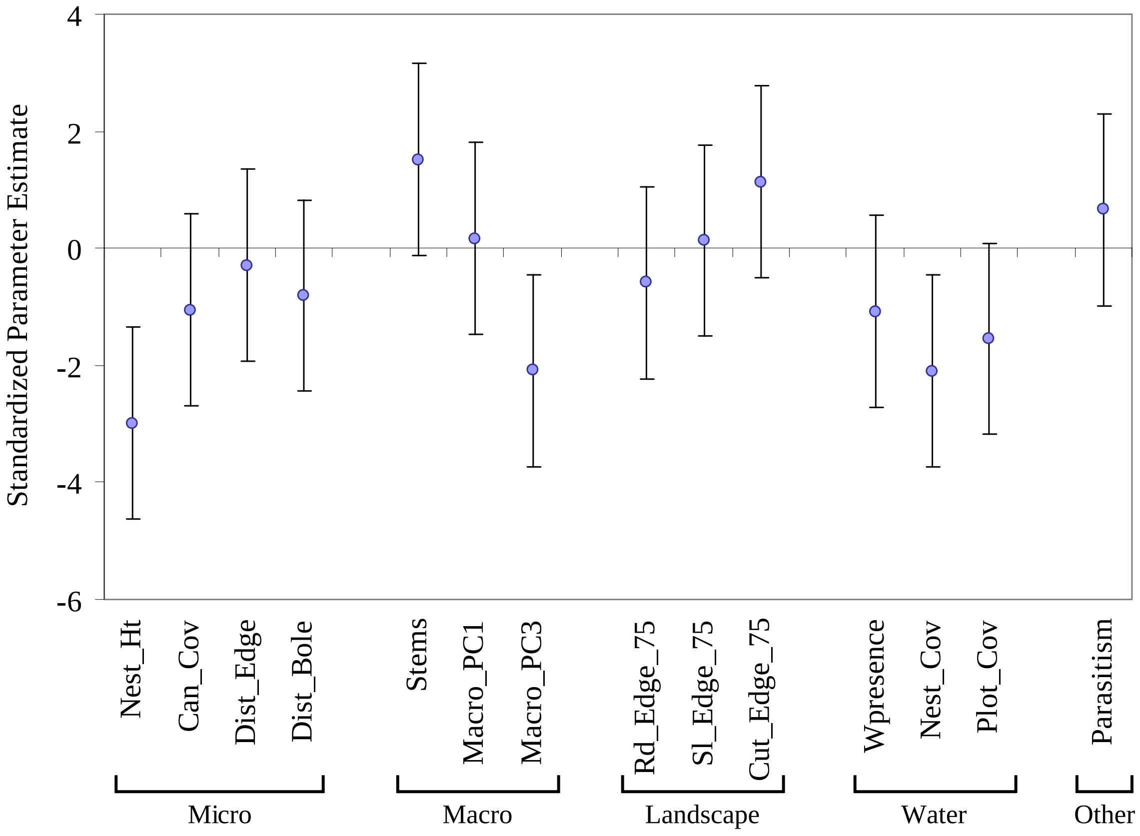


Figure 3.6: Standardized parameter estimates (*b/se*) of the variables included in the Acadian Flycatcher Cox regression Model A. Bars represent 90% confidence intervals. Parameter estimates were derived from the averaged model (see Table 3.3).

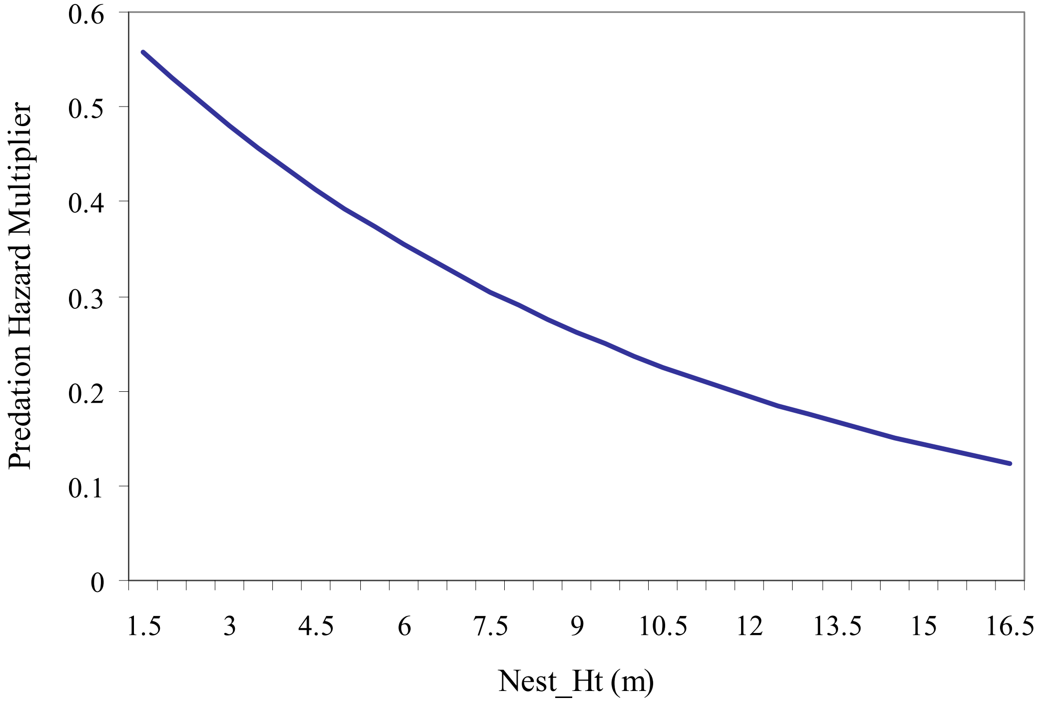


Figure 3.7: Relationship between Acadian Flycatcher nest height and the hazard of nest predation. The hazard multiplier is the exponentiated portion of the following equation:

$$h_i(t) = \lambda(t)\exp\left(\beta_{Nest\_Ht} * Nest\_Ht_i + \sum_{\substack{j=2 \\ \text{to } 14}}^{j} \beta_j * x_{ij}\right)$$

Where the hazard (*h*) of the predation event occurring for individual *i* at time (*t*) depends on the baseline hazard function (λ) at time (*t*), the parameter estimate for Nest_Ht, the value of Nest_Ht for individual *i*, and the parameter estimates and values of the other 13 covariates (*j*) in the averaged model. The baseline hazard, λ(*t*), is left unspecified. While the values of Nest_Ht are varied over its full range, all other continuous covariates are held constant at their mean values and class variables are set to 0. The resulting equation from which the above graph was made is as follows:

$$h_i(t) = \exp(-0.1008 * Nest\_Ht_i - 0.4314)$$

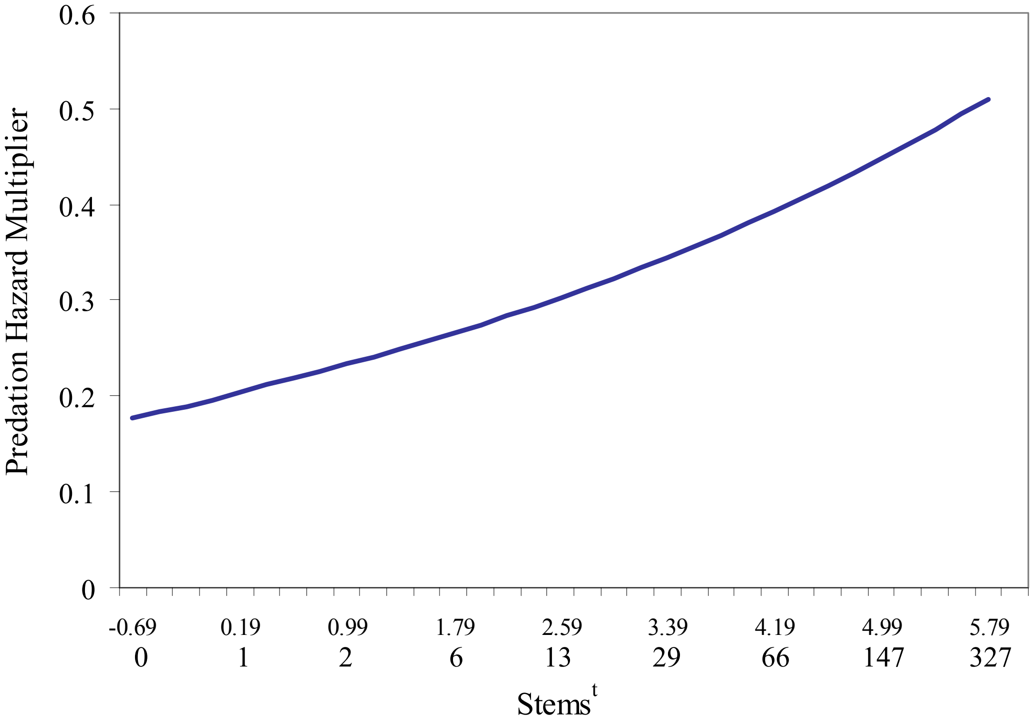


Figure 3.8: Relationship between the number of stems within a 5 m-radius circle around the nest and the hazard of nest predation for Acadian Flycatchers. The "t" denotes that the variable Stem was log transformed. The first set of values along the x-axis reflect the log transformed values used in the model, while the second set correspond to the actual stem count and are listed to provide the biological link and assist with interpretation. The hazard multiplier is the exponentiated portion of the following equation:

$$h_i(t) = \lambda(t)\ \exp(\beta_{\text{Stems}} * \text{Stems}_i + \sum_{\substack{j=2 \\ \text{to } 14}}^{j} \beta_j * x_{ij})$$

Where the hazard (*h*) of the predation event occurring for individual *i* at time (*t*) depends on the baseline hazard function (λ) at time (*t*), the parameter estimate for Stems, the value of Stems for individual *i*, and the parameter estimates and values of the other 13 covariates (*j*) in the averaged model. The baseline hazard, λ(*t*), is left unspecified. While the values of Stems are varied over its full range, all other continuous covariates are held constant at their mean values and class variables are set to 0. The resulting equation from which the above graph was made is as follows:

$$h_i(t) = \exp(0.1632 * \text{Stems}_i - 1.6171)$$

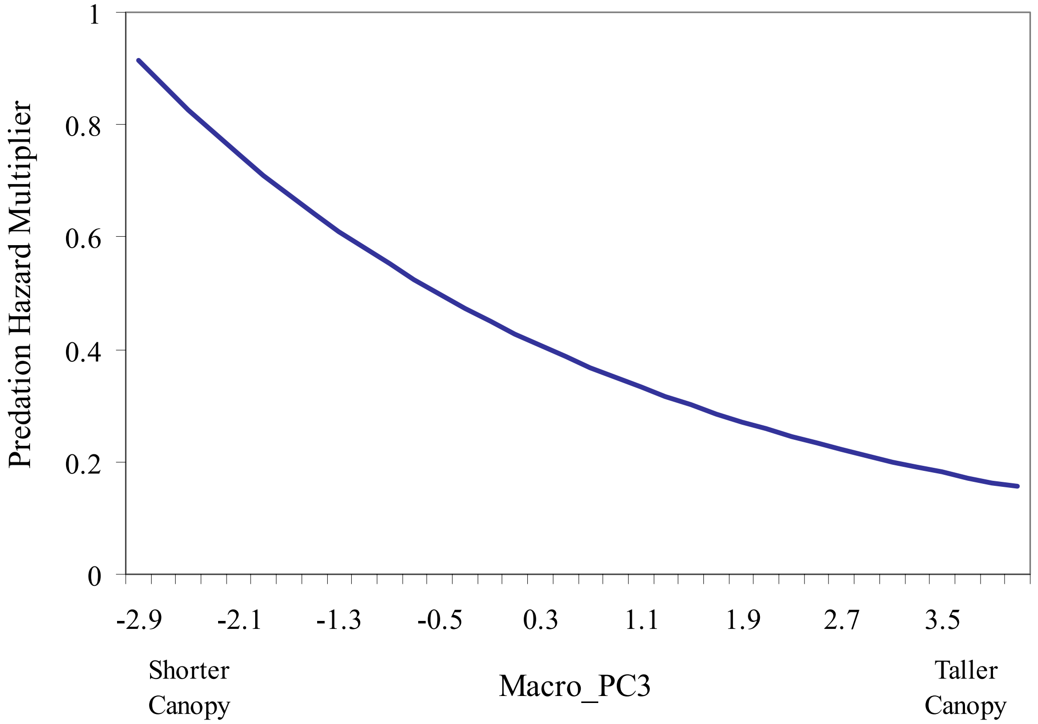


Figure 3.9: Relationship between Macro_PC3 and the hazard of nest predation for Acadian Flycatchers. The hazard multiplier is the exponentiated portion of the following equation:

$$h_{\mathrm{i}}(t) = \lambda(t)\ \exp(\beta_{\mathrm{Macro\_PC3}} * \mathrm{Macro\_PC3}_{\mathrm{i}} + \sum_{\substack{j=2 \\ \text{to } 14}}^{j} \beta_j * x_{ij})$$

Where the hazard (*h*) of the predation event occurring for individual *i* at time (*t*) depends on the baseline hazard function (λ) at time (*t*), the parameter estimate for Macro_PC3, the value of Macro_PC3 for individual *i*, and the parameter estimates and values of the other 13 covariates (*j*) in the averaged model. The baseline hazard, λ(*t*), is left unspecified. While the values of Macro_PC3 are varied over its full range, all other continuous covariates are held constant at their mean values and class variables are set to 0. The resulting equation from which the above graph was made is as follows:

$$h_{\mathrm{i}}(t) = \exp(-0.1780 * \mathrm{Macro\_PC3}_{\mathrm{i}} - 0.9853)$$

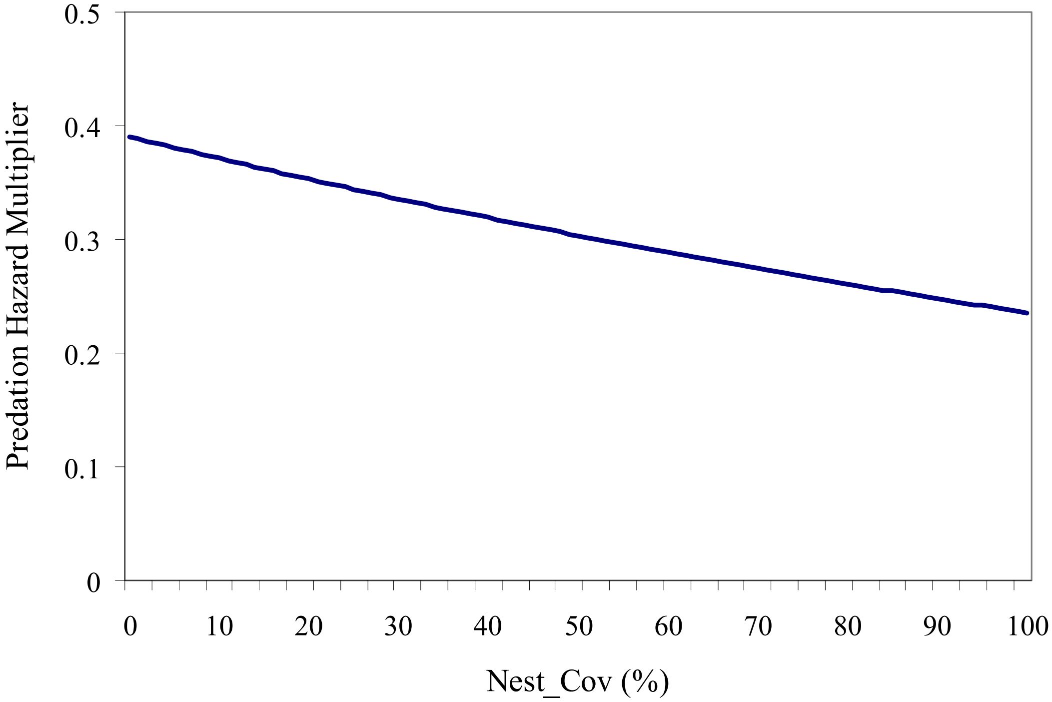


Figure 3.10: Relationship between the percent water coverage at the macro-scale (within an 11.3 m-radius circle around the nest) and the hazard of nest predation for Acadian Flycatchers. The hazard multiplier is the exponentiated portion of the following equation:

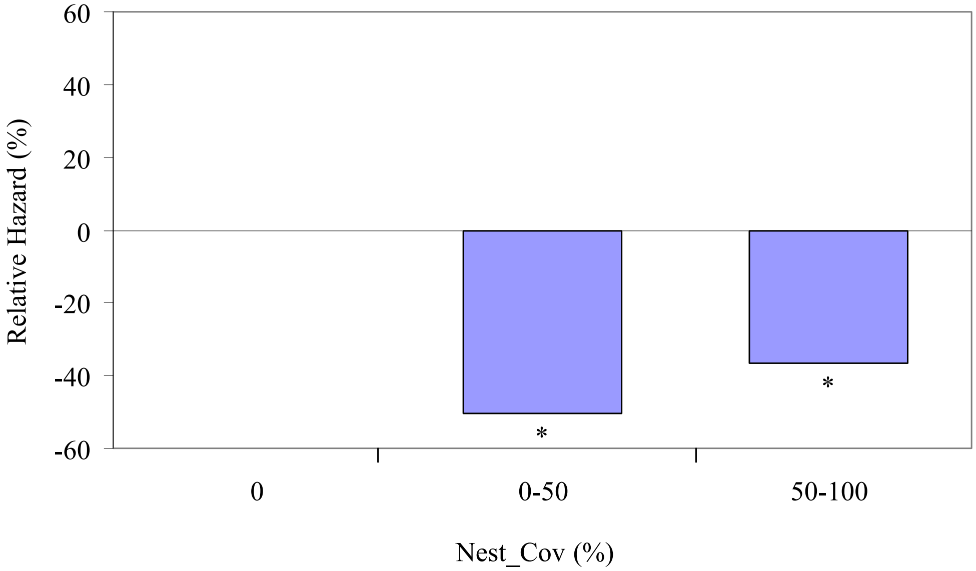
$$h_i(t) = \lambda(t)\exp(\beta_{Nest\_Cov} * Nest\_Cov_i + \sum_{\substack{j=2 \\ \text{to } 14}}^{j} \beta_j * x_{ij})$$

Where the hazard (*h*) of the predation event occurring for individual *i* at time (*t*) depends on the baseline hazard function (λ) at time (*t*), the parameter estimate for Nest_Cov, the value of Nest_Cov for individual *i*, and the parameter estimates and values of the other 13 covariates (*j*) in the averaged model. The baseline hazard, λ(*t*), is left unspecified. While the values of Nest_Cov are varied over its full range, all other continuous covariates are held constant at their mean values and class variables are set to 0. The resulting equation from which the above graph was made is as follows:

$$h_i(t) = \exp(-0.0050 * Nest\_Cov_i - 0.9406)$$

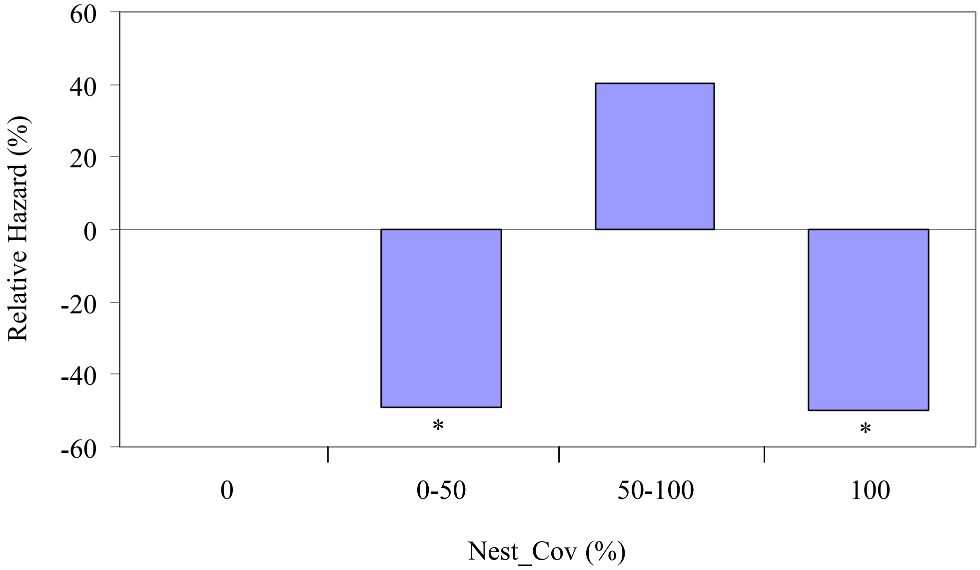
Figure 3.11: The relative hazard of predation among categories of percent water coverage at the macro-scale for Acadian Flycatcher nests. Data were derived from an alternate global model that included dummy variables describing categories of macro-scale water coverage, in addition to all non-water variables of Model A. (a) Water coverage at the macro-scale is broken into three categories, 0%, greater than 0% but less than 50%, and greater than or equal to 50%, where the second and third categories are compared to 0% water coverage. (b) Water coverage at the macro-scale is broken into four categories, 0%, greater than 0% but less than 50%, greater than or equal to 50% but less than 100%, and 100%, where the second, third, and forth categories are compared to 0% water coverage. Because 0% is the category to which the others are compared, its hazard is set to 0%. The percent hazards for the other categories are not absolute, but relative to the 0% category. An asterisk denotes significant difference from the category of comparison. Significance is based on the 90% confidence intervals of each covariate's parameter estimate.

(a)



60
40
20
0
-20
-40
-60
Relative Hazard (%)
*
*
0
0-50
50-100
Nest_Cov (%)

(b)



60
40
20
0
-20
-40
-60
Relative Hazard (%)
*
*
0
0-50
50-100
100
Nest_Cov (%)

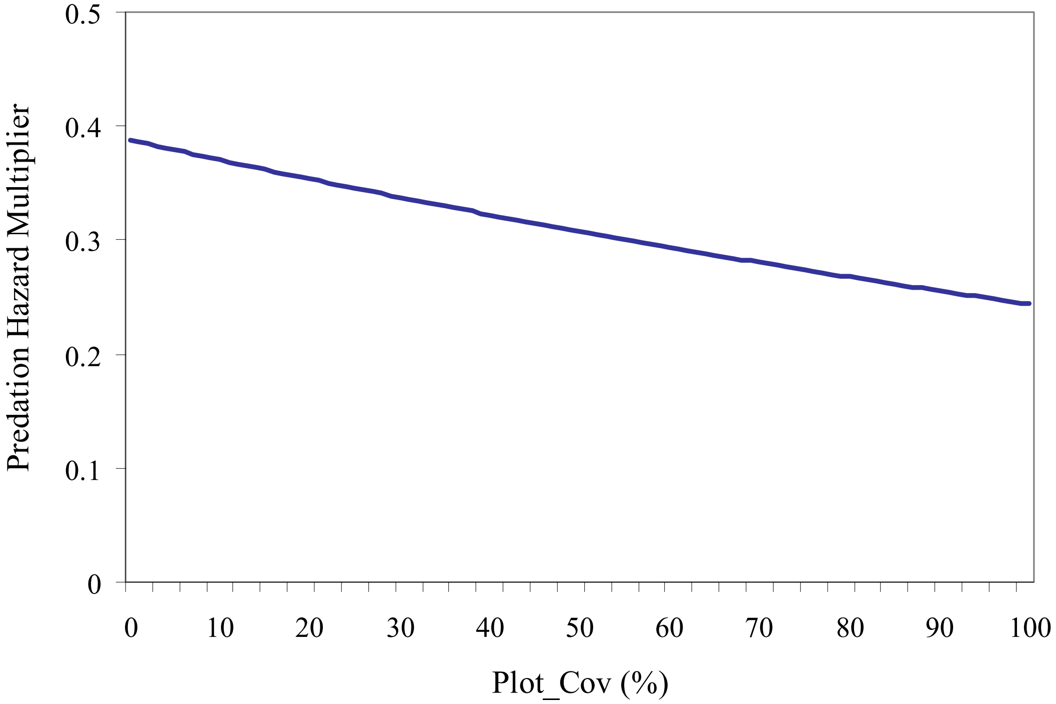


Figure 3.12: Relationship between the percent water coverage of the study plot and the hazard of nest predation for Acadian Flycatchers. The hazard multiplier is the exponentiated portion of the following equation:

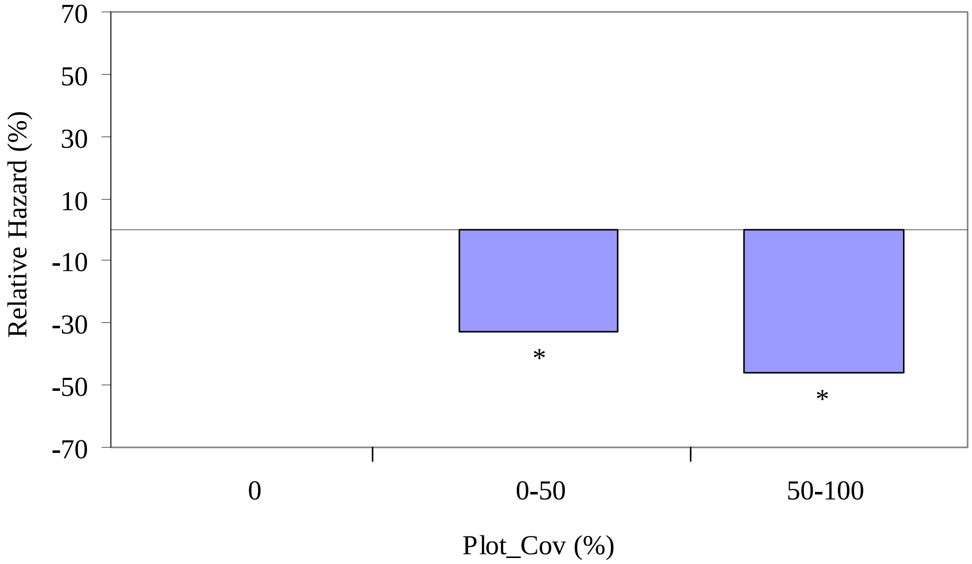
$$h_i(t) = \lambda(t)\,\exp\left(\beta_{Plot\_Cov} * Plot\_Cov_i + \sum_{\substack{j=2 \\ \text{to } 14}}^{j} \beta_j * x_{ij}\right)$$

Where the hazard (h) of the predation event occurring for individual i at time (t) depends on the baseline hazard function (λ) at time (t), the parameter estimate for Plot_Cov, the value of Plot_Cov for individual i, and the parameter estimates and values of the other 13 covariates (j) in the averaged model. The baseline hazard, $\lambda(t)$, is left unspecified. While the values of Plot_Cov are varied over its full range, all other continuous covariates are held constant at their mean values and class variables are set to 0. The resulting equation from which the above graph was made is as follows:

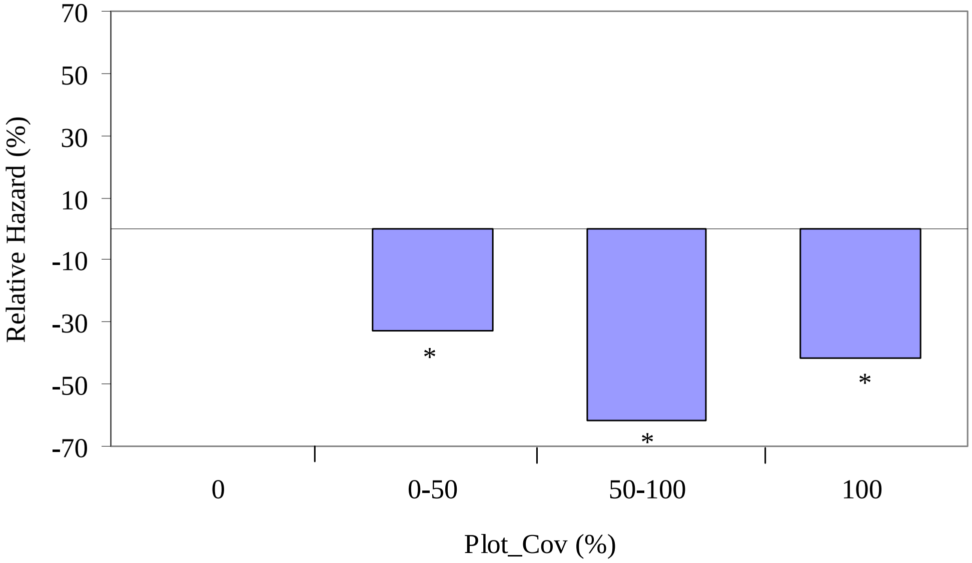
$$h_i(t) = \exp(-0.0046 * Plot\_Cov_i - 0.9470)$$

Figure 3.13: The relative hazard of predation among categories of percent water coverage at the plot-scale for Acadian Flycatcher nests. Data were derived from an alternate global model that included dummy variables describing categories of plot-scale water coverage, in addition to all non-water variables of Model A. (a) Water coverage at the plot-scale is broken into three categories, 0%, greater than 0% but less than 50%, and greater than or equal to 50%, where the second and third categories are compared to 0% water coverage. (b) Water coverage at the plot-scale is broken into four categories, 0%, greater than 0% but less than 50%, greater than or equal to 50% but less than 100%, and 100%, where the second, third, and forth categories are compared to 0% water coverage. Because 0% water coverage is the category to which the others are compared, its hazard is set to 0. The percent hazards for the other categories are not absolute, but relative to the 0% category. An asterisk indicates significant difference from the category of comparison. Significance is based on the 90% confidence intervals of each covariate's parameter estimate.

(a)


70
50
30
10
-10
-30
-50
-70
Relative Hazard (%)
*
*
0
0-50
50-100
Plot_Cov (%)

(b)


70
50
30
10
-10
-30
-50
-70
Relative Hazard (%)
*
*
*
0
0-50
50-100
100
Plot_Cov (%)

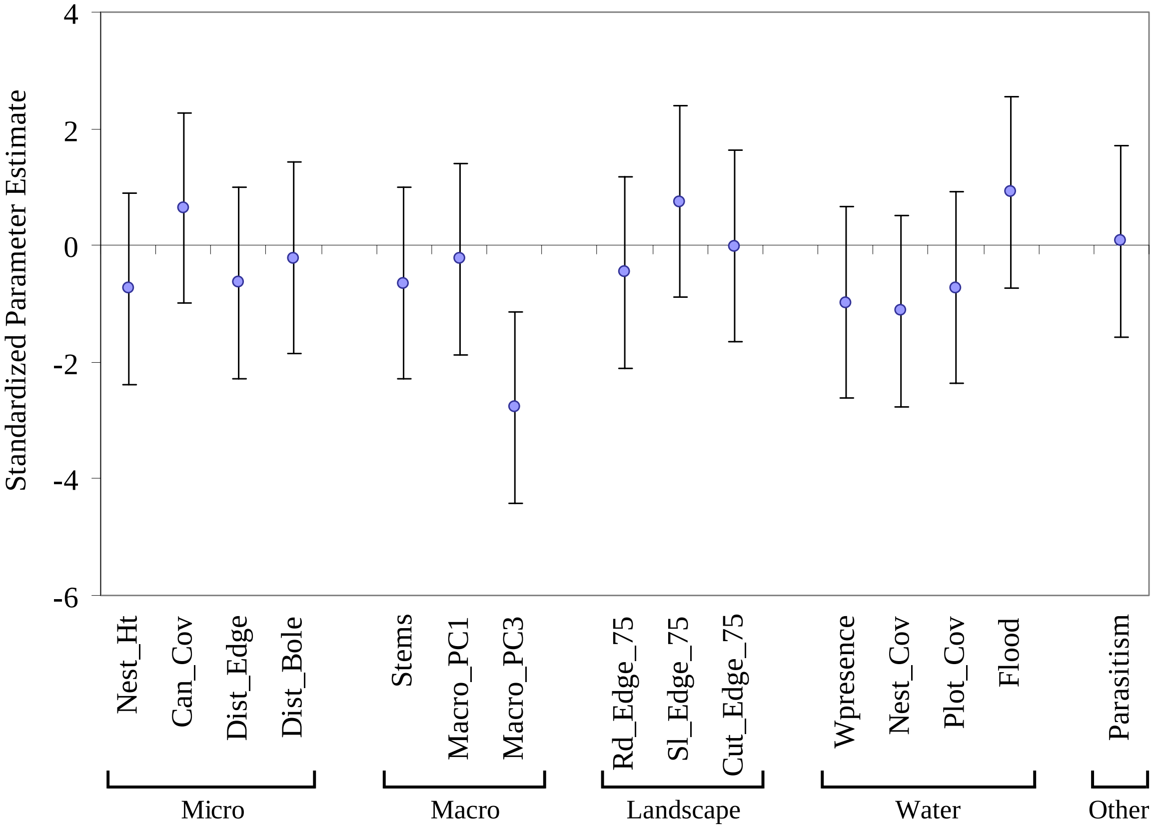


Figure 3.14: Standardized parameter estimates (*b/se*) of the variables included in the Acadian Flycatcher Cox regression Model B. Bars represent 90% confidence intervals. Parameter estimates were derived from the averaged model (see Table 3.7).

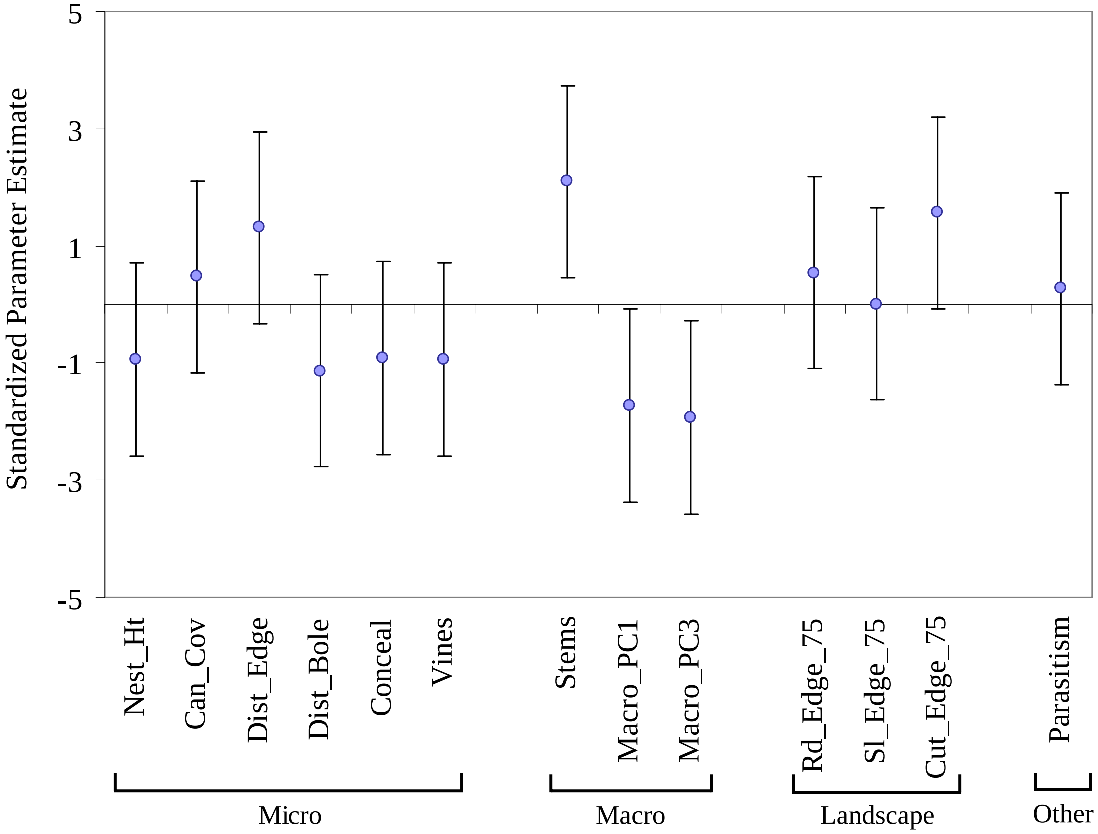


Figure 3.15: Standardized parameter estimates (*b/se*) of the variables included in the Acadian Flycatcher Cox regression Model C. Bars represent 90% confidence intervals. Parameter estimates were derived from the averaged model (see Table 3.8).

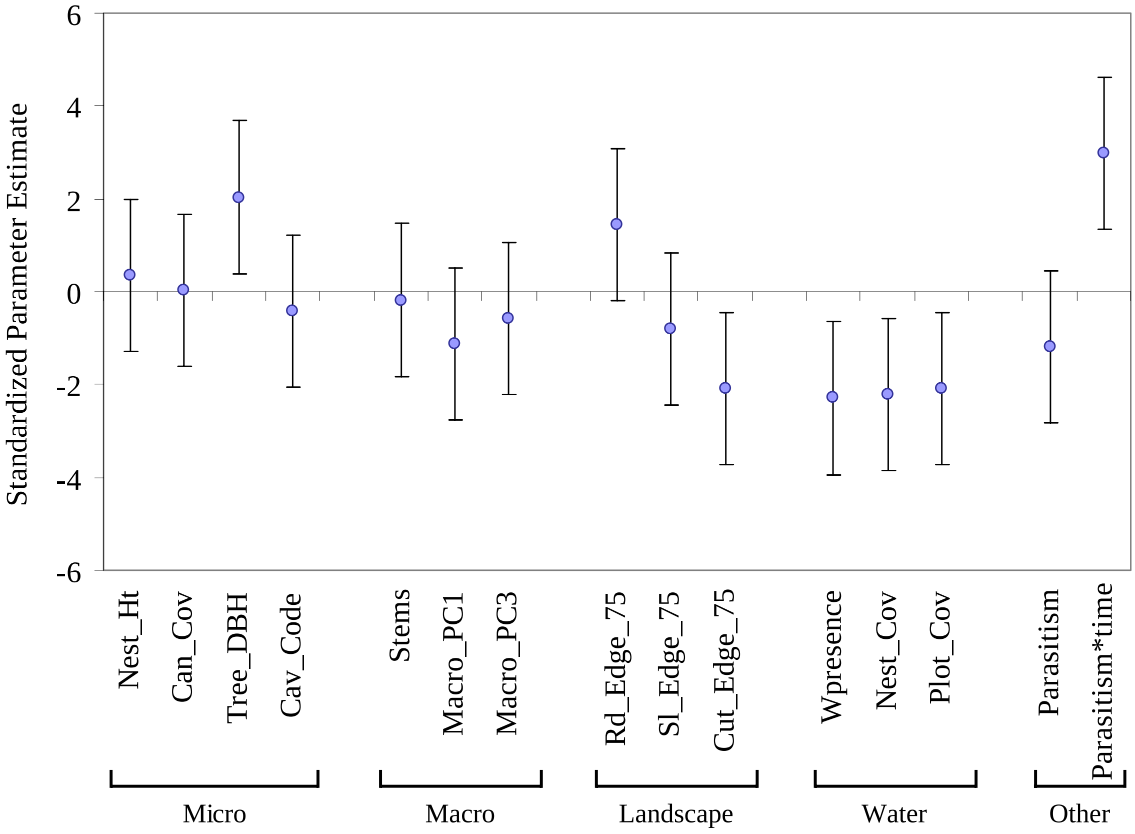


Figure 3.16: Standardized parameter estimates (*b/se*) of the variables included in the Prothonotary Warbler Cox regression Model A. Bars represent 90% confidence intervals. Parameter estimates were derived from the averaged model (see Table 3.10).

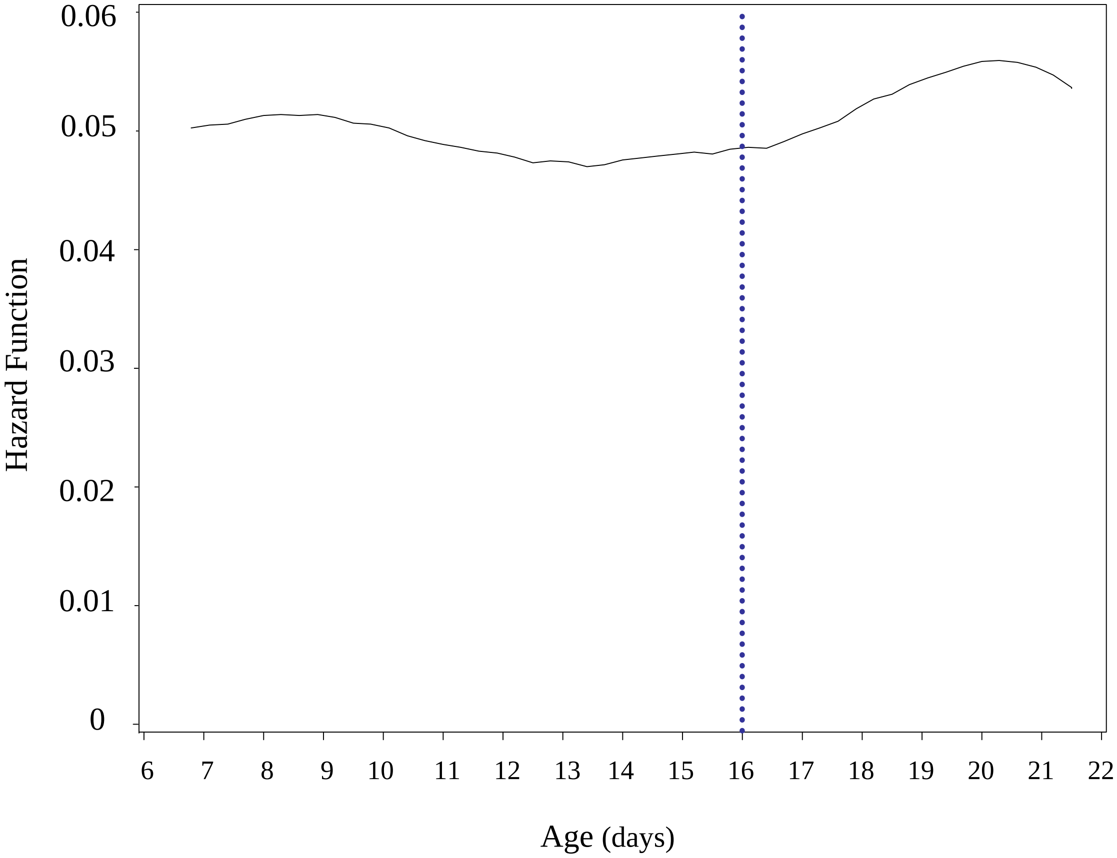


Figure 3.17: Baseline hazard function of the Prothonotary Warbler Cox regression Model B. By necessity, time-dependent covariates (water and parasitism variables) were excluded from the model to derive the baseline hazard function. Covariates were held constant at their mean values. The x-axis is age of the nest in days; the broken vertical line indicates the time at which the nest transitions from the egg stage to the nestling stage. A bandwidth of 6 days was used to create the smoothed hazard function.

