LANDSCAPE AND LOCAL EFFECTS ON AVIAN HABITAT USE AND BREEDING SUCCESS IN BOTTOMLAND HARDWOOD FORESTS OF THE MISSISSIPPI ALLUVIAL VALLEY

by

KIRSTEN R. HAZLER

(Under the Direction of Robert J. Cooper)

ABSTRACT

During the breeding season, nest predation and brood parasitism are critical factors influencing songbirds' reproductive success. Therefore, minimizing risk should be an important factor in selecting breeding habitat, whether at the scale of the patch, territory, or nest site. I examined these ideas in a landscape and local study of avian habitat selection, density, and breeding success in bottomland hardwood forests of the Mississippi Alluvial Valley.

At the local scale, I investigated how perceived risk from red-bellied woodpeckers (*Melanerpes carolinus*, nest predators) and brown-headed cowbirds (*Molothrus ater*, brood parasites) affected Acadian flycatcher (*Empidonax virescens*) territory settlement. Woodpecker risk was higher on vacant territories in only one of the two years, and apparent woodpecker avoidance appeared to be mediated indirectly through habitat preferences. Cowbird risk was higher on vacant territories in both years, and avoidance appeared to be mediated both by indirect habitat effects as well as a direct behavioral response.

I investigated landscape context and local vegetation effects on densities of Acadian flycatchers and four other migratory species, as well as on relative abundance of red-bellied woodpeckers and brown-headed cowbirds. In addition, for flycatchers I investigated the factors influencing nest survival and incidence of brood parasitism. Nest survival increased with increasing forest cover (and hence, decreasing agriculture) in the surrounding landscape. Acadian flycatchers were particulary sensitive to interior forest openings from patch cuts and other disturbances. We found that incidence of brood parasitism decreased with increasing distance from forest disturbances, and that population density decreased with increasing forest disturbance in the surrounding landscape. This is consistent with our finding that brown-headed cowbirds were positively associated with early successional forest cover in the landscape, including interior forest openings. We do not know how much influence red-bellied woodpeckers have as nest predators, but we did find that, at the landscape scale, flycatcher population density was negatively related to woodpecker abundance, after controlling for landscape context and vegetation effects.

INDEX WORDS: Nest survival, Brood parasitism, Territory settlement, Risk avoidance, Acadian Flycatcher, Red-bellied Woodpecker, Brown-headed Cowbird, Landscape effects, Habitat characteristics, Bottomland hardwood forests

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INTRODUCTION

I conducted my dissertation research in bottomland hardwood forests of the Mississippi Alluvial Valley (MAV), a region where reforestation is currently in progress to reverse decades of habitat loss and fragmentation due to the conversion of forests to agricultural uses. At the most basic level, my charge was to document breeding success and abundance of migratory songbirds in mature forests adjacent to either agricultural fields or fields that had been reforested. The underlying assumption was that reforested fields should buffer the adjacent forest from high rates of nest predation and brood parasitism which are often associated with the forest-agriculture interface, thereby improving reproductive success and increasing density of songbirds. From setting out to test this assumption, my research evolved into a more general examination of a variety of factors, at both landscape and local scales, that impact breeding bird populations.

In my research, I focused on the Acadian flycatcher (*Empidonax virescens*). This was an ideal species for this type of research because it is a mature forest obligate generally thought to be sensitive to habitat fragmentation, yet also occurs in sufficient numbers to generate reasonable sample sizes, with nests that are relatively easy to find (albeit not always easy to monitor). It is also a species with which I was familiar from previous studies, and a bird for which (truth in advertizing) I have a particular fondness. The other main characters in what I came to view as grand theater on the ecological stage were the brown-headed cowbird (*Molothrus ater*) and the red-bellied woodpecker (*Melanerpes carolinus*).

Prior to my arrival in the MAV, I was already aware, in theory, of the cowbird's brood parasitic lifestyle, but I had never truly experienced it. I had previously seen a few parasitized nests, but never had I seen and heard so many cowbirds in one place, nor found so many parasitized nests with two, three, or even four cowbird eggs. I was struck by how hard it must be for songbirds in the region to maintain their populations with such high parasitism pressure. Another eye-opening moment for me was witnessing the depredation of an Acadian flycatcher nest by red-bellied woodpeckers, while the agitated parents tried in vain to protect their young. I had never even considered woodpeckers as nest predators before, and soon found out that my surprise was quite common in the ornithological community. I was determined to find out more. My research in this area barely scratches the surface; I still cannot say whether red-bellied woodpeckers have a significant influence as nest predators, but I hope that my research inspires further investigations.

Because about half of the Acadian flycatcher nests were too high to observe the contents directly, I spent many, many hours in the field quietly observing parent behaviors at the nests as a means of monitoring their progress. This was in addition to the many, many hours spent following the birds as they sang their territory boundaries, chattered to their mates, lowered their bodies into the forks of branches to test the suitability of potential nest locations, gathered spider webs and other materials for nest construction, snapped their beaks and chased cowbirds, and, occasionally, attacked woodpeckers. I was (and am) fascinated by bird behavior and by the interspecific relationships that are likely influencing habitat selection at multiple scales.