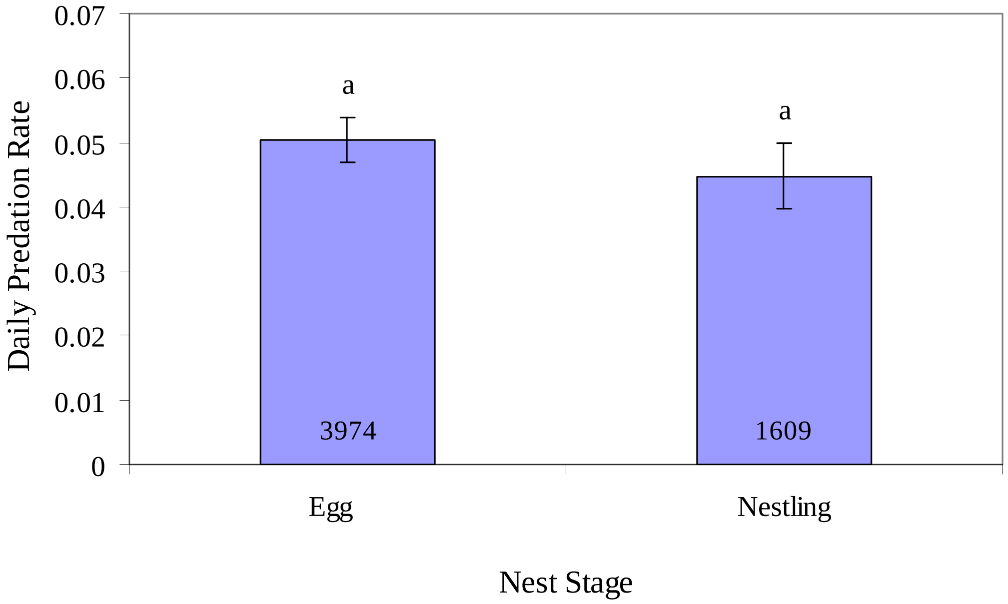


Figure 3.18: Comparison of daily predation rates during the egg stage and nestling stage of Prothonotary Warbler nests. Bars represent ± 1 SE. Letters above bars signify statistical differences between predation rates; like letters are not statistically different. Numbers within columns indicate the number of nest exposure days. Nests from all plots and years were combined (n=461).

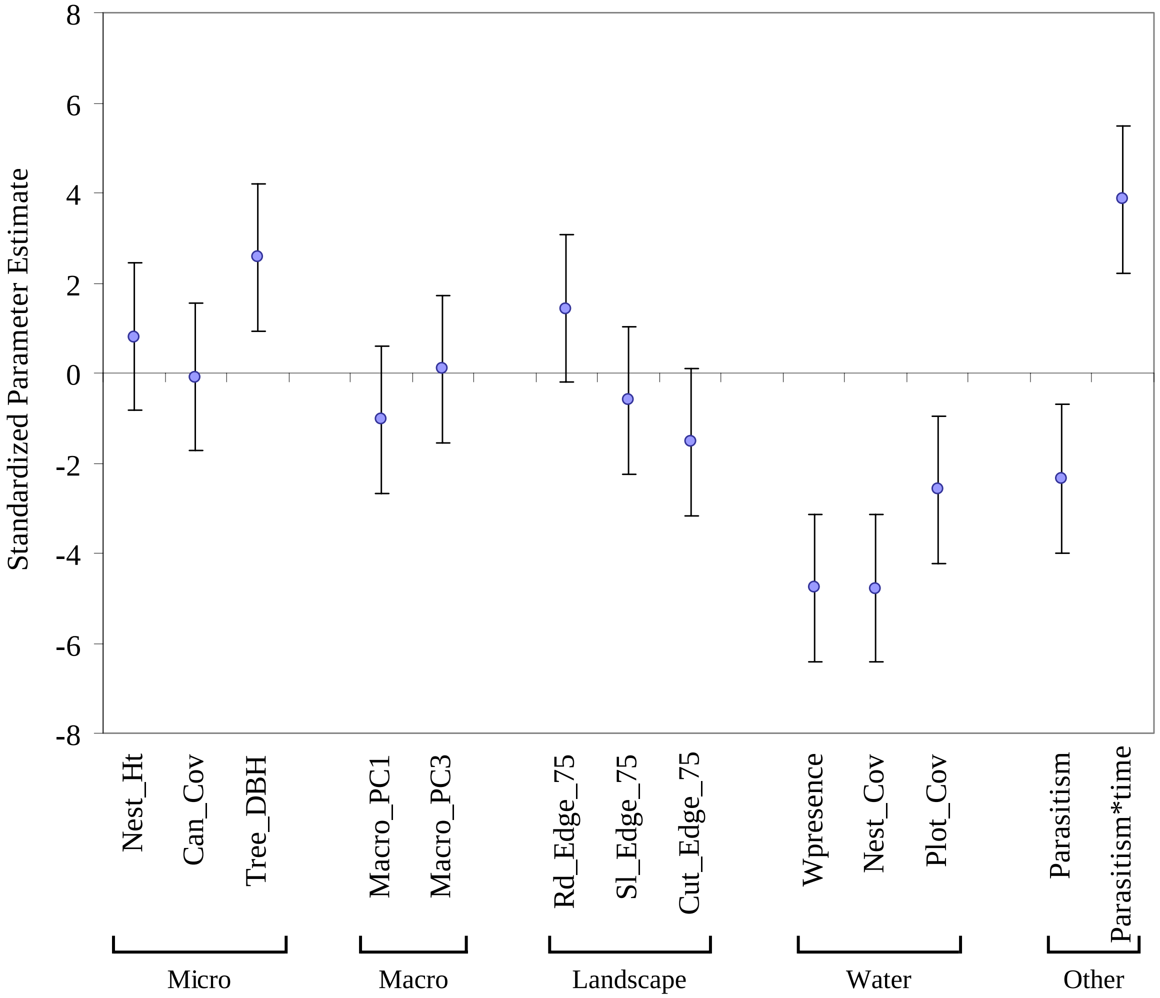


Figure 3.19: Standardized parameter estimates (*b/se*) of the variables included in the Prothonotary Warbler Cox regression Model B. Bars represent 90% confidence intervals. Parameter estimates were derived from the averaged model (see Table 3.11).

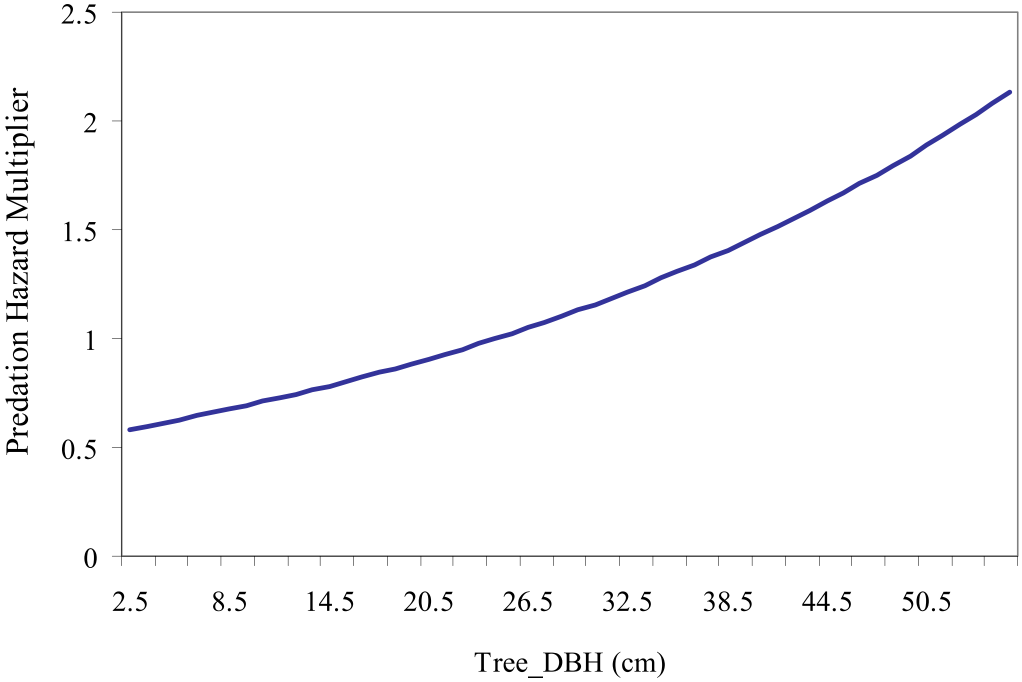


Figure 3.20: Relationship between the DBH of the nest tree and the hazard of nest predation for Prothonotary Warblers. The hazard multiplier is the exponentiated portion of the following equation:

$$h_i\,(t) = \lambda(t)\ \exp(\beta_{Tree\_DBH}{*}Tree\_DBH_i + \sum_{j=2 \text{ to } 12}^{j} \beta_j{*}x_{ij} + \beta_{Parasitism*time}{*}Parasitism_i(t))$$

Where the hazard (*h*) of the predation event occurring for individual *i* at time (*t*) depends on the baseline hazard function (λ) at time (*t*), the parameter estimate for Tree_DBH, the value of Tree_DBH for individual *i*, the parameter estimates and values of the other 12 covariates (*j*) in the averaged model, and time (*t*). The baseline hazard, λ(*t*), is left unspecified. While the values of Tree_DBH are varied over its full range, all other continuous covariates are held constant at their mean values, class variables are set to 0, and time is set to 0. The resulting equation from which the above graph was made is as follows:

$$h_i\,(t) = \exp(0.0244{*}Tree\_DBH_i - 0.5995)$$

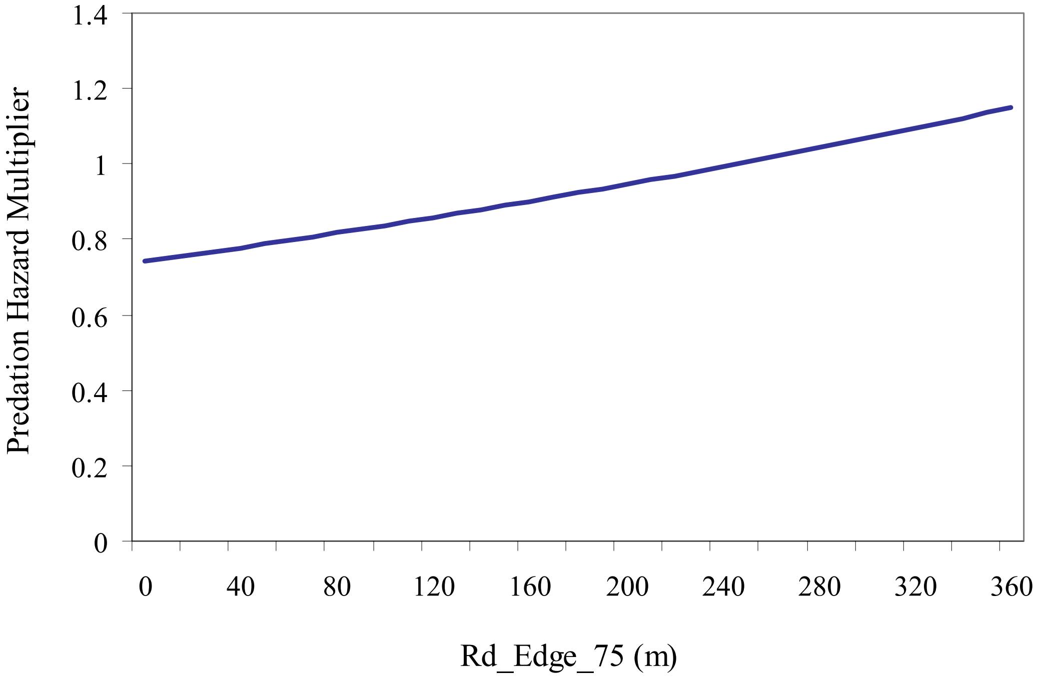


Figure 3.21: Relationship between the length of road within a 75 m-radius circle centered at a nest and the hazard of nest predation for Prothonotary Warblers. The hazard multiplier is the exponentiated portion of the following equation:

$$h_i(t) = \lambda(t)\exp(\beta_{Rd\_Edge\_75} * Rd\_Edge\_75_i + \sum_{\substack{j=2 \\ \text{to } 12}}^{j} \beta_j * x_{ij} + \beta_{Parasitism*time} * Parasitism_i(t))$$

Where the hazard (*h*) of the predation event occurring for individual *i* at time (*t*) depends on the baseline hazard function (λ) at time (*t*), the parameter estimate for Rd_Edge_75, the value of Rd_Edge_75 for individual *i*, the parameter estimates and values of the other 12 covariates (*j*) in the averaged model, and time (*t*). The baseline hazard, λ(*t*), is left unspecified. While the values of Rd_Edge_75 are varied over its full range, all other continuous covariates are held constant at their mean values, class variables are set to 0, and time is set to 0. The resulting equation from which the above graph was made is as follows:

$$h_i(t) = \exp(0.0012 * Rd\_Edge\_75_i - 0.2999)$$

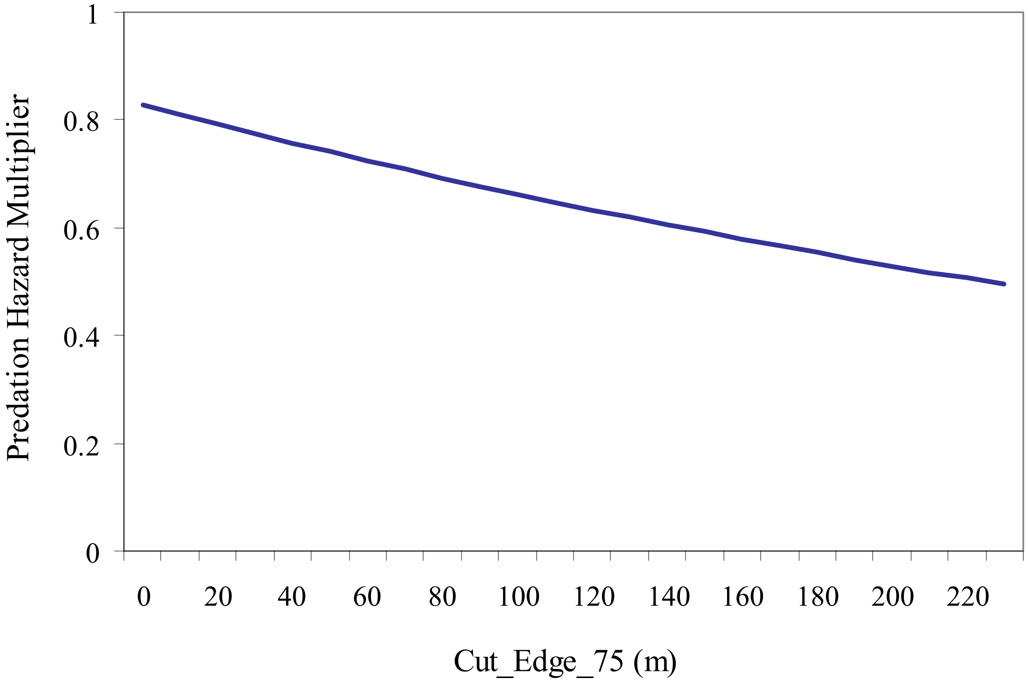


Figure 3.22: Relationship between the amount of patch cut edge within a 75 m-radius circle of a nest and the hazard of nest predation for Prothonotary Warblers. The hazard multiplier is the exponentiated portion of the following equation:

$$h_i(t) = \lambda(t)\ \exp(\beta_{\mathrm{Cut\_Edge\_75}} * \mathrm{Cut\_Edge\_75}_i + \sum_{\substack{j=2 \\ \text{to } 12}}^{j} \beta_j * x_{ij} + \beta_{\mathrm{Parasitism*time}} * \mathrm{Parasitism}_i(t))$$

Where the hazard (*h*) of the predation event occurring for individual *i* at time (*t*) depends on the baseline hazard function (λ) at time (*t*), the parameter estimate for Cut_Edge_75, the value of Cut_Edge_75 for individual *i*, the parameter estimates and values of the other 12 covariates (*j*) in the averaged model, and time (*t*). The baseline hazard, λ(*t*), is left unspecified. While the values of Cut_Edge_75 are varied over its full range, all other continuous covariates are held constant at their mean values, class variables are set to 0, and time is set to 0. The resulting equation from which the above graph was made is as follows:

$$h_i(t) = \exp(-0.0022 * \mathrm{Cut\_Edge\_75}_i - 0.1880)$$

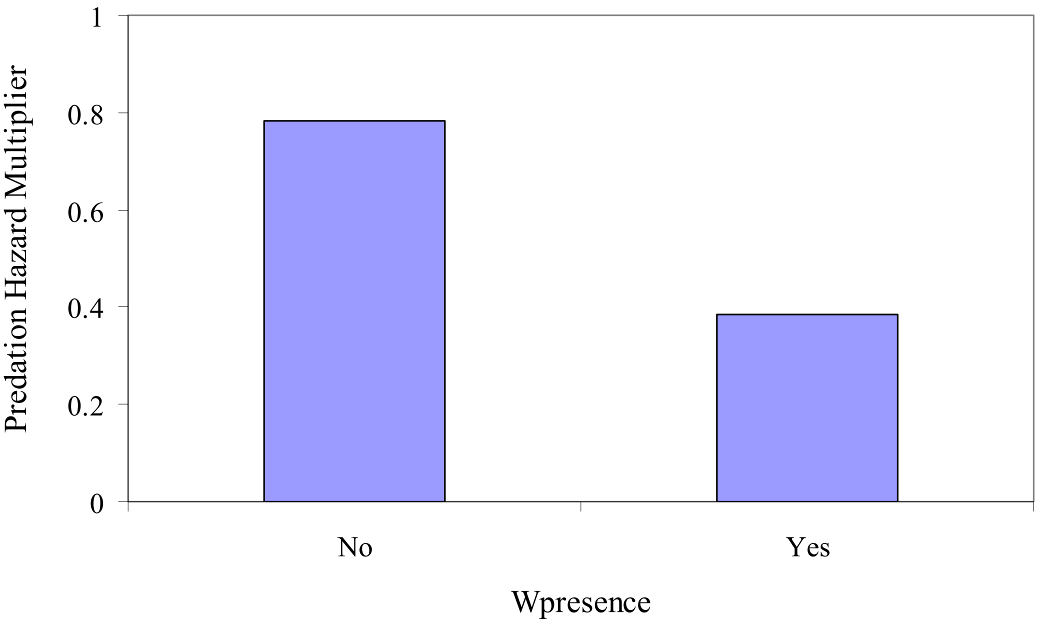


Figure 3.23: Relationship between the presence/absence of water at the micro-scale (directly under the nest) and the hazard of nest predation for Prothonotary Warblers. The hazard multiplier is the exponentiated portion of the following equation:

$$h_i(t) = \lambda(t)\ \exp(\beta_{\text{Wpresence}} * \text{Wpresence}_i + \sum_{\substack{j=2 \\ \text{to } 12}}^{j} \beta_j * x_{ij} + \beta_{\text{Parasitism*time}} * \text{Parasitism}_i(t))$$

Where the hazard (h) of the predation event occurring for individual i at time (t) depends on the baseline hazard function (λ) at time (t), the parameter estimate for Wpresence, the value of Wpresence for individual i, the parameter estimates and values of the other 12 covariates (j) in the averaged model, and time (t). The baseline hazard, $\lambda(t)$, is left unspecified. While the values of Wpresence are varied between 0 and 1, all other class variables are set to 0, continuous covariates are held constant at their mean values, and time is set to 0. The resulting equation from which the above graph was made is as follows:

$$h_i(t) = \exp(-0.7087 * \text{Wpresence}_i - 0.2461)$$

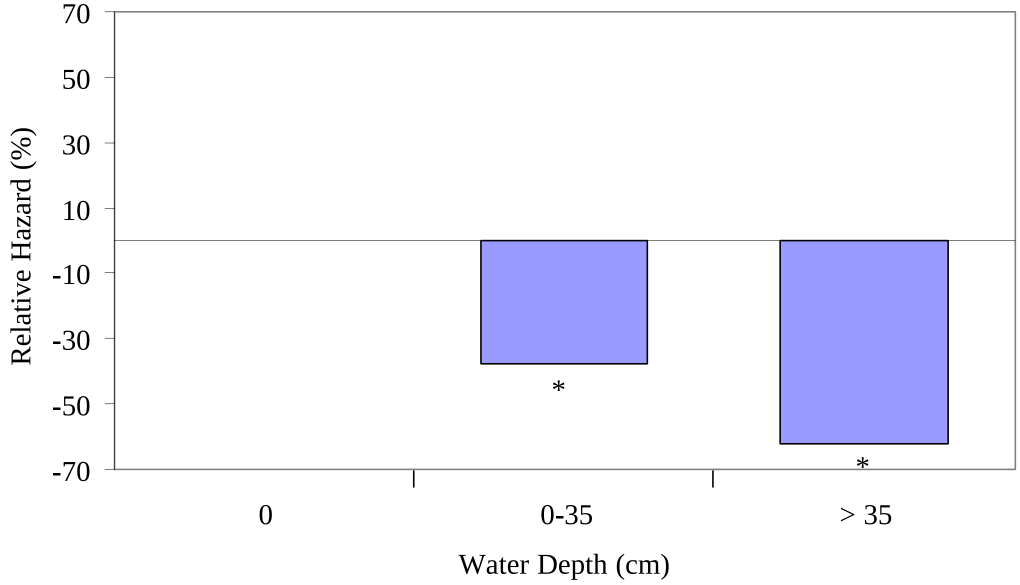


Figure 3.24: Comparison of the hazards of nest predation among categories of water depth directly beneath the nests of Prothonotary Warblers. Data were derived from an alternate global model that included dummy variables describing categories of micro-scale water depth, in addition to all non-water variables of Model B. Water depth is broken into three categories, 0 cm, greater than 0 but less than or equal to 35 cm, and greater than 35 cm. The hazards of nest predation for the second and third categories are compared to the hazard for nests that have 0 cm of water at the micro-scale. Because 0 cm is the category to which the others are compared, its hazard is set to 0%. The percent hazards shown for the 0-35 cm, and > 35 cm are not absolute, but relative to the 0 cm category. An asterisk indicates significant difference from the category of comparison. Significance is based on the 90% confidence intervals of each covariate's parameter estimate.

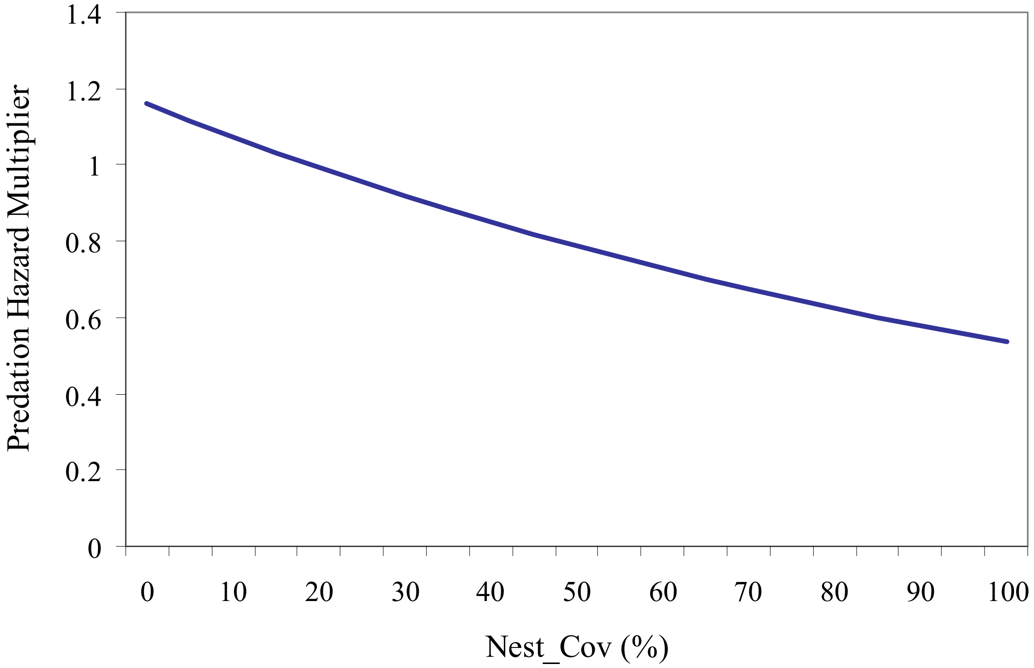


Figure 3.25: Relationship between the percent water coverage at the macro-scale (within an 11.3 m-radius circle around the nest) and the hazard of nest predation for Prothonotary Warblers. The hazard multiplier is the exponentiated portion of the following equation:

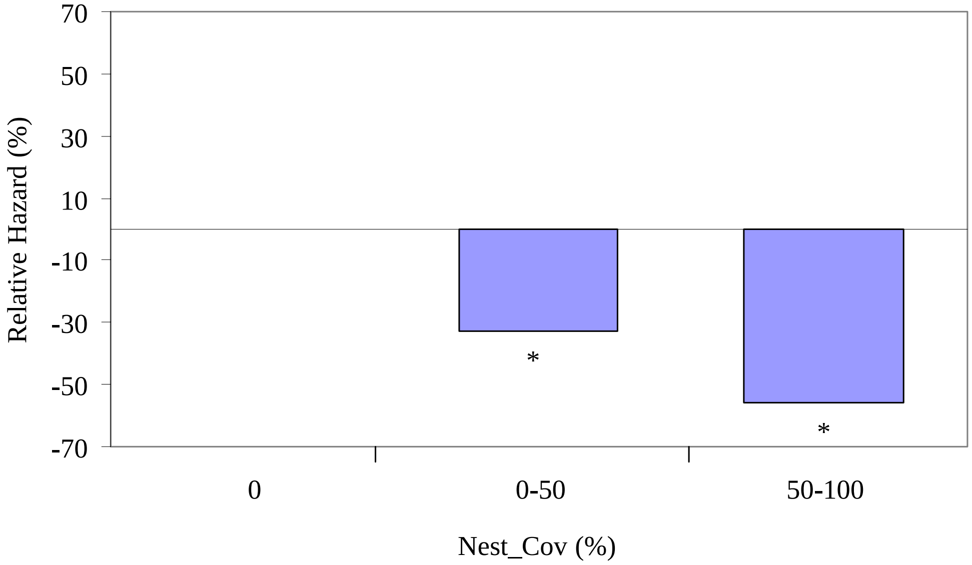
$$h_i(t) = \lambda(t)\ \exp(\beta_{Nest\_Cov} * Nest\_Cov_i + \sum_{\substack{j=2 \\ \text{to } 12}}^{j} \beta_j * x_{ij} + \beta_{Parasitism*time} * Parasitism_i(t))$$

Where the hazard (h) of the predation event occurring for individual i at time (t) depends on the baseline hazard function (λ) at time (t), the parameter estimate for Nest_Cov, the value of Nest_Cov for individual i, the parameter estimates and values of the other 12 covariates (j) in the averaged model, and time (t). The baseline hazard, $\lambda(t)$, is left unspecified. While the values of Nest_Cov are varied over its full range, all other continuous covariates are held constant at their mean values, class variables are set to 0, and time is set to 0. The resulting equation from which the above graph was made is as follows:

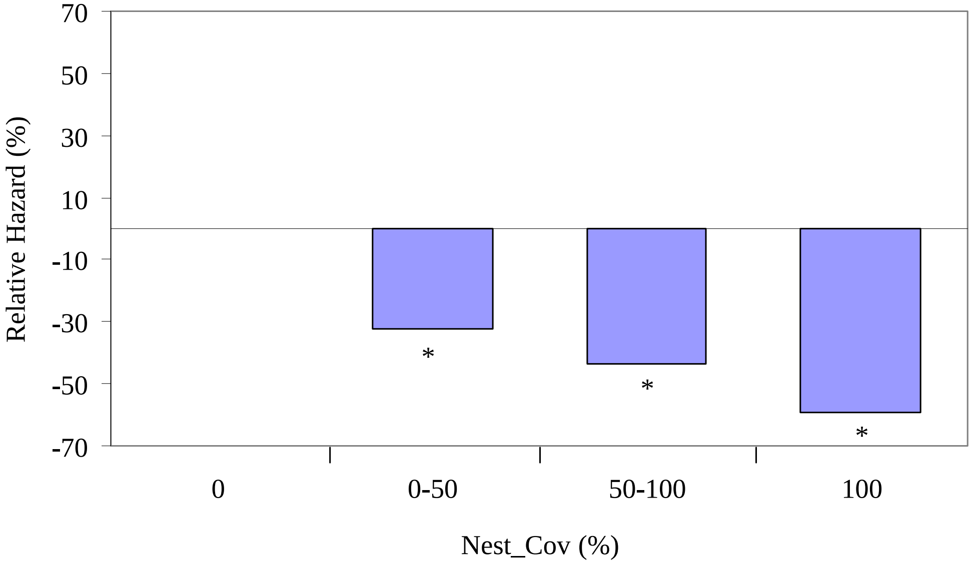
$$h_i(t) = \exp(-0.0077 * Nest\_Cov_i + 0.1480)$$

Figure 3.26: The relative hazard of predation among categories of percent water coverage at the macro-scale for Prothonotary Warbler nests. Data were derived from an alternate global model that included dummy variables describing categories of macro-scale water coverage, in addition to all non-water variables of Model B. (a) Water coverage at the macro-scale is broken into three categories, 0%, greater than 0% but less than 50%, and greater than or equal to 50%, where the second and third categories are compared to 0% water coverage. (b) Water coverage at the macro-scale is broken into four categories, 0%, greater than 0% but less than 50%, greater than or equal to 50% but less than 100%, and 100%, where the second, third, and forth categories are compared to 0% water coverage. Because 0% water coverage is the category to which the others are compared, its relative hazard is set to 0. The percent hazards for the other categories are not absolute, but relative to the 0% category. An asterisk indicates significant difference from the category of comparison. Significance is based on the 90% confidence intervals of each covariate's parameter estimate.

(a)


70
50
30
10
-10
-30
-50
-70
Relative Hazard (%)
*
*
0
0-50
50-100
Nest_Cov (%)

(b)


70
50
30
10
-10
-30
-50
-70
Relative Hazard (%)
*
*
*
0
0-50
50-100
100
Nest_Cov (%)

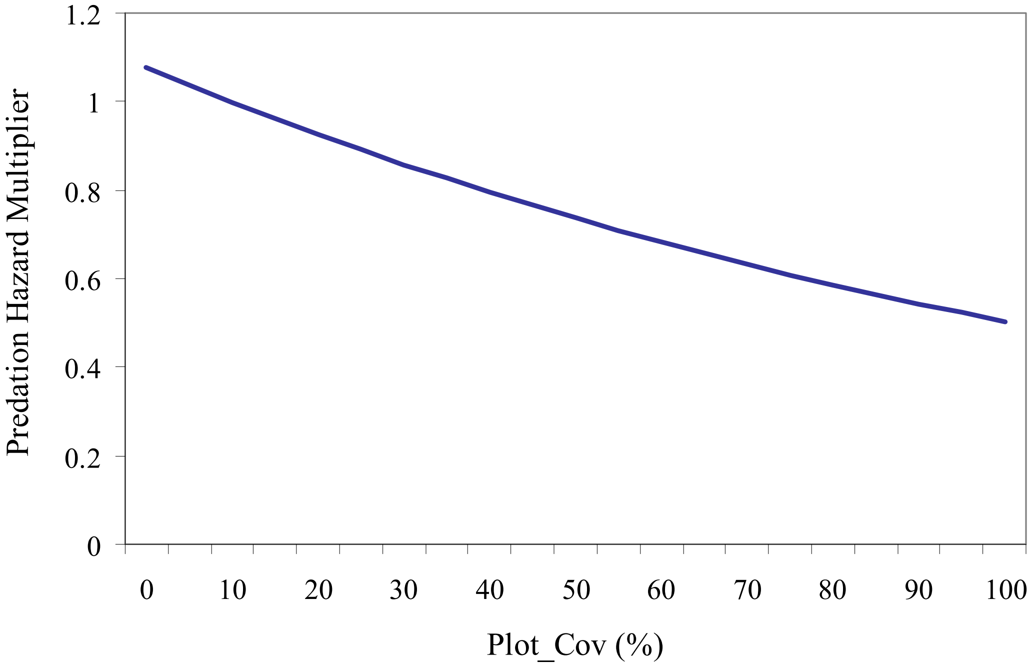


Figure 3.27: Relationship between the percent water coverage of the 50-ha study plot and the hazard of nest predation for Prothonotary Warblers. The hazard multiplier is the exponentiated portion of the following equation:

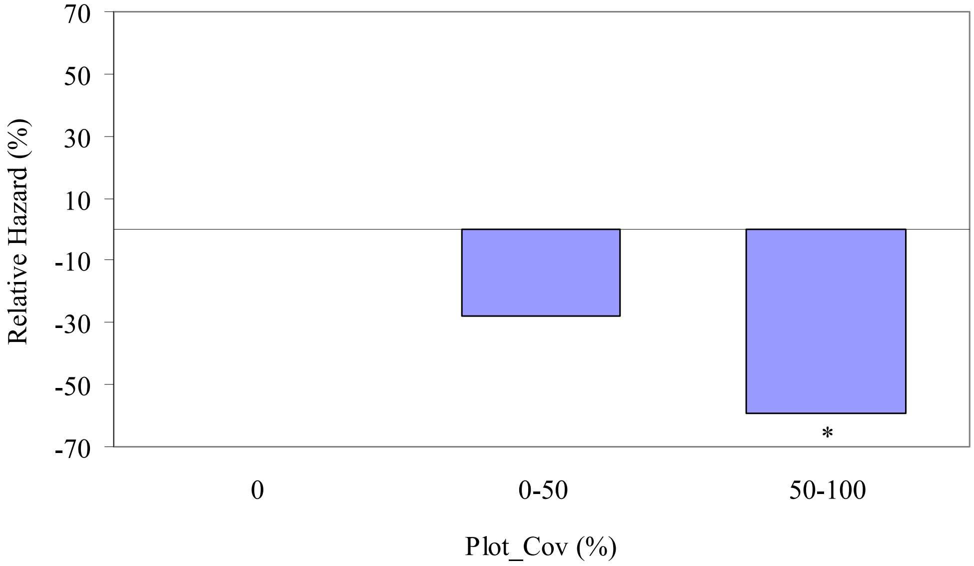
$$h_i(t) = \lambda(t)\ \exp(\beta_{\mathrm{Plot\_Cov}}{*}\mathrm{Plot\_Cov}_i + \sum_{\substack{j=2 \\ \text{to } 12}}^{j} \beta_j{*}x_{ij} + \beta_{\mathrm{Parasitism*time}}{*}\mathrm{Parasitism}_i(t))$$

Where the hazard (h) of the predation event occurring for individual i at time (t) depends on the baseline hazard function (λ) at time (t), the parameter estimate for Plot_Cov, the value of Plot_Cov for individual i, the parameter estimates and values of the other 12 covariates (j) in the averaged model, and time (t). The baseline hazard, $\lambda(t)$, is left unspecified. While the values of Plot_Cov are varied over its full range, all other continuous covariates are held constant at their mean values, class variables are set to 0, and time is set to 0. The resulting equation from which the above graph was made is as follows:

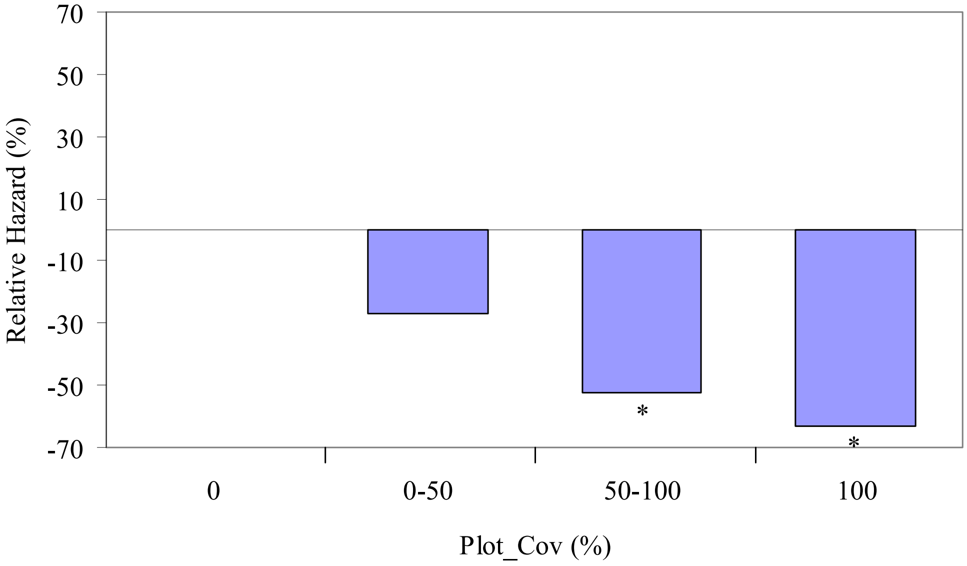
$$h_i(t) = \exp(-0.0076{*}\mathrm{Plot\_Cov}_i + 0.0754)$$

Figure 3.28: The relative hazard of predation among categories of percent water coverage at the plot-scale for Prothonotary Warbler nests. Data were derived from an alternate global model that included dummy variables describing categories of plot-scale water coverage, in addition to all non-water variables of Model B. (a) Water coverage at the plot-scale is broken into three categories, 0%, greater than 0% but less than 50%, and greater than or equal to 50%, where the second and third categories are compared to 0% water coverage. (b) Water coverage at the plot-scale is broken into four categories, 0%, greater than 0% but less than 50%, greater than or equal to 50% but less than 100%, and 100%, where the second, third, and forth categories are compared to 0% water coverage. Because 0% water coverage is the category to which the others are compared, its relative hazard is set to 0. The percent hazards for the other categories are not absolute, but relative to the 0% category. An asterisk indicates significant difference from the category of comparison. Significance is based on the 90% confidence intervals of each covariate's parameter estimate.

(a)


70
50
30
10
-10
-30
-50
-70
Relative Hazard (%)
*
0
0-50
50-100
Plot_Cov (%)

(b)


70
50
30
10
-10
-30
-50
-70
Relative Hazard (%)
*
*
0
0-50
50-100
100
Plot_Cov (%)

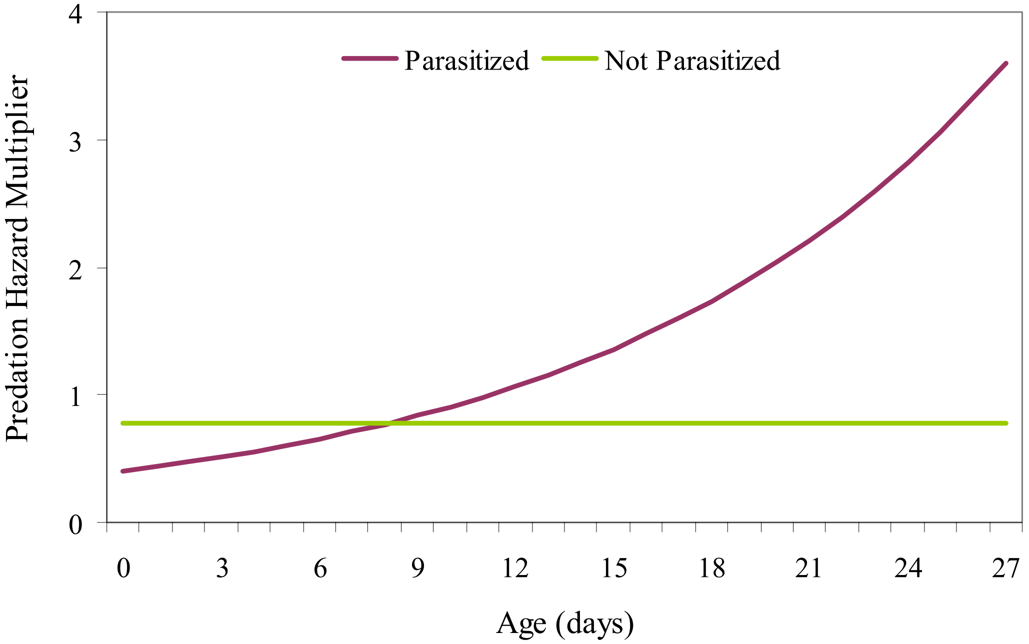


Figure 3.29: Relationship between parasitized and non-parasitized nests and the hazard of nest predation for Prothonotary Warblers. The x-axis is age of the nest in days. Parasitism interacted positively with time; the effect of parasitized nests on nest predation hazard changed throughout the nesting cycle, growing stronger as the age of the nest increased. The hazard multiplier is the exponentiated portion of the following equation:

$$h_i(t) = \lambda(t)\exp(\beta_{\text{Parasitism}}*\text{Parasitism}_i + \beta_{\text{Parasitism*time}}*\text{Parasitism}_i(t) + \sum_{\substack{j=3\\ \text{to } 13}}^{j} \beta_j * x_{ij})$$

Where the hazard (h) of the predation event occurring for individual i at time (t) depends on the baseline hazard function (λ) at time (t), the parameter estimate for Parasitism, the value of Parasitism for individual i, the parameter estimate for Parasitism*time, time (t), and the parameter estimates and values of the other 11 covariates (j) in the averaged model. The baseline hazard, $\lambda(t)$, is left unspecified. While the values of Parasitism are varied between 0 and 1, all other class variables are set to 0, continuous covariates are held constant at their mean values, and time is varied over the full range of the nesting cycle (day 0 to day 27). The resulting equation from which the above graph was made is as follows:

$$h_i(t) = \exp(-0.6628*\text{Parasitism}_i + 0.08110*\text{Parasitism}_i*\text{time} - 0.2461)$$

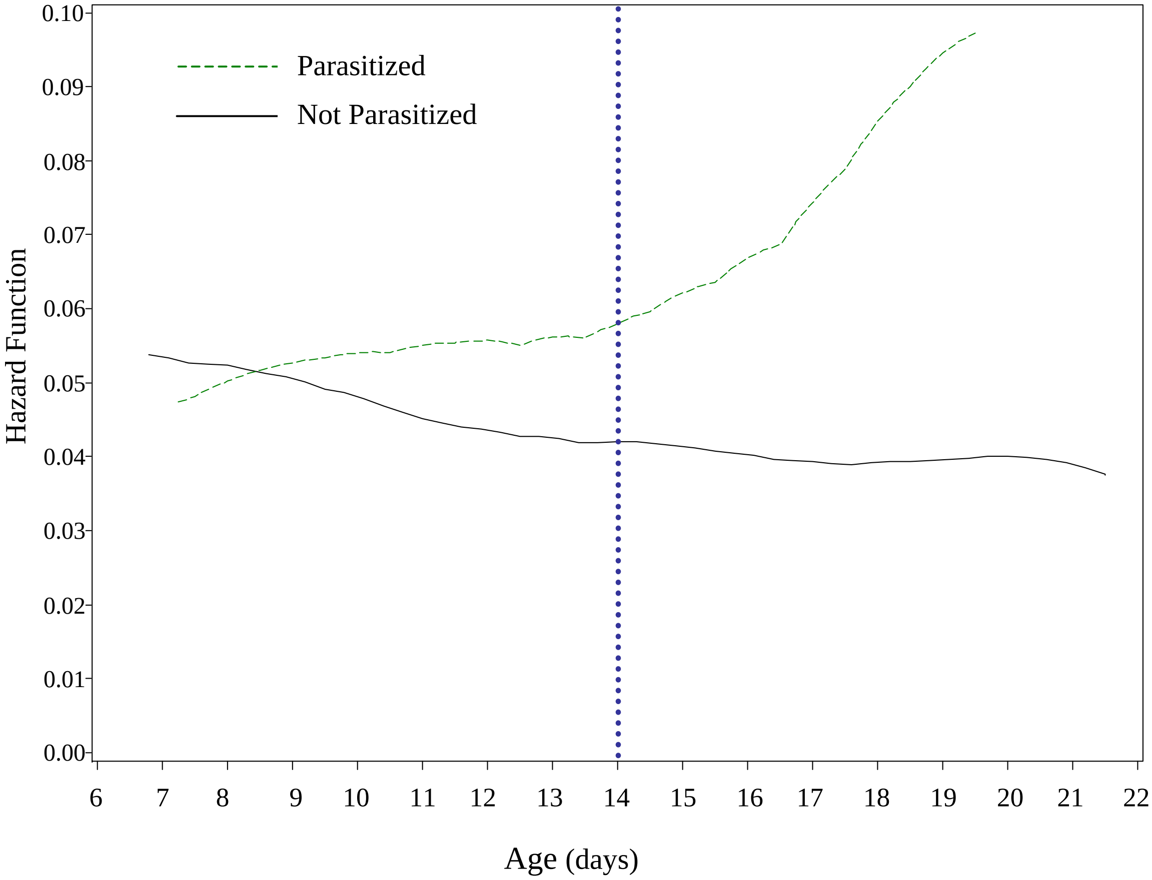
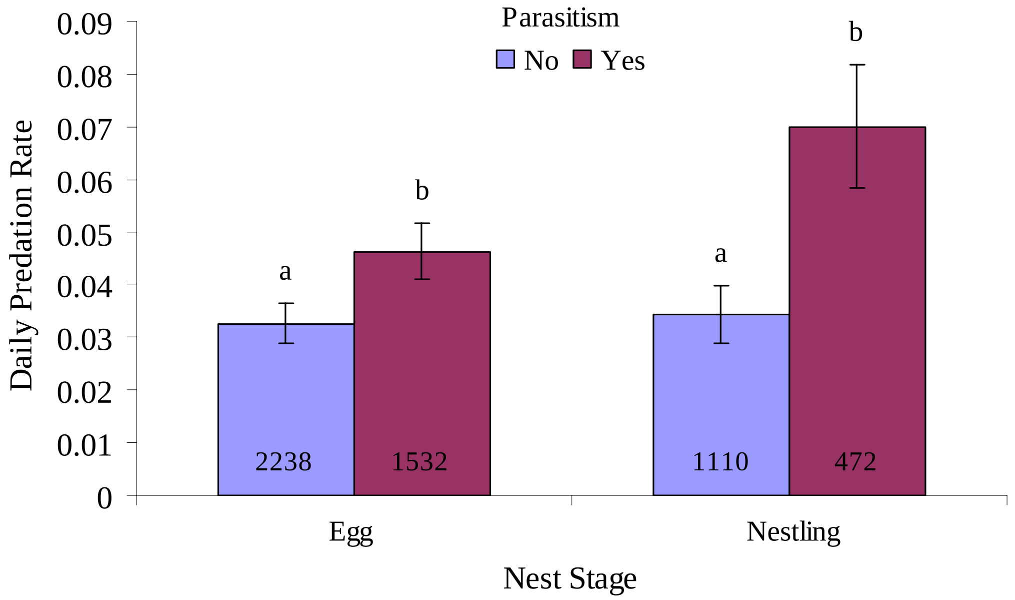


Figure 3.30: Baseline hazard functions of the Prothonotary Warbler Cox regression Model B, stratified by parasitism status of the nest. Parasitism was treated as a static covariate for the purpose of this figure, although it is treated as a time-dependent covariate in the actual model. By necessity, the time-dependent water covariates were excluded from the model to derive the baseline hazard function. Covariates were held constant at their mean values. The x-axis is age of the nest in days; the broken vertical line indicates the time at which the nest transitions from the egg stage to the nestling stage if the nest is parasitized. A bandwidth of 6 days was used to create the smoothed hazard function.