The unifying theme of this dissertation is the relationship between landscape context, local vegetation characteristics, and biotic interactions influencing habitat selection and breeding success in migratory songbirds, particularly the Acadian flycatcher. Chapter 1 is a brief literature review to introduce the reader to the subject matter. Chapter 2 is a manuscript that was published in Southeastern Naturalist, describing my discovery of nest predation by red-bellied woodpeckers and reviewing similar accounts from other researchers. Chapter 3 is an investigation of whether, and how, Acadian flycatcher settlement patterns at the local scale are influenced by woodpeckers and cowbirds. A much earlier version of this chapter was submitted to Animal Behavior but not accepted; a revised version will be submitted to Oikos. In Chapter 4, a manuscript that will be submitted to Landscape Ecology, I examine landscape and local effects on Acadian flycatcher nesting success. In Chapter 5, I investigate landscape and local effects on densities of 5 migratory species (including Acadian flycatchers), as well as the relative abundance of brown-headed cowbirds and red-bellied woodpeckers. A version of this chapter will be submitted to The Auk. I end with some concluding remarks in Chapter 6.

CHAPTER 1

LITERATURE REVIEW

Observed patterns of animal habitat use are the outcome of hierarchical processes of habitat selection (Hilden 1965, Johnson 1980, Cody 1985a, Hutto 1985, Orians and Wittenberger 1991, Jones 2001). The ability to assess the quality of available habitats (and microsites within habitats) directly impacts individuals' survival and reproductive potential, and should thus be strongly molded by natural selection (Cody 1985b, Pulliam and Danielson 1991, Stamps 1994, Jones 2001). A thorough understanding of the causes and consequences of habitat selection behavior is important from a conservation standpoint as natural habitats become increasingly rare, degraded, and fragmented. Without mechanistic understanding, we will be unable to predict how species will respond to changes in the landscape, and whether behaviors that have been favored by natural selection in the past will become maladaptive (Stamps 1994, Reed 1999).

To a large extent, of course, the value of a habitat for an animal depends on the amount of various resources it can provide. However, ecologists recognized early on that habitat selection is influenced by the social environment, not just the intrinsic quality of the habitat alone. Svärdson (1949) noted that interspecific competition would cause the habitat range of a species to contract, as individuals are confined to habitats in which they have a competitive advantage. In contrast, he hypothesized that where intraspecific competition was intense, a species would tend to occupy a broader range of habitats. The term "buffer effect" was introduced by Kluyver and Tinbergen (1953), referring to the same phenomenon. Brown (1969) expanded on the idea of the buffer effect, describing graphically how individuals should distribute themselves among habitats of varying quality, given that territoriality sets an upper limit on density and that productivity declines with increasing density. These concepts were further developed in the classic paper by Fretwell and Lucas (1970), in which the "ideal free" and "ideal dominant" distributions were introduced.

The Fretwell-Lucas models are based on the assumptions that animals are “ideal” in their ability to accurately assess habitats of different quality, and that habitat suitability decreases with increasing density. “Free” refers to the ability to enter and settle in any chosen habitat, uninhibited by the presence of conspecifics already settled there. The “ideal dominant” model (Fretwell and Lucas 1970), better known as the “ideal despotic” (Fretwell 1972), was introduced because it is more applicable to territorial organisms such as songbirds. Under this model, entry into a habitat is inhibited by established territorial individuals and density is limited. A newly arriving individual will have lower expected success (as measured, for example, in terms of reproductive output or another proxy of fitness) than the average of the individuals already settled. The resulting distribution is one in which superior habitats support higher densities as well as higher levels of success than inferior habitats. This is in contrast to the ideal free model, in which organisms distribute themselves among habitats such that density will always be higher in the higher quality habitat, but the average success of individuals is equivalent among habitats.

Fretwell and Lucas (1970) offered two possible reasons for why newly arriving birds under the ideal despotic model would have lower expected success in a patch than the habitat average. If a patch of habitat is relatively homogeneous, such that individual territories within it are roughly equal in quality, late-arriving individuals would have lower expected success due to "resistance" from established birds and possible risk of injury or death from territorial disputes. Conversely, in a heterogeneous habitat in which territories vary in quality, late-arriving individuals would have lower expected success because the best territories would already be taken. The latter idea appears to be the basis of the "ideal preemptive" distribution presented by Pulliam and Danielson (1991), although the authors do not discuss the ideal despotic model.

The ideal preemptive model is very similar to the ideal despotic, yielding the same prediction that density among patches should be positively related to expected fitness within the patches. However, the ideal despotic model focuses on habitat selection at the scale of habitat patches, whereas the ideal preemptive focuses on selection at the scale of individual territories. Pulliam and Danielson (1991) conceptualized a habitat patch as a heterogeneous entity, containing multiple potential territories of varying quality. This idea also forms the basis of the discussion of site selection by Rodenhouse et al. (1997). Under the ideal preemptive model, once a territory has been settled by an individual it is "preempted" and cannot be settled by another individual. However, entry into a habitat by newly arriving individuals is otherwise unrestricted, and the occupation of a territory "does not influence the expected reproductive success that can be achieved at any other site" (Pulliam and Danielson 1991, p. S52). In essence, the ideal preemptive model may be thought of as a specific case of the more general ideal despotic distribution. At the population level, average fitness typically declines with increasing density because territories vary in quality and increasingly poor territories are settled. However, the fitness of an individual occupying a specific territory is not affected by increasing density around it.