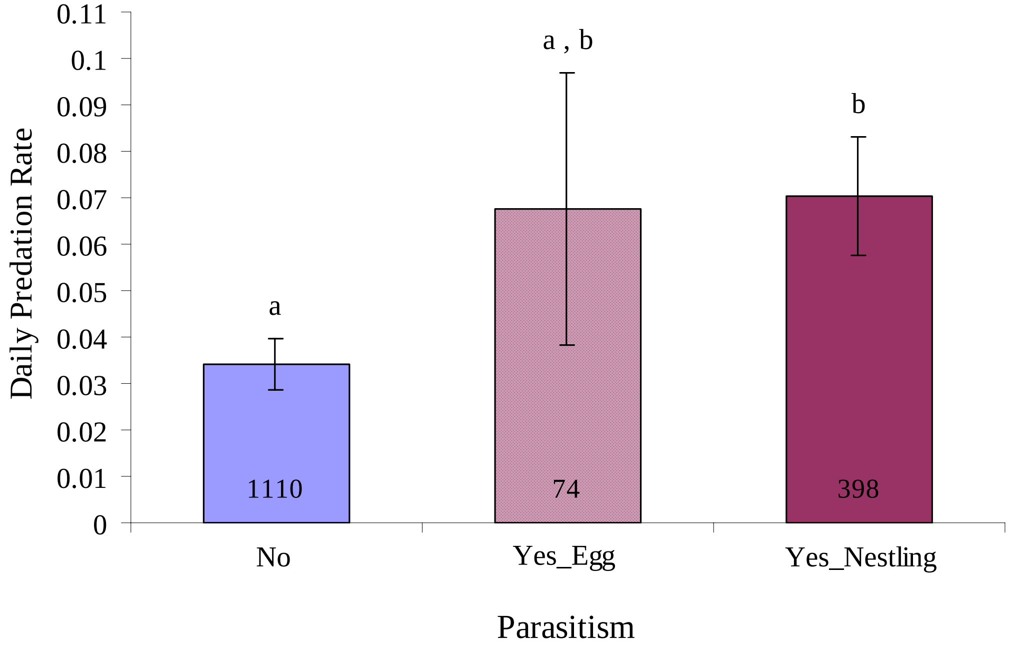
Figure 3.31: Daily predation rate of non-parasitized and parasitized Prothonotary Warbler nests. Bars represent ± 1 SE. Letters above bars signify statistical differences between the daily predation rates of the two groups; unlike letters are statistically different. Numbers within columns indicate the number of nest exposure days. Nests from all plots and years were combined (n=378).

Figure 3.32: (a) Comparison of daily predation rates during the egg and nestling stages of non-parasitized and parasitized Prothonotary Warbler nests. Parasitized nests within the nestling stage may contain cowbird eggs or nestlings. Bars represent ± 1 SE. Letters above bars signify statistical differences of predation rates within stages and of predation rates of like parasitism between stages; like letters are not statistically different, whereas unlike letters are statistically different. Numbers within columns indicate the number of nest exposure days (n=378). (b) Comparison of daily predation rates during the nestling stage of non-parasitized Prothonotary Warbler nests, parasitized nests containing one or more cowbird eggs, and parasitized nests containing one or more cowbird nestlings. Bars represent ± 1 SE. Letters above bars signify statistical differences; like letters are not statistically different, whereas unlike letters are statistically different. Numbers within columns indicate the number of nest exposure days (n=193).

(a)


Parasitism
No
Yes
Daily Predation Rate
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
a
b
a
b
2238
1532
1110
472
Egg
Nestling
Nest Stage

(b)


Daily Predation Rate
0.11
0.1
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
a
a , b
b
1110
74
398
No
Yes_Egg
Yes_Nestling
Parasitism

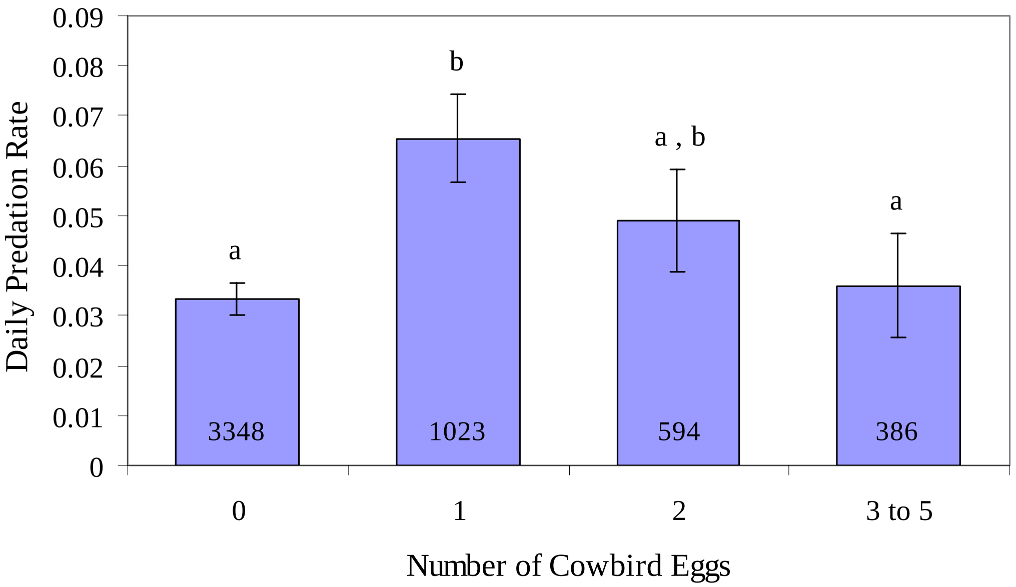


Figure 3.33: Comparison of daily predation rates among Prothonotary Warbler nests grouped by the number of cowbird eggs contained within each nest. Bars represent ± 1 SE. Letters above bars signify statistical differences between predation rates; like letters are not statistically different, whereas unlike letters are statistically different. Numbers within columns indicate the number of nest exposure days. Nests from all plots and years were combined (n=378).

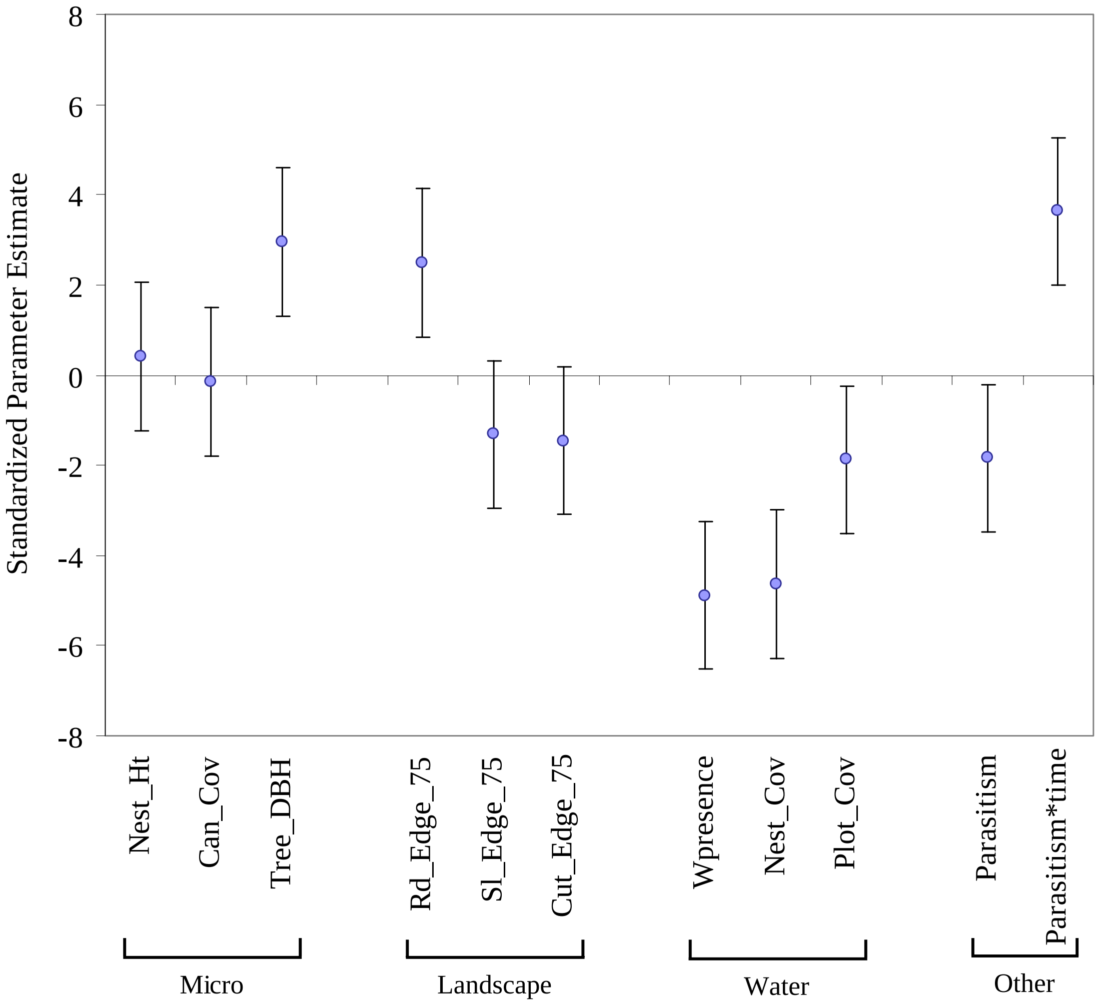


Figure 3.34: Standardized parameter estimates (*b/se*) of the variables included in the Prothonotary Warbler Cox regression Model C. Bars represent 90% confidence intervals. Parameter estimates were derived from the averaged model (see Table 3.16).

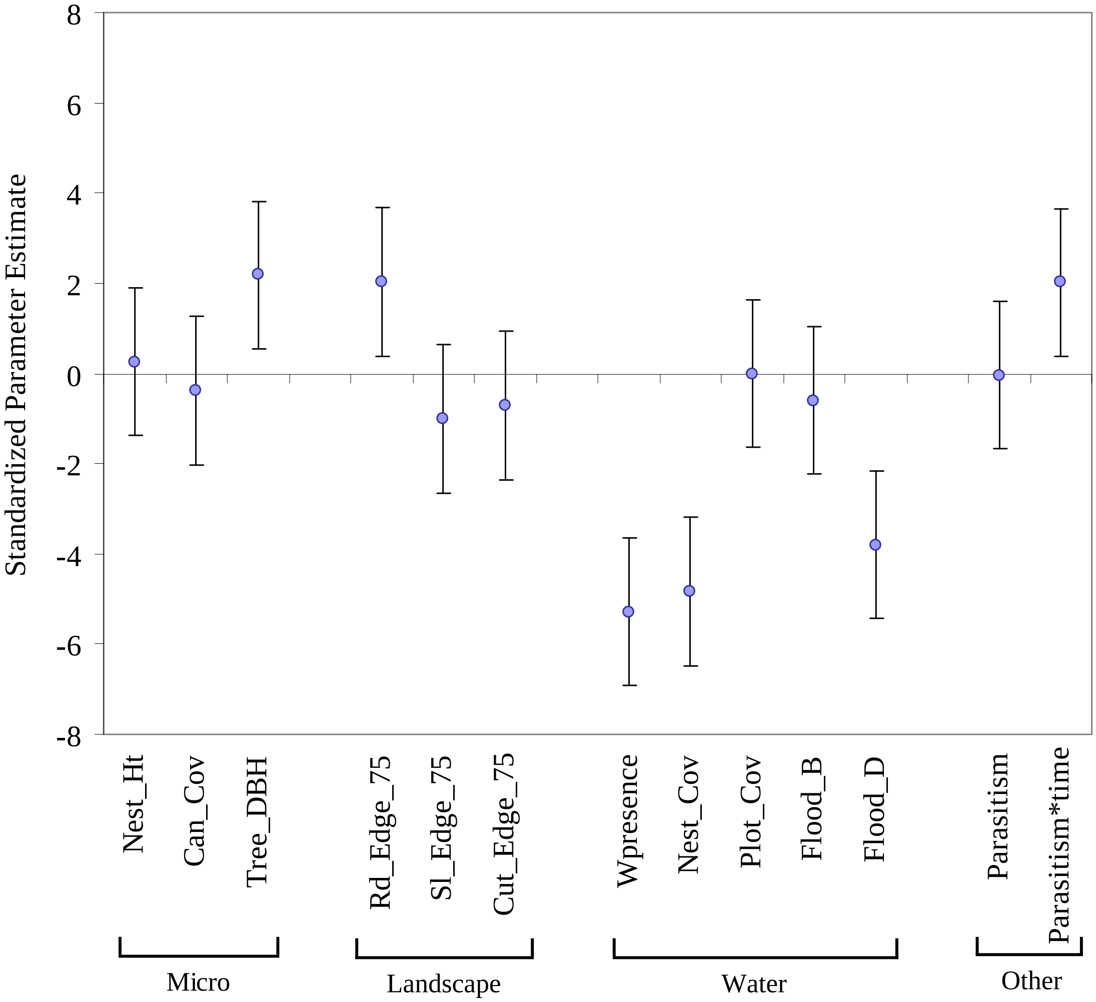


Figure 3.35: Standardized parameter estimates (*b/se*) of the variables included in the Prothonotary Warbler Cox regression Model D. Bars represent 90% confidence intervals. Parameter estimates were derived from the averaged model (see Table 3.17).

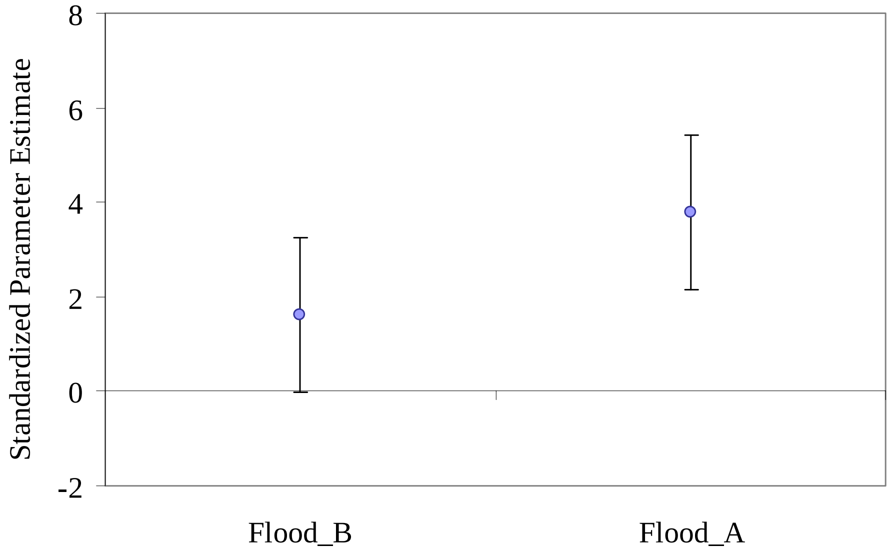


Figure 3.36: Standardized parameter estimates (*b/se*) of the flood stage dummy variables included in the Prothonotary Warbler Cox regression Model D. The full model was re-fit to leave out Flood_D ("During"), rather than Flood_A ("After"), and allow direct comparison of "Before" flooding to "During" flooding. Only flood stage variables are depicted here because the other variables are shown in Figure 3.35 and are identical. Bars represent 90% confidence intervals. Parameter estimates and standard errors were derived from the averaged model. Hazard Ratio is the estimated response to a change in the independent variable from Flood_B to Flood_D, or from Flood_A to Flood_D (other variables held fixed). Akaike Weight is the sum of relative AIC weight (Burnham and Anderson 1998) for those models in which the variable appears.

Variable		Parameter Estimate	Standard Error	90% Confidence Interval	Hazard Ratio	Akaike Weight
Water	Flood_B	0.4942	0.3063	{-0.0082 , 0.9966}	1.6392	0.0001
	Flood_A	0.6834	0.1800	{0.3882 , 0.9786}	1.9806	0.0001

Because Flood_A represents the comparison of "After" to "During" flooding, rather than "During" to "After", the standardized parameter estimate listed for Flood_A above is simply the negative of that displayed for Flood_D in Table 3.17, while the hazard ratio is simply the inverse and the standard error and Akaike weight are identical.

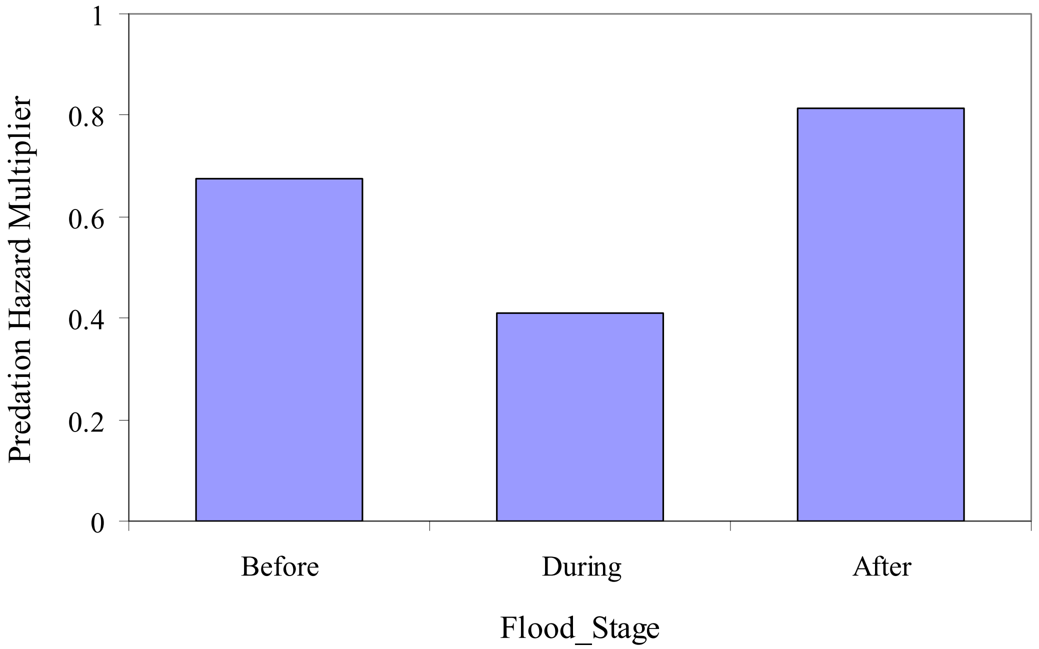


Figure 3.37: Relationship between the stage of flooding at the plot-scale and the hazard of predation for Prothonotary Warbler nests active during each stage. Flood stage is broken into three categories: before complete inundation, during complete inundation, and after complete inundation. During complete inundation, the plot is 100% covered with water; however, before and after complete inundation, the plot can be anywhere between 0% covered to less than 100% covered. The hazard multiplier is the exponentiated portion of the following equation:

$$h_i(t) = \lambda(t)\exp(\beta_{Flood\_B} * Flood\_B_i + \beta_{Flood\_D} * Flood\_D_i + \sum_{\substack{j=3 \\ \text{to } 12}}^{j} \beta_j * x_{ij} + \beta_{Parasitism*time} * Parasitism_i(t))$$

Where the hazard (h) of the predation event occurring for individual i at time (t) depends on the baseline hazard function (λ) at time (t), the parameter estimates for Flood_B and Flood_D, the values of Flood_B and Flood_D for individual i, the parameter estimates and values of the other 11 covariates (j) in the averaged model, and time (t). The baseline hazard, $\lambda(t)$, is left unspecified. While the values of Flood_B and Flood_D are varied between 0 and 1, all other class variables are set to 0, continuous covariates are held constant at their mean values, and time is set to 0. The resulting equation from which the above graph was made is as follows:

$$h_i(t) = \exp(-0.1892 * Flood\_B_i - 0.6834 * Flood\_D_i - 0.2050)$$

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APPENDICES

Appendix 3A: Description of the three different Cox regression models created to examine the survival of Acadian Flycatcher nests from predation. Years and spatial scales included in each model are marked with a crossed box, while years and spatial scales not included have an open box.

Model	Year(s)	Sample Size	Spatial Scales	Variables	Purpose
A	☒ 1996 ☒ 1997 ☒ 1998 ☒ 2000	339	☒ Micro-Scale ☒ Macro-Scale ☒ Landscape-Scale ☒ Water ☒ Other	Nest_Ht, Can_Cov, Dist_Edge, Dist_Bole Stems, Macro_PC1, Macro_PC3 Rd_Edge_75, Sl_Edge_75, Cut_Edge_75 Wpresence, Nest_Cov, Plot_Cov Parasitism	Examine all variables measured in each year
B	☒ 1996 ☐ 1997 ☐ 1998 ☐ 2000	117	☒ Micro-Scale ☒ Macro-Scale ☒ Landscape-Scale ☒ Water ☒ Other	Nest_Ht, Can_Cov, Dist_Edge, Dist_Bole Stems, Macro_PC1, Macro_PC3 Rd_Edge_75, Sl_Edge_75, Cut_Edge_75 Wpresence, Nest_Cov, Plot_Cov, **Flood** Parasitism	Examine effect of flood stage
C	☐ 1996 ☐ 1997 ☐ 1998 ☒ 2000	71	☒ Micro-Scale ☒ Macro-Scale ☒ Landscape-Scale ☐ Water ☒ Other	Nest_Ht, Can_Cov, Dist_Edge, Dist_Bole, **Conceal, Vines** Stems, Macro_PC1, Macro_PC3 Rd_Edge_75, Sl_Edge_75, Cut_Edge_75 Parasitism	Examine effect of micro-scale habitat characteristics, Conceal and Vines

Appendix 3B: Description of the four different Cox regression models created to examine the survival of Prothonotary Warbler nests from predation. Years and spatial scales included in each model are marked with a crossed box, while years and spatial scales not included have an open box.

Model	Year(s)	Sample Size	Spatial Scales	Variables	Purpose
A	☒ 1996 ☒ 1997 ☐ 1998 ☒ 2000	314	☒ Micro-Scale ☒ Macro-Scale ☒ Landscape-Scale ☒ Water ☒ Other	Nest_Ht, Can_Cov, Cav_Code Stems, Macro_PC1, Macro_PC3 Rd_Edge_75, Sl_Edge_75, Cut_Edge_75 Wpresence, Nest_Cov, Plot_Cov Parasitism, Parasitism*time	Examine **measured** variables at all spatial scales; thus exclude nests from 1998-breeding season
B	☒ 1996 ☒ 1997 ☒ 1998 ☒ 2000	461	☒ Micro-Scale ☒ Macro-Scale ☒ Landscape-Scale ☒ Water ☒ Other	Nest_Ht, Can_Cov Macro_PC1, Macro_PC3 Rd_Edge_75, Sl_Edge_75, Cut_Edge_75 Wpresence, Nest_Cov, Plot_Cov Parasitism, Parasitism*time	Include GIS extracted macro-scale habitat characteristics so could include nests from all years
C	☒ 1996 ☒ 1997 ☒ 1998 ☒ 2000	513	☒ Micro-Scale ☐ Macro-Scale ☒ Landscape-Scale ☒ Water ☒ Other	Nest_Ht, Can_Cov Rd_Edge_75, Sl_Edge_75, Cut_Edge_75 Wpresence, Nest_Cov, Plot_Cov Parasitism, Parasitism*time	Satisify skepticism concerning inclusion of GIS extracted macro-scale habitat characteristics
D	☒ 1996 ☐ 1997 ☒ 1998 ☐ 2000	280	☒ Micro-Scale ☐ Macro-Scale ☒ Landscape-Scale ☒ Water ☒ Other	Nest_Ht, Can_Cov Rd_Edge_75, Sl_Edge_75, Cut_Edge_75 Wpresence, Nest_Cov, Plot_Cov, **Flood_B, Flood_D** Parasitism, Parasitism*time	Examine effect of flood stage

CHAPTER 4

THE IMPORTANCE OF MULTI-SCALE HABITAT CHARACTERISTICS TO BROOD PARASITISM OF TWO BOTTOMLAND HARDWOOD FOREST SONGBIRDS: A LOGISTIC REGRESSION MODEL[1]

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[1] Gannon, J. and R.J. Cooper. To be submitted to *Ecological Applications*.

ABSTRACT

Population declines of forest-interior songbirds may be linked to increased brood parasitism resulting from a reduction and degradation of breeding habitat; bottomland hardwood forests of the southeastern U.S. are an example of one such habitat that has undergone severe reductions in the quantity and quality of breeding habitat and where parasitism by brood-parasitic cowbirds is high. We developed species-specific, multi-scale logistic regression models to investigate the relative importance of habitat characteristics to the brood parasitism of two neotropical migrant songbirds, the Acadian Flycatcher (*Empidonax virescens*) and the Prothonotary Warbler (*Protonotaria citrea*), breeding within the bottomland hardwood forests of the White River NWR. We demonstrated that the likelihood of brood parasitism was linked to local- and landscape-scale characteristics of the nest site and the surrounding habitat. Landscape-level characteristics describing proximity to external cowbird-feeding sites and exposure to internal canopy openings caused by patch cuts strongly influenced the probability of parasitism; nests located closer to feeding sites and exposed to more open canopy experienced increased rates of parasitism, however the magnitude of the effect was species-specific. Finer-scale characteristics of the nesting habitat and the nest-site, as well as temporal characteristics of the breeding season, were also influential; however, their influence was species-specific and tended to be less important. Local characteristics may be immaterial in areas saturated with cowbirds, but emerge as influential within areas more removed from cowbird seeding points. We conclude that although the factors influencing parasitism levels are complex, appropriate habitat management has the potential to reduce parasitism levels. In accordance with the conclusions of other researchers, we conclude that landscape-level management efforts to minimize cowbird-feeding areas and to decrease forest-interior disturbance that create open canopy will be most effective in decreasing levels of brood parasitism; however conservation efforts should consider all spatial scales when designing management plans to reduce parasitism.

INDEX WORDS: Bottomland hardwoods, Acadian Flycatcher, Prothonotary Warbler, Brood parasitism, Habitat characteristics, Open canopy, Cowbird feeding sites, Multiple spatial scales, Logistic regression

INTRODUCTION

Populations of many neotropical migratory songbirds have declined in recent decades (Robbins et al. 1989, Askins et al. 1990). Although the declines in many forest-dwelling neotropical migrant birds can be linked to a reduction in breeding and wintering habitats, the high degree of forest fragmentation and habitat loss in the eastern United States suggests that factors on the breeding grounds are the primary cause of migrant declines, presumably through decreased reproductive success (Robinson et al. 1995b). Low reproductive success resulting from increased rates of parasitism by Brown-headed Cowbirds (*Molothrus ater*) on the nests of forest-interior songbirds in these fragmented landscapes may have contributed to the population declines of neotropical migrants in North America (Mayfield 1977, Brittingham and Temple 1983, Hoover and Brittingham 1993).

Conservation of bird species will benefit from reducing the limiting nature of nest parasitism through knowledge of the birds' breeding biology, understanding their habitat requirements, and identifying and preserving the habitat features that positively affect their breeding productivity and survival (Martin 1992). Physical features of the breeding habitat influence opportunities for nesting, foraging, and protection from enemies (Cody 1981) and may ultimately reflect the suitability of a site for the reproduction and survival of breeding birds (Hilden 1965). Hence, to effectively manage for the conservation of songbird populations, it is critical to identify the specific habitat features that directly influence fitness components of reproduction and survival (Martin 1992). Given that brood parasitism by Brown-headed Cowbirds significantly decreases the reproductive success of many neotropical migrants (Brittingham and Temple 1983), it is important to identify the physical features of the nesting habitat that influence rates brood parasitism. Long-term solutions to maintaining populations of neotropical migrant birds include the identification of habitat features that directly impede the effectiveness of brood parasites at locating nests (Martin 1992). In addition, the identification and reduction of land use practices that augment brood parasite populations are necessary. As a result of reported declines, there has been a surge of research on neotropical migrant bird populations in recent years. Studies have considered effects of nest-site habitat characteristics, habitat fragmentation, and external and internal forest edges on the reproductive success of forest-interior neotropical migrants.

Several studies have examined the influences that habitat characteristics at the micro-scale (< 5-m radius) and nest-patch or macro-scale (5-m to 11.3-m radius) have on nest parasitism; however, results of published studies are mixed. Some studies have correlated increased rates of parasitism with canopy openness (Wolf 1987, Brittingham and Temple 1996), while others found no such relationship (Larison et al. 1998, Howe and Knopf 2000). Moorman et al. (2002) found an inverse relationship between ground cover and the probability of parasitism for a shrub-nesting songbird. Concealment by vegetation at the micro-scale and nest-patch scale has also been related to decreased rates of parasitism (Uyehara and Whitfield 2000); however, a review by Robinson et al. (1995a) failed to find a general effect of nest cover on parasitism levels. Conflicting reports on the effect of nest placement within the vertical strata of forested habitats also exist; some researchers found increased levels of parasitism on ground nests (Hahn and Hatfield 2000), others documented that canopy nests were more heavily parasitized (Robinson et al. 2000), while a general review found no preferences by brood parasitic cowbirds for a particular stratum (Robinson et al. 1995a). A correlation between proximity of perches within the nesting macro-habitat and increased probability of parasitism has also been documented (Anderson and Storer 1976, Clotfelter 1998, Hauber and Russo 2000, Budnick 2002; but see Brittingham and Temple 1983).

Fragmentation of extensive forests into smaller patches has occurred in many temperate forest regions due to conversion to agricultural or urban land uses. Forest fragments have a higher proportion of exterior edge than do larger more intact forests and are thus more influenced by the matrix in which they are embedded (DeGraaf 1995). Such influences can include higher rates of brood parasitism (Wilcove 1985). The adverse effects of habitat fragmentation and decreased proportion of forest cover on rates of nest parasitism are well documented (Robinson et al. 1995b, Donovan et al. 1995, Donovan et al. 1997, Annand and Thompson 1997). Brood parasitism by Brown-headed Cowbirds increases with forest fragmentation and proximity to agricultural landscapes because populations of cowbirds flourish in landscapes that offer a mixture of both feeding (agricultural) and breeding (forest) habitats (Donovan et al. 1997), and areas with high cowbird densities experience high parasitism rates (Hoover and Brittingham 1993). However, fragmentation caused by silvicultural practices in forest-dominated landscapes may not have the same effect (Thompson et al. 1992, Rodewald and Yahner 2001b).

Studies examining the effect of forest fragmentation on rates of nest parasitism have predominantly been conducted in agricultural landscapes where many have documented elevated rates of parasitism in association with increased forest fragmentation and the creation of external edge (Brittingham and Temple 1983, Donovan et al. 1997, Morse and Robinson 1999, Chalfoun et al. 2002a). Fewer studies have been conducted in forest-dominated landscapes fragmented by forestry practices, and evidence of increased parasitism within these landscapes and at the internal edges timber management creates has been equivocal. Both positive (Strelke and Dickson 1980, Moorman and Guynn 2001, Moorman et al. 2002) and non-existent (Morse and Robinson 1999) relationships between rates of parasitism or abundance of cowbirds and internal edge created by forestry practices have been reported. Additionally, a higher abundance of cowbirds within younger forest stands and plots treated by silvicultural practices has been documented (Thompson et al. 1992, Annand and Thompson 1997). Differences in landscape structure, edge type, permanence of edge, and abundance of cowbirds in agriculturally versus industrially fragmented forests may preclude generalization regarding nest parasitism within fragmented landscapes and at the external and internal edges they create.

Most studies examining effects of internal edge within forests have focused on the extensive openings created by silvicultural practices, disregarding narrow breaks in the forest canopy created by anthropogenic disturbances, such as recreational trails, roads, and utility right-of-way corridors, or by natural forest openings such as streams. Although forest edges are frequently associated with increases in edge-related brood parasitism, it is unclear whether narrow internal edges, man-made or natural, create the same edge conditions that attract cowbirds near edges adjacent to large, human-induced openings. Few studies have compared rates of parasitism along different types of edges, such as trails (Hickman 1980), roads (Rich et al. 1994), utility rights-of-way (Chasko and Gates 1982, Rich et al. 1994), and streams (Gates and Giffen 1991). Although few in number, these studies have reported increased abundance of cowbirds and increased rates of brood parasitism (Chasko and Gates 1982) in close proximity to the these internal edges. Additionally, a link was made between cowbird abundance along roads and utility right-of-way corridors and the presence of grass within the openings (Rich et al. 1994).

A more complete understanding of the factors that control populations of forest-nesting songbirds on their breeding grounds will require information on responses to habitat features at multiple scales. Studies have documented that rates of brood parasitism respond to habitat variation at the nest-site (Uyehara and Whitfield 200) and the nest-patch scale (Brittingham and Temple 1996), as well as to edge proximity (Chasko and Gates 1982) and the pattern of forest and interstitial land use in the surrounding landscape (Donovan et al. 1997). Although variables at several spatial scales have been investigated and show that both localized and landscape-level factors can have a profound effect on nest parasitism rates, further knowledge on the relative importance and the interaction of variables at multiple scales with respect to brood parasitism is necessary for comprehensive management of songbird populations. Despite this need, few studies have simultaneously investigated the relative importance of habitat characteristics at more than one spatial scale to the reproductive success of birds. To our knowledge, Rodewald and Yahner (2001a) have conducted the only multi-scale study that simultaneously investigated the relative influence of variables at three spatial scales on avian nesting success; however, the study did not specifically address parasitism. Many ecological processes that might affect nest parasitism operate at multiple spatial scales (Bergin et al. 2000) and are complex, potentially involving several interactions between variables at different spatial and temporal scales. Therefore, accurate interpretation of the mechanisms driving rates of nest parasitism will require viewing these ecological processes at multiple scales (Donovan et al. 1997) and proper management of songbird populations will require more studies to use a multi-scale approach.

A drastic example of forest habitat loss in the southeastern United States has been in bottomland hardwood forests of the Mississippi Alluvial Valley (MAV; MacDonald et al. 1979, Mitsch and Gosselink 1986); only about 20% of the original 9 to 10 million hectares of bottomland hardwood forests in the MAV remain (Yin et al. 1997). Conversion to agriculture, timber removal, and the construction of flood control and navigation structures have eliminated bottomland hardwood forests from much of the MAV and, as a result, agriculture has replaced forest as the dominant land cover within the MAV. Most of the remaining bottomland forest within the MAV exists as small patches surrounded by a sea of agriculture; within such a landscape, forest-nesting birds are exposed to an abundance of generalist predators and Brown-headed Cowbirds. In addition to actual losses of bottomland hardwood forests, the remaining bottomland hardwoods are in an ecologically degraded condition due to severe fragmentation, hydrologic alterations, and poor timber management practices (Allen 1997). The ecosystem changes within remaining bottomland hardwood forests of the MAV could negatively impact regional populations of neotropical migrants that depend on functioning bottomland forest ecosystems; this is especially true for those birds that reach their highest breeding densities within bottomland hardwood forests. For the above reasons, as well as the continued increase in timber removal, the bird conservation group Partners in Flight has identified bottomland hardwood forests as a habitat of regional concern (Hunter et al. 1993). Despite the importance and imperiled state of bottomland hardwood forests, there is a lack of long-term data sets on the nesting success of songbirds breeding within these forests, indicating that research within bottomland hardwood forests is needed.

The White River National Wildlife Refuge, located in the MAV of southeast Arkansas, is one of the largest remaining tracts of bottomland hardwood forest within the US. Although large (65,000 ha), the Refuge is narrow (4.5-15.5 km-wide) in shape and is surrounded by agricultural fields; as such, it is accessible to cowbirds that parasitize the nests of forest-interior songbirds breeding within the forest. The Refuge is managed by the USFWS for multiple uses, including wildlife diversity, waterfowl habitat, public recreational activities such as hunting and fishing, and timber. Consequently, logged areas, logging roads, and public access roads exist throughout the Refuge. It is unknown whether these features of the internal forest landscape exacerbate the already high rates of nest parasitism to which the breeding birds are exposed.

Previous research within the White River National Wildlife Refuge has focused on the reproductive success of two neotropical migrants, the Acadian Flycatcher (*Empidonax virescens*; Wilson 1997) and the Prothonotary Warbler (*Protonotaria citrea*; Wood 1999). Both of these species are declining within the Mississippi Alluvial Plain (Sauer et al. 2003) and, as a result of area sensitivity (Acadian Flycatcher and Prothonotary Warbler) and extreme habitat specificity (Prothonotary Warbler), Partners in Flight has given the Acadian Flycatcher a high-priority ranking for monitoring and management in the Southeast and has listed the Prothonotary Warbler as a species of high conservation priority throughout its breeding range (Hunter et al. 1993, Rich et al. 2004). Research on the micro- and macro-habitat characteristics of Acadian Flycatcher nests revealed no relationship with parasitism (Wilson 1997). Research on Prothonotary Warblers reported that parasitism levels were not related to plot-scale forest fragmentation caused by logging (patch and group cuts; Wood 1999). Within the Refuge, as well as elsewhere within bottomland hardwood forests, research investigating the effects of internal edges on rates of nest parasitism of forest-interior songbirds is lacking. Additionally, research that simultaneously investigates the relative importance of habitat characteristics at multiple spatial scales to nest parasitism is needed.

This study augments the scanty knowledge concerning brood parasitism of neotropical migrant songbirds within bottomland hardwood forests of the MAV. The study was conducted within the White River National Wildlife Refuge during the breeding seasons of 1996-2000. We examine brood parasitism of two common bottomland hardwood forest bird species, the Acadian Flycatcher and Prothonotary Warbler, in relation to physical characteristics of the nesting habitat at the micro-, macro-, and landscape scale. These physical characteristics include descriptions of nest placement, vegetation structure, proximity and exposure to internal forest canopy openings created by patch cuts, trails, and roads, and proximity to external forest edges.

STUDY AREA

The White River National Wildlife Refuge (NWR) is located in the southeast Arkansas portion of the Mississippi Alluvial Valley (Figure 2.4). It is located within the Lower White River Basin, within the flood plain of the lower White River, approximately 12 km above its confluence with the Mississippi River. The Refuge is a 65,000-ha managed, seasonally flooded, bottomland hardwood forest that extends approximately 104 km along the White River. It is one of the largest remaining contiguous bottomland hardwood forests in the United States (Harris and Gosselink 1990). Although large, the Refuge is narrow in shape (4.8-15.5 km-wide) and is surrounded by agricultural fields; as such, it contains generalist predators and cowbirds that prey upon and parasitize the nests of songbirds breeding within the forest. A grassy levee, on which cattle graze, runs parallel to the east side of the Refuge and serves as a foraging ground for large flocks of Brown-headed Cowbirds. Of the total Refuge area, about 91% is forested, 8% is in waterways and lakes, and less than 2% is grassland and cropland.

Within the Refuge, the dominant overstory tree species are overcup oak (*Quercus lyrata*), Nuttall oak (*Quercus nuttallii*), green ash (*Fraxinus pennsylvanica*), bitter pecan (*Carya* *aquatica*), American elm (*Ulmus americana*), cedar elm (*Ulmus crassifolia*), waterlocust (*Gleditsia aquatica*), sugarberry (*Celtis laevigata*), and cypress (*Taxodium distichum*). Understory vegetation is predominantly comprised of possumhaw (*Ilex decidua*), swamp privet (*Forestiera acuminata*), hawthorn (*Crataegus spp.*), and water elm (*Planera aquatica*), as well as seedlings and saplings of overstory tree species. For further description of this area, see Wilson and Cooper (1998a,b).

METHODS

PLOTS

In 1993, six 50-ha (500 m x 1000 m) plots were established within a single management compartment (Number 8) of the Refuge (Figure 2.5). The compartment was 1,376 ha in size and consisted of contiguous homogenous habitat. In the fall of 1995, three silvicultural treatments (no cut, selective cut, and patch cut) were randomly allocated to two plots each (Figure 2.5). The selective cut plots had 300.9 m^2 and 311.6 m^2 basal area of timber removed. Each of the two patch cut plots had four blocks (averaging 2.8 ha/block) of timber completely removed or felled (Figure 2.6). A 25-m grid system (21 columns x 41 rows) was established and maintained on each plot for use in navigation and nest location. Because of our interest in definable internal edges, this study focused solely on the no cut and patch cut plots; thus, all subsequent information applies only to these four plots.

NESTS

NEST SEARCHING

Intensive nest searches were conducted on all plots during the breeding seasons of 1996-1998 and 2000. Nest searching for Acadian Flycatchers started upon the arrival of the females in late April and continued through the end of July or early August (Figure 2.7a). For Prothonotary Warblers, nest searching began upon the arrival of the females in early April and continued through the breeding season until the males began to abandon territories (Figure 2.7b). Nest searching efforts varied between years and between species (Table 2.1). Once a nest was found, flagging tape was placed more than 5 meters from the nest and care was taken to approach the nest from different pathways on subsequent nest checks. The location of the nest was recorded as the distance and direction from the closest grid point with the use of a SONIN electronic distance estimator and a compass.

NEST MONITORING

Once a nest was located, its contents were noted. Mirror poles were used to examine nests when contents could not be seen from the ground. If nest height was too high for mirror poles (about 9 m for Acadian Flycatchers and 5 m for Prothonotary Warblers), the nest was observed from a distance using binoculars, and contents of the nest or nest stage were determined by observing the behavior of the adult birds; for example, brooding females indicated that the nest was still active, while delivering of food or disposing of fecal sacs indicated that the nest contained nestlings. In addition, the architectural structure of Acadian Flycatcher nests often made it possible to determine the status, if not stage, of the nests by looking through the bottom of nests while standing directly beneath it. Nests were visited every two to four days following Breeding Bird Inventory and Research Database (BBIRD) protocol (Martin et al. 1997) to determine clutch size, number of nestlings, number of fledglings, and fate of the nest as accurately as possible.

NEST FATE

Nest fates were recorded for the host species, for cowbirds if the nest was parasitized, and for the overall nest. Fates fell within three categories: successful, failed, or uncertain. A host was considered successful if one or more host young fledged. A cowbird was successful if one or more cowbird young fledged. A nest was considered successful if one or more young fledged, regardless of the species. Evidence for nest success followed BBIRD protocols (Martin et al. 1997). Nest failures were broken down into the following classifications: predation, parasitism, abandonment, adult mortality, flooding, physical causes such as weather or tree fall, and unknown. Uncertain nest fates occurred when there was insufficient information to determine success or failure. Nests were excluded from analysis if the nest failed prior to laying of the first egg or if observers caused mortalities.

NEST INITIATION

Nest initiation date (date when first host egg was laid) was determined in order to separate nests into initiation periods. The majority of nests were found in the building and laying stages (Table 2.5), thus, nest initiation day was apparent. When nests were found after egg laying commenced, nest initiation date was determined by backdating to the day that the first host egg was laid based upon the average length of species' laying, incubating, and nestling periods. Nests were separated into two initiation periods, early or late, based on the mean mid-point between the earliest and latest nest initiation dates for each year. Acadian Flycatcher nests initiated on or before June 18 were placed in the early initiation period and nests initiated after June 18 were placed in the late period. For Prothonotary Warblers, June 3 was the cutoff for early and late initiation periods.

NEST TERMINATION

If a nest failed or fledged between nest checks, the midpoint of the check was used as the termination date. If the fate of the nest was uncertain, the last active nest check was used as the termination date. Exposure days were determined by subtracting the date found, or the date initiated if the nest was found prior to the first egg, from the date terminated. Therefore, exposure days only included days that the nest was active and under observation.

NEST SUCCESS

Nesting success was calculated by the methods of Mayfield (1961, 1975), which estimates the probability of nest survival based on nest exposure days. Exposure days from nests with uncertain fates were included in the calculations. Nesting success was calculated for each species, using exposure days for only the host species.

A daily probability of nest survival and its standard error was calculated for each stage of the nesting period: the egg stage (from first egg to hatching) and the nestling stage (hatching to fledging). Nest-stage survival estimates were obtained by raising the daily survival probability of a given stage to the number of days in the respective stage. For Acadian Flycatchers, the egg stage is 15 days and the nestling stage is 14 days. For Prothonotary Warblers, the egg stage is 16 days (based on an average clutch size of five) and the nestling stage is 11 days. The overall probability of nest success was calculated as the product of the two stage survival probabilities. Calculating overall nest success in this manner assumes that mortality is constant within but not necessarily across the different nest stages. The standard error for overall nest success was calculated by the method of Hensler (1985). The daily probability of nest survival for the entire nesting period was calculated by raising the overall nest survival to the inverse of the number of days in the full nesting period (n), which for Acadian Flycatchers and Prothonotary Warblers is 29 days and 27 days, respectively. The standard error of the daily probability was approximated by dividing the standard error of overall nest success by [n*((daily survival probability)^(n-1))].

BROOD PARASITISM

DEFINITION AND RESTRICTIONS

A nest was considered parasitized if it contained one or more cowbird egg(s) or young. To maintain an ample sample size, rather than restricting nests to those found prior to egg laying, the "window of susceptibility" (Pease and Grzybowski 1995) was used to restrict the use of certain nests. Using nests found after the initiation date may underestimate the frequency of parasitism because parasitized nests that terminate prior to being found are not included. A good sample size for statistical analyses was prioritized over an accurate overall frequency of parasitism. The number of days that each species was susceptible to parasitism was calculated based on the following assumptions adapted from Pease and Grzybowski (1995) and Banks and Martin (2001): (1) cowbirds may lay eggs one day before hosts initiate their clutches; (2) cowbirds require 12 days of incubation (Lowther 1993); and (3) cowbirds may hatch up to two days after the host young hatch. For all analyses concerning parasitism, the number of susceptible days was used to restrict the use of each species' nests as follows:

ACADIAN FLYCATCHER – Using the aforementioned assumptions and assuming an average clutch size of three eggs, the Acadian Flycatcher is susceptible to brood parasitism for a six-day window. This window spans from one day prior to host initiation to three days after egg laying has completed. In other words, a nest that is five or more days old is no longer susceptible to parasitism. Nests that were recorded as non-parasitized, but terminated prior to reaching day five, or the closing of the susceptibility window, were excluded from all parasitism analyses.

PROTHONOTARY WARBLER – Using the aforementioned assumptions and assuming an average clutch size of five eggs, the Prothonotary Warbler is susceptible to brood parasitism for a seven-day window. This window spans from one day prior to host initiation to two days after egg laying has completed. In other words, a nest that is six or more days old is no longer susceptible to parasitism. Nests that were recorded as non-parasitized, but terminated prior to reaching day six, or the closing of the susceptibility window, were excluded from all parasitism analyses.

ACADIAN FLYCATCHER AND PROTHONOTARY WARBLER – Nests that were found in the nestling stage and recorded as non-parasitized were excluded from the analyses under the assumption that cowbird eggs that failed to hatch could be present but not visible. Lastly, nests in which the status of parasitism could not be ascertained with certainty (e.g., high nests outside of the reach of a mirror pole) were excluded from analyses.

FREQUENCY, RATE, AND INTENSITY

The frequency of brood parasitism by Brown-headed Cowbirds was estimated for each species as the number of parasitized nests divided by the total number of nests. For Prothonotary Warblers, daily parasitism rate was estimated as the number of cowbird eggs divided by the number of susceptible days ("instantaneous parasitism rate"; Pease and Grzybowski 1995). For parasitized nests that terminated before day six, the number of susceptible days equaled the age of the nest at termination plus one. Nests that terminated on or after day six were susceptible to parasitism for seven days. The intensity of parasitism was estimated as the mean number of cowbird eggs per parasitized nest. Parasitism rate and intensity were not calculated for Acadian Flycatchers owing to the difficulty of seeing into their high nests to obtain an accurate count of cowbird eggs.

HABITAT MEASUREMENTS

MICRO-SCALE

At the end of the breeding season, when nests were no longer active, habitat characteristics were measured at the micro-scale, right at the nest (Table 2.2, Figure 2.8). The measurements included characteristics of the nest substrate and nest placement. These measurements were based on BBIRD protocol (Martin et al. 1997).

For each nest, we used a densiometer to measure the percentage of canopy cover in the four cardinal directions; the four measurements were then averaged to obtain an overall percent canopy cover. Nest heights of both species were measured with the use of a clinometer unless the nest was within reach of a measuring pole (< 5 m). For Acadian Flycatchers, an additional measurement of nest placement included the distance of the nest from the edge of the nest branch. For Prothonotary Warblers, we measured width and height of the cavity entrance. Based on histograms of the two cavity entrance dimensions, we grouped width and height into four and five size categories, respectively (Figure 2.9). The product of a cavity's width and height was used to assign it one of five codes that described its overall cavity entrance size (Figure 2.9). The cavity code was treated as a continuous variable for modeling purposes, where cavities of code 1 were smaller than average, cavities of code 2 were average size, and cavities of code 3 and 4 were incrementally larger than average. Cavities that were open in height (i.e., had no top), regardless of width, were assigned a cavity code of 5; these cavities were considered to represent the upper extreme of the size continuum. We also recorded cavity type (split or hole). Splits were natural openings created by injury/decay of the tree with an entrance greater in height than width. Holes were natural or excavated cavities with a circular shape.

MACRO-SCALE

At the end of the breeding season, habitat characteristics were measured at the macro-scale, within an 11.3 m-radius circle (0.04 ha) centered at each nest (Table 2.2, Figure 2.8). Our measurements were modified from the methods developed by James and Shugart (1970). Within each 0.04-ha plot, we recorded the species and diameter at breast height (DBH) for all trees with a DBH ≥ 10 cm, thus obtaining the number of trees and the average DBH for the nest plot. Estimates of percent canopy cover and canopy height were obtained using a densiometer and a clinometer, respectively. These measurements were taken in the four cardinal directions and then averaged to obtain an overall percent canopy cover and canopy height for the nest plot. The nest plot was divided into four quadrants and within each 0.01-ha quadrant we measured the distance from the nest to the closest tree ≥ 10 cm DBH; if no tree ≥ 10 cm DBH was present within the quadrant, we measured the distance to the nearest tree beyond the 11.3 m-radius circle. The four distances were averaged to provide an indicator of openness around the nest site. Within a 5 m-radius circle around each nest, we recorded the number of woody stems (trees and saplings < 10 cm DBH). The same macro-scale measurements were taken at 15 recurring, systematically selected grid points per 50-ha plot each year.

LANDSCAPE SCALE

Habitat characteristics were measured at the landscape scale (Table 2.3, Figure 2.8). Distances from each nest to the exterior forest edge and to the levee were measured in ArcView GIS 3.2 (ESRI 1999). In an attempt to target landscape features relevant to parasitism, canopy openings within the study area were mapped. Roads, sloughs, and other water bodies greater than 5-meters wide were combined with patch cuts to create an ArcView shapefile of canopy openings (Figure 2.11). The closest distance from each nest to a canopy opening was determined. In addition, the percent of open canopy within 200 meters of each nest was measured. A 200 m-radius buffer is equivalent to 12.5 ha and was chosen for two reasons: 1) to correspond with the breeding home range of a female cowbird (average 9.7 ha, range 4.7-16 ha; McGeen and McGeen 1968) and 2) to provide an adequate range of values for the percent of open canopy.

DATA ANALYSIS

VARIABLE TRANSFORMATIONS

A logit transformation was applied to percent micro-canopy cover, percent macro-canopy cover, and percent open canopy within 200 meters of a nest. A log transformation was used on the macro-habitat variable, tree distance. A square root transformation was applied to the Acadian Flycatcher micro-habitat variable, branch edge distance. Transformations were applied to obtain a more balanced distribution of the data. More specifically, because the variables were to be used as predictors in linear models, transformations more clearly distinguished among values near support boundaries (e.g., proportions near 0/1) and reduced the influence of highly-skewed values (e.g., distances).

PRINCIPAL COMPONENTS ANALYSIS

MACRO-HABITAT VARIABLES – Principal components analysis (PCA) was performed on a set of five interrelated macro-habitat variables. The PCA procedure was used to simplify the representation of the information by creating a reduced set of new, uncorrelated variables which could then be used as covariates in models. The original five variables included tree count, average DBH, average canopy height, and the transformed versions of tree distance and macro-canopy cover. Macro-habitat measurements taken at the nest sites of both bird species and at sampling grid points were combined for all years (n=1033) to run the PCA.

OPEN CANOPY – Principal components analysis was executed on two highly correlated variables describing nest exposure to open canopy at the landscape scale: distance to open canopy and the transformed version of percent open canopy within 200 meters of a nest. Measures of openness taken from the nest locations of both bird species were combined for all years (n=1012) to run the PCA.

GIS EXTRACTION OF MACRO-HABITAT PRINCIPAL COMPONENTS

Macro-habitat features were not measured at Prothonotary Warbler nests in 1998 because of logistical constraints. The missing values prevented statistical analyses of data including both macro-habitat variables and 1998 nests; that is, we had to choose between using macro-habitat variables and dropping all nests from the year 1998 or dropping the macro-habitat variables and including nests from 1998. To remedy this situation, we created an interpolated coverage of the macro-habitat principal components to extract and impute habitat values for Prothonotary Warbler nests monitored during the 1998-breeding season (see Chapter 2 for details).

NEST SURVIVAL, PARASITISM FREQUENCY, RATE, AND INTENSITY

Nest success was compared between parasitized and non-parasitized nests of Acadian Flycatchers and Prothonotary Warblers using the program CONTRAST (Hines and Sauer 1989), which performs chi-square tests for comparisons among rate estimates. Additionally, survival probabilities of Prothonotary Warbler nests were compared between nests containing varying numbers of cowbird eggs. For both species, the frequency of parasitism was compared among years and among plots using a chi-square test of equal proportions; the yearly comparison was completed combining over all plots and individually by each plot, while the plot comparison was completed over all years and by individual years. For Prothonotary Warbler nests, the daily rate and intensity of parasitism were compared among plots. Rates of parasitism were compared using program CONTRAST. Parasitism intensity was compared using the non-parametric Kruskal-Wallis test.

LOGISTIC REGRESSION MODELS

All analyses were performed using SAS Release 8.02 (SAS Institute 2001). We used logistic regression to create exploratory models that investigated which habitat characteristics at three spatial scales were related to nest parasitism (Tables 4.2 and 4.7). The landscape scale variables, distance to forest/agriculture edge and distance to levee, were not included in the analysis because, as a result of refuge shape and plot design, they were synonymous with plot assignment (Figures 2.5 and 4.1). The above landscape variables and plot could not both be included in the analysis because of their high correlation; plot was chosen because it not only explained the landscape differences, but it controlled for other nuisance differences. Plots were represented by a combination of three dummy variables, treatment, replicate, and a treatment*replicate interaction (Appendix 4A). This representation of plot allowed us to investigate treatment effects, create interactions between treatment type (no cut or patch cut) and other covariates, as well as control for individual plot differences. Separate models were created for each bird species, combining all years and plots. The nest was the experimental unit and parasitized/not parasitized was the dichotomous response variable, where 1=parasitized and 0=not parasitized.

Explanatory variables were tested for problematic multicollinearity using the variance inflation factor, tolerance, and condition index diagnostics. The diagnostics were derived by performing a weighted least squares regression using linear combinations adjusted by the weight matrix of the maximum likelihood algorithm (PROC LOGISTIC, PROC REG; Allison 1999). All variables were centered to remove collinearity with the intercept. The data were screened for influential observations using diagnostic statistics outputted from PROC LOGISTIC (Allison 1999). In addition to using box plots to look for obvious outliers, we used the hat matrix diagonal statistic to identify extreme observations. The C statistic was used to identify observations with undue influence on overall regression coefficients, and DFBETAs were used to identify observations with undue influence on specific parameter estimates. Each statistic was plotted against the nest observations to visually identify problematic observations. Variables were tested for linearity by plotting the logit of parasitism frequency against each explanatory variable.

A limited number of interactions between main effects were created based on knowledge of the system. PROC LOGISTIC was used to screen the interactions by adding them one at a time to a model containing all explanatory variables and excluding those with a p-value greater than 0.2 from further consideration. Interaction terms that met the criteria were used to produce all possible combinations of interaction terms, while imposing a limit of three terms per combination (i.e., all possible one interaction term, two interaction term, and three interaction term combinations). The interaction term combinations were added one at a time to the full model (i.e., all main effects) and the augmented models were compared to each other, as well as to the model containing only main effects and no interactions. We compared models by Akaike's Information Criterion (AIC; Akaike 1973). We balanced fit of the model with model complexity and chose the most parsimonious model that provided the largest improvement in model fit. This model was used as the global model. The fit of the global model was tested with the Hosmer and Lemeshow Goodness-of-Fit Test (1989).

We created candidate models from the explanatory variables within the global model. All candidate models included dummy variables describing the study year and plot. In addition to these variables, three additional variables were allowed per candidate model. Using these requirements and restrictions, all one-, two-, and three-variable combinations were created from the set of explanatory variables within the global model (SAS macro, APLR; C.T. Moore, USGS Patuxent Wildlife Research Center, unpublished software). The list of all possible models was filtered to exclude models that included an interaction term without both main effects. Despite steps we took to reduce the size of the candidate model set (a priori construction of candidate variable set, enforcement of upper size limit for any model, and specification of inclusion criteria for specific variables), the resulting set of candidate models was large, but within reason for the exploratory nature of our analysis (Burnham and Anderson 1998).

We used the information-theoretic approach described by Burnham and Anderson (1998) to compare models; this approach uses AIC as the basis for comparison. Models were ranked by AIC, corrected for small sample size (AICc), from smallest to largest. We used the Δ AICc values (AICc – minimum AICc) and the Akaike model weights (w_i) to determine if there was one "best" model among our set of candidate models. Akaike model weights indicate the relative likelihood of the model, given the data and the set of candidate models (Burnham and Anderson

1998). A given w_i is considered to be the weight of evidence in favor of model *i* being the actual best model; the weights are normalized so that the relative likelihoods sum to 1 (Burnham and Anderson 1998). We considered a top-ranked model to be "best" if the ratio of the top-ranked model to the second-ranked model was at least 10 (i.e, $w_1/w_2 \geq 10$). When we did not find one best model, we followed the recommendation of Burnham and Anderson (1998) and performed model averaging. Model averaging incorporates model selection uncertainty into estimates of parameters and estimates of their precision to produce unconditional parameter estimates, standard errors, and confidence intervals (Burnham and Anderson 1998). All candidate models were included in the scope of the averaged model, and inferences were made from the resulting averaged model. To quantify the relative evidence of importance for each predictor variable (x_j) included in the averaged model, we summed the Akaike model weights (w_i) across all of the candidate models where variable *j* occurred (Burnham and Anderson 1998). To provide an idea of how the Akaike model weights were distributed among the candidate models, we calculated the 95% confidence set of candidate models. To do so, we summed the Akaike model weights of the ranked models from largest to smallest until that sum reached 0.95; the corresponding subset of models is a type of confidence set on the best model (Burnham and Anderson 1998).

Plots of standardized parameter estimates and their 90% confidence intervals were created to facilitate comparisons of relative effect sizes among the covariates included in the top-selected or the averaged models. Standardized parameter estimates are the quotient of the model coefficients and their standard errors (that is, $b/se(b)$). In addition to effect sizes, the plots indicate whether estimates were precise enough, relative to effect size, to conclude if and how the variables affect nest parasitism. We used 90%, as opposed to 95%, confidence intervals to reduce the probability of committing a Type II error; in ecological situations, an incorrect conclusion that a variable is not important (Type II error) may be more detrimental to the resource than incorrectly concluding that a variable is important (Type I error; Johnson 1999). The probability of parasitism was plotted against each variable whose 90% confidence interval did not span 0 and that had large Akaike weights relative to the other variables in the model.

Comparison of the probability of parasitism between years and between plots was limited by the dummy coding for year and for Trt, Rep, Trt*Rep. To compare the probability of parasitism between all years, the model was re-fit twice, each time leaving out a different year for comparison. To compare the probability of parasitism between all plots, the model was re-fit three additional times, each time re-coding the Trt, Rep, Trt*Rep variables such that each plot in turn was coded as (0,0,0), making its estimate equal to the intercept value (Appendix 4B). Re-fitting the model in this manner was necessary because, due to model averaging, the covariance matrices between variables were not available.

PROTHONOTARY WARBLER – The data set for Prothonotary Warblers had a large number of missing values. In particular, macro-scale habitat features were not measured in 1998. Because of this limitation, three different data sets were used to run the logistic regression analysis so that hypotheses could be fully (albeit separately) investigated with as much information as available. The first data set included all variables of interest that were measured during all years (n=270; Model A). This data set included macro-scale variables and thus excluded all nests from the 1998-breeding season because they lacked macro-scale habitat measurements. The second data set included all years and variables at all spatial scales, including the GIS extracted values for the macro-habitat variables from 1998 (n=317; Model B). To satisfy skepticism concerning the inclusion of the GIS extracted macro-habitat variables, the third data set included all years, but excluded macro-scale variables (n=343; Model C).

SPATIAL AUTOCORRELATION

We tested for positive spatial autocorrelation among neighboring nests of the same species with respect to parasitism fate. We used two different programs, ROOKSCASE (Sawanda 1999) and GeoDa (Anselin 2003), specifying an irregular lattice and a 200-m lag to calculate Moran's I (Moran 1950). The index was compared to the z-score for the null hypothesis of a random spatial distribution to determine whether the nests in our sample dataset exhibited a spatially correlated pattern of nest parasitism within a breeding season. Moran's I ranges in value from –1 to 1; a positive value indicates a clustering of nest fates, where nests within the given distance interval are more similar to each other than expected by random, whereas a negative value indicates that nests are more dissimilar to each other than expected by random. Although Moran's I detects clustering, it does not convey the nature of the spatial clustering; that is, it does not distinguish whether the cluster is of parasitized nests or of non-parasitized nests. We considered spatial correlation among nests pre- and post-modeling, using raw nest fates (i.e., parasitized/not parasitized) and logistic regression residuals from the global model, respectively. If the raw fates of nests were spatially correlated, we expected that the inclusion of spatially explicit independent variables in the logistic regression model would account for the correlation, as would be manifested by spatial independence of the residuals.

RESULTS

NEST SURVIVAL, PARASITISM FREQUENCY, RATE, AND INTENSITY

Totals of 441 Acadian Flycatcher and 579 Prothonotary Warbler nests were monitored on the four study plots during the breeding seasons of 1996-1998 and 2000 (Table 2.1). For both species, the majority of nests were found in the building and laying stages (Table 2.5). After age restrictions were applied to the nests for the purpose of studying brood parasitism by Brown-headed Cowbirds, 320 Acadian Flycatcher and 463 Prothonotary Warbler nests remained. Brood parasitism was prevalent for both Acadian Flycatcher and Prothonotary Warbler nests, with 33% and 43% of nests parasitized, respectively (Table 4.1); however, it accounted for only a small proportion of nest failures (12% and 8%, respectively; Table 2.6). Although parasitism was not directly responsible for a considerable amount of nest failures, it significantly reduced the nest success of both Acadian Flycatchers and Prothonotary Warblers (χ^2=21.26, df=1, p<0.0001 and χ^2=38.32, df=1, p<0.0001, respectively; Figure 4.2).

Breeding home ranges of female cowbirds within the study area overlapped and multiple parasitism (i.e., when more than one female cowbird lays an egg in the same host nest) was common for Prothonotary Warbler nests. Forty-one percent of parasitized nests contained more than one cowbird egg (Table 4.1). The mean number of cowbird eggs contained within parasitized nests was 1.6 ± 0.06, with a range of one to five eggs. Whether a nest was parasitized once or subjected to multiple parasitism events did not appear to affect nest success (χ^2=0.36, df=2, p=0.836; Figure 4.3).

Parasitism frequency of Acadian Flycatcher and Prothonotary Warbler nests varied by year and by plot (Figure 4.4). Acadian Flycatcher nests located on plot F, the plot nearest to the levee, experienced significantly higher frequencies of parasitism than did nests on plots A, D, or E (χ^2=15.25, df=1, p<0.0001, χ^2=12.40, df=1, p=0.0004, and χ^2=8.29, df=1, p=0.0040, respectively; Figure 4.5a). Similarly, the frequency of parasitism for Prothonotary Warbler nests located on plot F was significantly higher than for those located on plots A or E (χ^2=8.73, df=1, p=0.003 and χ^2=6.22, df=1, p=0.013, respectively; Figure 4.5b). Furthermore, the daily rate of parasitism was significantly higher for Prothonotary Warbler nests located on plot F than those located on the other three plots (χ^2=6.81, df=1, p=0.009, χ^2=4.04, df=1, p=0.045, and χ^2=7.46, df=1, p=0.006; Figure 4.6a). Parasitism intensity, or the mean number of cowbird eggs per parasitized nests, did not differ among plots (χ^2=5.58, df=3, p=0.134; Figure 4.6b).

PARASITISM MODELS

ACADIAN FLYCATCHER

The logistic regression global model included variables measured at the micro-, macro-, and landscape scale (Table 4.2); these variables resulted in a number of covariates that included main effects and interactions. The global model contained 11 covariates: six dummy variables representing two covariates of Year and Plot, six continuous variables, one dichotomous variable, and two interaction terms (Table 4.3). The response variable modeled was parasitism, where 0=not parasitized and 1=parasitized. The overall fit of the global model was good, allowing us to conclude that the coefficient for at least one of the covariates in the model was not 0 (Hosmer and Lemeshow 1989; χ^2=3.57, df=8, p=0.894). There were 292 nests, including 98 parasitism events, with a complete set of data for all variables. Candidate models contained the study year and plot, and could include up to three additional variables from the global model, resulting in a total of 78 candidate models. Based on the ΔAICc values and the Akaike model weights, there was not one model among our set of candidate models that best explained the probability of parasitism. The 95% confidence set of candidate models included 62 models. All candidate models were averaged to obtain unconditional parameter estimates and unconditional estimates of their standard errors and confidence intervals (Table 4.3). All inferences were based on the averaged model.

The relative effect sizes of the variables in the averaged model are shown as standardized coefficient estimates in Figure 4.7. This figure shows how strongly and in what direction each of the covariates in the model affected the probability of parasitism. The 90% confidence intervals for the standardized parameter estimates of micro-scale Can_Cov and Dist_Edge, as well as macro-scale Macro_PC2, all spanned 0, indicating that these variables were either unimportant or that our estimates were too imprecise, relative to effect size, to conclude whether or how these variables affected the probability of nest parasitism. However, the predictor variables we considered spanned fairly wide ranges (Table 4.4), such that we expected to be able to detect biologically meaningful effects. The probability of parasitism was related to the covariates Year, Plot (Trt, Rep, Trt*Rep), micro-scale Nest_Ht, macro-scale Macro_PC1, landscape-scale Open, and Season (Figure 4.7).

Parasitism was lower during the breeding season of 1996 than during any other year. The predicted odds of parasitism for nests in the year 1996 were 66.9%, 67.9%, and 72.9% lower than the odds of parasitism for nests in the years 1997, 1998, and 2000, respectively (Table 4.5). The confidence interval of the dummy variable Trt*Rep, the interaction between plot treatment and treatment replicate, revealed that replicate plots of the same treatment did not behave the same with respect to the probability of parasitism and the effect of treatment could not be interpreted in isolation of the other two variables, Rep and Trt*Rep. Combining the three variables Trt, Rep, and Trt*Rep, allowed us to reproduce the four study plots, A, D, E, and F (Appendix 4A). However, because Trt interacted with the variables Macro_PC1 and Open, the plots could not be compared in their absence. Holding Macro_PC1 and Open at their mean values, the probability of parasitism was higher on plot F than on the other three plots. The predicted odds of parasitism for nests on plot F were 3.96, 3.91, and 3.24 times the odds of parasitism for nests on plots A, D, and E, respectively (Table 4.5).

We individually examined the relationship between the probability of parasitism and the variables Nest_Ht, Macro_PC1, Open, and Season. To do so, we considered the model intercept, the parameter for the variable of interest, and the range of values for the variable of interest; because the variables were centered prior to analysis, the outcome is the probability of parasitism when all other variables included in the model are at their mean values. Under these conditions, we calculated the percent change in the predicted odds of parasitism that was associated with a one-unit increase in the variable of interest. To examine the relationship between the probability of parasitism and the dichotomous variable, Season, we compared the predicted odds of parasitism between its two values.

The probability of parasitism was positively associated with nest height (Table 4.3, Figure 4.7). Our model predicted that a one-meter increase in nest height is associated with a 7.3% increase in the predicted odds of parasitism (Table 4.3, Figure 4.8). The mean nest height of parasitized nests was higher than that of non-parasitized nests (Table 4.6).

The macro-habitat variable Macro_PC1 interacted positively with plot treatment; thus, to examine the relationship between the probability of parasitism and Macro_PC1, we considered each plot separately while varying the values of Macro_PC1 (Figure 4.9). Under these conditions, our model predicted that on control plots A and F, a one-unit increase in Macro_PC1 is associated with a 15.4% decrease in the predicted odds of parasitism (Table 4.3). Whereas, on patch cut plots D and E, a one-unit increase in Macro_PC1 is associated with a 33.8% increase in the predicted odds of parasitism. The probability of parasitism was highest on plot F in areas with many, small, closely spaced trees, possibly where the forest is frequently disturbed and consequently younger. The probability of parasitism was lowest on plot A in areas with few, large, widely spaced trees, possibly where the forest is rarely disturbed and older; however, the probability of parasitism was equally low on patch cut plots D and E in areas of the opposite type. On average, parasitized nests were in areas with more, smaller trees that were spaced closer together (Table 4.6).

The landscape-scale variable Open interacted positively with plot treatment; thus, to examine the relationship between the probability of parasitism and exposure to open canopy, we considered each plot separately while varying the values of Open (Figure 4.10). Under these conditions, our model predicted that on control plots A and F, a one-unit increase in Open is associated with a 2.1% decrease in the predicted odds of parasitism (Table 4.3). Whereas, on patch cut plots D and E, a one-unit increase in Open is associated with a 40.7% increase in the predicted odds of parasitism. The probability of parasitism was highest on plot F, regardless of proximity/exposure to areas of open canopy, however, the probability of parasitism on plots D and E approached that of plot F for nests that were located in close proximity to large canopy openings. The probability of parasitism on patch cut plots D and E was lower than that of plot A in areas of closed canopy, however, exceeded plot A with increased exposure to open canopy. On average, parasitized nests were less exposed to open canopy than non-parasitized nests (Table 4.6).

The probability of parasitism was negatively associated with time of the breeding season (Table 4.3, Figure 4.7). Our model predicted that the odds of parasitism for nests initiated in the second half of the breeding season were 38.3% lower than the odds of parasitism for nests initiated in the first half of the breeding season (Table 4.3, Figure 4.11). On average, a greater proportion of non-parasitized nests were initiated in the second half of the breeding season than were parasitized nests (Table 4.6).

Nest distance from the levee, a landscape-scale characteristic, was not included in the model because, as a result of refuge shape and study design, it was synonymous with plot assignment (Figures 2.5 and 4.1b) and was highly correlated with plot. We chose to include plot (in the form of Trt, Rep, and Trt*Rep), rather than levee distance, in the model because it not only contained information on distance from levee, but it controlled for unexplained variability; additionally, it allowed us to incorporate important interactions between plot treatment and other covariates in the model that could not be built-in with levee distance. However, when we modeled the probability of parasitism using levee distance in place of plot assignment, we found that levee distance was included in candidate models containing 99% of the Akaike weight and was the most important non-forced covariate included in the model. The averaged logistic regression model revealed a negative relationship between the probability of parasitism and distance from the levee and predicted that a one-meter increase in distance from the levee was associated with a 0.04% decrease in the predicted odds of parasitism (Figure 4.12). Simply looking at the log odds of parasitism with respect to distance from the levee revealed that the probability of parasitism decreased as distance from the levee increased, with a dramatic drop in parasitism around 1400 meters from the levee (Figure 4.13). On average, parasitized nests were located closer to the levee (Table 4.6).

PROTHONOTARY WARBLER

The logistic regression global model included variables measured at three spatial scales: micro, macro, and landscape (Table 4.7). Of the two macro-scale principal components included in the global model, only the GIS extracted values for Macro_PC1 were deemed acceptable to use in lieu of actual measurements for nests from the 1998 season (Table 2.17). Yearly differences in data availability, specifically the lack of macro-scale measurements during 1998, made it necessary to fit logistic regression models to three separate data sets (Models A, B, and C).

Model A included all measured variables of interest from all three spatial scales. As such, Model A excluded nests from the 1998-breeding season because they lacked macro-scale habitat measurements. Model B used all variables at all spatial scales from all years, and thus included the GIS extracted macro-habitat values for the nests from the 1998-breeding season. Model C excluded all macro-scale variables and included all years.

MODEL A – The first model (Model A) included all variables from all spatial scales, but excluded nests from 1998. The global model contained 10 covariates: five dummy variables representing two covariates of Year and Plot, five continuous variables, two dichotomous variables, and one interaction term (Table 4.8). The overall fit of the global model was good, allowing us to conclude that the coefficient for at least one of the covariates in the model was not 0 (Hosmer and Lemeshow 1989; χ^2= 6.44, df=8, p=0.598). There were 270 nests, including 95 parasitism events, with a complete set of data for all the variables. Candidate models contained the study year and plot, and could include up to three additional variables from the global model, resulting in a total of 71 candidate models. Based on the ΔAICc values and the Akaike model weights, there was not one model among our set of candidate models that best explained the probability of parasitism. The 95% confidence set of candidate models included 9 models. All candidate models were averaged to obtain unconditional parameter estimates and unconditional estimates of their standard errors and confidence intervals (Table 4.8). The 90% confidence interval of the macro-scale variable Macro_PC2 spanned 0 and had a relatively low Akaike weight, allowing us to conclude that Macro_PC2 was not an important factor for nest parasitism (Table 4.8 and Figure 4.14). We decided to drop Macro_PC2 as a variable of interest and to fit a second model (Model B) to an augmented data set, using the GIS extracted values for Macro_PC1 and nests from 1998, for the following three reasons: (1) the little evidence for an effect of Macro_PC2, (2) the substantial reductions in sample size caused by missing data for macro-scale features in 1998, and (3) the acceptable performance of GIS extracted values for Macro_PC1 (Table 2.17).

MODEL B – The second model (Model B) included all variables from all spatial scales, except Macro_PC2, and nests from all years. The global model contained 9 covariates: six dummy variables representing two covariates of Year and Plot, four continuous variables, two dichotomous variables, and one interaction term (Table 4.9). The overall fit of the global model was good, allowing us to conclude that the coefficient for at least one of the covariates in the model was not 0 (Hosmer and Lemeshow 1989; χ^2= 9.34, df=8, p=0.314). There were 317 nests, including 123 parasitism events, with a complete set of data for all the variables. Candidate models contained the study year and plot, and could include up to three additional variables from the global model, resulting in a total of 48 candidate models. Based on the ΔAICc values and the Akaike model weights, there was not one model among our set of candidate models that best explained the probability of parasitism. The 95% confidence set of candidate models included 6 models. All candidate models were averaged to obtain unconditional parameter estimates and unconditional estimates of their standard errors and confidence intervals (Table 4.9).

The effect of Macro_PC1 on the probability of nest parasitism was consistent in Model A and Model B (Tables 4.8 and 4.9); the parameter estimates, standard errors, and weights were almost identical. The equivalent estimates for Macro_PC1, in addition to the judgment that the GIS extracted values of Macro_PC1 were unbiased and not significantly different from the actual values (Table 2.17), gave us little reason to conclude that the use of extracted values in Model B was inappropriate. In addition to the effect of Macro_PC1, the signs and magnitudes of the parameter estimates, the standard errors, and the weights of the other covariates in Models A and B closely corresponded with each other (Tables 4.8 and 4.9), further satisfying concern about the use of the extracted values.

The relative effect sizes of the averaged model are shown as standardized coefficient estimates in Figure 4.15. The 90% confidence interval for the standardized parameter estimate of micro-scale Can_Cov spanned 0, indicating that it was either unimportant or that our estimate was too imprecise, relative to effect size, to conclude whether or how this variable affected the probability of nest parasitism. However, the predictor variables we considered spanned fairly wide ranges (Table 4.10), such that we expected to be able to detect biologically meaningful effects. The probability of parasitism was related to the covariates Year, Plot (Trt, Rep, Trt*Rep), micro-scale Cav_Code and Cav_Split, macro-scale Macro_PC1, landscape-scale Open, and Season. (Figure 4.15).

Parasitism was higher during the breeding season of 1998 than any other year. The predicted odds of parasitism for nests in the year 1998 were 3.12, 2.37, and 3.02 times the odds of parasitism for nests in the years 1996, 1997, and 2000, respectively (Table 4.11). The confidence interval of the dummy variable Trt*Rep, the interaction between plot treatment and treatment replicate, revealed that replicate plots of the same treatment did not behave the same with respect to the probability of parasitism and, therefore, the effect of treatment could not be interpreted in isolation of the other two variables, Rep and Trt*Rep. Combining the three variables Trt, Rep, and Trt*Rep, allowed us to reproduce the four study plots, A, D, E, and F (Appendix 4A). However, because Trt interacted with the variable Open, the plots could not be compared in its absence. Holding Open at its mean value, the probability of parasitism was higher on plot F than on plots A and E, and higher on plot D than on plot A. The predicted odds of parasitism for nests on plot F were 2.86 and 2.02 times the odds of parasitism for nests on plots A and E, respectively (Table 4.11). Additionally, the predicted odds of parasitism for nests on plot D were 1.99 times the odds of parasitism for nests on plot A (Table 4.11).

We individually examined the relationship between the probability of parasitism and the variables Cav_Code, Cav_Split, Macro_PC1, Open, and Season. To do so, we considered the model intercept, the parameter for the variable of interest, and the range of values for the variable of interest; because the variables were centered prior to analysis, the resulting outcome reflects the response when all other variables included in the model are at their mean values. Under these conditions, we determined the percent increase in the predicted odds of parasitism that was associated with a one-unit increase in the continuous variable of interest. For dichotomous variables, we compared the predicted odds of parasitism between their two values.

The probability of parasitism was positively related to the size of the nest cavity entrance (Table 4.9, Figure 4.15). Our model predicted that a one-unit increase in cavity size was associated with a 66% increase in the predicted odds of parasitism (Table 4.9, Figure 4.16). In this model, we treated cavity code as a continuous variable, assuming a linear relationship between cavity size entrance and the probability of parasitism; however, a simple comparison of percent of nests parasitized by cavity size suggested that there is a threshold of cavity size, above which parasitism frequency is increased (Figure 4.17). Nests with cavity entrances larger than average (cavity code > 2) were subjected to higher percentages of parasitism (Figure 4.17a) and more frequent multiple parasitism (Figure 4.17b) than were nests with average or below average cavity entrances. The overall percentage of nests parasitized was 38.8%; if cowbirds parasitized nests without regard to cavity entrance size, we would expect about 39% of nests within each cavity entrance category to be parasitized. However, nests of different cavity codes were not equally parasitized (χ^2 test of equal proportions: χ^2=19.43, df=4, p=0.0006); nests with small to average cavity entrances were parasitized less than expected while nests with larger than average cavity entrances were parasitized more than expected (Figure 4.17a). The mean cavity size of parasitized nests was larger than that of non-parasitized nests (Table 4.12).

The probability of parasitism was positively associated with split cavities (Table 4.9, Figure 4.15). When examining the relationship between the probability of parasitism and the type of cavity (hole/split), our model predicted that the odds of parasitism for nests located in split cavities were 207% higher than the odds of parasitism for nests located in non-split cavities (Table 4.9, Figure 4.18). On average, split cavities were more common among parasitized nests than among non-parasitized nests (Table 4.12).

The probability of parasitism was negatively associated with the macro-habitat variable Macro_PC1 (Table 4.9, Figure 4.15). Our model predicted that a one-unit increase in

Macro_PC1 is associated with a 15% decrease in the predicted odds of parasitism (Table 4.9, Figure 4.19). Nests located in older, less disturbed forests, with fewer and larger trees spaced further apart, experienced less parasitism. On average, parasitized nests were in areas with more, smaller trees that were spaced closer together (Table 4.12).

The landscape-scale variable Open interacted positively with plot treatment; thus, to examine the relationship between the probability of parasitism and exposure to open canopy, we considered each plot separately while varying the values of Open (Figure 4.20). Under these conditions, our model predicted that on control plots A and F, a one-unit increase in Open is associated with an 18% decrease in the predicted odds of parasitism (Table 4.9). Whereas, on patch cut plots D and E, a one-unit increase in Open is associated with a 37% increase in the predicted odds of parasitism. When nest exposure to canopy openings was low, plots A and F had a higher probability of parasitism; however, at high levels of Open, when nests were located in close proximity to large canopy openings, the probability of parasitism was greater on plots D and E. On average, parasitized nests were less exposed to open canopy than were non-parasitized nests (Table 4.12).

The probability of parasitism was negatively associated with time of the breeding season (Table 4.9, Figure 4.15). When examining the relationship between the probability of parasitism and the time of the breeding season that the nest was initiated, our model predicted that the odds of parasitism for nests initiated in the second half of the breeding season were 65% lower than the odds of parasitism for nests initiated in the first half of the breeding season (Table 4.9, Figure 4.21). On average, a greater proportion of non-parasitized nests were initiated in the second half of the breeding season than were parasitized nests (Table 4.12).

Landscape-level nest distance from the levee was not included in the model because, as a result of refuge shape and plot design, it was synonymous with plot assignment (Figures 2.5 and 4.1b) and was highly correlated with plot. We chose to include plot (in the form of Trt, Rep, and Trt*Rep), rather than levee distance, in the model because it not only contained information on distance from levee, but it controlled for unexplained variability; additionally, it allowed us to incorporate interactions between plot treatment and other covariates in the model that could not be built-in with levee distance. However, when we modeled the probability of parasitism using levee distance in place of plot assignment, we found that levee distance was included in candidate models containing 69% of the Akaike weight and was one of the most important non-forced covariates included in the model. The averaged logistic regression model revealed a negative relationship between the probability of parasitism and distance from the levee and predicted that a one-meter increase in distance from the levee was associated with a 0.03% decrease in the predicted odds of parasitism (Figure 4.22). Simply looking at the log odds of parasitism with respect to distance from the levee revealed that the probability of parasitism decreased as distance from the levee increased, with a substantial drop around 2200 meters from the levee (Figure 4.23). On average, parasitized nests were located closer to the levee (Table 4.12).

MODEL C – We fit a third model (Model C) to satisfy skepticism concerning the inclusion of the Macro_PC1 GIS extracted values in Model B. The data set for the third model excluded all macro-scale variables and included available nests from all years. The global model contained 8 covariates: six dummy variables representing two covariates of Year and Plot, three continuous variables, two dichotomous variables, and one interaction term (Table 4.13). The overall fit of the global model was good, allowing us to conclude that the coefficient for at least one of the covariates in the model was not 0 (Hosmer and Lemeshow 1989; χ^2= 11.17, df=8, p=0.193). There were 343 nests, including 137 parasitism events, with a complete set of data for all the variables. Candidate models contained the study year and plot, and could include up to three additional variables from the global model, resulting in a total of 31 candidate models. Based on the ΔAICc values and the Akaike model weights, there was not one model among our set of candidate models that best explained the probability of parasitism. The 95% confidence set of candidate models included 7 models. All candidate models were averaged to obtain unconditional parameter estimates and unconditional estimates of their standard errors and confidence intervals (Table 4.13). The signs and magnitudes of the parameter estimates, the standard errors, and the weights of the covariates in Models B and C closely corresponded with each other (Tables 4.9 and 4.13). In addition, the relative effects of the variables in Models B and C were analogous to each other (Figures 4.15 and 4.24). The concordance of covariate estimates among Models A, B, and C (Tables 4.8, 4.9, and 4.13) led us to conclude that it was reasonable to use the GIS extracted macro-scale variable, Macro_PC1, in Model B. Thus, we present Model B as our final model.