Pulliam and Danielson (1991) took their model further and explicitly considered the consequences of imperfect settlement decisions. This is a critical theoretical development. Animals are not “ideal” because they rarely, if ever, have perfect information as the basis of their behavioral decisions. Proximate cues are not always reliable, and sometimes lead to maladaptive choices and ecological traps (Gates and Gysel 1978, Misenhelter and Rotenberry 2000, Flaspohler et al. 2001). Even if proximate cues were perfect indicators of habitat quality, an animal cannot sample every available territory or habitat patch before making a settlement decision, especially if changes in the landscape make habitat sampling more cumbersome (Jones 2001). To thoroughly understand and predict animal distribution patterns and population dynamics, we need a better understanding of how animals acquire the information used to make settlement decisions, and the fitness consequences of those decisions.

The basic Fretwell-Lucas models and related models (e.g., Rosenzweig 1985, Parker and Sutherland 1986, Morris 1995, Morris et al. 2001) emphasize competition, assuming that habitat suitability declines with increasing density and that competitors have a repulsive effect on each other. These fundamental assumptions can no longer be accepted so readily (Stamps 1994). When population density is critically low, the benefits of clustering can outweigh the costs of competition, and attractive forces may prevail over repulsion (Allee et al. 1949). But the Allee effect can operate even under normal circumstances. Conspecific attraction is typically associated with colonial species (e.g., Forbes and Kaiser 1994), but there is increasing recognition that it also occurs among territorial animals. Empirically, field researchers have noticed a tendency for territorial birds to cluster together, leaving apparently suitable intervening habitat unoccupied (e.g., Nice 1937, Lack 1948, Hinde 1952, Sherry and Holmes 1985). Conspecific attraction in territorial birds has been investigated in several recent studies (Muller et al. 1997, Pöysä et al. 1998, Ramsay et al. 1999, Ward and Schlossberg 2004, Ahlering et al. 2006, Mills et al. 2006). Conservation biologists may be able to capitalize on this phenomenon, using artificial conspecific cues to attract species of concern to suitable but unoccupied habitat patches (Ward and Schlossberg 2004).

Proximity of conspecifics can have a positive effect on fitness by providing easier access to potential mates (including extra-pair copulations), predator protection, or interspecific territory defense (reviewed by Stamps 1988, Stamps 1994). In addition to these benefits, conspecifics can be an important source of “public information” (Valone 1989, Doligez et al. 2002, Valone and Templeton 2002, Danchin et al. 2004, Doligez et al. 2004b), providing cues about rich foraging areas, danger from predators, or the likelihood of successful breeding. Inexperienced (younger) individuals, in particular, are more likely to rely on socially-acquired information about resource quality (Nocera et al. 2006). The conveyance and utilization of public information is not restricted to conspecifics. Other species with similar requirements may also provide useful information about habitat quality (Danchin et al. 2004). Several manipulative experiments suggest that heterospecific attraction is prevalent in boreal forests, where migratory passerines appear to use resident species as indicators of high quality breeding patches (Mönkkönen et al. 1990, Mönkkönen et al. 1997, Forsman et al. 1998, Thomson et al. 2003). The relative importance of positive (attractive) and negative (repulsive) interactions between potential competitor species is expected to vary along environmental gradients due to differences in relative density (Mönkkönen et al. 2004).

Although there has been a tendency to focus on food resources as the primary determinant of intrinsic habitat quality (Stamps 1994), predation risk is a cost that must be weighed against the benefits to be accrued from occupying a particular area (Hilden 1965, Lima and Dill 1990, Moody et al. 1996). There are many examples of animals modifying behavioral decisions, including habitat selection, based on perceived predation risk (reviewed by Lima and Dill 1990). Foraging animals often shift to safer but potentially less profitable microhabitats when they perceive an elevated risk of predation (Werner et al. 1983, Caldwell 1986, Lima 1988, Kullberg 1998, Brown and Kotler 2004, Winterrowd and Devenport 2004, Butler et al. 2005, Foam et al. 2005). However, there is less information on the extent to which animals use risk assessment in decisions involving a longer time commitment than a foraging bout, such as the choice of a breeding territory or nest site. This is arguably a more important decision, because once an individual has invested time and energy in a particular breeding location, the individual is relatively immobile and committed (Getty 1981). Yet it is also a more problematic decision because an assessment of conditions at the time of settlement may or may not be an accurate assessment of future conditions.