SPATIAL AUTOCORRELATION

ACADIAN FLYCATCHER – Examining the raw nest fates, we found positive spatial autocorrelation among the Acadian Flycatcher nests located within 200 meters of each other during the 1996- and 1997-breeding seasons; however, the spatial pattern of nest fates during the 1998- and 2000-breeding seasons were not significantly different from random (Table 4.14a). When considering the regression residuals for each nest, we found evidence for positive spatial autocorrelation among nests during the 1997-breeding season (Table 4.14a). We conclude that the spatially explicit variables included in our model accounted for the spatial pattern in nest parasitism among nests during the 1996-breeding season, but not the 1997-breeding season. Visual interpretation of the nest fates during the 1997-breeding season revealed the cause of the positive spatial autocorrelation; the majority of nests (76%) located on study plot F were parasitized, whereas nearly all of the nests (95%) located on study plot D were not parasitized. Under these circumstances, it was impossible for nests within 200 meters of each other to not be similar.

PROTHONOTARY WARBLER – Examining both the raw nest fates and the residuals, we found evidence of positive spatial autocorrelation among the Prothonotary Warbler nests located within 200 meters of each other during the 1997-breeding season (Table 4.14b). Hence, we conclude that our model did not successfully account for all of the spatial pattern in nest parasitism during this season. We do not, however, expect the spatial autocorrelation to generate bias in our model (Diniz-Filho et al. 2003); rather, we view it as useful in identifying the need to investigate mechanisms operating at different spatial scales than we explicitly incorporated into our model.

DISCUSSION

NEST SURVIVAL, PARASITISM FREQUENCY, RATE, AND INTENSITY

Acadian Flycatcher and Prothonotary Warbler nests both suffered from frequent parasitism within our study area. Parasitism frequencies for Acadian Flycatchers were within the range of frequencies reported in various other studies (Walkinshaw 1961, Robinson and Wilcove 1994, Whitehead and Taylor 2002), while Prothonotary Warblers suffered higher frequencies within our study area than the frequencies commonly reported (Petit 1999).

High levels of parasitism within our study area were expected; although the refuge is large (65,000 ha), it is long and narrow in shape and surrounded on all sides by agriculture (row crops) and on one side by a grassy levee containing grazing cattle. As such, the landscape is ideal for cowbirds, providing a mixture of both feeding and breeding habitat all within the extent of their home range (Donovan et al. 1997).

Failure of the entire host clutch/brood due directly to parasitism events (i.e., nest abandonment, hatching failure of host eggs, trampling/starvation of host young by cowbird young) was low relative to the frequency of parasitism for both species; however, parasitized nests suffered significantly reduced success compared with non-parasitized nests. Basic nest success (the probability of successfully fledging one host young) ignores partial nest losses caused by brood parasitism, such as cowbird egg removal and partial hatching/nestling failure, that diminish overall host reproductive success or fecundity (young/female). Research has documented that successful parasitized nests of both Acadian Flycatchers and Prothonotary Warblers have smaller clutches and fledge fewer young per nest than do successful non-parasitized nests, accounting for a 77-90% and 22-53% reduction in total expected output, respectively (Walkinshaw 1961, Whitehead and Taylor 2002; but see Trine et al. 1998; Petit 1991, 1999, Hoover 2001). The exceptionally high reduction in reproductive success of parasitized Acadian Flycatcher nests, in comparison to Prothonotary Warbler nests, may be in part owing to their small clutches and long incubation and nestling periods that permit cowbird nestlings a greater competitive advantage (Rothstein and Robinson 1998, Trine et al. 1998). Acadian Flycatchers discontinue incubation upon hatching of the first egg; consequently, because cowbird eggs usually hatch first, this behavior causes incomplete incubation of host eggs and often hatching failure (Walkinshaw 1961). Acadian Flycatchers can successfully rear a mixed brood of host and cowbird young if host eggs hatch first; however, if cowbird eggs hatch first, Acadian Flycatchers are not successful in fledging their own young (Walkinshaw 1961, Wilson and Cooper 1998b). Prothonotary Warblers, however, are often successful at fledging host young along with cowbird young (Petit 1999).

An additional cost of brood parasitism that has been reported, but is often ignored, is increased probability of nest predation (Dearborn 1999, Thompson et al. 1999, Budnick 2002). Our study did not find an increase in the probability that parasitized Acadian Flycatcher nests would be preyed upon (Figure 3.6), however, we found a positive relationship between parasitism and predation for Prothonotary Warbler nests (Figures 3.19, 3.29-3.32). Potential explanations for this relationship include increased noise and host activity at parasitized nests that increase the conspicuousness of nests to potential predators. Alternatively, if cowbirds and nest predators use similar cues for locating nests, the relationship could be an artifact of correlation between nest/host characteristics that make the nest vulnerable to identification by both cowbirds and predators (McLaren and Sealy 2000; see Chapter 3 for a more detailed discussion).

Although our data show that direct nest failure due to parasitism is low compared with parasitism frequency, these values grossly underestimate the negative effect that parasitism has on the reproductive success of Acadian Flycatchers and Prothonotary Warblers. In general, the negative effect of parasitism is understated because it has additional costs that are not fully considered; researchers lack information on individual female fecundity (Smith 1981, May and Robinson 1985) and ignore increased risk of nest predation that is often associated with parasitism. Although parasitism is often considered a secondary threat to the reproductive success of neotropical migrant songbirds, it may be more significant than generally acknowledged (Grzybowski and Pease 2000). While birds renest within a few days of losing nests to predation (Roth and Johnson 1993), acceptor species will consume an entire nesting attempt raising cowbirds. Therefore, depending upon reduction in young produced per nest and whether a host species is single- or dooble-brooded, a relatively low parasitism rate could have the same negative impact as a relatively high predation rate (Roskaft and Moksnes 1998).

Multiple parasitism was prevalent within our study area – a common occurrence when local cowbird abundance is high, especially relative to host density (Rothstein et al. 1984, Rothstein and Robinson 1998). Although the per capita success rate of cowbird eggs is inversely proportional to the number of cowbird eggs in a nest (Friedmann 1963), overlap of laying areas is unavoidable when cowbird abundance is high. In terms of host nest success, there did not appear to be a cost to additional parasitism events. However, an increased reduction in fecundity, which we did not measure, is likely to have occurred (e.g., Trine 2000).

The frequency of parasitism varied annually for both species. Annual variation in parasitism levels is a common finding in parasitism studies (Petit 1989, Roth and Johnson 1993, Bielefeldt and Rosenfield 1997, Trine et al. 1998, Petit and Petit 2000, Budnick 2002) and is often explained by annual fluctuations in local cowbird abundances (Petit 1991). High annual variability in parasitism levels highlights the need for long-term data sets when monitoring for conservation management of species negatively affected by brood parasitism.

Nests of both species located on plot F suffered significantly higher levels of parasitism than did nests located on the other three study plots. The refuge is long and narrow (only 4.5 km-wide at the study location) in shape and is bordered on both sides by agricultural fields of rice, soybean, and winter wheat that supply ideal feeding opportunities for cowbirds. Additionally, a grassy levee containing grazing cattle runs parallel to the east side of the refuge and harbors large flocks of foraging cowbirds. Because cowbirds have large home ranges and will routinely commute up to 7 km between breeding and feeding sites, the nests located within the entire width of the refuge at our study location are at risk of being parasitized. Indeed, cowbirds were found over the entire study area. One might expect to find higher parasitism levels on plots A and F, because they are closest to the forest-agricultural edge, than on plots D and E which are located in the interior of the refuge. Alternatively, if cowbirds saturate the entire study area, they may be limited by host availability and may need to infiltrate all areas of the refuge to find non-parasitized host nests; thus, we might expect to see equally high frequencies of parasitism across the study plots. Although the vast non-forested matrix in which the refuge is embedded provides ample feeding opportunities, cowbirds show a preference for foraging with grazing cattle (Rothstein et al. 1980, Verner and Ritter 1983, Robinson et al. 1993, Goguen and Mathews 2000) and parasitism frequencies are correlated with local abundances of cowbirds (Hoover and Brittingham 1993). Even within fragmented landscapes that offer abundant feeding opportunities and are saturated with cowbirds, studies have reported decreasing gradients of brood parasitism stemming from livestock feed sites (Morse and Robinson 1999, Goguen and Mathews 2000). Although cowbirds will travel long distances between feeding and breeding sites, it is not the norm (Smith et al. 2000); they will only go as far as needed to fulfill their needs and on average travel much shorter distances between feeding and breeding sites (e.g., Thompson 1994, Thompson and Dijak 2000). It is likely that cowbirds foraging on the levee saturate the breeding habitat of the nearby forest and, due to host limitation, disperse from there to minimize overlap between breeding territories and to locate non-parasitized hosts. Excessive overlap between breeding territories would result in high frequencies of multiple parasitism, intense competition between breeding female cowbirds, and decreased cowbird reproductive success (Friedmann 1963, Trine 2000). The diffusion of cowbirds from the levee is supported by the fact that although parasitism frequencies were higher closer to the levee, the mean number of parasitic eggs per parasitized nest did not differ among plots.

PARASITISM MODELS

GENERAL

To account for the lack of macro-habitat measurements taken at Prothonotary Warbler nests during the 1998-breeding season, we created three different logistic regression models for this species. These three models differed in the variables and years included. Model A included all variables from all spatial scales, while excluding nests from the year 1998, and demonstrated that the macro-scale variable, Macro_PC2, was not related to the probability of brood parasitism. Based on Model A, we concluded that further consideration of Macro_PC2 was not warranted. Model B included all variables and nests from all years, necessitating the inclusion of GIS extracted values for the macro-scale variable Macro_PC1. Model C included nests from all years while excluding all macro-scale variables. Comparison of Models A, B and C led us to conclude that use of the extracted values for Macro_PC1 was reasonable. For this reason, of the three models (Models A, B, and C) we created for Prothonotary Warblers, we selected Model B as our final model; hence, the following discussion applies to the covariates of Model B and includes variables from the micro-, macro-, and landscape scale while incorporating data from all years of the study.

For both Acadian Flycatchers and Prothonotary Warblers, each Model presented was originally comprised of a large number of candidate models. Burnham and Anderson (1998) suggest that this approach is justifiable for observational studies when inference is based on the Akaike weights of all models, rather than on one single best model. Accordingly, we followed the recommendation of Burnham and Anderson (1998) and implemented model averaging to incorporate model selection uncertainty into the parameter estimates, and estimates of their precision, of our final Model.

The likelihood of parasitism for both species was linked to local- and landscape-scale characteristics of the nest site and the surrounding habitat. Although Acadian Flycatchers and Prothonotary Warblers differ greatly in the characteristics of their nest sites, habitat selection, and reproductive requirements, we found distinct similarities between the function of variables in relation to the likelihood of parasitism for both species; these similarities were most likely owing to the behavior of their shared brood parasitic enemy, the Brown-headed Cowbird. Shared variables in the parasitism models of both species included Year, Plot (Trt, Rep, Trt*Rep), micro-scale canopy cover, macro-scale canopy cover, macro-scale age/disturbance, landscape scale canopy cover, time of the breeding season, and distance from the levee. Other variables reflected species-specific nesting ecologies. For open-cup nesting Acadian Flycatchers, these variables included micro-scale nest measurements of nest height and nest distance from branch edge. For cavity nesting Prothonotary Warblers, these variables included micro-scale cavity descriptions of cavity entrance size and cavity type. We first discuss the results of shared variables for both species and then discuss the species-specific variables.

ANNUAL VARIATION AND PLOT PLACEMENT

Annual variability in parasitism frequencies was substantial for both species and thus inclusion of year in the models was necessary to capture random effects not measured by the variables that described nest-site and nesting habitat characteristics. Annual variation in parasitism levels is often explained by annual fluctuations in local cowbird abundances. However, variable local abundance of cowbirds was not solely responsible for differences in annual parasitism levels because relative parasitism levels among years for each species did not strictly coincide. For Acadian Flycatchers, parasitism levels were lowest during the 1996-breeding season (20%) and comparably high during the 1997-, 1998-, and 2000-breeding seasons (39-43%); however, Prothonotary Warbler nests suffered from the highest parasitism frequencies during the 1998-breeding season (55%), whereas frequencies were lower during the other years (33-39%). It is possible that the annual discrepancy between species reflects a host preference of female cowbirds. Although cowbirds are generalist brood parasites, they express host preferences, which vary among regions and landscapes depending upon the local population of available hosts (Friedmann 1929). Annual fluctuation in availability of a preferred host can generate variable parasitism pressures on less preferred hosts, which may depend on the ranked preference of each host (Trine et al. 1998).

We expected distance from the levee to have a strong effect on the probability of parasitism, but we also needed to control for unexplained variability related to plot. Because our study plots are arranged perpendicular to the levee, inherent in them is a distance gradient from the levee. Thus, we incorporated study plot into our models in the form of three dummy variables describing the plot treatment, plot replicate, and the interaction between the two. We used this approach, as opposed to directly including the plot, because we anticipated interactions to exist between some of our other covariates and plot treatment and needed a way to include those interactions in our model. Because plots A and F are both no-cut plots, but they exist at the two extremes of the levee distance gradient, it is not surprising that the interaction between plot treatment and replicate was important. Additionally, interactions between plot treatment and the habitat variables for Macro_PC1 and Open were anticipated because of the large amount of disturbed habitat and open canopy on the patch-cut plots as opposed to the no-cut plots.

We expected nests located on plot F to have a higher probability of being parasitized than nests located on the other three study plots. We found this to be true for Acadian Flycatcher nests; however, although Prothonotary Warbler nests suffered from significantly higher frequencies of parasitism on plot F, after controlling for various nest and habitat characteristics, nests located on plot F were more likely to be parasitized than were nests located on plots A and E, but not on plot D. We believe the relationship demonstrated for Acadian Flycatcher and Prothonotary Warbler nests is explained by the proximity of plot F to the grassy levee, a popular cowbird-feeding site. In the absence of other effects, we might expect to find a decreasing linear gradient of parasitism from the levee. Although parasitism on plot F was the greatest, we did not find a decreasing linear gradient of parasitism. Although plot A is the furthest from the levee, it is near the forest-agricultural edge on the opposite side of the refuge, an additional source of cowbirds. Additionally, a large gravel road with grassy sides runs parallel to plot A and provides cowbird feeding opportunities as well as a route by which cowbirds can infiltrate the interior forest from the neighboring non-forest matrix. Based solely on proximity to exterior cowbird-feeding sites, we might expect plot D, which is located in the center of the refuge, to have lower exposure to cowbirds and thus have the lowest probability of parasitism. For Prothonotary Warblers, nests located on plot D, however, did not benefit from their interior location, possibly because cowbirds saturate all available forested habitat at our study location and because plot D, as a patch-cut plot, has a large amount of open canopy and disturbed forest that attract cowbirds (see discussion below on open canopy). Although plot E is also a patch-cut plot, the cuts are smaller and less intrusive within the plot core than they are on plot D.

NEST PLACEMENT AND VEGETATION STRUCTURE: MICRO- AND MACRO-SCALE

Characteristics of the nest-site and the nesting habitat describing micro- and macro-scale canopy cover were unimportant to the likelihood of parasitism. Both variables were included as surrogate descriptions of overhead nest concealment. The expectation was that increased nest cover would decrease parasitism (e.g., Brittingham and Temple 1996, Burhans 1997, Larison et al. 1998, Uyehara and Whitfield 2000) by concealing nests from cowbirds that were flying overhead or sitting on an overhead perch. We found, however, that nest cover did not affect the probability of parasitism, a finding that paralleled the results of several other studies (e.g., Smith 1981, Clotfelter 1998, Hauber and Russo 2000, Howe and Knopf 2000, Banks and Martin 2001). Reduced canopy cover does not always correlate with higher frequencies of parasitism. The lack of association between nest concealment and parasitism may be due to the searching behavior of female cowbirds. For example, mixed results might occur if cowbirds predominantly search for and parasitize nests below the canopy (Norman and Robertson 1975, Wiley 1988, Briskie et al. 1990, Hahn and Hatfield 2000; but see Robinson et al. 2000). Additionally, if cowbirds locate nests by observing host-activity rather than directly searching for nests, a conclusion that has been strongly supported in the literature (Norman and Robertson 1975, Lowther 1979, Clotfelter 1998, Rothstein and Robinson 1998, Banks and Martin 2001, Robinson and Robinson 2001), nest concealment would not be expected to hinder nest location by cowbirds. Although nest cover at the macro-scale may help conceal host activities within the vicinity of the nest (e.g., Larison et al. 1998) or decrease nest-searching efficiency of cowbirds by increasing the number of potential nest sites to be searched (Martin 1993, Budnick 2002), it did not have an influence on parasitism outcome in our study. In addition to providing nest cover, we thought macro-scale canopy cover might be related to local cowbird abundance within the forest; specifically, low macro-scale canopy cover might attract cowbirds and increase parasitism. Although this was the case with canopy cover at a larger spatial scale (200-m radius; see discussion below), it was not the case at this fine spatial scale (11.3-m radius). Thus, cowbirds seem to be responding to nest habitat characteristics at a broader spatial scale. In addition to spatial scale, cowbirds may respond to large openings in the canopy rather than to canopy cover per se.

As we predicted, parasitized nests of both species were more often located in disturbed macro-habitats, containing more small/young and closely spaced trees, than were non-parasitized nests, and the probability of parasitism decreased as trees within the nesting macro-habitat were fewer, larger, and more widely spaced. Similar vegetation characteristics examined at the nest-patch scale of shrub-nesting Song Sparrows (*Melospiza melodia*), showed no effect on parasitism (Larison et al. 1998), while Brittingham and Temple (1996) reported the opposite parasitism response when they combined results of several ground-, shrub-, and canopy-nesting species. Although the offending species, the Brown-headed Cowbird, remained the same, results may be host species-specific as well as habitat-specific, precluding generalizations and revealing the need for community-wide studies. Nevertheless, in support of our findings, several studies have documented increased relative abundance of cowbirds within disturbed/regenerating forest habitat when compared with undisturbed mature forest (Thompson et al. 1992, Annand and Thompson 1997, Moorman and Guynn 2001).

For Acadian Flycatchers, the relationship between macro-habitat disturbance/age was contingent upon plot treatment, making generalizations inappropriate and less useful. A negative relationship between the probability of parasitism and the number/size/distribution of trees was found on the no-cut plots (i.e., decreased parasitism in older, less disturbed macro-habitats containing fewer, large, widely spaced trees); however, the opposite was true on patch-cut plots. Although we did not address understory vegetation, it is likely that more disturbed/younger areas possessed a denser understory of seedlings, saplings, grasses, ivy, and vines. An increase in stem density (data not shown), and possibly understory density, was present within the forest adjacent to patch cuts. Large canopy openings, such as those created by patch cuts, modify the abiotic environment (including increased sunlight and wind exposure, increased air temperature, and decreased air and soil moisture), producing changes in the abundance and distribution of plant species in the adjacent forest (Murcia 1995). Wind exposure along edges may increase tree falls, creating further disturbance and, along with increased sunlight, promoting new plant growth. These types of edge effects are known to extend 50 m into the forest interior (Murcia 1995). Within patch-cut plots of our study, the interior forest more removed from the patch cuts was most likely less disturbed, with a less developed understory. Within forests, cowbirds may observe host activity by walking along the forest floor, a technique that would be disrupted by a dense understory (Norman and Robertson 1975, Uyehara and Whitfield 2000). Thus, nests located within more disturbed macro-habitats may benefit from a denser understory and experience less parasitism. Along these lines, Moorman et al. (2002) demonstrated decreased parasitism on shrub-nesting Hooded Warblers (*Wilsonia citrina*) with increased ground cover. Within patch-cut plots, macro-habitats further from the disturbed patch-cut edge may have been more conducive for locating host nests, thus accounting for the opposite trend observed on patch-cut plots. Still, the probability of parasitism was greatest on plot F regardless of the value for

Macro_PC1; suggesting that, at close proximity to cowbird foraging areas, local habitat characteristics are irrelevant.

LANDSCAPE-SCALE CHARACTERISTICS

OPEN CANOPY – Exposure of nests to open canopy had a different effect on the probability of parasitism on no-cut plots A and F than on patch-cut plots D and E. Canopy openings on plots A and F were relatively few and consisted mostly of narrow, low-use ATV trails, whereas plots D and E contained large openings associated with patch cuts, as well as wider, higher-use roads. For Acadian Flycatchers, no effect of open canopy was found on no-cut plots, while a positive relationship was found on patch-cut plots. The probability of parasitism was highest on plot F, regardless of nest exposure to open canopy, and high on plot A at low levels of open canopy. However, Acadian Flycatcher nests exposed to high levels of open canopy on patch-cut plots D and E had higher probabilities of parasitism than did nests that were equally exposed on plot A. This pattern of parasitism is compatible with the notion that, within forested landscapes, cowbirds are limited by feeding opportunities and parasitism is driven by proximity to foraging areas while other habitat characteristics are of secondary importance (Thompson et al. 2000). Under this premise, areas close to cowbird-feeding sites suffer the highest levels of parasitism and are saturated with cowbirds in all available habitat, making edge effects a non-existent phenomenon (Morse and Robinson 1999, Robinson and Robinson 1999, Thompson et al. 2000). However, areas further from influential feeding sites are more sheltered from cowbirds; in such areas, penetration of the forest interior may be facilitated by large openings in the canopy (Winslow et al. 2000). Additionally, if cowbirds are less abundant further from feeding sites, their breeding habitat preferences may be expressed as they disperse from these sites.

For Prothonotary Warblers, we again found a positive relationship between exposure to open canopy and parasitism on patch-cut plots; though, we observed a negative relationship on no-cut plots. The probability of parasitism was highest on plots F and A at low to medium levels of open canopy; however, at high levels of open canopy, the probability of parasitism for nests located on patch-cut plots exceeded that for nests located on the no-cut plots. Given the low amount of open canopy on plots A and F and the proximity of these plots to cowbird foraging areas, it follows that we would not find a positive relationship between parasitism and open canopy on these plots. However, a logical explanation for the negative relationship that we detected for Prothonotary Warblers on these plots eludes us.

For Acadian Flycatcher and Prothonotary Warbler nests located on patch-cut plots, proximity to large canopy openings increased the probability of parasitism. The higher mean canopy closure of parasitized nests seems counter-intuitive; however, this misleading value is the result of combining nests over all plots, ignoring proximity to foraging sites, and is a mere artifact of high parasitism levels on plot F, which has very little open canopy. Numerous studies have documented increased relative abundance of cowbirds and/or increased levels of parasitism in close proximity to canopy openings within forested landscapes created by timber cuts (patchcuts and clearcuts; Strelke and Dickson 1980, Evans and Gates 1997, Winslow et al. 2000, Moorman et al. 2002; but see Morse and Robinson 1999), utility corridors (Chasko and Gates 1982, Rich et al. 1994, Evans and Gates 1997), roads and trails (Hickman 1990, Rich et al. 1994), and streams (Gates and Giffen 1991, Evans and Gates 1997). Similarly, nests located within forested plots containing small (< 0.6 ha) canopy openings created by timber cuts have shown increased levels of parasitism (Robinson and Robinson 2001; but see Robinson and Robinson 1999, Twedt et al. 2001). Results of these and other studies indicate that internal disturbances within forests may allow cowbirds to infiltrate forest interiors and range throughout the landscape. Gates and Evans (1998) reported that the core breeding ranges selected by female cowbirds contained higher numbers of seedlings and saplings, large snags, and more open canopy than non-use areas. Thus, although levels of parasitism are lower in more heavily forested landscapes, local patterns of disturbances that create canopy openings in such areas may increase cowbird densities and elevate levels of parasitism.

Large canopy openings associated with patch-cuts, while not providing feeding opportunities for cowbirds, provide a wider diversity of potential host species from which to choose, including forest-interior, shrub, and forest-shrub edge species, and may contain a higher density of potential hosts (MacArthur and MacArthur 1961, Gates and Gysel 1978, Chasko and Gates 1982, Swift et al. 1984). Cowbirds within areas that are saturated with conspecifics may be limited by breeding opportunities. In such instances, cowbird abundance and parasitism levels are often increased in areas of high host density (Thompson et al. 2000). In addition to host density, tree lines adjacent to large openings provide ample perches from which cowbirds may observe host-activity, facilitating the location and parasitism of host nests (Clotfelter 1998, Hauber and Russo 2000, Budnick 2002; but see Brittingham and Temple 1996). Although we did not collect data on cowbird abundance, overall host density, cowbird-host preferences, or perches, all of the above could potentially explain the observed pattern of increased parasitism probability in close proximity to large canopy openings.

LEVEE – As discussed earlier, the probability of parasitism for both species decreased as the distance from the levee increased. Although we did not explicitly include levee distance as a variable in the main model, it was incorporated by inclusion of plot treatments, plot replicates, and the treatment*replicate interaction. Our alternate model, which replaced plot descriptors with levee distance, demonstrated the importance of the levee and revealed the expected inverse relationship between the probability of parasitism and proximity from a prominent cowbird-feeding site. Separate from the logistic regression model, simply examining the effect of levee distance on the log odds of parasitism was informative. Although the probability of parasitism was high across the entire width of the study area, it decreased considerably at a distance of 1400 m and 2200 m for Acadian Flycatchers and Prothonotary Warblers, respectively. This incursion of parasitism into the forest interior was much larger than the 0-50 m-edge interval historically considered (Paton 1994) and the 300-m threshold documented by Brittingham and Temple (1983). Our finding, however, corresponds with the 1.5-km average commuting distance between feeding and breeding sites reported by Thompson (1994). It is also analogous to results reported by Morse and Robinson (1999) and Goguen and Mathews (2000), who documented a decreasing gradient in cowbird abundance, and a concomitant decline in the rate of parasitism, with increasing distance from cowbird-feeding sites, over distances of 800 meters and 8-12 kilometers, respectively. These declining parasitism gradients were observed regardless of local factors such as the presence of edge, clearcuts, and varying forest stand ages, suggesting that parasitism pressure is driven by the spatial arrangement of cowbird-feeding sites within the landscape and that local-scale habitat characteristics are of secondary importance. Prothonotary Warbler nests located within the furthest distance interval from the levee exhibited a minor increase in the probability of being parasitized, most likely due to proximity to the west forest-agricultural edge.

TEMPORAL SCALE

Nests of both species initiated in the first half of the breeding season had a greater probability of being parasitized than did nests initiated in the second half of the breeding season. This finding is congruous with other studies that have also reported a decline in parasitism toward the end of the breeding season (e.g., Petit 1989, 1991, Wilson 1997; Smith et al. 2000). The degree of temporal overlap between the cowbird laying season and the breeding seasons of the Acadian Flycatcher and Prothonotary Warbler may explain the observed seasonal variation in parasitism rates. When a host's breeding season overlaps only slightly with the cowbird's, parasitism levels are lower than when the breeding seasons of the two species coincide (Elliott 1978, Petrinovich and Patterson 1978). Acadian Flycatchers initiate nests from early May through mid-August, while Prothonotary Warblers initiate nests from mid-April to late July. Although the cowbird-breeding season extends from the beginning of April to the beginning of August, the majority of eggs are deposited during the months of May and June (Lowther 1993). Thus, parasitism pressure on Acadian Flycatcher nests initiated in July and August and on Prothonotary Warbler nests initiated in July is alleviated. While both Acadian Flycatchers and Prothonotary Warblers initiate nests during the months of heaviest cowbird activity, Acadian

Flycatchers continue to initiate nests well past the time that cowbirds are laying eggs; thus, it would seem that the effect of the time of breeding season on parasitism levels would be stronger for Acadian Flycatchers than for Prothonotary Warblers. However, we found that the opposite was true; the effect of the time of breeding season on parasitism levels was stronger for Prothonotary Warblers than for Acadian Flycatchers. Prothonotary Warblers initiate nests early in the breeding season compared with other songbirds within the area; thus, they likely receive the full brunt of cowbird parasitism during the month of April. The inordinately heavy parasitism levels suffered early in the breeding season, combined with the decline of parasitism during the month of July, may explain the strong decrease in parasitism that we observed during the later half of the Prothonotary Warbler-breeding season.

SPECIES-SPECIFIC MICRO-HABITAT CHARACTERISTICS

ACADIAN FLYCATCHER – Acadian Flycatcher nests located higher in the canopy had a greater probability of being parasitized. This positive relationship between nest height and parasitism emerged despite the fact that Acadian Flycatchers show a tendency to nest higher as the breeding season progresses (Wilson and Cooper 1998a) and enjoy reduced parasitism later in the breeding season. Some studies have reported increased rates of parasitism on high nests (Robinson et al. 2000), while others have found the opposite effect (Hahn and Hatfield 1995) or no effect (Clotfelter 1998, Banks and Martin 2001, Budnick 2002; also see review in Robinson et al. 1995a). If cowbirds behave similarly to aerial nest predators, higher nests may simply be more conspicuous and accessible; however, documented nest-searching behavior of cowbirds (Norman and Robertson 1975) does not support the conclusion that these nests should be more heavily parasitized.

It has been suggested that flycatchers counteract high rates of nest predation by making nests less accessible to ground predators through increased nest height (Murphy 1983). Nest height is also positively correlated with nest concealment (Wilson and Cooper 1998a), another potential nesting characteristic that may serve to decrease nest predation. Previous analyses of

Acadian Flycatcher data within the refuge suggested that when the nests of individual females are depredated, their re-nesting attempt tends to be located higher in the canopy and often in a tree of a different species (Cooper, unpublished data), further supporting the notion that higher nests are an attempt to avoid nest predation. Higher nests did have lower risk of nest predation (Table 3.3, Figures 3.6 and 3.7); however, they suffered from increased brood parasitism. Assuming nest predation causes a greater reduction in reproductive output per female, this may be an evolutionary trade-off that Acadian Flycatchers must accept.

The location of Acadian Flycatcher nests relative to nest-branch edge did not affect the probability of parasitism. We suspected that nests located within the interior canopy of the nest tree, as opposed to on the nest-branch edge, would be more concealed and less exposed to parasitism. However, the probability of parasitism does not appear to be related to nest concealment. Cowbirds most likely locate nests by observing host-activity, not by identifying more exposed nests (Hauber and Russo 2000). Acadian Flycatchers have a tendency to build their nests on small branches, away from the tree bole and at the branch edge, over open air (Whitehead and Taylor 2002), possibly as a technique for predator avoidance and to allow aerial access and departure from nests. This tendency did not appear to increase rates of brood parasitism.

PROTHONOTARY WARBLER – In North America, cavity nesters are generally less likely to be parasitized than open-cup nesters (reviewed in Robinson et al. 1995a); however, Prothonotary Warblers are an exception to this generalization (Friedmann 1963, Petit 1991). Nonetheless, certain characteristics of their cavity nests may benefit them by reducing parasitism pressure. As predicted, there was a positive relationship between size of the cavity entrance and the probability of parasitism. Nests located in cavities of average size or smaller (width $\leq$ 5.5 cm, height $\leq$ 6.5 cm) were parasitized less frequently than were nests located in cavities with larger entrances. Nests located in cavities with smaller entrances likely encounter lower parasitism levels because smaller cavities limit access to larger female cowbirds attempting to lay eggs; similar relationships have been reported by studies of the cavity-nesting Yellow-shouldered Blackbird (*Agelaius xanthomus*; Post and Wiley 1976), Eastern Bluebird (*Sialia sialis*; Woodward and Woodward 1979), House Wren (*Troglodytes aedon*; Kattan 1998), and Prothonotary Warbler (Hoover 2001). This idea is also supported by an anecdotal observation within our study area of a dead female cowbird stuck inside the entrance of a small cavity (Wood personal communication). It is also possible that larger cavity entrances increase the conspicuousness of nests and allow female cowbirds to more easily locate them. However, because there was a threshold of cavity entrance size, above which parasitism frequency was higher, rather than a linear increase, the limitation explanation is more probable.

Prothonotary Warbler nests located in natural splits, as opposed to excavated or natural circular cavities, were parasitized more heavily. The entrances of split cavities are elongated in height, while variable in width; thus, split cavities may have provided easier access to nests by large female cowbirds. However, because split cavities could potentially be limiting in their width, they may simply be more conspicuous to female cowbirds. Nest conspicuousness may be germane to the probability of parasitism regardless of whether cowbirds identify nest locations based on host-activity or by actively searching.

CONSERVATION AND MANAGEMENT IMPLICATIONS

Recent studies have suggested that in addition to threatening local populations of endangered species, parasitism may threaten regional populations of abundant, widespread species (Bohning-Gaese et al. 1993, Rothstein and Robinson 1998). Thus, management efforts to reduce cowbird numbers and parasitism levels are essential to conservation efforts of forest-nesting neotropical songbirds. Results of our and others' studies indicate that management to decrease parasitism levels is both necessary and possible. The best and most permanent way to reduce impact of cowbirds on forest-interior neotropical migrants is through landscape-level management (Robinson et al. 1993). Because cowbirds are associated with agriculture, human settlements, and external and internal edges, the best management strategy is to maintain large areas of contiguous forest in which edge habitat and potential feeding areas are eliminated. The ultimate solution must involve changing land-use practices and configurations that reduce cowbird-feeding areas (Robinson et al. 1993).

Cowbird numbers and parasitism levels are regulated at several spatial scales and consideration of all spatial scales should be taken when designing management plans to reduce parasitism. The surrounding landscape in which forested tracts are embedded must be considered before carrying out local-scale management efforts. For example, if cowbird numbers are driven by large-scale biogeographic and regional-landscape patterns, management efforts directed solely at local-scale features such as internal edges will be ineffective; thus, large-scale factors should be considered first to determine the local-scale management efforts that are needed and most likely to be effective. Within any biogeographic context, however, conservation efforts to reduce the number of cowbirds should focus on minimizing the interspersion of cowbird feeding areas within forested landscapes (Thompson et al. 2000). Based on known cowbird commuting distances (Rothstein et al. 1984, Thompson 1994), protecting birds from parasitism may require management at a much larger scale than originally thought (Trine et al. 1998); Thompson et al. (2000) suggest that cowbird feeding habitat should be reduced within a 2- to 10-km radius of the areas in which parasitism is a concern. Vegetative management or modification of current agricultural practices could also be used to make feeding habitats less suitable to cowbirds. Secondarily, managers should consider local-scale habitat features such as internal edge. Before implementing changes to local habitat features, however, it is important to be aware that the same habitat features that decrease parasitism in one species may increase parasitism in another. Local-scale management efforts to reduce parasitism would benefit from a better understanding of fine-scale factors such as: the influence of edge, cowbird breeding habitat preferences, host densities, and nest-site and nest-patch habitat features of community-wide host species. Cowbird trapping is only recommended as a stop-gap measure to protect endangered host species with restricted distributions, and, even then, is only effective at small scales (Robinson et al. 1993).

Within the current boundaries of the White River NWR and our study area, potential management strategies include: removal of cattle from the levee during the breeding season, prohibiting mowing of the levee and of roadsides during the breeding season, and decreasing disturbance within the forest interior that create open canopy of any size. As for the last suggestion, keeping roads as narrow as possible and re-vegetating logging roads will help reduce the amount of open canopy within the forest. Additionally, Robinson et al. (1993) recommend that in this moderately fragmented landscape, if logging cannot be avoided, low-volume, single-tree selection should be used instead of group selection or clearcuts that open gaps in the canopy and potentially provide cowbirds with additional access to forest-interior hosts. Single-tree selection is an actively used silvicultural technique at White River NWR; however, due to logistical constraints, we did not address plots treated with the single-tree selection method. If specifically targeting to reduce parasitism on Prothonotary Warblers, additional management could involve manually restricting the entrance size of cavities to limit cowbird access to the nests, or possibly using nest boxes.

SUMMARY/CONCLUSION

The probability that Acadian Flycatcher and Prothonotary Warbler nests would be parasitized was linked to local- and landscape-scale characteristics of the nest site and the surrounding habitat. Outside of annual variation, distance from the levee, a landscape-level characteristic, had the largest effect on Acadian Flycatcher parasitism and seemed to be the driving force in determining whether or not a nest would be parasitized. Finer-scale characteristics of the nesting habitat and the nest-site, as well as finer temporal characteristics of the breeding season, were also important, but to a much lesser extent. Local characteristics may be immaterial in areas saturated with cowbirds, but emerge as influential within areas more removed from cowbird seeding points where influence of the feeding site has declined (Robinson et al. 1995a,b, Gates and Evans 1998, Thompson et al. 2000). For Prothonotary Warblers, distance from the levee, exposure to open canopy, and time of breeding season had large effects on parasitism probability. However, for this species, micro-scale nest-site characteristics, namely cavity entrance size and type, also were highly important.

Whether cowbirds are locally associated with edge or with host-density may be related to factors limiting cowbird numbers at the landscape scale (Thompson et al. 2000). Specifically, in areas where cowbirds are constrained by landscape or biogeographic factors, most parasitism should occur near feeding areas (to minimize commuting) or in areas of high host density (to maximize parasitism opportunities). Thompson et al. (2000) demonstrated that within an area where overall cowbird abundance and parasitism levels were low, parasitism was higher near forest-agricultural edges (feeding area) and at interior edges created by timber harvest (potential area of high host density). Alternatively, in an area with high overall cowbird abundance and parasitism levels, parasitism was not related to edge and was instead related to local host abundance. In general, cowbird-edge association is found in forest-dominated landscapes where feeding opportunities are limited and in severely fragmented landscapes where breeding opportunities are limited, but does not exist in moderately fragmented areas where there are ample opportunities for both feeding and breeding (Gates and Evans 1998).

The situation at the White River NWR, however, is unique; although the refuge is an extensive tract of forest, it is embedded in a sea of agriculture. As such, the landscape is teeming with cowbirds. In this setting, cowbirds encounter both limited feeding and limited breeding opportunities, which interact with interesting outcomes. The uncoupling of cowbird feeding and breeding sites and the preference to breed within forests further complicates the situation. Within the refuge, feeding opportunities are limited by virtue of being forested; however, feeding sites are plentiful at the forest-agricultural boundaries, including a popular site on the levee. Owing to exceptional cowbird mobility and the narrow shape of the refuge, cowbird access to the interior forest in not limited and their presence is evident in all parts of the forest. Although cowbirds use distinct areas for feeding and breeding and are capable of commuting long distances between feeding and breeding grounds, they will travel only as far as necessary to meet both of these needs. Cowbirds probably saturate the available breeding habitat in the forest adjacent to feeding sites, but then due to limited breeding opportunities, spread further into the forest in search of non-parasitized hosts. It is likely, that in this situation, local-scale habitat features (including internal edge) and nest-site features of hosts have little to no influence on parasitism levels at close proximity to the feeding sites. However, cowbird intrusion into the forest interior may be facilitated by disturbances and openings in the canopy. As cowbirds diffuse into the forest interior and are less influenced by proximity to the feeding site, the effects of local-scale features may have more influence on parasitism levels felt by hosts. In general, cowbirds probably settle within an area based on features at the landscape scale, but then local habitat characteristics and host species behavior are likely used to further refine selection of suitable breeding habitats and nests (Evans and Gates 1997).

Within the cowbird/parasitism literature, the relative importance of habitat characteristics at the micro-, macro-, and landscape scale, as well as nest characteristics, host preferences, and host activity, remains unclear and further research on these topics is warranted. Although the same habitat features had the same general effect on parasitism of both focal species in our study, the magnitude of the effect varied. It is likely that cowbird preference for host species, as well as unmeasured characteristics of the nesting habitat, influence parasitism levels; predilection for particular hosts may even override effects of the micro- and macro-scale habitat. Additionally, because cowbirds are known to locate and parasitize nests based on observing host-activity, host behavior at the nest is likely important. Studies have demonstrated that hosts (both females and males) that are more active within the vicinity of the nest have a higher probability of having their nest parasitized (McLean 1987, Uyehara and Narins 1995, Clotfelter 1998, Banks and Martin 2001). Thus, research on host behavior at the nest would help elucidate the factors that influence the likelihood of parasitism. Cowbirds have different effects on host species even within the same habitat, making community-wide studies in various habitat types, landscapes, and regions essential to fully understand the dynamics of cowbird parasitism. Additionally, spatial patterns of parasitism have been shown to vary at both large and small scales among different host species (Winslow et al. 2000) and may result from variation in the behavior of cowbirds and/or hosts. Because female cowbirds have large breeding ranges and are often territorial (Darley 1983, Rothstein et al. 1986), it is conceivable that the behavior of individual females could influence patterns of parasitism at local scales, making control of spatial autocorrelation a concern. Lastly, nearly all parasitism studies are based on correlations between descriptions of habitat features and cowbird abundance and/or parasitism levels of hosts. While correlative studies may reveal common patterns, to confirm these patterns, experimental data at the appropriate scales are needed (Robinson and Smith 2000). Although the factors influencing parasitism levels are complex, results of this study and others suggest that appropriate habitat management has the potential to reduce parasitism levels.

TABLES

Table 4.1: Summary of parasitism of Acadian Flycatcher and Prothonotary Warbler nests. Multiple parasitism is the percent of parasitized nests that contain more than one cowbird egg. Mean number of cowbird eggs pertains to parasitized nests only. Mean number of cowbird nestlings pertains only to parasitized nests that contain cowbird nestlings. Cowbird hatching success is the number of cowbird nestlings divided by the number of cowbird eggs per nest, averaged over all nests that were still active past day 18 (the last possible day for cowbird eggs to hatch and fledge successfully). Means are calculated over nests from all years and plots. Sample size is provided in parentheses.

	Acadian Flycatcher	
Parasitism (n=320)	(%)	33
	Prothonotary Warbler	
Parasitism (n=463)	(%)	43
Multiple Parasitism (n=198)	(%)	41
Daily Parasitism Rate (n=463)	Mean ± SE	0.11 ± 0.007
No. Cowbird Eggs (n=198)	Mean ± SE	1.6 ± 0.06
	Min	1
	Max	5
No. Cowbird Nestlings (n=64)	Mean ± SE	1.4 ± 0.07
	Min	1
	Max	3
Cowbird Hatching Success (n=71)	Mean ± SE	0.64 ± 0.04

Table 4.2: Justification for inclusion of predictor variables in the logistic regression analysis and their expected relationship to the probability of parasitism of Acadian Flycatcher nests. See Tables 2.2, 2.3, and 2.14 for variable descriptions.

Variable	**Justification and Expected Relationship**
Micro-Scale	
Nest_Ht	Higher nests may be more obvious to Brown-headed Cowbirds because cowbirds tend to search for nests from prominent perches. Expected relationship to probability of parasitism: positive.
Can_Cov	More canopy cover may provide concealment. Expected relationship to probability of parasitism: negative.
Dist_Edge	Further distance from branch edge may provide concealment. Expected relationship to probability of parasitism: negative
Macro-Scale	
Macro_PC1	Few, large, spread out trees may reflect areas with less disturbance and may attract fewer Brown-headed Cowbirds. Expected relationship to the probability of parasitism: negative.
Macro_PC2	Less canopy cover may attract Brown-headed Cowbirds because provides improved look-out perches. Expected relationship to probability of parasitism: negative.
Landscape Scale	
Open	Open canopy may attract Brown-headed Cowbirds and serve as points of forest infiltration. Expected relationship to probability of parasitism: positive.
Other	
Season	Dichotomous variable: 0=nest initiated on or before June 18, 1= nest initiated after June 18. Brown-headed Cowbirds have an earlier breeding season than Acadian Flycatchers, therefore expect nest initiated late to have decreased probability of parasitism. Expected relationship: negative.
Trt, Rep, Trt*Rep	Set of dummy variables for plot treatment, plot replicate, and treatment*replicate interaction; together the three variables reproduce the four study plots. This representation allows us to investigate treatment effects and to make interactions between treatment and other variables. Plot contains the gradient of levee_dist, as well as serves as a nuisance variable for unexplained variability. Cowbirds forage on the levee. Expected relationship: Plot F will have increased probability of parasitism.
Year	Set of dummy variables representing different years of the study. Nuisance variable to control for annual variability; no expectations.