Birds in the northern hemisphere tend to respond more strongly to predation risk to their nestlings than to risk to themselves (Ghalambor and Martin 2001), so it is likely that minimizing nest predation is a driving force in breeding habitat selection (Fontaine and Martin 2006). There is some evidence that birds prefer "safe" nest sites (Martin and Roper 1988, Møller 1988, Kelly 1993, Martin 1995, Forstmeier and Weiss 2004), although in some situations the level of risk at any particular nest location may be inherently unpredictable (Martin 1995, Wilson and Cooper 1998). Several authors have found lower songbird densities in areas of relatively high predation risk, and suggested that risk avoidance, rather than direct predation, was the cause of the observed pattern (Sodhi et al. 1990, Suhonen et al. 1994, Norrdahl and Korpimäki 1998, Forsman et al. 2001).

Preference for safe nest sites, territories, or habitat patches might be mediated indirectly by structural features of the habitat (Lima 1993, Murphy et al. 1997, Butler et al. 2005), site fidelity contingent on the individual's own past reproductive success (Blancher and Robertson 1985, Schmidt 2001), the use of public information from conspecifics (Boulinier and Danchin 1997, Pärt and Doligez 2003, Doligez et al. 2004a, Ward 2005, Poysa 2006), or heterospecific habitat copying (Parejo et al. 2005). Alternatively, birds might assess risk directly via cues emitted from the predators themselves. Dusky warblers (*Phylloscopus fuscatus*) placed their nests in safer (but thermally less optimal) locations when the abundance of an important nest predator (Siberian chipmunk, *Tamias sibiricus*) was high (Forstmeier and Weiss 2004). Unoccupied shrike (*Lanius collurio*) territories were more likely to become occupied the following year if avian nest predators moved away (Roos and Pärt 2004). The timing of pied flycatcher (*Ficedula hypoleuca*) territory and nest box occupancy was unimodally related to the distance from sparrowhawk (*Accipiter nisus*) nests, presumably due to a trade-off between the predation risk to adult flycatchers and partial protection from avian nest predators afforded by the presence of sparrowhawks (Thomson et al. 2006). These examples support the idea that direct assessment of predation risk is a factor in breeding habitat selection.

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CHAPTER 2

COMMON, BUT COMMONLY OVERLOOKED: RED-BELLIED WOODPECKERS AS SONGBIRD NEST PREDATORS[1]

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[1] Hazler, K.R., D.E.W. Drumtra, M.R. Marshall, R.J. Cooper, and P.B. Hamel. 2004. Southeastern Naturalist 3(3):467-474.

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ABSTRACT

Woodpeckers in North America are not widely recognized as nest predators. In this paper, we describe several eyewitness accounts of songbird nest predation by Red-bellied Woodpeckers (*Melanerpes carolinus*), document evidence that songbirds recognize woodpeckers as nest predators, and show that our observations are consistent with previously published notes. We believe that this species, commonly overlooked, may be an important predator of songbird nests in many eastern North American forests.

INTRODUCTION

In the ornithological literature, there is much emphasis on determinants of nesting success because this is such a fundamental component of individual fitness, population dynamics, and avian conservation (e.g., Donovan and Thompson 2001; Martin 1998; Paton 1994). From a conservation standpoint, knowledge of the nest predator community is important for predicting how landscape changes (e.g., habitat fragmentation) will affect breeding bird communities (Andren 1995). Preconceived notions about which taxa are potential nest predators are likely to affect study design and interpretation.

In discussions with researchers at ornithological conferences, we have found that woodpeckers are not generally recognized as nest predators. In a summary of nest predation studies, Paton (1994) listed various birds, mammals, and snakes as "primary predators". However, corvids were the only avian taxa listed. Gates and Gysel (1978) mentioned several species of mammals, snakes, corvids, and raptors as potential nest predators, but said nothing about woodpeckers. Among eastern North American woodpeckers, Bent (1939) included only Red-headed Woodpeckers *(Melanerpes erythrocephalus*) as nest predators, based on eyewitness accounts. In summarizing previous work, largely based on the accounts in Bent (1939) and Ehrlich et al. (1988), Hamel (1992) also listed Red-headed Woodpeckers as the only eastern woodpecker that fed on eggs and nestlings.

Shackelford et al. (2000) described the Red-bellied Woodpecker (*M. carolinus*) as a "generalistic and opportunistic feeder," and cited several references showing that this species will eat bird eggs (Brackbill 1969; Rodgers 1990) and nestlings (Conner 1974; Grimes 1947; Neill and Harper 1990; Watt 1980). Through our research on the productivity of Neotropical migratory birds in bottomland hardwood forests, we have come to view the Red-bellied Woodpecker as a potentially important nest predator. The objective of this communication is to dispel the widely held notion that corvids and raptors are the only significant avian nest predators. Herein, we describe several eyewitness accounts of songbird nest predation by Red-bellied Woodpeckers, document evidence that songbirds recognize woodpeckers as nest predators, and show that our observations are consistent with previously published notes.