Table 4.3: Model averaged results from the logistic regression analysis of Acadian Flycatcher nest parasitism. Sample size equaled 292 nests, including 98 parasitism events. There were 78 candidate models; the six dummy variables for Year and Plot (Trt, Rep, Trt*Rep) were forced into each model, while up to three more variables, for a maximum of nine, were allowed to enter the model. The 78 candidate models were averaged to obtain unconditional estimates of parameters and their standard errors and confidence intervals. Odds Ratio is the estimated change in the odds of a parasitism event for each one-unit increase in the independent variable (other variables held fixed), Akaike Weight is the sum of relative AIC weight (Burnham and Anderson 1998) for those candidate models in which the variable appears, and # Models is the number of candidate models in which the variable appears. An asterisk denotes an interaction between two variables. A "t" indicates variables that were transformed prior to analysis. Variables were centered. Effects coding was used for year dummy variables. Years are compared to 2000.

Variable		Parameter Estimate	Standard Error	90% Confidence Interval	Odds Ratio	Akaike Weight	# Models
Year	1996	-0.8873	0.2455	{-1.2899 , -0.4846}	0.4118	1	78
	1997	0.2198	0.2156	{-0.1337 , 0.5733}	1.2458	1	78
	1998	0.2477	0.3200	{-0.2771 , 0.7725}	1.2811	1	78
Plot	Trt	0.0128	0.4142	{-0.6666 , 0.6921}	1.0128	1	78
	Rep	1.3770	0.3632	{0.7814 , 1.9726}	3.9629	1	78
	Trt*Rep	-1.1876	0.5543	{-2.0967 , -0.2785}	0.3050	1	78
Micro	Nest_Ht	0.0708	0.0564	{-0.0218 , 0.1634}	1.0734	0.3197	24
	Can_Cov^{t}	0.0743	0.1281	{-0.1357 , 0.2843}	1.0771	0.1941	24
	Dist_Edge^{t}	-0.0028	0.2498	{-0.4124 , 0.4068}	0.9972	0.1682	24
Macro	Macro_PC1	-0.1673	0.1697	{-0.4456 , 0.1109}	0.8459	0.4123	30
	Macro_PC2	0.0046	0.1479	{-0.2379 , 0.2471}	1.0046	0.1695	24
Landscape	Open	-0.0208	0.1308	{-0.2353 , 0.1936}	0.9794	0.2155	30
Other	Season	-0.4834	0.3512	{-1.0594 , 0.0926}	0.6167	0.3671	24
	Trt*PC1	0.4582	0.2168	{0.1027 , 0.8137}	1.5812	0.2611	7
	Trt*Open	0.3624	0.3080	{-0.1427 , 0.8676}	1.4368	0.0519	7
	Intercept	-1.0787	0.2830	{-1.5429 , -0.6146}	0.3400	1	78

Table 4.4: Mean micro, macro, and landscape characteristics of Acadian Flycatcher nest sites. Means were calculated for the nests and variables included in the logistic regression model (n=292). Variables in *italics* were not included in the model, but were used to derive the principal component macro-scale variables, Macro_PC1 and Macro_PC2, and the principal component landscape-scale variable, Open. Season is a dichotomous variable, thus the value listed is the mean of the 0/1 values, or the proportion of nests initiated in the second half of the breeding season. Years and plots were combined to compute all means. See Tables 2.2, 2.3, and 2.14 for variable descriptions.

Variable	**Mean ± SE**	**Min**	**Max**
Nest_Ht (m)	6.64 ± 0.14	1.50	16.47
Can_Cov (%)	96 ± 0.26	65	100
Dist_Edge (cm)	69 ± 2.43	10	250
Macro_PC1	0.1789 ± 0.0783	-2.9797	5.8378
Macro_PC2	0.5044 ± 0.0595	-2.1862	2.9627
Macro_CanCov (%)	96 ± 0.29	62	100
Trees (#)	24.8 ± 0.55	4	56
DBH (cm)	21.2 ± 0.29	12.0	49.1
Tree_Dist (m)	5.21 ± 0.08	1.71	10.05
Open	0.0291 ± 0.0793	-3.8903	1.8179
Open_Dist (m)	87.4 ± 3.71	0	276.4
Open_Percent (%)	9.47 ± 0.64	0	40.58
Season	0.22	----	----

Table 4.5: Contrasts between years and between plots, with regards to the probability of parasitism, based on model averaged results from the logistic regression analysis of Acadian Flycatcher nest parasitism. Models were re-fit several times in order to achieve all year by year comparisons and all plot by plot comparisons. Reference coding was used for all dummy variables. Values for plots are derived from contrasts using the dummy variables, Trt, Rep, and Trt*Rep (Appendix 4B). Only the contrasts whose 90% confidence intervals did not overlap zero are shown. Odds Ratio is the estimated odds of parasitism for year 1996 compared to another year, or for plot F compared to another plot, keeping all other variables in the averaged model fixed.

Contrast	Parameter Estimate	Standard Error	90% Confidence Interval	Odds Ratio
Year				
1996 vs 1997	-1.1070	0.3505	{-1.6819 , -0.5322}	0.3305
1996 vs 1998	-1.1350	0.4853	{-1.9309 , -0.3390}	0.3214
1996 vs 2000	-1.3070	0.3904	{-1.9473 , -0.6667}	0.2706
Plot				
F vs A	1.3770	0.3632	{0.7814 , 1.9726}	3.9629
F vs D	1.3642	0.4081	{0.6949 , 2.0336}	3.9126
F vs E	1.1748	0.3909	{0.5337 , 1.8159}	3.2375

Table 4.6: Mean micro, macro, and landscape characteristics of Acadian Flycatcher nest sites by parasitism event. Means were calculated for the nests and variables included in the logistic regression model. Means were computed post analyses and were not used to investigate potential variable effects. Means are presented simply for the purpose of documentation. Forst_Dist and Levee_Dist are shown because they are associated with Plot. Variables in *italics* were not included in the model, but were used to derive the principal component macro-scale variables, Macro_PC1 and Macro_PC2, and the principal component landscape-scale variable, Open. Season is a dichotomous variable, thus the value listed is the proportion of nests that were initiated in the second half of the breeding season. Years and plots were combined to compute all means. Sample size is provided in parentheses. See Tables 2.2, 2.3, and 2.14 for variable descriptions.

Variable	**Parasitism**	
	Parasitized	**Not Parasitized**
	Mean ± SE (n=98)	Mean ± SE (n=194)
Nest_Ht (m)	7.07 ± 0.26	6.43 ± 0.17
Can_Cov (%)	97 ± 0.33	96 ± 0.35
Dist_Edge (cm)	71 ± 4.20	68 ± 2.99
Macro_PC1	0.0764 ± 0.1349	0.2307 ± 0.0962
Macro_PC2	0.4499 ± 0.0982	0.5320 ± 0.0746
Macro_CanCov (%)	96 ± 0.40	96 ± 0.38
Trees (#)	26.0 ± 1.00	24.1 ± 0.64
DBH (cm)	21.1 ± 0.47	21.2 ± 0.38
Tree_Dist (m)	5.10 ± 0.13	5.26 ± 0.11
Forst_Dist (m)	2616.7 ± 77.35	2551.0 ± 67.11
Levee_Dist (m)	1944.7 ± 143.90	2560.7 ± 105.86
Open	-0.1806 ± 0.1417	0.1351 ± 0.0948
Open_Dist (m)	94.4 ± 6.66	83.8 ± 4.46
Open_Percent (%)	7.82 ± 1.08	10.30 ± 0.79
Season	0.17	0.24

Table 4.7: Justification for inclusion of predictor variables in the logistic regression analysis and their expected relationship to the probability of parasitism of Prothonotary Warbler nests. See Tables 2.2, 2.3, and 2.14 for variable descriptions.

Variable	Justification and Expected Relationship
Micro-Scale	
Can_Cov	More canopy cover may provide concealment. Expected relationship to probability of parasitism: negative.
Cav_Code	Large cavity entrances may make nests more obvious. Small cavity entrances may limit or prevent cowbird access to the nest. Expected relationship to probability of parasitism: positive.
Cav_Split	Split cavities tend to have larger entrances than non-split, or circular, cavities due to the elongated height of the entrance. Large cavity entrances may make nests more obvious. Small cavity entrances may limit or prevent cowbird access to the nest. Expected relationship to probability of parasitism: positive.
Macro-Scale	
Macro_PC1	Few, large, spread out trees may reflect areas with less disturbance and may attract fewer Brown-headed Cowbirds. Expected relationship to probability of parasitism: negative.
Macro_PC2	Less canopy cover may attract Brown-headed Cowbirds because provides improved look-out perches. Expected relationship to probability of parasitism: negative.
Landscape Scale	
Open	Open canopy may attract Brown-headed Cowbirds and serve as points of forest infiltration. Expected relationship to probability of parasitism: positive.
Other	
Season	Dichotomous variable: 0=nest initiated on or before June 3, 1= nest initiated after June 3. Breeding seasons of cowbirds and Prothonotary Warblers closely overlap, however, expect late nests will have decreased probability of parasitism. Expected relationship: negative.
Trt, Rep, Trt*Rep	Set of dummy variables for plot treatment, plot replicate, and treatment*replicate interaction; together the three variables reproduce the four study plots. This representation allows us to investigate treatment effects and to make interactions between treatment and other variables. Plot contains the gradient of levee_dist, as well as serves as a nuisance variable for unexplained variability. Cowbirds forage on the levee. Expected relationship: Plot F will have increased probability of parasitism.
Year	Set of dummy variables representing different years of the study. Nuisance variable to control for annual variability; no expectations.

Table 4.8: Model averaged results from the logistic regression analysis of Prothonotary Warbler nest parasitism (Model A). Analysis included all variables of interest that were measured during each year at all spatial scales, and thus excluded data from 1998. Sample size equaled 270 nests, including 95 parasitism events. There were 71 candidate models; the five dummy variables for Year and Plot (Trt, Rep, Trt*Rep) were forced into each model, while up to three more variables, for a maximum of eight, were allowed to enter the model. The 71 candidate models were averaged to obtain unconditional estimates of parameters and their standard errors and confidence intervals. Odds Ratio is the estimated change in the odds of a parasitism event for each one-unit increase in the independent variable (other variables held fixed), Akaike Weight is the sum of relative AIC weight (Burnham and Anderson 1998) for those candidate models in which the variable appears, and # Models is the number of candidate models in which the variable appears. An asterisk denotes an interaction between two variables. A "t" indicates variables that were transformed prior to analysis. Variables were centered. Effects coding was used for year dummy variables. Years are compared to 2000.

Variable		Parameter Estimate	Standard Error	90% Confidence Interval	Odds Ratio	Akaike Weight	# Models
Year	1996	-0.0930	0.2123	{-0.4412 , 0.2551}	0.9112	1	71
	1997	0.1871	0.1973	{-0.1365 , 0.5107}	1.2058	1	71
Plot	Trt	0.7273	0.4309	{0.0206 , 1.4341}	2.0696	1	71
	Rep	1.1122	0.3927	{0.4681 , 1.7562}	3.0409	1	71
	Trt*Rep	-1.3387	0.5709	{-2.2750 , -0.4023}	0.2622	1	71
Micro	Can_Cov^{t}	0.0856	0.1463	{-0.1544 , 0.3255}	1.0893	0.0918	23
	Cav_Code	0.4451	0.2084	{0.1033 , 0.7869}	1.5606	0.4409	23
	Cav_Split	1.2374	0.4348	{0.5243 , 1.9504}	3.4465	0.7336	23
Macro	Macro_PC1	-0.1705	0.1072	{-0.3462 , 0.0053}	0.8433	0.2796	23
	Macro_PC2	0.2321	0.2028	{-0.1005 , 0.5647}	1.2612	0.1490	23
Landscape	Open	-0.0430	0.1362	{-0.2664 , 0.1805}	0.9579	0.0823	29
Other	Season	-1.1776	0.3344	{-1.7260 , -0.6292}	0.3080	0.9942	23
	Trt*Open	0.5623	0.2882	{0.0897 , 1.0350}	1.7548	0.0014	7
	Intercept	-1.0582	0.3207	{-1.5841 , -0.5323}	0.3471	1	71

Table 4.9: Model averaged results from the logistic regression analysis of Prothonotary Warbler nest parasitism (Model B). Analysis included variables at all spatial scales, including extracted macro-scale values for 1998, and included data from all years. Sample size equaled 317 nests, including 123 parasitism events. There were 48 candidate models; the six dummy variables for Year and Plot (Trt, Rep, Trt*Rep) were forced into each model, while up to three more variables, for a maximum of nine, were allowed to enter the model. The 48 candidate models were averaged to obtain unconditional estimates of parameters and their standard errors and confidence intervals. Odds Ratio is the estimated change in the odds of a parasitism event for each one-unit increase in the independent variable (other variables held fixed), Akaike Weight is the sum of relative AIC weight (Burnham and Anderson 1998) for those candidate models in which the variable appears, and # Models is the number of candidate models in which the variable appears. An asterisk denotes an interaction between two variables. A "t" indicates variables that were transformed prior to analysis. Variables were centered. Effects coding was used for year dummy variables. Years are compared to 2000.

Variable		Parameter Estimate	Standard Error	90% Confidence Interval	Odds Ratio	Akaike Weight	# Models
Year	1996	-0.3609	0.2284	{-0.7355 , 0.0137}	0.6970	1	48
	1997	-0.0854	0.1961	{-0.4070 , 0.2362}	0.9181	1	48
	1998	0.7755	0.2702	{0.3324 , 1.2187}	2.1717	1	48
Plot	Trt	0.6877	0.3945	{0.0407 , 1.3347}	1.9891	1	48
	Rep	1.0514	0.3711	{0.4429 , 1.6600}	2.8618	1	48
	Trt*Rep	-1.3924	0.5237	{-2.2513 , -0.5336}	0.2485	1	48
Micro	Can_Cov^t	0.0315	0.1429	{-0.2029 , 0.2658}	1.0320	0.0636	17
	Cav_Code	0.5090	0.1956	{0.1882 , 0.8299}	1.6637	0.7031	17
	Cav_Split	1.1212	0.4678	{0.3539 , 1.8884}	3.0685	0.6090	17
Macro	Macro_PC1	-0.1653	0.1041	{-0.3361 , 0.0054}	0.8476	0.2229	17
Landscape	Open	-0.1955	0.1222	{-0.3959 , 0.0048}	0.8224	0.2286	22
Other	Season	-1.0569	0.2975	{-1.5449 , -0.5690}	0.3475	0.9881	17
	Trt*Open	0.5113	0.2512	{0.0994 , 0.9233}	1.6675	0.0039	6
	Intercept	-0.7229	0.2957	{-1.2079 , -0.2379}	0.4854	1	48

Table 4.10: Mean micro, macro, and landscape characteristics of Prothonotary Warbler nest sites. Means were calculated for the nests and variables included in the logistic regression models. Variables in *italics* were not included in the model, but were used to derive the principal component macro-scale variables, Macro_PC1 and Macro_PC2, and the principal component landscape-scale variable, Open. Cav_Split and Season are dichotomous variables; thus, the values listed are the proportion of nests that had split cavities and the proportion of nests that were initiated in the second half of the breeding season. Years and plots were combined to compute all means. Sample size is based on the nests used in Model B (n=317), with the exception of Macro_PC2 and the original macro-scale habitat variables (n=270). See Tables 2.2, 2.3, and 2.14 for variable descriptions.

Variable	**Mean ± SE**	**Min**	**Max**
Can_Cov (%)	91 ± 0.45	30	100
Cav_Code	2.3 ± 0.05	1	5
Cav_Ht (cm)	7.19 ± 0.39	2.5	50
Cav_Wid (cm)	4.69 ± 0.09	2	18.5
Cav_Split	0.19	----	----
Macro_PC1	-0.2504 ± 0.0716	-3.7503	3.5460
Macro_PC2	-0.2482 ± 0.0587	-2.6604	2.5967
Macro_CanCov (%)	91 ± 0.39	62	100
Trees (#)	28.4 ± 0.58	5	65
DBH (cm)	21.1 ± 0.29	13.6	40.5
Tree_Dist (m)	4.72 ± 0.08	1.23	8.45
Open	-0.0278 ± 0.0740	-3.8526	1.8732
Open_Dist (m)	90.1 ± 3.57	0	271.9
Open_Percent (%)	7.72 ± 0.52	0	41.22
Season	0.3	----	----

Table 4.11: Contrasts between years and between plots, with regards to the probability of parasitism, based on Model B averaged results from the logistic regression analysis of Prothonotary Warbler nest parasitism. Models were re-fit several times in order to achieve all year by year comparisons and all plot by plot comparisons. Reference coding was used for all dummy variables. Values for plots are derived from contrasts using the dummy variables, Trt, Rep, and Trt*Rep (Appendix 4B). For Year, only those contrasts whose 90% confidence intervals did not overlap zero are shown. For Plot, all contrasts are provided, however, those whose 90% confidence intervals did not overlap zero are indicated with an asterisk. Odds Ratio is the estimated odds of parasitism for year 1998 compared to another year, or for a given plot compared to another plot, keeping all other variables in the averaged model fixed.

Contrast	Parameter Estimate	Standard Error	90% Confidence Interval	Odds Ratio
Year				
1998 vs 1996	1.1364	0.4201	{0.4474 , 1.8254}	3.1156
1998 vs 1997	0.8610	0.3850	{0.2295 , 1.4924}	2.3654
1998 vs 2000	1.1047	0.4360	{0.3896 , 1.8198}	3.0183
Plot				
F vs A*	1.0514	0.3711	{0.4429 , 1.6600}	2.8618
F vs D	0.3637	0.4319	{-0.3445 , 1.0720}	1.4387
F vs E*	0.7047	0.3822	{0.0779 , 1.3315}	2.0233
E vs A	0.3467	0.3566	{-0.2381 , 0.9316}	1.4144
E vs D	-0.3410	0.3886	{-0.9783 , 0.2964}	0.7111
D vs A*	0.6877	0.3945	{0.0407 , 1.3347}	1.9891

Table 4.12: Mean micro, macro, and landscape characteristics of Prothonotary Warbler nest sites by parasitism event. Means were calculated for the nests and variables included in the logistic regression models. Means were computed post analyses and were not used to investigate potential variable effects. Means are presented simply for the purpose of documentation. Forst_Dist and Levee_Dist are shown because they are associated with Plot. Variables in *italics* were not included in the model, but were used to derive the principal component macro-scale variables, Macro_PC1 and Macro_PC2, and the principal component landscape-scale variable, Open. Cav_Split and Season are dichotomous variables; thus, the values listed are the proportion of nests that had split cavities and the proportion of nests that were initiated in the second half of the breeding season. Years and plots were combined to compute all means. Sample size is based on the nests used in Model B (n=317) and is provided in parentheses, with the exception of Macro_PC2 and the original macro-scale habitat variables (n=270; 95 parasitized and 175 not parasitized). See Tables 2.2, 2.3, and 2.14 for variable descriptions.

Variable	**Parasitism**	
	Parasitized	**Not Parasitized**
	Mean ± SE (n=123)	Mean ± SE (n=194)
Can_Cov (%)	91 ± 0.49	90 ± 0.67
Cav_Code	2.6 ± 0.09	2.1 ± 0.06
Cav_Ht (cm)	8.87 ± 0.79	6.19 ± 0.40
Cav_Wid (cm)	5.04 ± 0.18	4.48 ± 0.11
Cav_Split	0.29	0.12
Macro_PC1	-0.3251 ± 0.1066	-0.2030 ± 0.0955
Macro_PC2	-0.1796 ± 0.1037	-0.2854 ± 0.0711
Macro_CanCov (%)	91 ± 0.74	91 ± 0.47
Trees (#)	29.2 ± 0.98	28.0 ± 0.72
DBH (cm)	20.5 ± 0.44	21.4 ± 0.37
Tree_Dist (m)	4.75 ± 0.13	4.70 ± 0.10
Forst_Dist (m)	2579.8 ± 77.37	2512.6 ± 68.32
Levee_Dist (m)	2267.5 ± 133.92	2588.5 ± 107.70
Open	-0.2692 ± 0.1373	0.1252 ± 0.0824
Open_Dist (m)	101.1 ± 6.57	83.2 ± 4.02
Open_Percent (%)	7.34 ± 0.89	7.95 ± 0.64
Season	0.20	0.37

Table 4.13: Model averaged results from the logistic regression analysis of Prothonotary Warbler nest parasitism (Model C). Analysis excluded macro-scale variables and included nests from all years. Sample size equaled 343 nests, including 137 parasitism events. There were 31 candidate models; the six dummy variables for Year and Plot (Trt, Rep, Trt*Rep) were forced into each model, while up to three more variables, for a maximum of nine, were allowed to enter the model. The 31 candidate models were averaged to obtain unconditional estimates of parameters and their standard errors and confidence intervals. Odds Ratio is the estimated change in the odds of a parasitism event for each one-unit increase in the independent variable (other variables held fixed), Akaike Weight is the sum of relative AIC weight (Burnham and Anderson 1998) for those candidate models in which the variable appears, and # Models is the number of candidate models in which the variable appears. An asterisk denotes an interaction between two variables. A "t" indicates variables that were transformed prior to analysis. Variables were centered. Effects coding was used for year dummy variables. Years are compared to 2000.

Variable		Parameter Estimate	Standard Error	90% Confidence Interval	Odds Ratio	Akaike Weight	# Models
Year	1996	-0.3373	0.2192	{-0.6969 , 0.0222}	0.7137	1	31
	1997	-0.0475	0.1870	{-0.3542 , 0.2592}	0.9536	1	31
	1998	0.6786	0.2167	{0.3232 , 1.0341}	1.9712	1	31
Plot	Trt	0.5864	0.3681	{-0.0172 , 1.1900}	1.7975	1	31
	Rep	0.9738	0.3534	{0.3943 , 1.5534}	2.6481	1	31
	Trt*Rep	-1.2230	0.4956	{-2.0358 , -0.4101}	0.2944	1	31
Micro	Can_Cov^t	0.0532	0.1381	{-0.1734 , 0.2797}	1.0546	0.1081	12
	Cav_Code	0.4105	0.1693	{0.1327 , 0.6882}	1.5075	0.7269	12
	Cav_Split	0.9097	0.4141	{0.2305 , 1.5888}	2.4835	0.6403	12
Landscape	Open	-0.1630	0.1218	{-0.3628 , 0.0368}	0.8496	0.2547	16
Other	Season	-0.8660	0.2769	{-1.3202 , -0.4119}	0.4206	0.9604	12
	Trt*Open	0.4789	0.2416	{0.0826 , 0.8751}	1.6142	0.0139	5
	Intercept	-0.7446	0.2671	{-1.1827 , -0.3065}	0.4749	1	31

Table 4.14: Moran's I and values of significance for spatial autocorrelation among the nest fates of (a) Acadian Flycatcher nests and (b) Prothonotary Warbler nests located within a 200 meter distance interval. The # Pairs column indicates the number of neighboring nests used for the analysis within each breeding season. The analysis was conducted twice: once using the raw nest fates (parasitized/not parasitized) and once using the residuals from the logistic regression model. A p-value of 0.05 was considered significant and significant p-values are indicated in bold. We were only concerned with positive spatial autocorrelation.

(a) Acadian Flycatcher

Year	# Pairs	Raw			Residual		
		Moran's I	z-score	p-value	Moran's I	z-score	p-value
1996	363	0.1234	2.6675	**0.004**	0.0496	1.1938	0.117
1997	339	0.2942	5.8377	**<0.001**	0.1425	2.9383	**0.002**
1998	29	0.0320	0.3552	0.359	-0.0824	-0.2787	0.390
2000	99	0.0365	0.5434	0.295	0.0092	0.2639	0.397

(b) Prothonotary Warbler

Year	# Pairs	Raw			Residual		
		Moran's I	z-score	p-value	Moran's I	z-score	p-value
1996	216	-0.0181	-0.0895	0.464	0.0038	0.2624	0.397
1997	292	0.2124	3.8912	**<0.001**	0.1646	3.0563	**0.001**
1998	66	0.1110	1.1361	0.127	0.0470	0.5942	0.278
2000	129	-0.0460	-0.3754	0.352	-0.1422	-1.5378	0.062

FIGURES

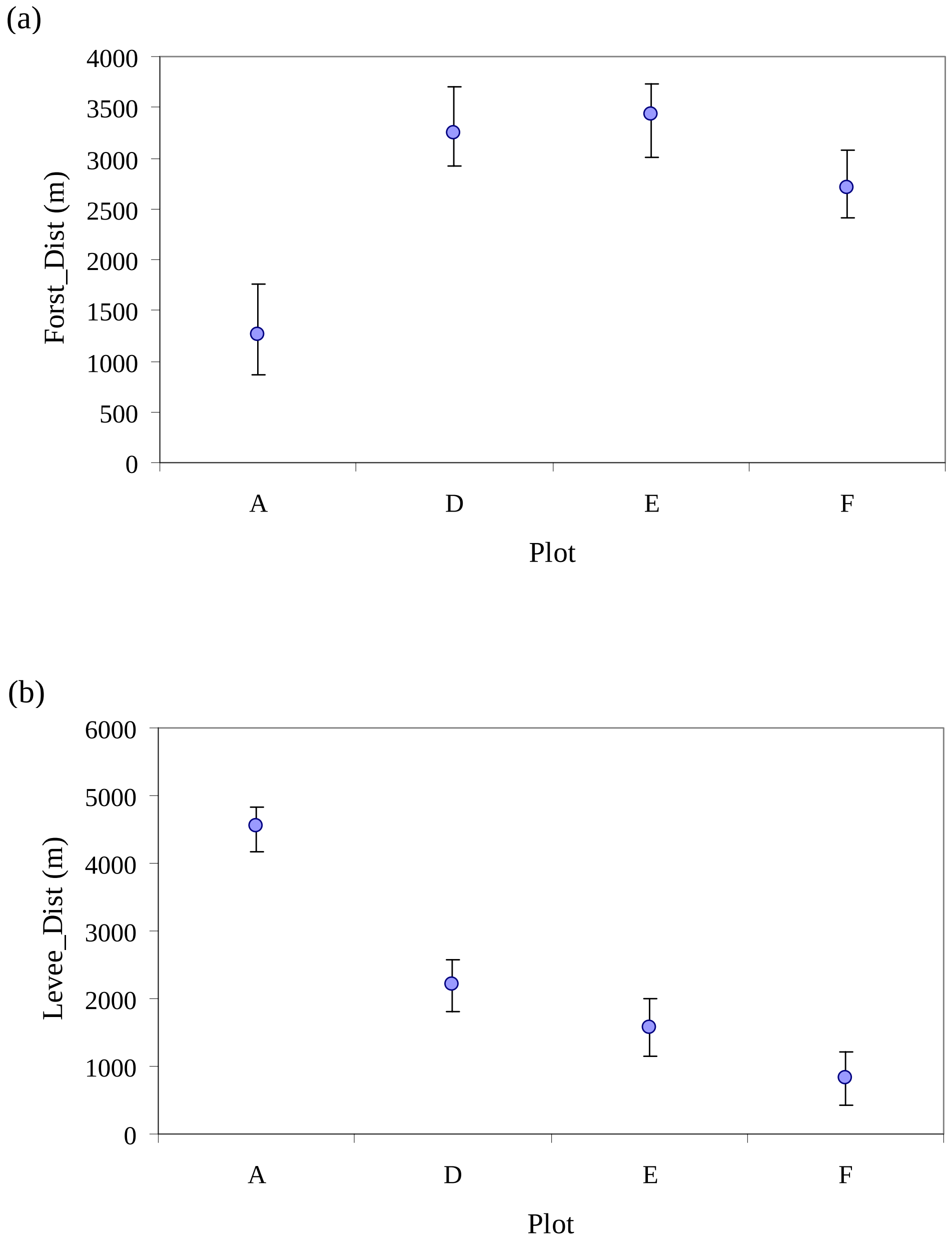
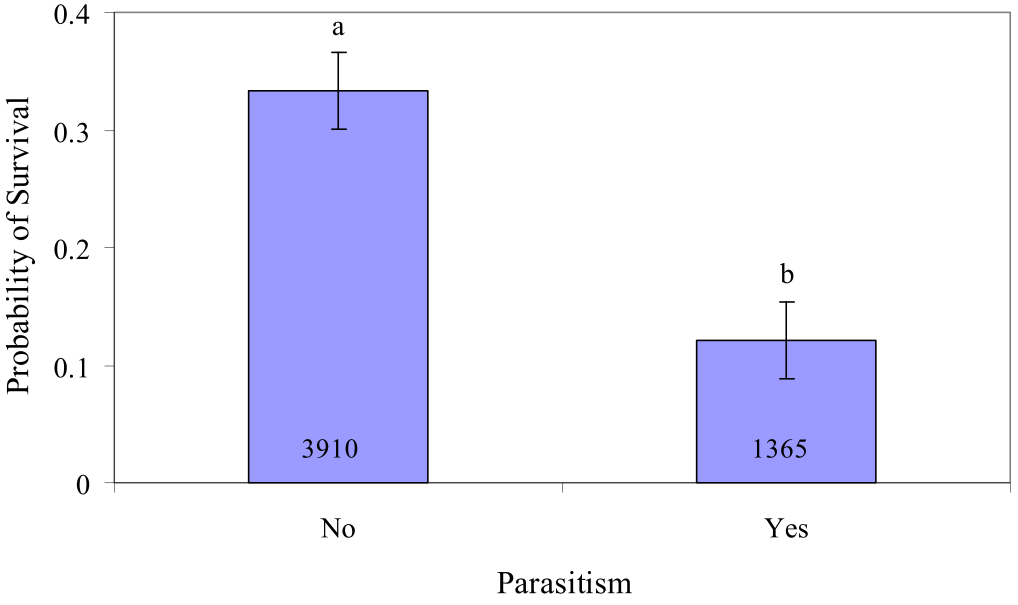


Figure 4.1: Relationship between study plot and (a) distance to forest/agriculture edge and (b) distance to levee. Plots are spaced across the width of the narrow refuge; where plot A is closest to the west edge, plot F is closest to the east edge, and plots D and E are in the middle, the furthest from either edge. Plots are located at a linear distance gradient from the levee; where plot F is closest and plot A furthest from the levee. Points represent mean distances for all nests of each plot. Bars represent the range of the distances per plot.

(a) Acadian Flycatcher



(b) Prothonotary Warbler

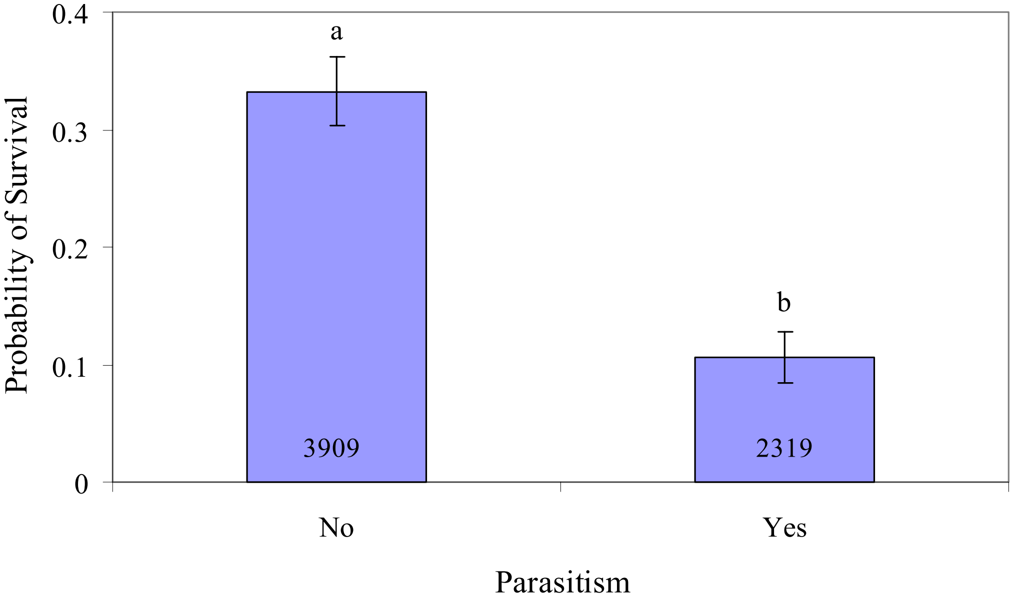


Figure 4.2: Mayfield estimates of survival for parasitized and non-parasitized nests of (a) Acadian Flycatchers and (b) Prothonotary Warblers. Bars represent ± 1 SE. Letters above bars signify statistical difference; unlike letters are statistically different. Numbers within columns indicate the number of nest exposure days. Nests from all plots and years were combined.

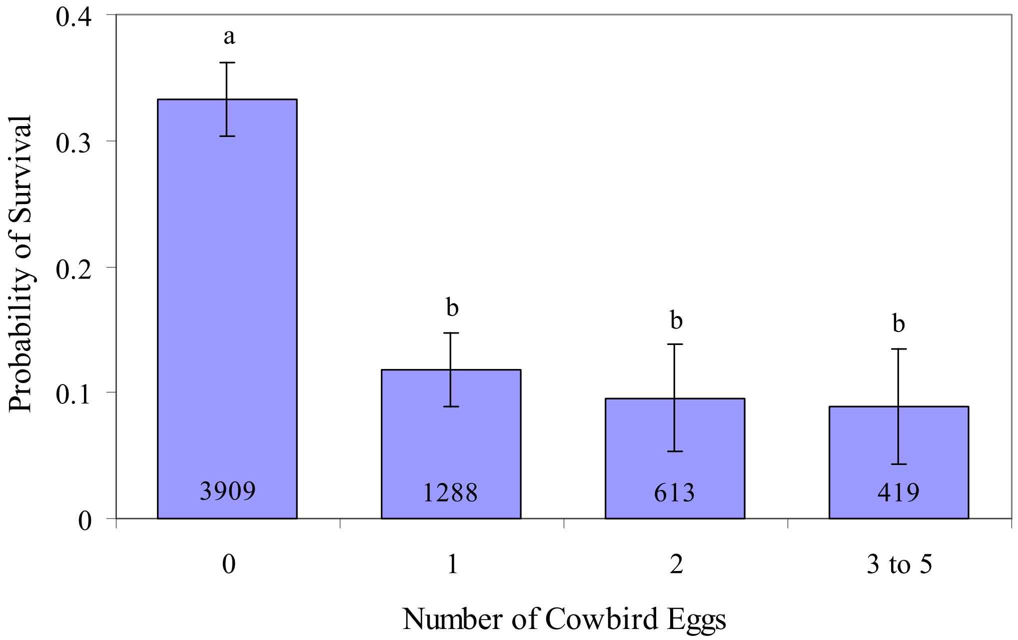
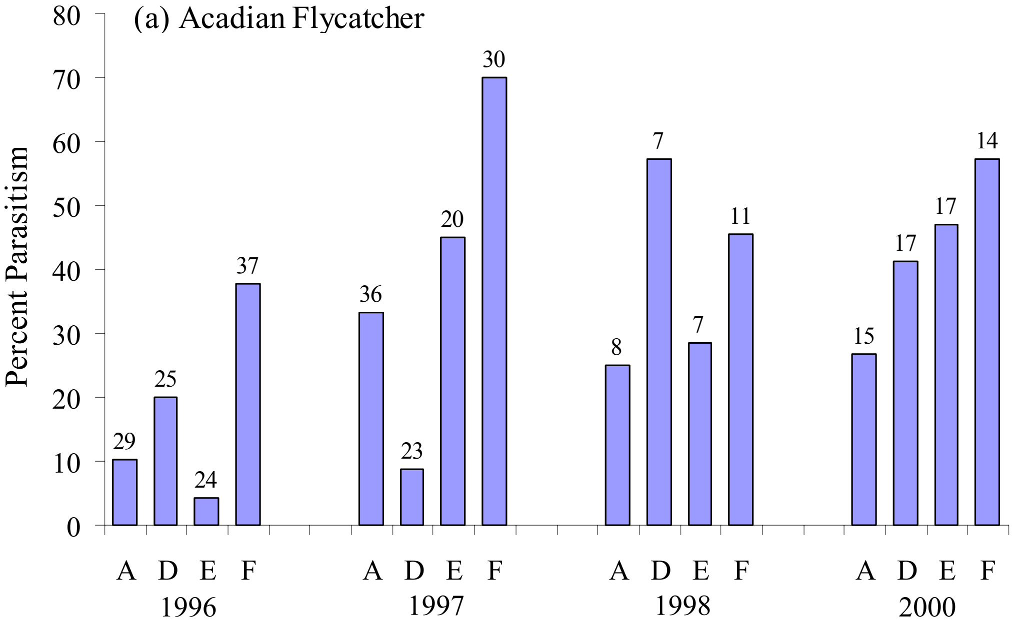


Figure 4.3: Mayfield survival of Prothonotary Warblers by number of parasitic eggs per nest. Bars represent ± 1 SE. Numbers within columns indicate the number of nest exposure days. Letters above columns signify statistical differences; like letters are not statistically different, whereas unlike letters are statistically different. Nests from all plots and years were combined.



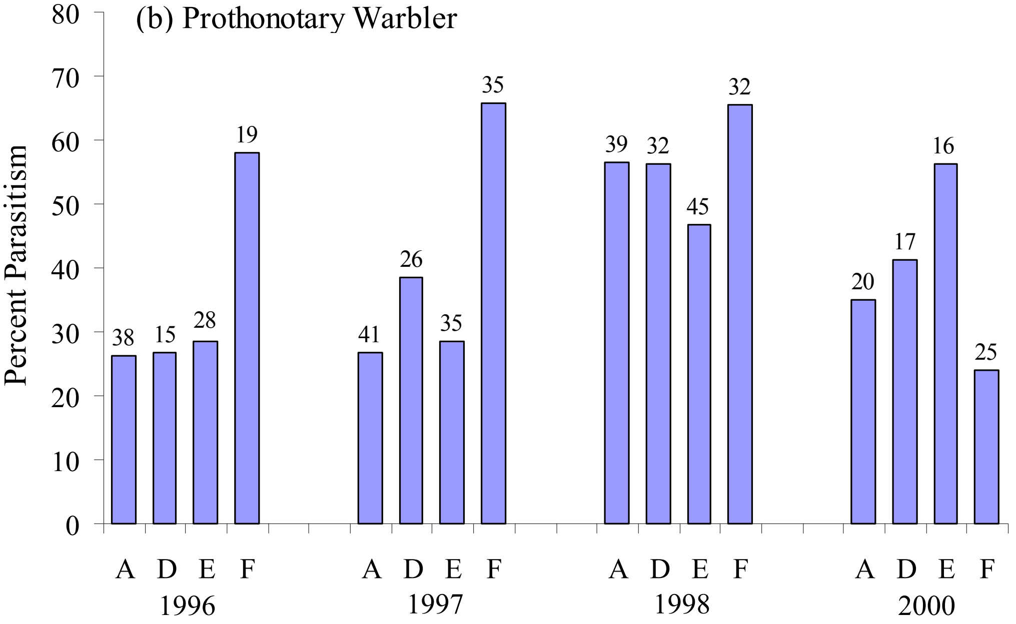


Figure 4.4: The percent of (a) Acadian Flycatcher and (b) Prothonotary Warbler nests that were parasitized by year and plot. Numbers above columns indicate sample size. The frequency of parasitism for both species varied by year (χ^2=14.71, df=3, p=0.0021 and χ^2=15.18, df=3, p=0.0017) and by plot (χ^2=20.93, df=3, p=0.0001 and χ^2=9.99, df=3, p=0.0186).

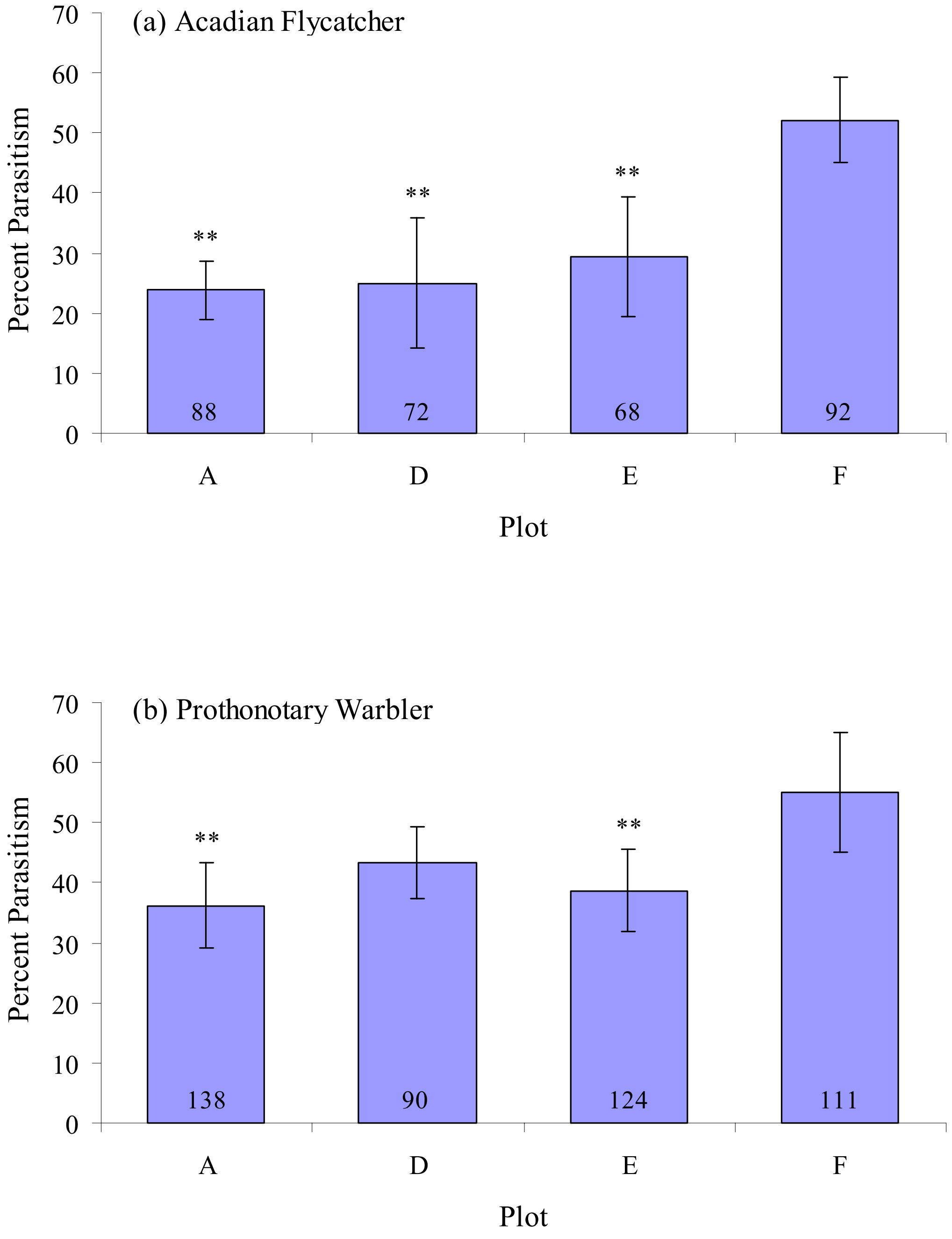


Figure 4.5: The percent of (a) Acadian Flycatcher and (b) Prothonotary Warbler nests that were parasitized on each study plot. Nests from all years were combined. Numbers within columns indicate sample size. Asterisks above the columns signify statistical differences from plot F.