STUDY AREAS AND METHODS

Our observations are derived from our studies of songbird nesting success in several bottomland hardwood forests in the Mississippi Alluvial Valley between 1993 and 2002. These forests include portions of Meeman-Shelby Forest State Park and Wildlife Management Area near Memphis, Tennessee; Chickasaw National Wildlife Refuge (NWR) near Ripley, Tennessee; White River NWR near Stuttgart, Arkansas;

Tensas River NWR near Tallulah, Louisiana; and Delta National Forest (NF) near Vicksburg, Mississippi. These forests are dominated, to varying degrees, by Nuttall oak (*Quercus nuttallii* Palmer), overcup oak (*Q. lyrata* Walt.), sweetgum (*Liquidambar styraciflua* L.), sugarberry (*Celtis laevigata* Willd.), and water hickory (*Carya aquatica* Nutt.). Green ash (*Fraxinus pennsylvanica* Marsh.), elms (*Ulmus* spp.), and other oaks are also common. At the Meeman-Shelby and Chickasaw sites, eastern cottonwood (*Populus deltoides* Bartr. ex Marsh.), sycamore (*Platanus occidentalis* L.), and pecan (*Carya illinoensis* (Wang) K. Koch) are also dominant canopy species.

Red-bellied Woodpeckers were abundant at our study sites (Durham et al. 1988; personal observations; unpublished data). For example, in point count surveys conducted at White River NWR, 1994-2000, we recorded a mean of 0.97 detections per count (s = 0.9; n = 2119 unlimited radius, 5 min point counts). In these surveys, Red-bellied Woodpeckers were detected almost 5 times more frequently than corvids and raptors combined.

We searched for songbird nests following standard protocols (Martin and Geupel 1993). We usually checked nests at 2-4 day intervals. Although we found nests of most common species on the study sites, we focused our field efforts on Acadian Flycatchers (*Empidonax virescens*), Blue-gray Gnatcatchers (*Polioptila caerulea*), and Prothonotary Warblers (*Protonotaria citrea*). Most Prothonotary Warbler nests were accessible from the ground or a canoe, but we checked higher nests with a mirror pole. When possible, we checked Acadian Flycatcher nest contents with a mirror pole, but nests were frequently too high. All Blue-gray Gnatcatcher nests were too high to check with a mirror pole. To determine if the high nests were active, we stood 10-20 m away (horizontal distance) and watched the nest for up to 30 min to see if adult birds visited the nest. This allowed us to observe several predation events and to observe anti-predatory behaviors exhibited by songbirds against woodpeckers.

EYEWITNESS ACCOUNTS

In the following accounts, we use the word "attack" to describe defensive behaviors involving actual physical contact between songbirds and woodpeckers, such as pecking or striking. We use the word "harass" to denote aggressive maneuvers, such as repeated close swooping, that seemed intended to drive the woodpecker away but did not involve direct physical contact.

We observed two predation events on the Meeman-Shelby Forest site. At 10:00 CST on 11 May 1993, we saw a male Red-bellied Woodpecker at the nest of a Blue-gray Gnatcatcher, approximately 20 m high in a 25 m tall boxelder (*Acer negundo*). The woodpecker repeatedly stabbed his bill into the nest, then flew south with what appeared to be a nestling. The woodpecker visited the nest three more times. Each time, he stabbed into it, took what appeared to be a nestling, and flew in the same direction. During each of these trips, the female gnatcatcher attacked the woodpecker at the nest by landing on his back and pecking him, but with no apparent effect. The nest had been active for ≥14 days, and the gnatcatcher had been incubating or perhaps brooding nestlings on 8 May. On 13 May, we saw the female gnatcatcher dismantling and moving the nest.

On 26 June 1994, at ~10:00, we observed a Red-bellied Woodpecker consuming the eggs of an Acadian Flycatcher nest, which was 13 m high, also in a boxelder. The woodpecker perched on the edge of the nest while hanging upside down, then curled its head up, over, and into the nest cup. It returned to the nest twice. The adult flycatcher attacked the woodpecker, striking it several times. Later, fresh egg shell and yolk were found beneath the nest. The next day, the nest was empty, and no flycatchers were observed in the vicinity.

We witnessed a possible third nest predation event at Meeman-Shelby on 7 July 1994. We had discovered an Acadian Flycatcher nest in the construction phase on 25 June, and the female had been incubating eggs or brooding new hatchlings on the morning of 7 July. At ~16:00, we observed two Red-bellied Woodpeckers within 10 m of the nest, about 6 m high in a boxelder. The flycatcher pair harassed the woodpeckers and eventually drove them away from the nest, which was empty at that point. We suspect that the nest had been depredated by the woodpeckers, but cannot confirm our suspicion. We did not find any egg shell or yolk beneath the nest, and we observed no activity around the nest the next day.

We witnessed one predation event on the Tensas River NWR. At 07:47 on 9 June 2000, we discovered a Red-bellied Woodpecker depredating an Acadian Flycatcher nest. One woodpecker perched at the nest rim, while a second woodpecker perched on a branch nearby. A third woodpecker was within 15 m. Both flycatcher parents repeatedly swooped at the woodpecker at the nest, calling continuously. However, their nest defense was ineffectual. After a few minutes, the first woodpecker flew off with an egg in its beak. The two other woodpeckers flew off as well and were never observed at the nest, although they may have taken contents prior to the observation. The flycatcher parents continued to call and flutter around the nest for at least 10 min after the woodpeckers departed. One flycatcher had disheveled breast feathers. At 11:05, we returned to check the status of the nest and found it intact with no sign of damage. Although it was too high to view contents with a mirror, this nest was quite threadbare and appeared to be empty from below. The parents were neither seen nor heard at this time.

At White River NWR, we found the nest of an Indigo Bunting (*Passerina cyanea*) as it was being depredated by a Red-bellied Woodpecker at 10:25 on 23 April 1998. The woodpecker perched on the nest rim, removed one egg, then flew off with the egg in its bill. We did not detect the bunting parents during this predation event. However, within 15 min the female bunting flew to the nest two times and checked its contents. The nest was located 4.3 m high in a sugarberry, and contents were not checked with a mirror pole until the following day. At that time, the nest was empty. On 27 April, the Indigo Bunting pair initiated a second clutch in the same nest. This second nest was depredated 10-11 days into incubation but the identity of the predator was unknown.

We have circumstantial evidence that woodpeckers have removed contents from many Prothonotary Warbler nests at White River NWR. In our experience, this secondary cavity-nester typically places its nest just below the opening of a hole in a dead trunk. Frequently, the cavity wall opposite the opening is thin, and nest contents tend to be gathered against this back wall (DEWD, pers. obs.). In many instances when nest checks revealed that the contents were missing, the back wall had a freshly excavated hole, implicating a woodpecker as the nest predator. Based on such observations from 1994-2000, we attributed 145 (17%) of 874 depredations of Prothonotary Warbler nests to woodpeckers. While we could not identify the species of woodpecker responsible, Red-bellied Woodpeckers comprised 64% of all woodpecker detections in the area (unpubl. data).

Additional behavioral observations indicate that adult birds of potential prey species recognize the Red-bellied Woodpecker as a threat. For example, on 5 and 11 June 1993, at Chickasaw NWR, adult Eastern Wood-Pewees (*Contopus virens*) flew from their nest, >15 m high in a sweetgum, and harassed adult Red-bellied Woodpeckers that came within 10 m of the nest. [A Cerulean Warbler (*Dendroica cerulea*) nest was 12 m higher in the same tree, but we did not observe any aggressive behavior by Cerulean Warblers directed against Red-bellied Woodpeckers.] On 8 May 2000 at 11:00, a pair of color-banded Prothonotary Warblers chased a Red-bellied Woodpecker near their nest at White River NWR. The nest contained four warbler eggs and two Brown-headed Cowbird (*Molothrus ater*) eggs. On 19 May at 13:20, when the nest contained two 7-day-old cowbird nestlings, we observed the same male warbler attacking a Red-bellied Woodpecker. On 29 June at 11:50, a different banded female Prothonotary Warbler chipped and dove at a Red-bellied Woodpecker less than 5 m from her nest. When the nest was checked 2 h later, none of the 5-day-old nestlings were missing.

On 11 separate occasions, we observed Blue-gray Gnatcatchers harassing or attacking Red-bellied Woodpeckers on the Meeman-Shelby Forest site. The woodpeckers were usually within 10 m of the nest, but did not seem to be trying to prey upon its contents. In contrast, gnatcatcher parents did not interact aggressively with a Red-headed Woodpecker foraging within about 20 m of their nest, even though they were nearby.

In Delta NF, we twice witnessed Acadian Flycatchers harassing Red-bellied Woodpeckers. On 2 July 2002 at 09:04, a female flycatcher perched 15 m from her active nest, calling. A Red-bellied Woodpecker, first heard about 25 m away, came within 15 m of the nest. The flycatcher then harassed the woodpecker until it flew away. On 25 July, a flycatcher adult and its chick were seen perched together on a branch approximately 15 m above the ground. About 7 m away, a Red-bellied Woodpecker clung to a hickory trunk 2-3 m lower than the flycatchers. The adult flycatcher repeatedly swooped at the head of the woodpecker while loudly snapping its beak. After each swoop, it returned briefly to perch with the chick. The chick appeared to be watching the proceedings. At White River NWR and Meeman-Shelby Forest, we made additional observations of aggressive behaviors directed at Red-bellied Woodpeckers by Acadian Flycatchers.

In contrast to aggressive maneuvers, Acadian Flycatchers occasionally react to the presence of woodpeckers with stealth. We observed this twice in Delta NF. At 08:23 on 6 July 2001, a female flycatcher was calling and foraging within a 15 m radius of her active nest while the male sang nearby. After 8 min of observation, the female flew to the nest and began incubating. After a few seconds, a Red-bellied Woodpecker came within 15 m of the nest and began calling and drumming. The flycatcher immediately flew off the nest and did not interact with the woodpecker. She returned to the nest and resumed incubating after an additional 7 min had passed and the woodpecker had moved farther away. On 6 June 2002, while an Acadian Flycatcher incubated her eggs, a Red-bellied Woodpecker came within 5 m of the nest and perched in an adjacent tree. The flycatcher immediately flew off the nest in silence and appeared to watch the woodpecker from 7 m away.