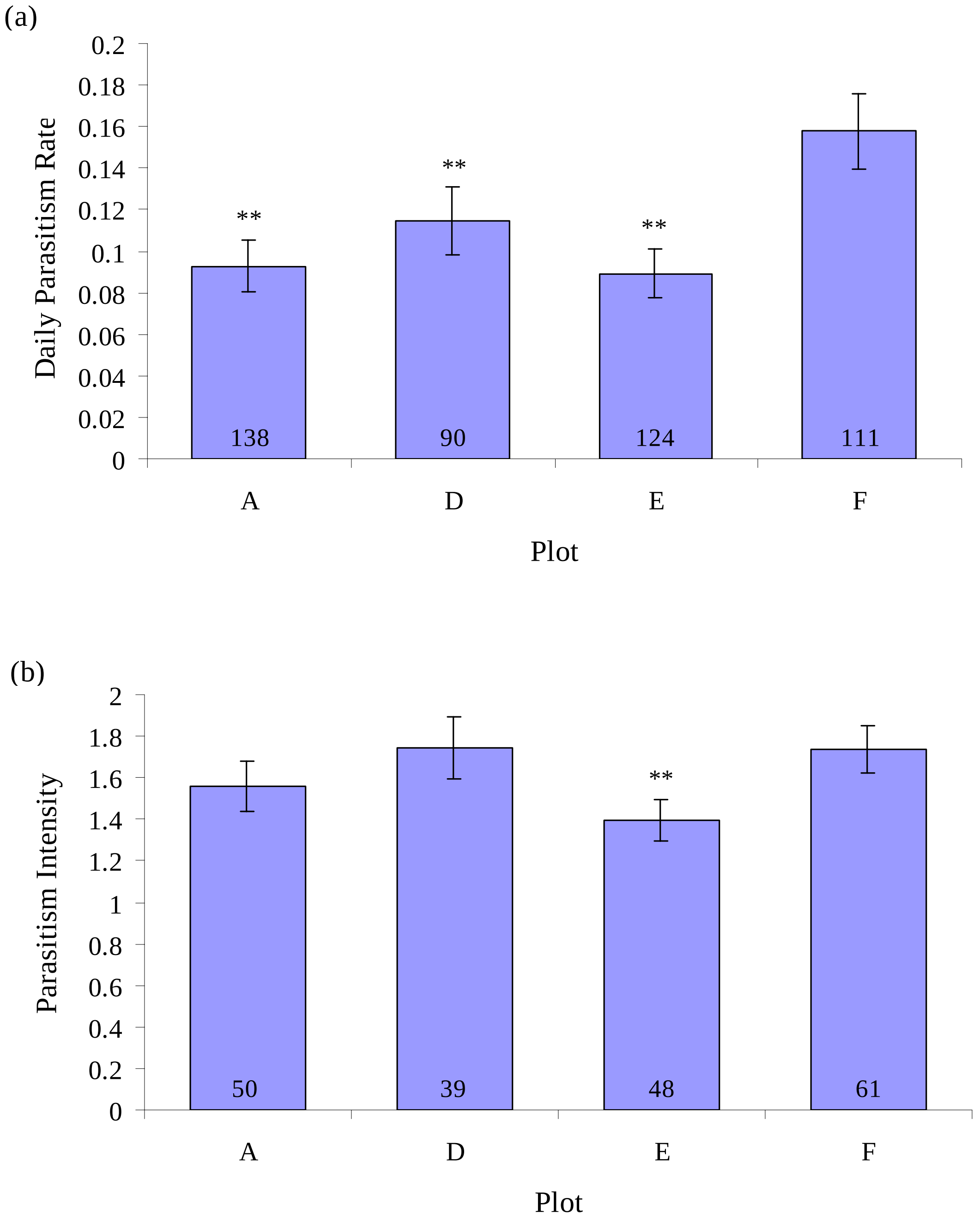


Figure 4.6: (a) A comparison of daily parasitism rate of Prothonotary Warbler nests by plot. Bars represent ± 1 SE. Numbers within columns indicate sample size. Asterisks above the columns signify statistical differences from plot F. (b) A comparison of mean number of parasitic eggs per parasitized Prothonotary Warbler nest by plot. Bars represent ± 1 SE. Numbers within columns indicate sample size. An asterisk above a column signifies statistical difference from plot F.

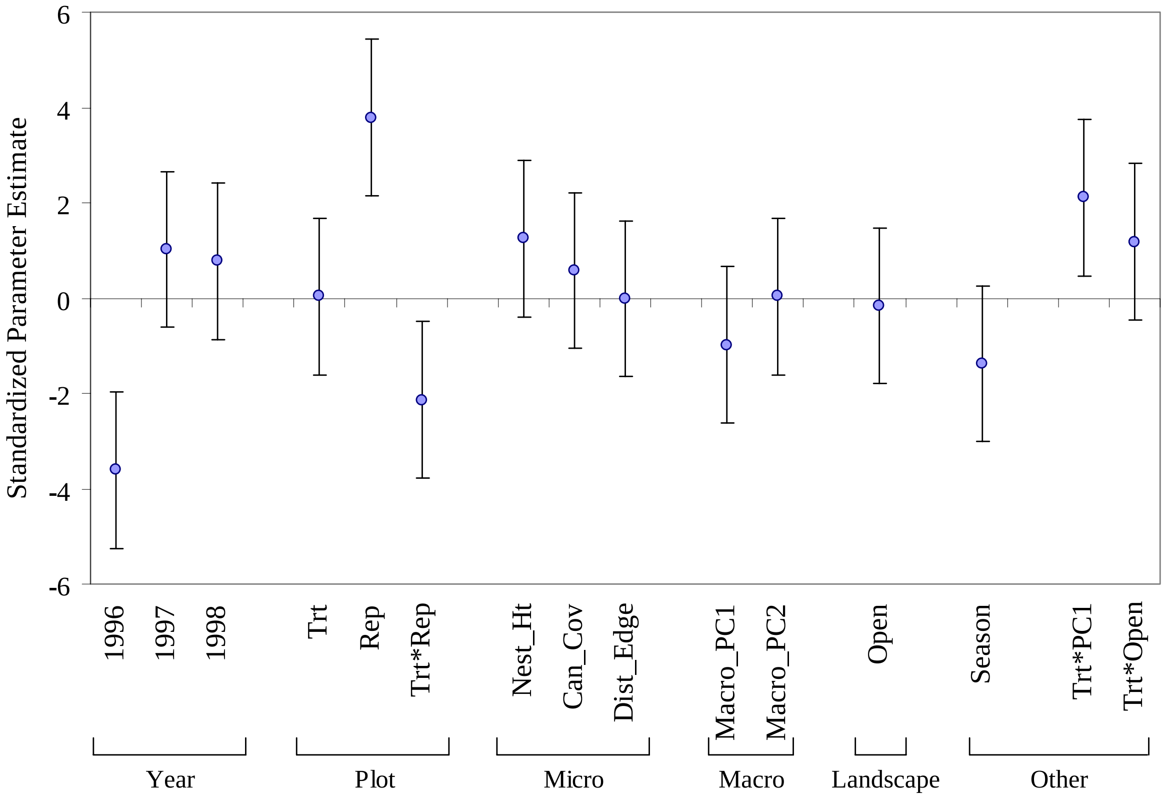


Figure 4.7: Standardized parameter estimates (*b/se*) of the variables included in the Acadian Flycatcher logistic regression model. Bars represent 90% confidence intervals. Parameter estimates were derived from the average model (see Table 4.3).

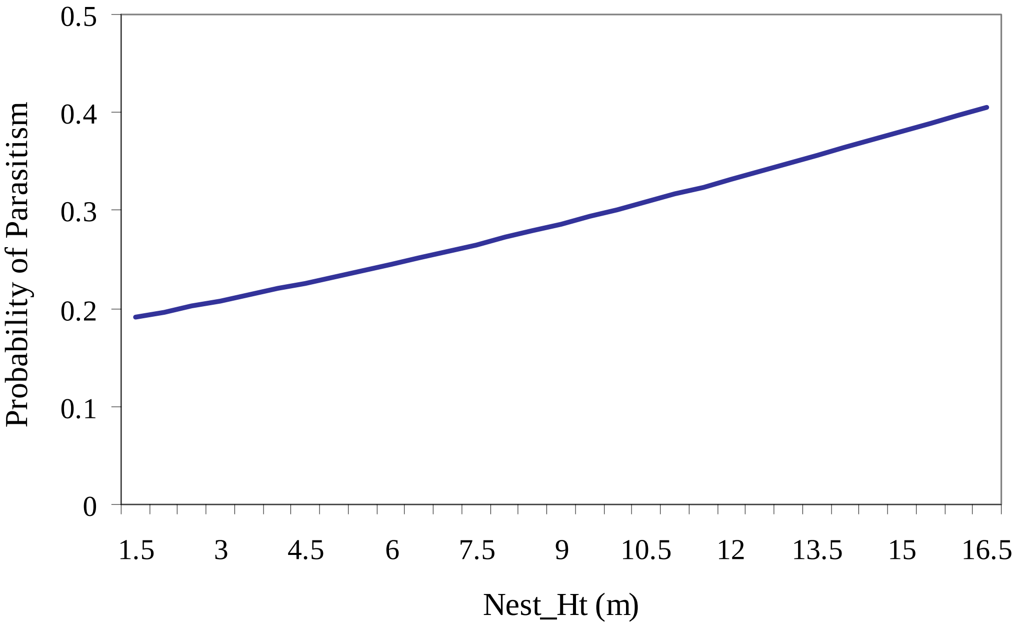


Figure 4.8: Relationship between Acadian Flycatcher nest height and the probability of parasitism. The probability of parasitism is derived from the following equation:

$$p_i = \exp(\text{Intercept} + \beta_{\text{Nest\_Ht}} * \text{Nest\_Ht}_i)/(1 + \exp(\text{Intercept} + \beta_{\text{Nest\_Ht}} * \text{Nest\_Ht}_i))$$

Where the probability (*p*) that an individual nest is parasitized depends on the model intercept, the parameter estimate for Nest_Ht, and the value of Nest_Ht for individual *i*. Values of Nest_Ht are varied over its full range. Because we centered all variables prior to analysis, the outcome of the above equation is the probability of parasitism when all other variables included in the model are at their mean values. See Table 4.3 for the values of the intercept and the parameter estimate used in the above equation.

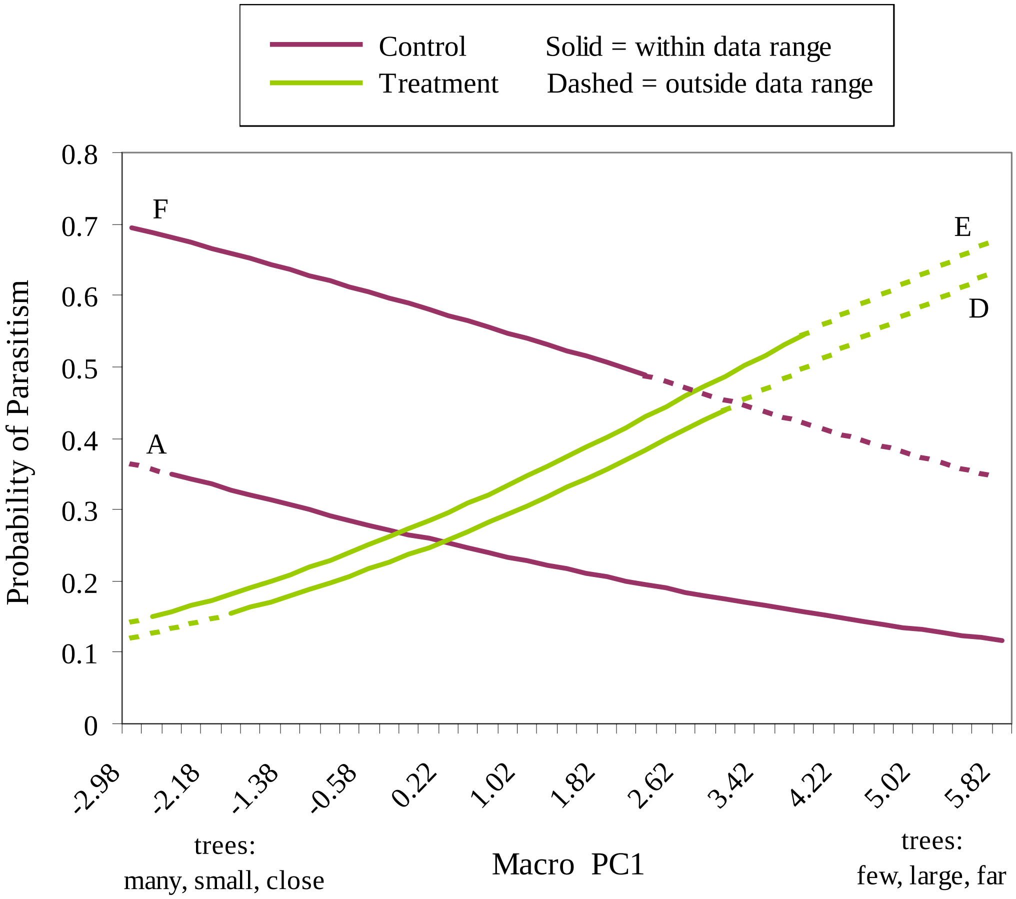


Figure 4.9: Relationship between Macro_PC1 and the probability of parasitism of Acadian Flycatcher nests. Macro_PC1 interacts with plot treatment, thus, four lines are depicted, one for each plot. The probability of parasitism is derived from the following equation:

$$p_{\text{i}} = \frac{\exp(\text{Intercept} + \beta_{\text{Macro\_PC1}}*\text{Macro\_PC1}_{\text{i}} + \beta_{\text{Trt}}*\text{Trt}_{\text{i}} + \beta_{\text{Rep}}*\text{Rep}_{\text{i}} + \beta_{\text{Trt*Rep}}*\text{Trt*Rep}_{\text{i}} + \beta_{\text{Trt*PC1}}*\text{Trt}_{\text{i}}*\text{Macro\_PC1}_{\text{i}})}{(1 + \exp(\text{Intercept} + \beta_{\text{Macro\_PC1}}*\text{Macro\_PC1}_{\text{i}} + \beta_{\text{Trt}}*\text{Trt}_{\text{i}} + \beta_{\text{Rep}}*\text{Rep}_{\text{i}} + \beta_{\text{Trt*Rep}}*\text{Trt*Rep}_{\text{i}} + \beta_{\text{Trt*PC1}}*\text{Trt}_{\text{i}}*\text{Macro\_PC1}_{\text{i}}))}$$

Where the probability (*p*) that an individual nest is parasitized depends on the model intercept, the parameter estimates for Macro_PC1, Trt, Rep, Trt*Rep, and Trt*PC1, and the values of Macro_PC1, Trt, Rep, and Trt*Rep for individual *i*. Values of Macro_PC1 are varied over its full range. Values of Trt, Rep, and Trt*Rep are varied between the values of 0 and 1 to represent the study plots (see Appendix 4A). Because we centered all variables prior to analysis, the outcome of the above equation is the probability of parasitism when all other variables included in the model are at their mean values. See Table 4.3 for the values of the intercept and the parameter estimates used in the above equation.

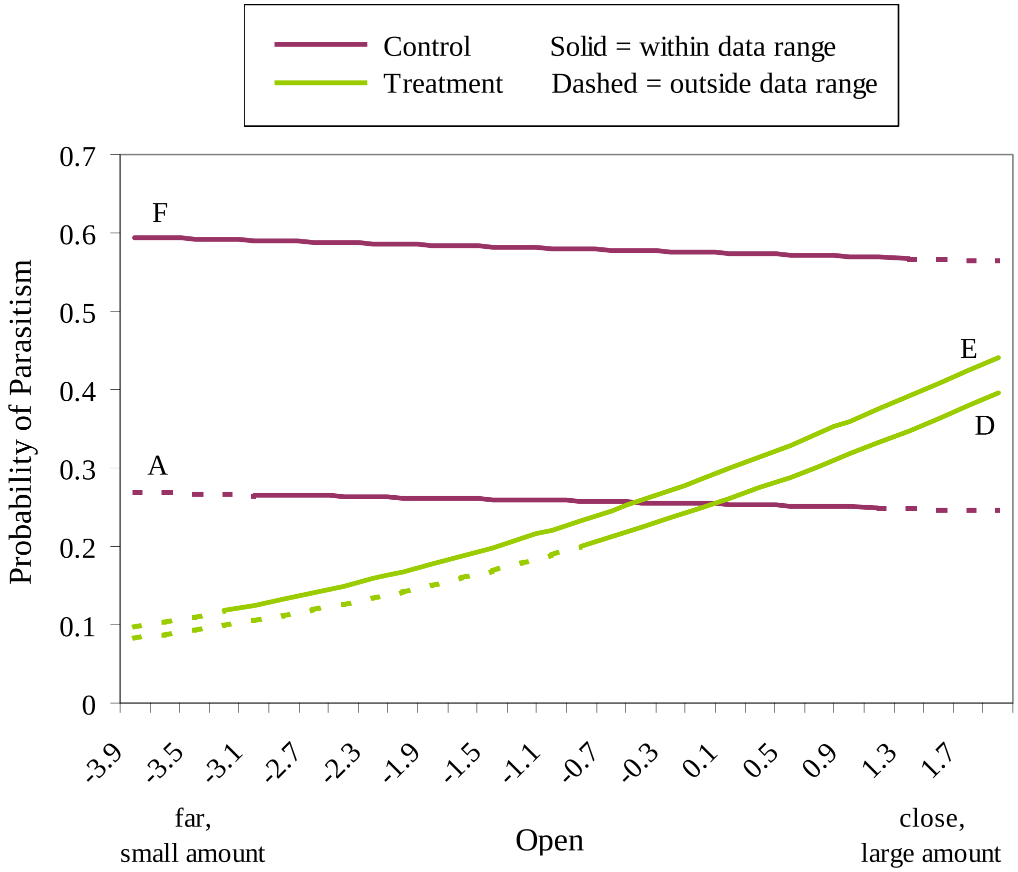


Figure 4.10: Relationship between open canopy and the probability of parasitism of Acadian Flycatcher nests. The variable Open interacts with plot treatment, thus, four lines are depicted, one for each plot. The probability of parasitism is derived from the following equation:

$$p_{\mathrm{i}} = \frac{\begin{array}{c}\exp(\mathrm{Intercept} + \beta_{\mathrm{Open}}{*}\mathrm{Open}_{\mathrm{i}} + \beta_{\mathrm{Trt}}{*}\mathrm{Trt}_{\mathrm{i}} + \beta_{\mathrm{Rep}}{*}\mathrm{Rep}_{\mathrm{i}} + \beta_{\mathrm{Trt*Rep}}{*}\mathrm{Trt}{*}\mathrm{Rep}_{\mathrm{i}} + \\ \beta_{\mathrm{Trt*Open}}{*}\mathrm{Trt}_{\mathrm{i}}{*}\mathrm{Open}_{\mathrm{i}})\end{array}}{\begin{array}{c}(1 + \exp(\mathrm{Intercept} + \beta_{\mathrm{Open}}{*}\mathrm{Open}_{\mathrm{i}} + \beta_{\mathrm{Trt}}{*}\mathrm{Trt}_{\mathrm{i}} + \beta_{\mathrm{Rep}}{*}\mathrm{Rep}_{\mathrm{i}} + \beta_{\mathrm{Trt*Rep}}{*}\mathrm{Trt}{*}\mathrm{Rep}_{\mathrm{i}} + \\ \beta_{\mathrm{Trt*Open}}{*}\mathrm{Trt}_{\mathrm{i}}{*}\mathrm{Open}_{\mathrm{i}}))\end{array}}$$

Where the probability (*p*) that an individual nest is parasitized depends on the model intercept, the parameter estimates for Open, Trt, Rep, Trt*Rep, and Trt*Open, and the values of Open, Trt, Rep, and Trt*Rep for individual *i*. Values of Open are varied over its full range. Values of Trt, Rep, and Trt*Rep are varied between the values of 0 and 1 to represent the study plots (see Appendix 4A). Because we centered all variables prior to analysis, the outcome of the above equation is the probability of parasitism when all other variables included in the model are at their mean values. See Table 4.3 for the values of the intercept and the parameter estimates used in the above equation.

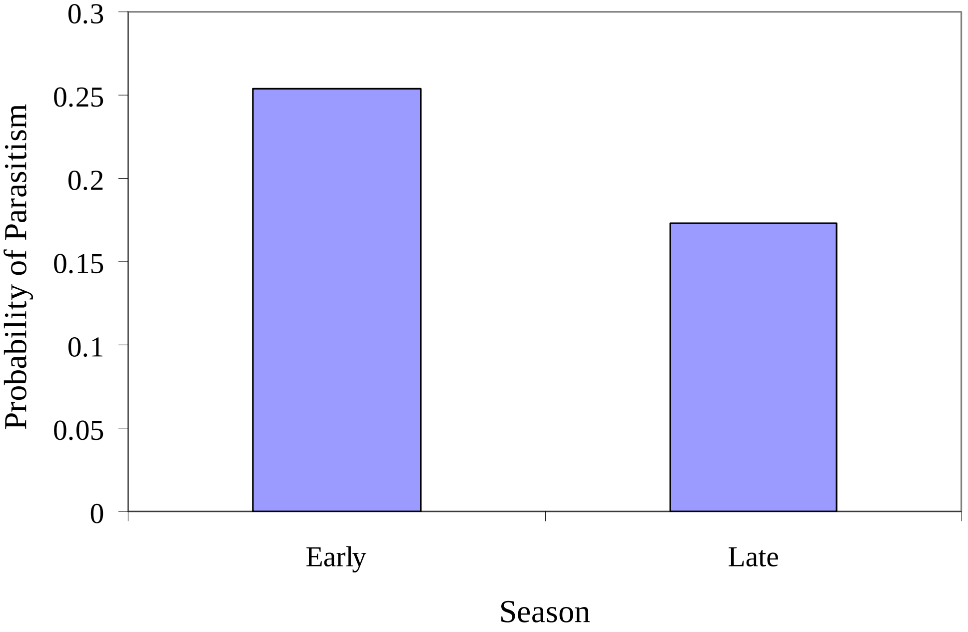


Figure 4.11: Relationship between the time of the breeding season and the probability of parasitism of Acadian Flycatcher nests. The probability of parasitism is derived from the following equation:

$$p_{\mathrm{i}} = \exp(\mathrm{Intercept} + \beta_{\mathrm{Season}}*\mathrm{Season}_{\mathrm{i}})/(1 + \exp(\mathrm{Intercept} + \beta_{\mathrm{Season}}*\mathrm{Season}_{\mathrm{i}}))$$

Where the probability (p) that an individual nest is parasitized depends on the model intercept, the parameter estimate for Season, and the value of Season for individual i. Values of Season are varied between the two values of 0 and 1. Because we centered all variables prior to analysis, the outcome of the above equation is the probability of parasitism when all other variables included in the model are at their mean values. See Table 4.3 for the values of the intercept and the parameter estimate used in the above equation.

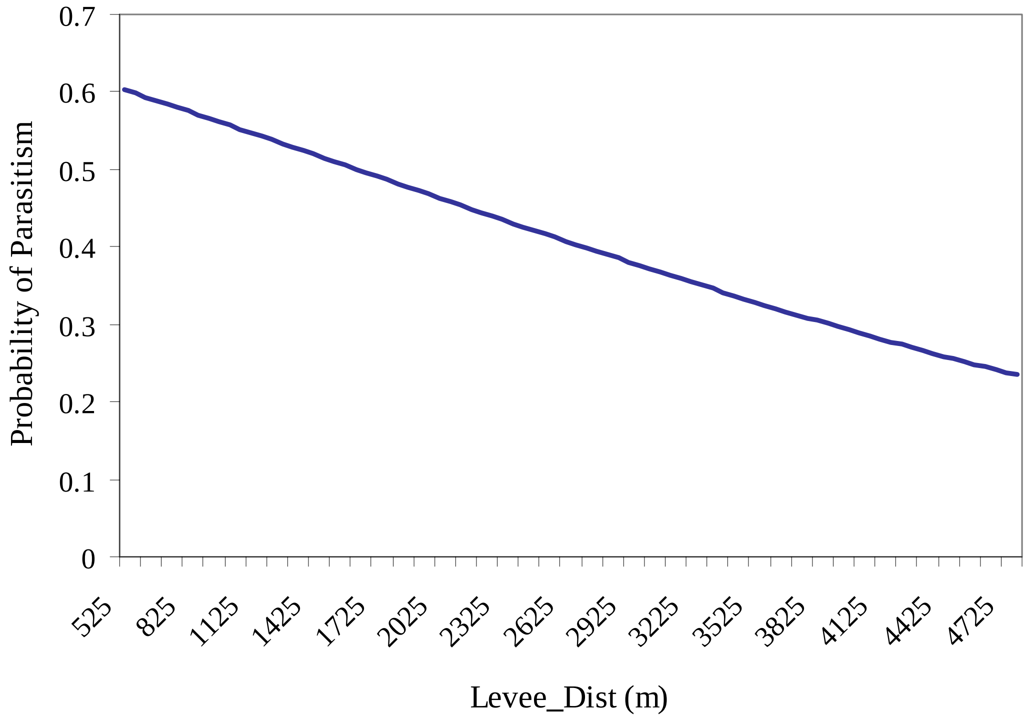


Figure 4.12: Relationship between Acadian Flycatcher nest distance from the levee and the probability of parasitism. The parameter estimates used to create this figure were derived from an alternate averaged model that used levee distance and a treatment*levee_distance interaction in the place of the plot descriptors, replicate and the treatment*replicate interaction. Outside of this change, all variables in the alternate model were the same and included: Year, Trt, Nest_Ht, Can_Cov, Dist_Edge, Macro_PC1, Macro_PC2, Open, Levee_Dist, Season, Trt*PC1, Trt*Open, and Trt*Levee. The probability of parasitism is derived from the following equation:

$$p_\mathrm{i} = \frac{\exp(\mathrm{Intercept} + \beta_{\mathrm{Levee}}*\mathrm{Levee}_\mathrm{i} + \beta_{\mathrm{Trt}}*\mathrm{Trt}_\mathrm{i} + \beta_{\mathrm{Trt*Levee}}*\mathrm{Trt}_\mathrm{i}*\mathrm{Levee}_\mathrm{i})}{(1 + \exp(\mathrm{Intercept} + \beta_{\mathrm{Levee}}*\mathrm{Levee}_\mathrm{i} + \beta_{\mathrm{Trt}}*\mathrm{Trt}_\mathrm{i} + \beta_{\mathrm{Trt*Levee}}*\mathrm{Trt}_\mathrm{i}*\mathrm{Levee}_\mathrm{i}))}$$

Where the probability (p) that an individual nest is parasitized depends on the model intercept, the parameter estimates for Levee, Trt, and Trt*Levee, and the values of Levee and Trt for individual i. Values of Levee are varied over its full range. Because there was zero evidence for an interaction effect between Trt and Levee, Trt is set to 0. Because we centered all variables prior to analysis, the outcome of the above equation is the probability of parasitism when all other variables included in the model are at their mean values. Intercept = -0.2726 and $\beta_{\mathrm{Levee}} = -0.0004$.

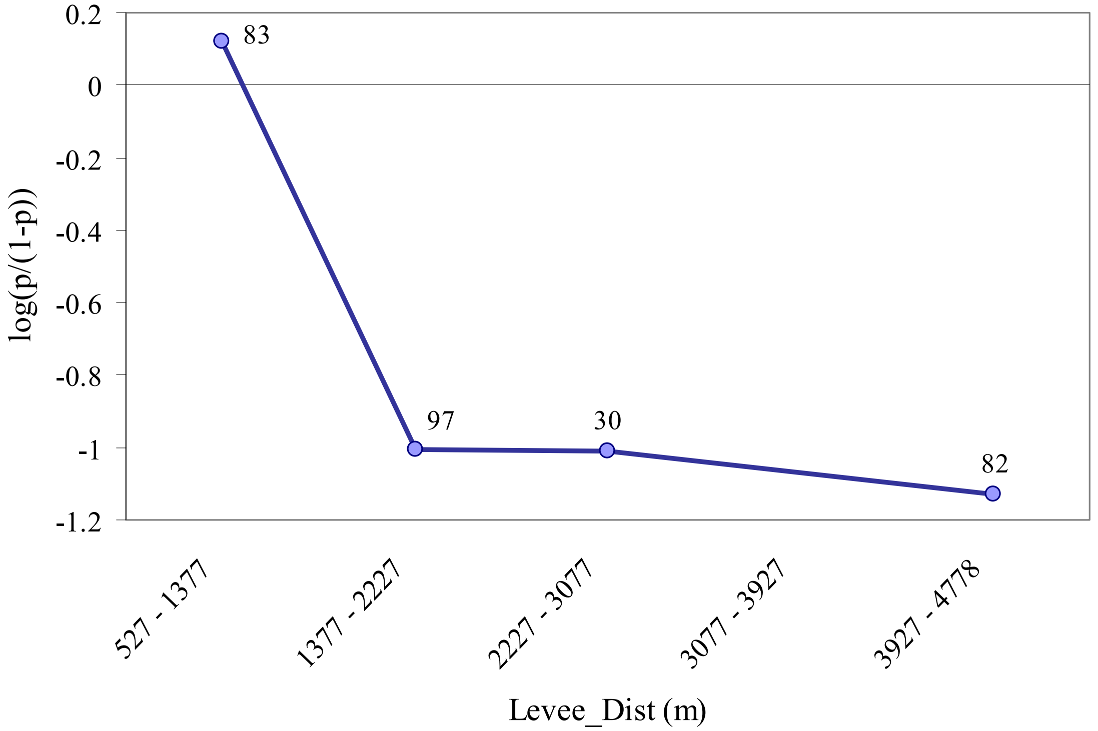


Figure 4.13: Relationship between distance to levee and the logit form of the probability of parasitism of Acadian Flycatcher nests. Levee distances were divided into five equal distance groups. No nests were located within the fourth distance group. Numbers above points indicate the number of nests within each distance group.

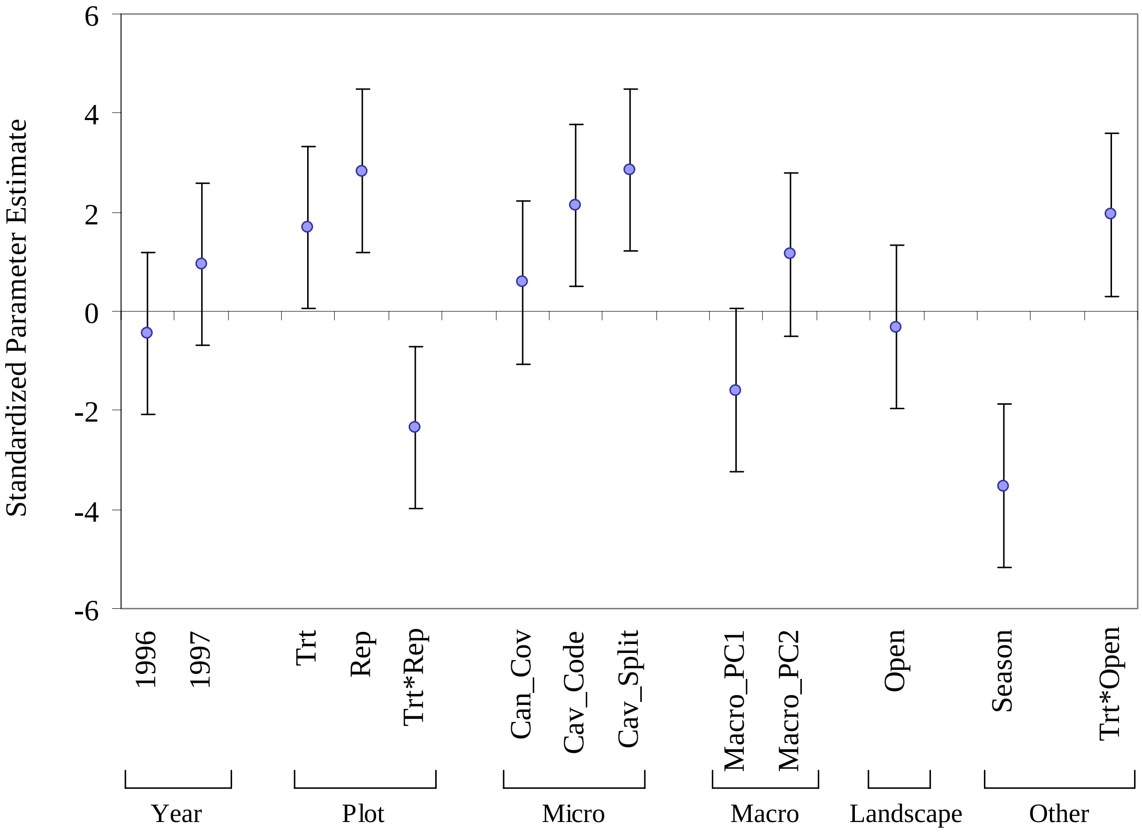


Figure 4.14: Standardized parameter estimates (*b/se*) of the variables included in the Prothonotary Warbler logistic regression Model A. Bars represent 90% confidence intervals. Parameter estimates were derived from the averaged model (see Table 4.8).

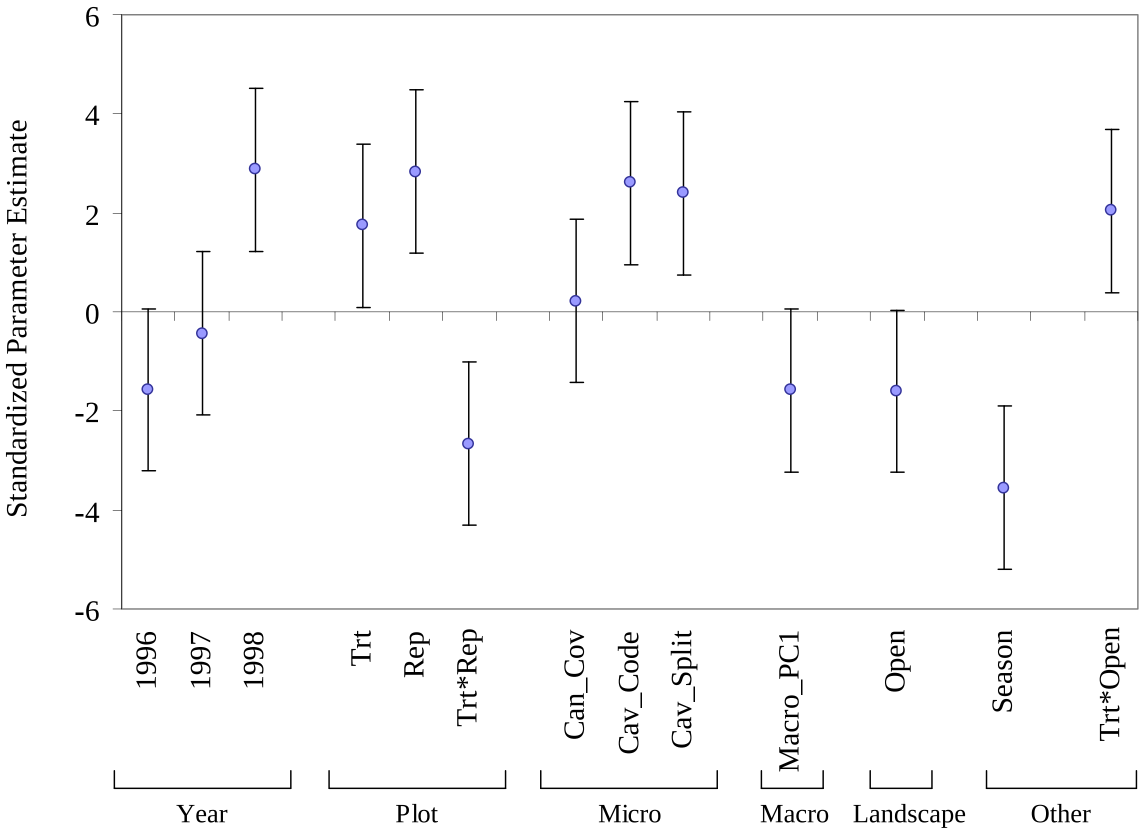


Figure 4.15: Standardized parameter estimates (*b/se*) of the variables included in the Prothonotary Warbler logistic regression Model B. Bars represent 90% confidence intervals. Parameter estimates were derived from the average model (see Table 4.9).

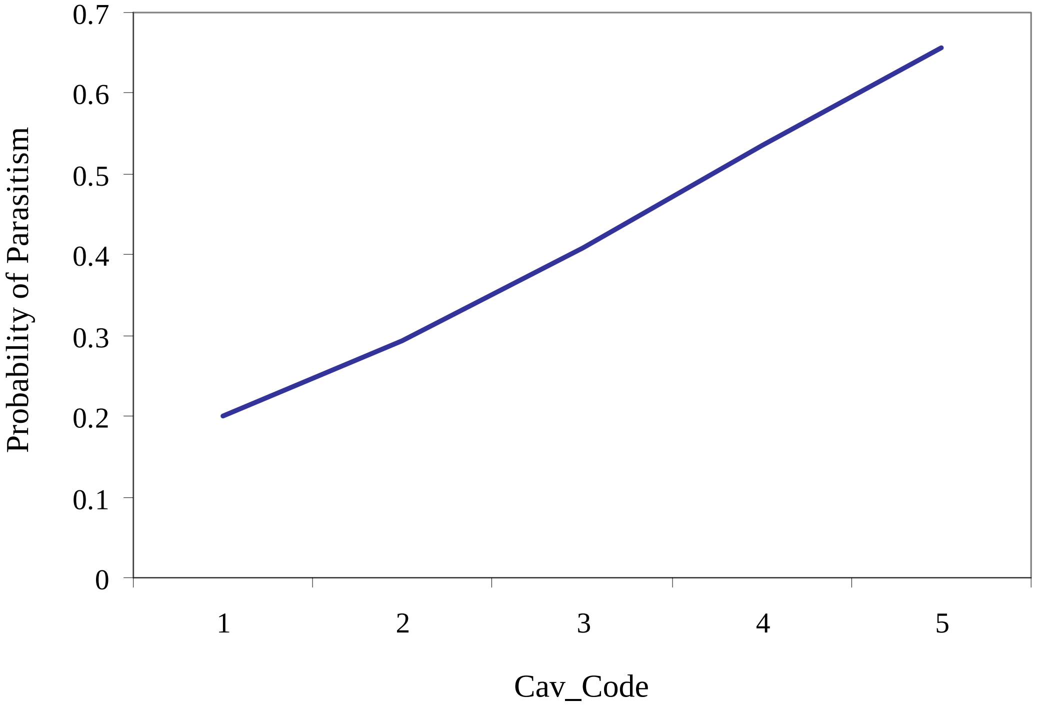


Figure 4.16: Relationship between cavity entrance size and the probability of parasitism of Prothonotary Warbler nests, where Cav_Code is treated as a continuous variable. The probability of parasitism is derived from the following equation:

$$p_i = \exp(\text{Intercept} + \beta_{\text{Cav\_Code}} * \text{Cav\_Code}_i)/(1 + \exp(\text{Intercept} + \beta_{\text{Cav\_Code}} * \text{Cav\_Code}_i))$$

Where the probability (p) that an individual nest is parasitized depends on the model intercept, the parameter estimate for Cav_Code, and the value of Cav_Code for individual i. Values of Cav_Code are varied over its full range. Because we centered all variables prior to analysis, the outcome of the above equation is the probability of parasitism when all other variables included in the model are at their mean values. See Table 4.9 for the values of the intercept and the parameter estimate used in the above equation.

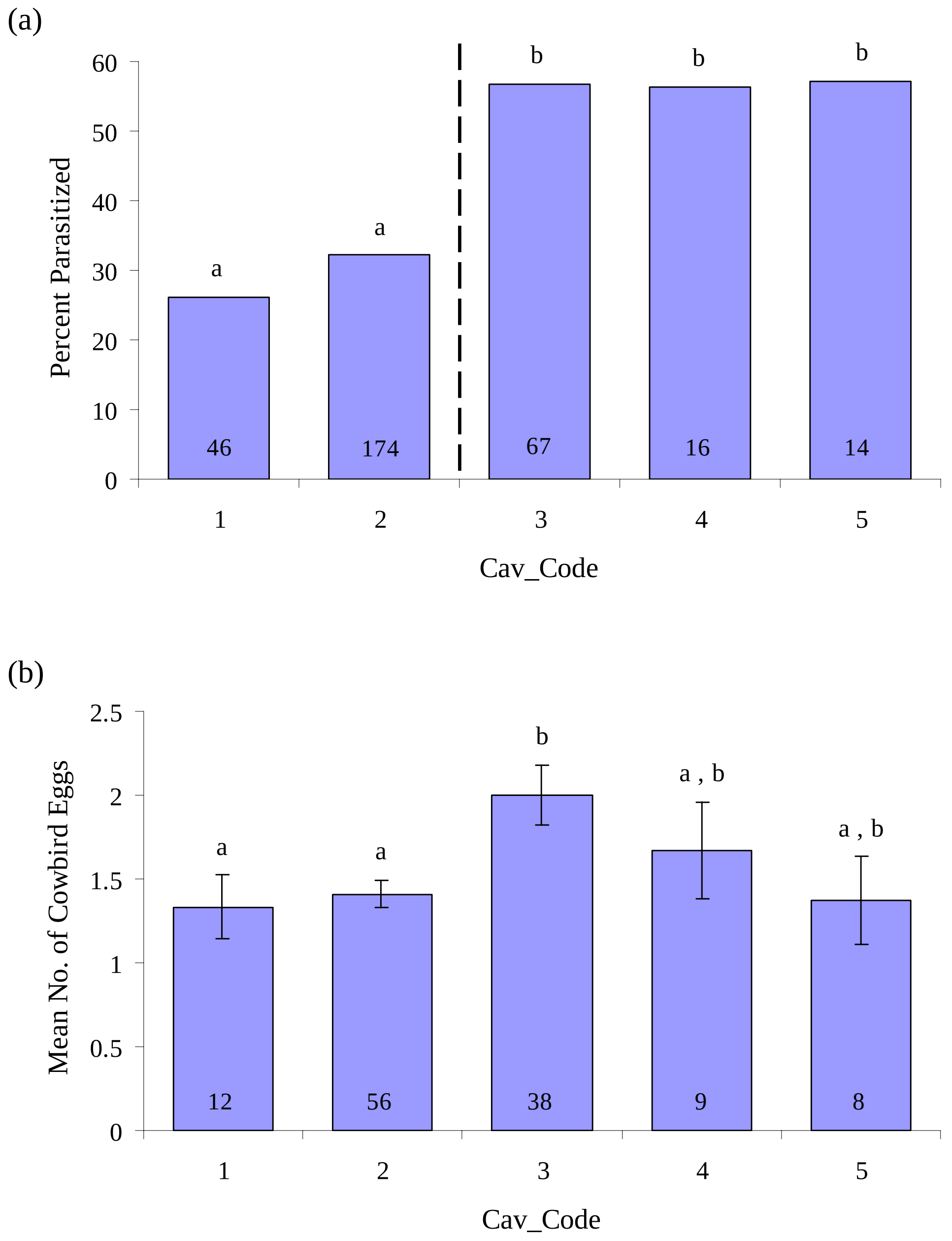


Figure 4.17: (a) Percent of Prothonotary Warbler nests that were parasitized by cavity entrance size of the nest, where Cav_Code is presented as a categorical variable. The dashed line indicates a threshold in cavity entrance size, below which parasitism frequency is lower, and above which parasitism frequency is higher. Overall, parasitism equaled 38.8%. (b) Mean number of parasitic cowbird eggs per parasitized nest by cavity entrance size of the nest. Numbers within columns indicate the number of nests sampled. Bars represent ± 1 SE. Letters above columns signify statistical differences; like letters are not statistically different, whereas unlike letters are statistically different.