Red-bellied Woodpeckers may also be a threat to other woodpeckers. On 12 May 2002 in Delta NF, we observed a Red-bellied Woodpecker investigating multiple cavities. At the time, this bird had an active nest with young nearby. The Red-bellied Woodpecker was harassed by a Downy Woodpecker (*Picoides pubscens*) for several minutes before finally leaving the area.

DISCUSSION

In Europe, Nilsson (1984) found that woodpeckers (*Dendrocopos* spp.) were responsible for 48% and 17%, respectively, of the predation on tit (*Parus* sp.) nest boxes and natural nests. The author also reported several direct observations of Great Spotted Woodpeckers (*D. major*) robbing tit nests. Onnebrink and Curio (1991) employed models of the Great Spotted Woodpecker in experimental tests of nest defense behavior by tits, underlining the recognized importance of this nest predator.

In North America, Short (1982) listed four species of *Melanerpes* [Red-headed (*M. erythrocephalus*), Acorn (*M. formicivorus*), Gila (*M. uropygialis*) and Red-bellied Woodpecker] as known predators of bird eggs or nestlings. Boyd and Ellison (in review) recently added the Golden-fronted Woodpecker (*M. aurifrons*) to the list. The remaining *Melanerpes* species have not been recognized as nest predators. However, we suspect that further study of these species will reveal that nest depredation is a common behavior across the genus.

After watching a Red-bellied Woodpecker consume an Acadian Flycatcher nestling, Traill (1991) suggested that "nest predation…by Red-bellied Woodpeckers might be one of the limiting factors in the breeding success of these small woodland birds." Red-bellied Woodpeckers have been documented as nest predators in several other published notes as well (Table 2.1). The frequency and extent of woodpecker predation on bird nests is unknown, and anecdotal observations are insufficient for assessing the impact of particular predators on the dynamics of songbird populations in various regions and habitat types. Nonetheless, our observations add to the growing evidence that Red-bellied Woodpeckers (and other woodpecker species) frequently consume songbird eggs and nestlings, and are potentially an important nest predator in some areas. Although our personal observations are restricted to bottomland hardwood forests in the Mississippi Alluvial Valley, the Red-bellied Woodpecker is common in a variety of forest types (Shackelford et al. 2000). We believe that this species, commonly overlooked as a predator, may be a significant factor affecting songbird nesting success in many eastern North American forests.

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Table 2.1. Documented instances of nest predation by Red-bellied Woodpeckers.

Citation	State	Prey Species	Nesting Stage
This paper	Tennessee	Blue-gray Gnatcatcher	nestlings
		Acadian Flycatcher	eggs, nestlings[1]
	Louisiana	Acadian Flycatcher	eggs
	Arkansas	Indigo Bunting	eggs
		Prothonotary Warbler	nestlings[1]
J.A. Jackson, pers. comm.	Mississippi	Red-cockaded Woodpecker (*Picoides borealis*)	nestlings
		Eastern Bluebird (*Sialia sialis*)	eggs
Traill, 1991	N. Carolina	Acadian Flycatcher	nestlings
Neill and Harper 1990	Illinois	House Wren (*Troglodytes aedon*)	nestlings
Rodgers 1990	S. Carolina	Domestic Fowl (*Gallus gallus*)	eggs
Watt 1980	Maryland	American Redstart (*Setophaga ruticilla*)	nestlings
Conner 1974	Virginia	Carolina Chickadee (*Poecile carolinensis*)	nestlings
Brackbill 1969	Maryland	House Sparrow (*Passer domesticus*)	eggs
Grimes, 1947	Florida	Hairy Woodpecker (*Picoides villosus*)	nestlings[1]

[1] Unconfirmed, but likely based on circumstantial evidence

CHAPTER 3

RISKY BUSINESS: TERRITORY SETTLEMENT BY ACADIAN FLYCATCHERS UNDER THREAT OF NEST PREDATION AND BROOD PARASITISM [1]

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[1] Hazler, K.R., R.J. Cooper, and D.J. Twedt. To be submitted to Oikos.

ABSTRACT

We hypothesized that, for songbirds, minimizing risk from avian nest predators and brood parasites is an important factor in selecting a breeding site. Through the early part of two breeding seasons (2001-2002), we spot-mapped locations of Acadian flycatchers (*Empidonax virescens*, territory selectors), red-bellied woodpeckers (*Melanerpes carolinus*, nest predators) and brown-headed cowbirds (*Molothrus ater*, brood parasites) in a 56-ha study area within an extensive bottomland hardwood forest. We were thereby able to determine the order of flycatcher territory settlement in relation to perceived risk (detections/ha over a 30-day survey period) from woodpeckers and cowbirds, while accounting for habitat characteristics. In both years, perceived cowbird risk was higher on vacant than on occupied territories (2001 mean difference = 1.15, SE = 0.60; 2002 mean difference = 1.97, SE = 0.69). Perceived woodpecker risk was higher on vacant territories in 2001 only (mean difference = 1.27, SE = 0.59). We used an information-theoretic framework to evaluate the relative effects of woodpecker risk, cowbird risk, a floristic index of the wetland gradient, and distance to the nearest edge on flycatcher territory settlement. Flycatchers selected somewhat drier sites along the wetland continuum, resulting in indirect avoidance of woodpeckers and cowbirds due to their opposing response. However, flycatchers appeared to directly avoid cowbirds as well; cowbird risk was the variable with the largest effect size. For each 1-unit increase in perceived cowbird risk, the likelihood of selecting a territory was reduced by 17.5%. There was little support for an effect of woodpecker risk, and none for an edge effect. After accounting for philopatry in a set of post-hoc models for 2002 only, there was little support for additional habitat effects, but evidence for cowbird avoidance remained.