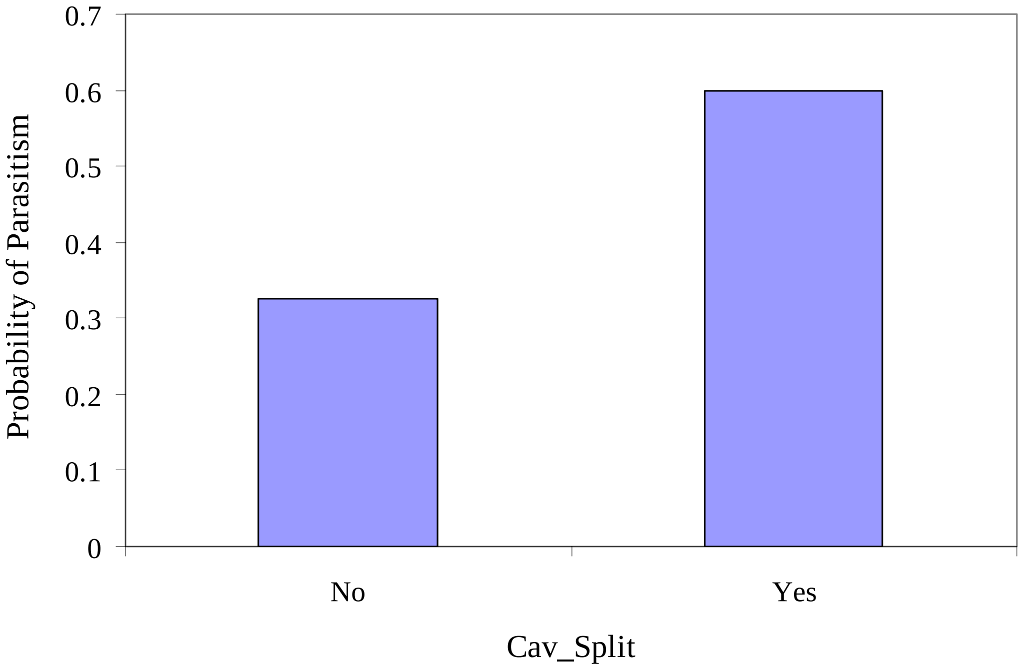


Figure 4.18: Relationship between cavity type (circular or split) and the probability of parasitism of Prothonotary Warbler nests. The probability of parasitism is derived from the following equation:

$$p_i = \exp(\text{Intercept} + \beta_{\text{Cav\_Split}}*\text{Cav\_Split}_i)/(1 + \exp(\text{Intercept} + \beta_{\text{Cav\_Split}}*\text{Cav\_Split}_i))$$

Where the probability (*p*) that an individual nest is parasitized depends on the model intercept, the parameter estimate for Cav_Split, and the value of Cav_Split for individual *i*. Values of Cav_Split are varied between the values 0 and 1. Because we centered all variables prior to analysis, the outcome of the above equation is the probability of parasitism when all other variables included in the model are at their mean values. See Table 4.9 for the values of the intercept and the parameter estimate used in the above equation.

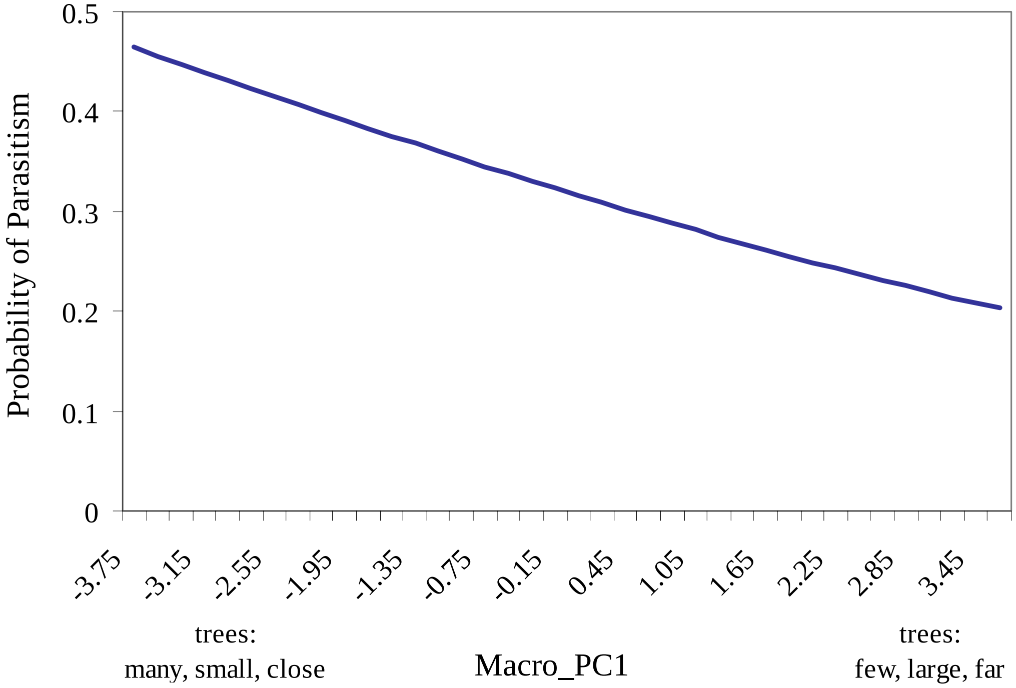


Figure 4.19: Relationship between Macro_PC1 and the probability of parasitism of Prothonotary Warbler nests. The probability of parasitism is derived from the following equation:

$$p_i = \exp(\text{Intercept} + \beta_{\text{Macro\_PC1}} * \text{Macro\_PC1}_i)/(1 + \exp(\text{Intercept} + \beta_{\text{Macro\_PC1}} * \text{Macro\_PC1}_i))$$

Where the probability (*p*) that an individual nest is parasitized depends on the model intercept, the parameter estimate for Macro_PC1, and the value of Macro_PC1 for individual *i*. Values of Macro_PC1 are varied over its full range. Because we centered all variables prior to analysis, the outcome of the above equation is the probability of parasitism when all other variables included in the model are at their mean values. See Table 4.9 for the values of the intercept and the parameter estimate used in the above equation.

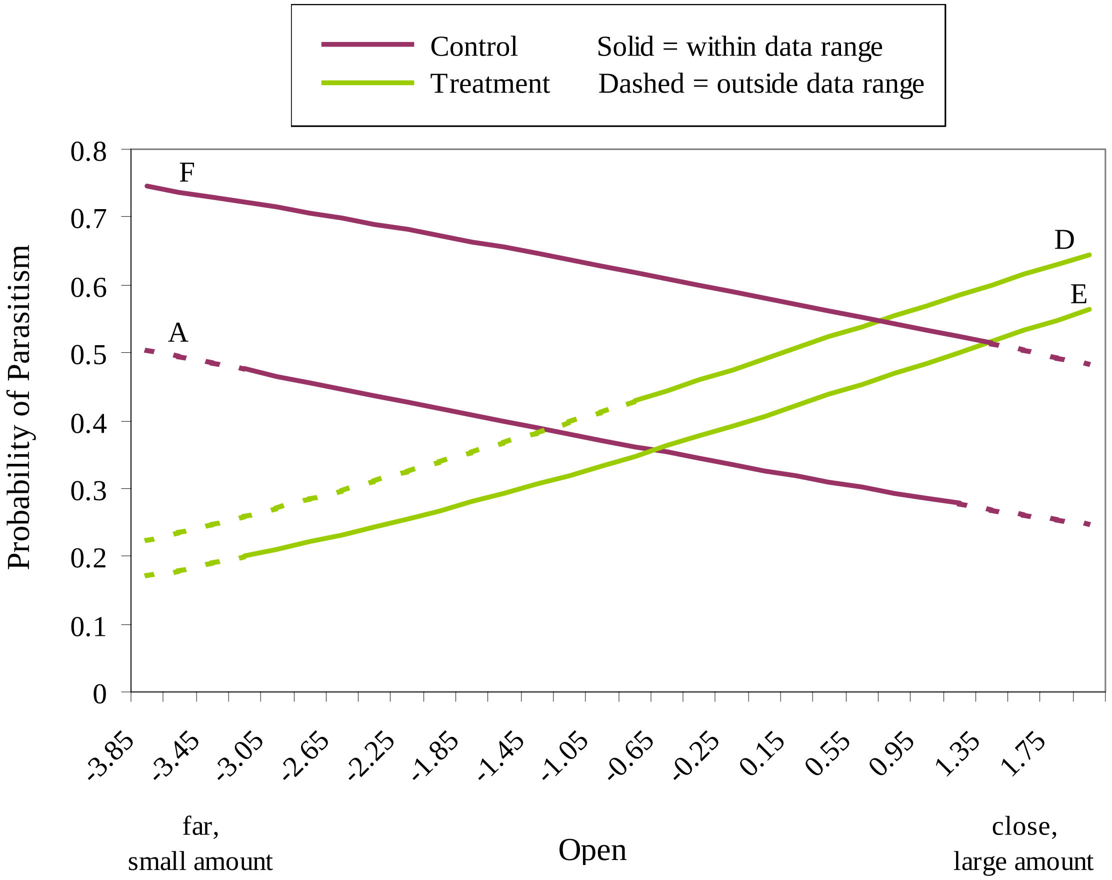


Figure 4.20: Relationship between exposure to open canopy and the probability of parasitism of Prothonotary Warbler nests. The variable Open interacts with plot treatment, thus, four lines are depicted, one for each plot. The probability of parasitism is derived from the following equation:

$$p_{\mathrm{i}} = \frac{\exp(\mathrm{Intercept} + \beta_{\mathrm{Open}}{*}\mathrm{Open}_{\mathrm{i}} + \beta_{\mathrm{Trt}}{*}\mathrm{Trt}_{\mathrm{i}} + \beta_{\mathrm{Rep}}{*}\mathrm{Rep}_{\mathrm{i}} + \beta_{\mathrm{Trt*Rep}}{*}\mathrm{Trt}{*}\mathrm{Rep}_{\mathrm{i}} + \beta_{\mathrm{Trt*Open}}{*}\mathrm{Trt}_{\mathrm{i}}{*}\mathrm{Open}_{\mathrm{i}})}{(1 + \exp(\mathrm{Intercept} + \beta_{\mathrm{Open}}{*}\mathrm{Open}_{\mathrm{i}} + \beta_{\mathrm{Trt}}{*}\mathrm{Trt}_{\mathrm{i}} + \beta_{\mathrm{Rep}}{*}\mathrm{Rep}_{\mathrm{i}} + \beta_{\mathrm{Trt*Rep}}{*}\mathrm{Trt}{*}\mathrm{Rep}_{\mathrm{i}} + \beta_{\mathrm{Trt*Open}}{*}\mathrm{Trt}_{\mathrm{i}}{*}\mathrm{Open}_{\mathrm{i}}))}$$

Where the probability (p) that an individual nest is parasitized depends on the model intercept, the parameter estimates for Open, Trt, Rep, Trt*Rep, and Trt*Open, and the values of Open, Trt, Rep, and Trt*Rep for individual *i*. Values of Open are varied over its full range. Values of Trt, Rep, and Trt*Rep are varied between the values of 0 and 1 to represent the study plots (see Appendix 4A). Because we centered all variables prior to analysis, the outcome of the above equation is the probability of parasitism when all other variables included in the model are at their mean values. See Table 4.9 for the values of the intercept and the parameter estimates used in the above equation.

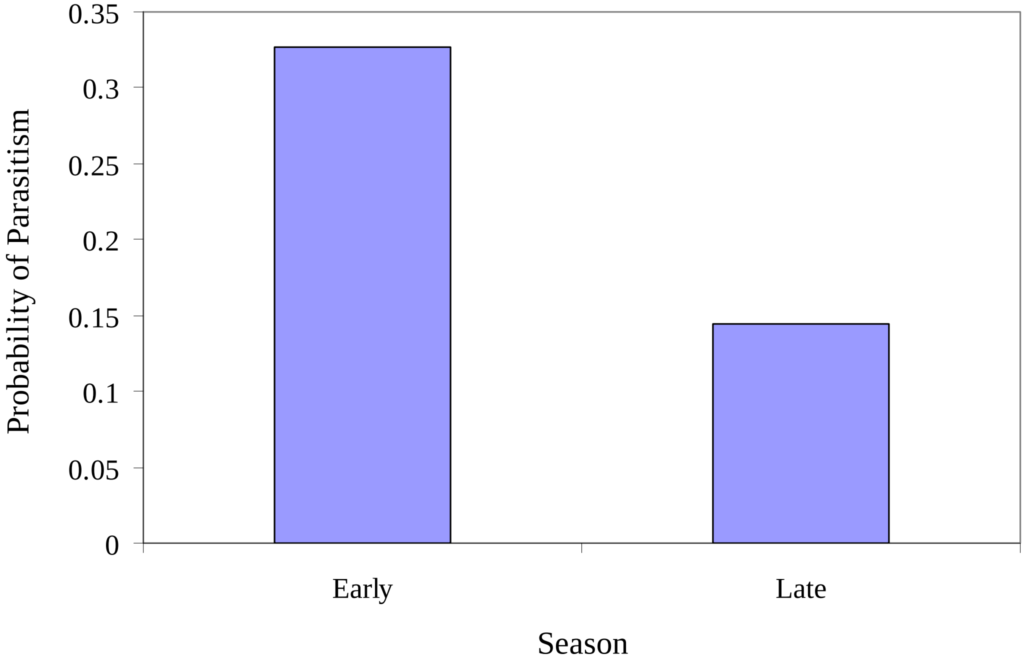


Figure 4.21: Relationship between the time of the breeding season and the probability of parasitism of Prothonotary Warbler nests. The probability of parasitism is derived from the following equation:

$$p_i = \exp(\text{Intercept} + \beta_{\text{Season}} * \text{Season}_i)/(1 + \exp(\text{Intercept} + \beta_{\text{Season}} * \text{Season}_i))$$

Where the probability (*p*) that an individual nest is parasitized depends on the model intercept, the parameter estimate for Season, and the value of Season for individual *i*. Values of Season are varied between the two values of 0 and 1. Because we centered all variables prior to analysis, the outcome of the above equation is the probability of parasitism when all other variables included in the model are at their mean values. See Table 4.9 for the values of the intercept and the parameter estimate used in the above equation.

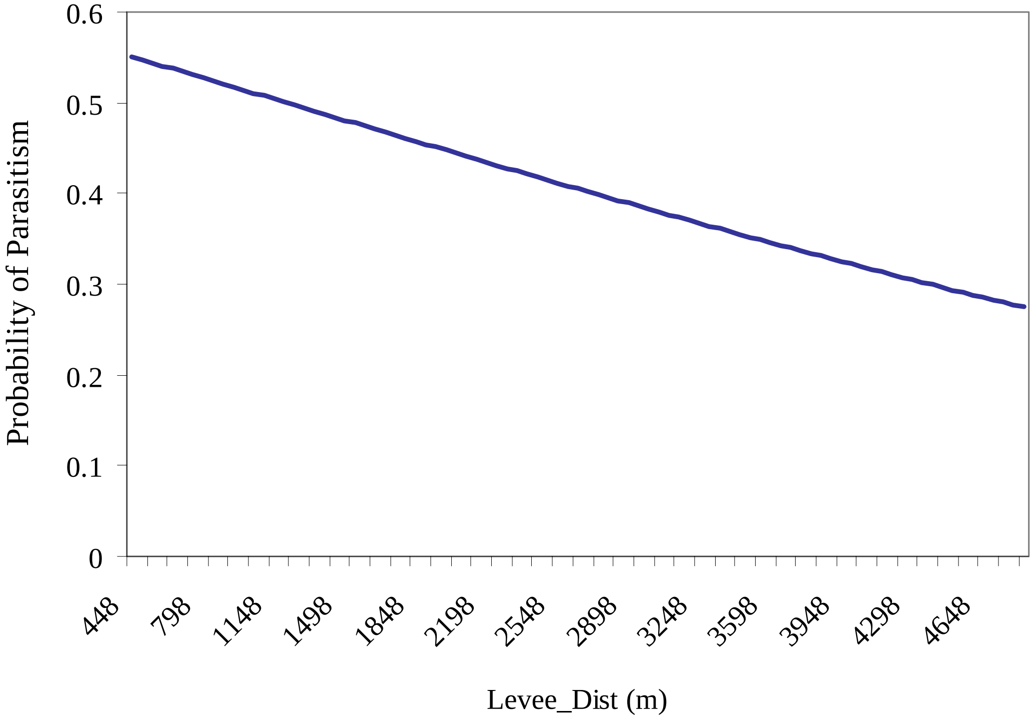


Figure 4.22: Relationship between Prothonotary Warbler nest distance from the levee and the probability of parasitism. The parameter estimates used to create this figure were derived from an alternate model that used levee distance and a treatment*levee_distance interaction in the place of the plot descriptors, replicate and the treatment*replicate interaction. Outside of this change, all variables in the alternate model are the same and include: Year, Trt, Can_Cov, Cav_Code, Cav_Split, Macro_PC1, Open, Levee_Dist, Season, Trt*Open, and Trt*Levee. The probability of parasitism is derived from the following equation:

$$p_{\mathrm{i}} = \frac{\exp(\mathrm{Intercept} + \beta_{\mathrm{Levee}}*\mathrm{Levee}_{\mathrm{i}} + \beta_{\mathrm{Trt}}*\mathrm{Trt}_{\mathrm{i}} + \beta_{\mathrm{Trt*Levee}}*\mathrm{Trt}_{\mathrm{i}}*\mathrm{Levee}_{\mathrm{i}})}{(1 + \exp(\mathrm{Intercept} + \beta_{\mathrm{Levee}}*\mathrm{Levee}_{\mathrm{i}} + \beta_{\mathrm{Trt}}*\mathrm{Trt}_{\mathrm{i}} + \beta_{\mathrm{Trt*Levee}}*\mathrm{Trt}_{\mathrm{i}}*\mathrm{Levee}_{\mathrm{i}}))}$$

Where the probability (p) that an individual nest is parasitized depends on the model intercept, the parameter estimates for Levee, Trt, and Trt*Levee, and the values of Levee and Trt for individual i. Values of Levee are varied over its full range. Because there was little evidence for an interaction effect between Trt and Levee, Trt is set to 0. Because we centered all variables prior to analysis, the outcome of the above equation is the probability of parasitism when all other variables included in the model are at their mean values. Intercept = -0.3347 and β_{Levee} = -0.0003.

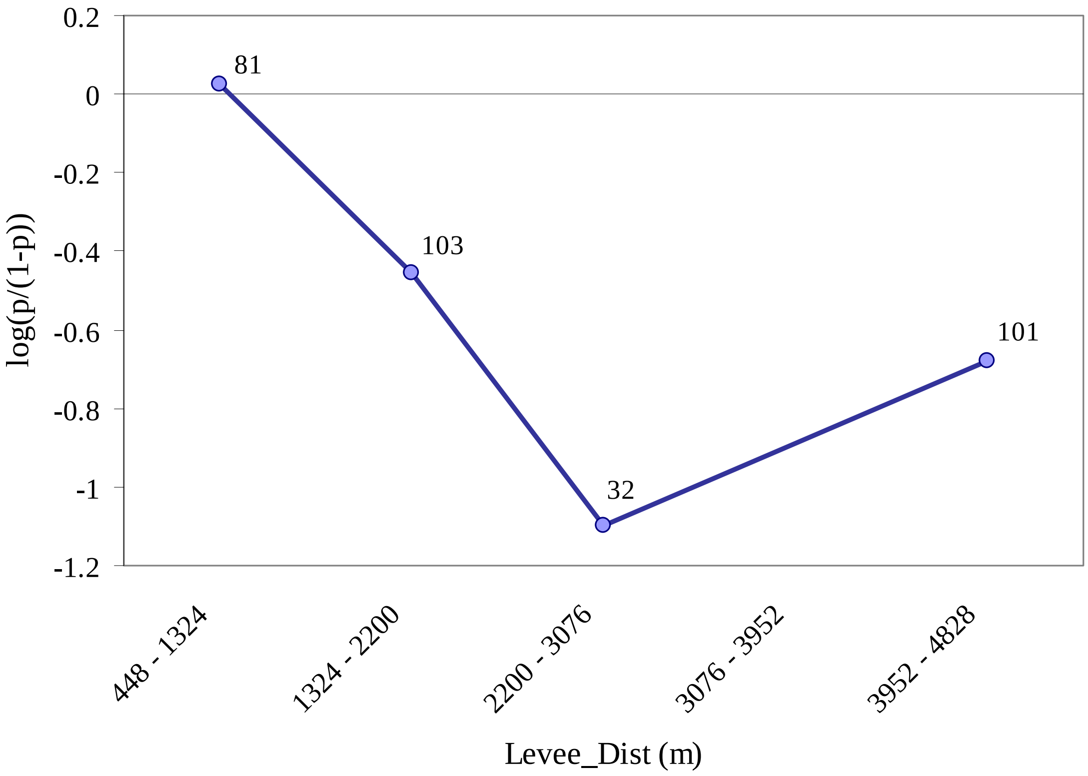


Figure 4.23: Relationship between distance to levee and the logit form of the probability of parasitism of Prothonotary Warbler nests. Levee distances were divided into five equal distance groups. No nests were located within the fourth distance group. Numbers above points indicate the number of nests within each distance group.

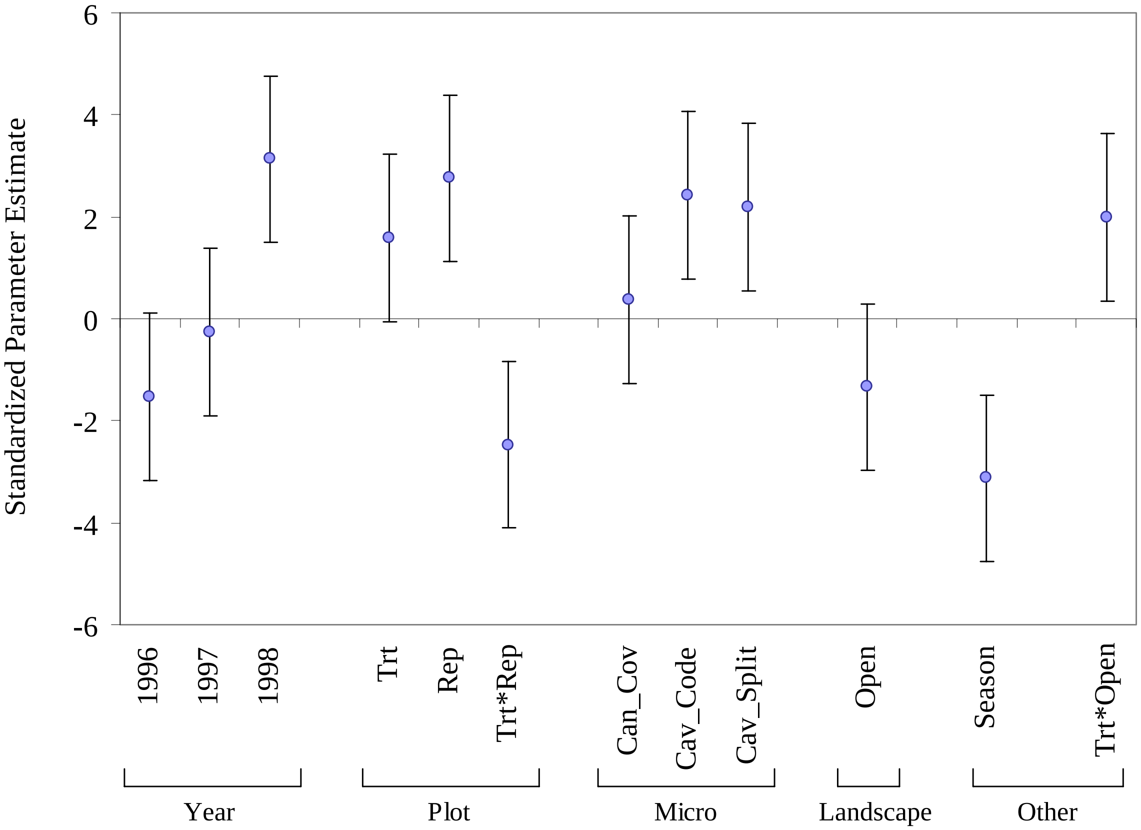


Figure 4.24: Standardized parameter estimates (*b/se*) of the variables included in the Prothonotary Warbler logistic regression Model C. Bars represent 90% confidence intervals. Parameter estimates were derived from the averaged model (see Table 4.13).

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APPENDICES

Appendix 4A: Definition and coding of the dummy variables used to represent the four study plots. Combining all three variables (Trt, Rep, and Trt*Rep) in the manner depicted completely reproduces the four study plots.

Definition

Trt = Treatment; 0 = no cut, 1 = patch cut
Rep = Replicate; 0 = first plot of like treatment, 1 = second plot of like treatment
Trt*Rep = Interaction of Treatment and Replicate

Dummy Coding				Reconstruction
	Trt	Rep	Trt*Rep	
Plot A	0	0	0	Plot A = Intercept
Plot D	1	0	0	Plot D = Intercept + Trt
Plot E	1	1	1	Plot E = Intercept + Trt + Rep + Trt*Rep
Plot F	0	1	0	Plot F = Intercept + Rep

Appendix 4B: Dummy coding used to re-fit the logistic regression model in order to compare the probability of parasitism between plots. The original coding only allowed for two plot comparisons. Re-coding the dummy variables and re-fitting the model three additional times allowed us to make all six plot comparisons.

Model	Dummy Coding				Reconstruction	Comparisons
		Trt	Rep	Trt*Rep		
Original	Plot A	0	0	0	Plot A = Intercept	
	Plot D	1	0	0	Plot D = Intercept + Trt	Plot D vs Plot A
	Plot E	1	1	1	Plot E = Intercept + Trt + Rep + Trt*Rep	Plot F vs Plot A
	Plot F	0	1	0	Plot F = Intercept + Rep	
		Trt	Rep	Trt*Rep		
Re-fit_1	Plot A	1	1	1	Plot A = Intercept + Trt + Rep + Trt*Rep	
	Plot D	0	0	0	Plot D = Intercept	Plot E vs Plot D
	Plot E	0	1	0	Plot E = Intercept + Rep	Plot F vs Plot D
	Plot F	1	0	0	Plot F = Intercept + Trt	
		Trt	Rep	Trt*Rep		
Re-fit_2	Plot A	1	0	0	Plot A = Intercept + Trt	
	Plot D	0	1	0	Plot D = Intercept + Rep	Plot A vs Plot E
	Plot E	0	0	0	Plot E = Intercept	Plot D vs Plot E
	Plot F	1	1	1	Plot F = Intercept + Trt + Rep + Trt*Rep	
		Trt	Rep	Trt*Rep		
Re-fit_3	Plot A	0	1	0	Plot A = Intercept + Rep	
	Plot D	1	1	1	Plot D = Intercept + Trt + Rep + Trt*Rep	Plot A vs Plot F
	Plot E	1	0	0	Plot E = Intercept + Trt	Plot E vs Plot F
	Plot F	0	0	0	Plot F = Intercept	

CHAPTER 5

THE IMPORTANCE OF MULTI-SCALE HABITAT CHARACTERISTICS TO NEST PREDATION AND BROOD PARASITISM OF TWO BOTTOMLAND HARDWOOD FOREST SONGBIRDS: A SUMMARY

Populations of many neotropical migratory songbirds have declined in recent decades (Robbins et al. 1989, Askins et al. 1990). Although the declines in many forest-dwelling neotropical migrant birds can be linked to a reduction in breeding and wintering habitats, the high degree of forest fragmentation and habitat loss in the eastern United States suggests that factors on the breeding grounds are the primary cause of migrant declines, presumably through decreased reproductive success (Robinson et al. 1995b). Increased rates of nest predation (Wilcove 1985) and brood parasitism (Brittingham and Temple 1983) suffered by forest-interior songbirds in these fragmented landscapes may be a cause of their decline in North America (Robbins et al. 1989, Askins et al. 1990).

The pervasive nature of nest predation and brood parasitism indicate that the nesting season is a critical period for maintenance of bird populations (Martin 1993). Physical features of the breeding habitat influence opportunities for nesting, foraging, and protection from enemies (Cody 1981) and may ultimately reflect the suitability of a site for the reproduction and survival of breeding birds (Hilden 1965). Nest predation is the main cause of reproductive failure in passerine birds (Ricklefs 1969) and brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) significantly decreases the reproductive success of many neotropical migrants (Brittingham and Temple 1983). Thus, to effectively manage for the conservation of songbird populations, it is critical to identify the specific features of the nesting habitat that influence rates of nest predation and brood parasitism. In addition, the identification and reduction of land use practices that augment predator and brood parasite populations are necessary.

As a result of reported declines, there has been a surge of research on neotropical migrant bird populations in recent years. Studies have documented that rates of nest predation and brood parasitism respond to habitat variation at the nest-site (Martin 1993) and the nest-patch scale (Bowman and Harris 1980), as well as to edge proximity (Gates and Gysel 1978) and the pattern of forest and interstitial land use in the surrounding landscape (Donovan et al. 1997). Although an increasing number of studies are showing that both localized and landscape-level factors can have a profound effect on nest predation and parasitism rates, few studies have simultaneously investigated the relative importance of habitat characteristics at more than one spatial scale to the reproductive success of birds. Many ecological processes that might affect nest predation and parasitism operate at multiple spatial scales (Bergin et al. 2000) and are complex, potentially involving several interactions between variables at different spatial and temporal scales. Therefore, accurate interpretation of the mechanisms driving rates of nest predation and parasitism will require viewing these ecological processes at multiple scales (Donovan et al. 1997) and proper management of songbird populations will require more studies to use a multi-scale approach.

A drastic example of forest habitat loss in the southeastern United States has been in bottomland hardwood forests (MacDonald et al. 1979, Mitsch and Gosselink 1986). It is estimated that 55% of the existing bottomland hardwoods are found in the Mississippi Alluvial Valley (MAV; Mitsch and Gosselink 1986), however, only about 20% of the original 9 to 10 million hectares of bottomland hardwood forests in the MAV remain (Yin et al. 1997). Conversion to agriculture, timber removal, and the construction of flood control and navigation structures have eliminated bottomland hardwood forests from much of the MAV and, as a result, agriculture has replaced forest as the dominant land cover within the MAV. Most of the remaining bottomland forest within the MAV exists as small patches surrounded by agriculture; within such a landscape, forest-nesting birds are exposed to an abundance of generalist predators and Brown-headed Cowbirds. In addition to actual losses of bottomland hardwood forests, the remaining bottomland hardwoods are in an ecologically degraded condition due to severe fragmentation, hydrologic alterations, and poor timber management practices (Allen 1997). The ecosystem changes within remaining bottomland hardwood forests of the MAV could negatively impact regional populations of neotropical migrants that depend on functioning bottomland forest ecosystems; this is especially true for those birds that reach their highest breeding densities within bottomland hardwood forests. Accordingly, the bird conservation group Partners in Flight has identified bottomland hardwood forests as a habitat of regional concern (Hunter et al. 1993). Despite the importance of and the imperiled state of bottomland hardwood forests, there is a lack of long-term data sets on the reproductive success of songbirds breeding within bottomland hardwood forests.

Our study addressed the need for information on avian nesting success within bottomland hardwood forests, as well as the need for research that simultaneously investigates the influence of habitat characteristics at multiple spatial scales on avian nesting success. The study was conducted within the White River National Wildlife Refuge (NWR) during the breeding seasons of 1996-2000. The White River NWR, located in the MAV of southeast Arkansas, is one of the largest remaining contiguous tracts of bottomland hardwood forest within the US. Although large (65,000 ha), the Refuge is narrow (4.5-15.5 km-wide) in shape and embedded within an agricultural landscape; as such, it contains an abundance of generalist predators and cowbirds that prey upon and parasitize the nests of forest-interior songbirds breeding within the forest. We focused on the nesting success of two common bottomland songbirds, the Acadian Flycatcher (*Empidonax virescens*) and the Prothonotary Warbler (*Protonotaria citrea*). Both of these species are declining within the Mississippi Alluvial Plain and, as a result of area sensitivity (Acadian Flycatcher and Prothonotary Warbler) and extreme habitat specificity (Prothonotary

Warbler), Partners in Flight has given the Acadian Flycatcher a high-priority ranking for monitoring and management in the Southeast and has listed the Prothonotary Warbler as a species of high conservation priority throughout its breeding range (Hunter et al. 1993, Rich et al. 2004). We simultaneously investigated the relative importance of nesting habitat characteristics at multiple spatial scales to the nest survival of our two focal birds from predation and to the likelihood of brood parasitism. We examined nest predation and brood parasitism in relation to physical characteristics of the nesting habitat at the micro-, macro-, and landscape scale. These physical characteristics included descriptions of nest placement, vegetation structure, proximity and exposure to various internal edges such as roads, sloughs, and patch cuts, and proximity to external edges. Additionally, we investigated how the seasonal flooding pattern (i.e., timing, magnitude, duration, and spatial extent) influenced nest survival from predation.

We developed species-specific Cox regression models to assess the importance of multi-scale characteristics of the nesting habitat to the risk of nest predation. We demonstrated that risk of nest predation was influenced by habitat characteristics of the micro-scale nest site, the macro-scale nest patch, and the landscape-scale study plot. For Acadian Flycatchers, these characteristics (relationships) included micro-scale nest height (−), macro-scale stem density (+) and canopy height (−), and the presence of water at the macro- and plot-scale (−). Nest height was the most important characteristic we considered, whereas macro-scale canopy height and water were of secondary importance. Macro-scale features of Prothonotary Warbler nesting habitat were not related to the risk of nest predation; however, risk was related to micro-scale nest-tree diameter (+), landscape-scale exposure to roads (+) and patch cuts (−), as well as to the presence of water at the micro-, macro-, and plot-scale (−). Additionally, brood parasitism of Prothonotary Warbler nests increased their risk of being preyed upon. Water and parasitism were by far the most important characteristics we considered for Prothonotary Warblers. For both species, there were many features of the nest site that were not associated with predation risk, suggesting that safe nest sites may not exist in an environment with an abundance and diversity of predators (Filliater et al. 1994). While we investigated many of the same habitat characteristics for each species, the direction and magnitude of their relationships with nest predation risk, as well as their relative importance, varied between species; thus, highlighting the need for species-specific studies when managing an area for multiple species.

We used our existing knowledge of the potential predator species within our study area, where possible using information of their behavior and foraging strategies, to explain the relationships we observed between the nesting habitat and the risk of nest predation. Our theories relied heavily on the supposition that Acadian Flycatcher nests are primarily preyed upon by rat snakes (*Elaphe obsoleta*), squirrels (*Glaucomys volans* and *Sciurus niger*), and avian species (*Melanerpes carolinus* and *Cyanocitta cristata*), whereas these same predators, in addition to raccoons (*Procyon lotor*), depredate Prothonotary Warbler nests. These predator assumptions were based on species-specific nest-site attributes (i.e., high open-cup nests located on branch edges versus low cavity nests located within snags), as well as the remains of depredated nests and anecdotal evidence. Our insight into the actual mechanisms that produced the patterns we observed was limited by our lack of predator identification. Future research within our study area would benefit immensely from a predator-focused nest study that identified predators responsible for depredations and studied their abundance, spatial distribution, and behavior relative to the habitat and their prey. This type of information would help clarify the intricacies of predator-prey interactions that currently elude us and would help us understand how particular management practices might affect these interactions.

Using species-specific logistic regression models, we demonstrated that the probability that Acadian Flycatcher and Prothonotary Warbler nests would be parasitized was linked to local- and landscape-scale characteristics of the nest site and the surrounding habitat. Outside of annual variation, distance from the levee (−), a landscape-level characteristic, had the largest effect on Acadian Flycatcher parasitism and seemed to be the driving force in determining whether or not a nest would be parasitized. Finer-scale characteristics of the nest site, namely micro-scale nest height (+), and the nesting habitat, specifically macro-scale age/disturbance (−/+) and landscape-scale exposure to open canopy (+), as well as finer temporal characteristics of the breeding season (−), were also important, but to a lesser extent. Local characteristics may be immaterial in areas saturated with cowbirds (e.g., the forest adjacent to the levee), but emerge as influential within areas more removed (> 1.5 km) from cowbird seeding points where influence of the feeding site has declined (Robinson et al. 1995a,b, Gates and Evans 1998, Thompson et al. 2000). For Prothonotary Warblers, distance from the levee (−), macro-scale age/disturbance (−), landscape-scale exposure to open canopy (+), and time of breeding season (−) had large effects on parasitism probability. However, for this species, micro-scale nest-site characteristics, namely cavity entrance size and type, also were very influential, demonstrating that nests located in smaller-entrance cavities may escape high levels of parasitism. Of the habitat characteristics that we investigated for both species, they demonstrated the same directional relationship with the probability of parasitism, while exhibiting different magnitudes and relative importance between species.

Although the White River NWR is an extensive tract of forest, it is embedded within an agricultural landscape, and as such, is replete with cowbirds. In this setting, cowbirds encounter both limited feeding and limited breeding opportunities, which interact with interesting outcomes. The uncoupling of cowbird feeding and breeding sites and the preference to breed within forests further complicates the situation. Within the Refuge, feeding opportunities are limited by virtue of being forested; however, feeding sites are plentiful at the forest-agricultural boundaries, including a popular site on the levee. Owing to exceptional cowbird mobility and the narrow shape of the Refuge, cowbird access to the interior forest in not limited and their presence is evident in all parts of the forest. Although cowbirds use distinct areas for feeding and breeding and are capable of commuting long distances between feeding and breeding grounds, they will travel only as far as necessary to meet both of these needs. Cowbirds probably saturate the available breeding habitat in the forest adjacent to feeding sites, but then due to limited breeding opportunities, spread further into the forest in search of non-parasitized hosts. It is likely, that in this situation, local-scale habitat features (including internal edge) and nest-site features of hosts have little to no influence on parasitism levels at close proximity to the feeding sites. However, cowbird intrusion into the forest interior may be facilitated by disturbances and openings in the canopy. As cowbirds diffuse into the forest interior and are less influenced by proximity to the feeding site, the effects of local-scale features may have more influence on parasitism pressure felt by hosts. In general, cowbirds probably settle within an area based on features at the landscape scale, but then local habitat characteristics and host species behavior are likely used to further refine selection of suitable breeding habitats and nests (Evans and Gates 1997).

It is well documented that both nest predation and brood parasitism increase with increased forest fragmentation at the landscape scale (Faaborg et al. 1995, Robinson et al. 1995a,b, Donovan et al. 1997, Hartley and Hunter 1998); likewise, the findings our study reveal similar relationships between these two events and characteristics of the nesting habitat at finer-scales. Specifically, the risk of nest predation and the likelihood of brood parasitism both increased with increased exposure to human-induced disturbances. We showed that nest predation increased with increasing exposure to forest-interior roads, while parasitism increased with proximity to a human-associated cowbird-feeding site and with exposure to canopy openings, created by roads and patch cuts, within the forest. While we did not observe an increased risk of nest predation to be associated with the presence of patch cuts, we investigated this possibility at only one spatial scale and thus advise against concluding that patch cuts are benign in nature at this time. Overall, our findings indicate that human-induced disturbances within the forest-interior and adjacent to the forest may reduce the reproductive success of songbirds by increasing their risk of nest predation and parasitism. We further linked these two events by revealing a positive relationship between brood parasitism and nest predation, independent of similar habitat characteristics.

Although it is generally assumed that nest predation has a larger negative effect on reproductive success of songbirds than does parasitism by cowbirds, the relative effects of nest predation and brood parasitism on the seasonal fecundity (young produced per female per year) of songbirds are often ignored. In addition to reducing clutch size, as well as hatching and fledgling success, parasitism may decrease seasonal fecundity by precluding second nesting attempts or by increasing the risk of nest predation (Pease and Gryzbowski 1995); thus, brood parasitism may have a much larger effect than generally acknowledged (Schmidt and Whelan 1999, Grzybowski and Pease 2000). Although nest predation and parasitism studies provide invaluable information, because a female may re-nest after losing a nest to predation, after abandoning a parasitized nest, or after successfully fledging a brood, they are imperfect surrogates for knowing the impact of nest predation and parasitism on seasonal fecundity (Grzybowski and Pease 2000). Studies that gather demographic parameters of seasonal fecundity and survival are necessary to fully assess the health and persistence of songbird populations.

Although the factors influencing nest predation and brood parasitism are complex, results of this study and others suggest that appropriate habitat management applied at the proper scale has the potential to reduce the limiting nature of these two events on songbird reproductive success. Obviously, maintaining the Refuge as a large, contiguous forested habitat is necessary. At a smaller scale, findings of our study suggest that management efforts aimed at reducing disturbances within the forest interior may decrease levels of both nest predation and parasitism. Limiting the creation and width of new roads, in addition to re-vegetating existing non-essential roads, will aid in this effort. Continued investigation of alternative timber harvesting techniques that reduce the creation of edge and open canopy is warranted; possibilities include combining multiple medium-sized cuts into fewer large cuts, making cuts circular in shape, or using uneven-aged single-tree selection as opposed to large even-aged cuts. It is encouraged that Refuge managers and researchers continue to work closely, initiating harvesting operations/treatments so that pre- and post-treatment studies can be conducted. Designing and implementing studies in an adaptive management framework may allow researchers and managers to effectively implement management prescriptions and research in the future, and may facilitate greater experimental rigor and design (Sallabanks et al. 2000). It is imperative at all times to be aware that while a particular habitat manipulation may benefit one species, it may be detrimental to another. Thus, in addition to maintaining a monitoring program during the application of management prescriptions, examining the potential effects of management efforts on other species within the community will be necessary.

In addition to internal disturbances, our study highlighted the importance of flooding on nest predation. As a seasonally flooded bottomland hardwood forest, water is a dominant feature of the Refuge and a dominant characteristic of the nesting habitat. We found that floodwater played a central role in reducing predation pressure on nests. For this reason, we strongly recommend that current and future projects that may affect the flooding patterns (timing, magnitude, duration, and spatial extent) within the Refuge be required to undergo a thorough investigation of their potential effects on the breeding success of songbirds nesting within the Refuge. As a species that is intimately tied to both bottomland hardwood forest habitat and water, the Prothonotary Warbler may make an ideal indicator of bottomland forest ecosystem integrity.

Our study also revealed the strong influence that the levee has on brood parasitism within the Refuge. Clearly, nests located closer to the levee suffered from increased levels of parasitism from brood parasitic cowbirds that use the levee as a popular foraging site. We suggest that prohibiting cattle from foraging on the levee during the breeding season will decrease the local abundance of cowbirds, thus reducing the levels of parasitism. Additionally, we recommend that mowing of the levee, roadsides, campgrounds, and fields should also be prohibited during the breeding season, as they also provide foraging opportunities for cowbirds. Limiting the interspersion of cowbird foraging opportunities within breeding grounds is the key to decreasing brood parasitism (Thompson et al. 2000).

Bottomland hardwood forests are the most productive and ecologically important wetland ecosystems in the world today (Conner 1994), contain some of the richest and most diverse plant and animal life found in North America (Mitsch and Gosselink 1986), and are of hemispheric importance to neotropical migratory birds as prime breeding habitat (Hunter et al. 1993). Drastic loss of this habitat has occurred and what remains is in an ecologically degraded condition, making it a habitat of regional concern (Hunter et al. 1993). As a forested wetland, the importance of hydrology to this ecosystem cannot be stressed enough. Conservation of this habitat, and the species that live within it, should be a management priority.

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