INTRODUCTION

Theoretical models of habitat settlement (Fretwell and Lucas 1970, Rosenzweig 1981, Pulliam and Danielson 1991, Rodenhouse et al. 1997) typically assume that animals are able to assess habitat quality and preferentially settle in the best habitat patch available. More realistically, however, individuals have only partial knowledge of the components of habitat quality, and may not always choose the best available breeding and/or foraging sites. As a consequence, average fitness and population growth are not fully maximized (Pulliam and Danielson 1991). To understand and predict population dynamics, empirical data are needed to determine how well individuals assess habitat quality when establishing breeding territories.

The suitability of a habitat for survival and reproduction depends on resource availability (food, nesting sites, etc.) as well as the risk of predation, parasitism, and other threats. Thus, theoretically optimal habitat selection can be viewed as a cost-benefit analysis: animals face tradeoffs between maximizing resources and minimizing risk (Lima and Dill 1990). Resource and risk assessment may be mediated by indirect cues, such as vegetation structure, or direct cues, such as predator vocalizations. There is, however, limited information on the specific mechanisms and accuracy of resource and risk assessment.

Animals can assess imminent predation risk and modify their behavior accordingly; there is ample evidence for this especially from studies of foraging behavior (Lima and Dill 1990). However, the extent to which animals use risk assessment in decisions involving long-term commitments, such as the choice of a breeding territory, is largely unknown. Getty (1981) observed that once time and energy have been invested in a particular breeding location, an individual is relatively immobile and committed. Unlike an animal engaging in a short-term foraging bout, the animal selecting a breeding site is unable to quickly adjust its location at a later time if it turns out to be unsuitable.

Several authors have found lower songbird densities in areas of relatively high predation risk, and suggested that risk avoidance, rather than direct predation, was the cause of the observed pattern (Sodhi et al. 1990, Suhonen et al. 1994, Norrdahl and Korpimäki 1998, Forsman et al. 2001). While supportive of the notion that birds preferentially choose safer territories, the shortcoming of these studies is that they inferred process (i.e., settlement) from pattern (i.e., density), but did not document the process itself. Direct predation effects could not necessarily be ruled out. In addition, although habitat characteristics were generally considered, the studies did not always control for habitat features that may have influenced the observed patterns.

In addition to nest depredation, brood parasitism represents a significant risk for many songbirds. In North America, brown-headed cowbirds (*Molothrus ater*) parasitize more than 220 species (Ortega 1998), and have been implicated in population declines of many of these (Brittingham and Temple 1983). Cowbirds play a role as nest predators as well (Arcese et al. 1996, Hoover and Robinson 2007). Host species are often aggressive toward adult cowbirds (Rothstein 1990, McLean and Maloney 1998), suggesting that they recognize them as a threat. Although some species eject cowbird eggs or desert parasitized nests, many species accept cowbird eggs and rear their young (Rothstein 1975). Acceptance of cowbird eggs may be due to the host's inability to recognize foreign eggs, inability to eject or bury foreign eggs, or the cost associated with abandoning the nest (Rothstein and Robinson 1998).

Until recently, host species' acceptance of dissimilar cowbird eggs has been an enigma without a fully satisfactory explanation. However, it now appears that "mafia-like" relatiatory behavior by cowbirds makes it more beneficial for some hosts to accept than to reject a cowbird egg (Hoover and Robinson 2007). If host behavior is thus constrained to accept cowbird eggs, host species might be able to reduce their probability of parasitism by avoiding areas of high parasitism risk. Although Schmidt's (2001) model of songbird population dynamics assumed that host assessment of parasitism risk was not possible, this assumption has not been empirically tested.

We examined territory settlement by male Acadian flycatchers (*Empidonax viresecens*) in relation to spatial patterns of perceived risk from an avian nest predator (red-bellied woodpecker, *Melanerpes carolinus*) and a brood parasite (brown-headed cowbird). Although Acadian flycatcher nests are subject to predation by a wide variety of nest predators, we focused on the red-bellied woodpecker because, although it is known from the literature and from personal observations to depredate nests, it is often overlooked as a potential nest predator (Hazler et al. 2004). Therefore, studies are needed to establish what impact this common species may have on songbird populations.

We hypothesized that areas of lower woodpecker and cowbird activity, and therefore presumably lower risk of predation and parasitism, would be settled first with later settlers forced to establish territories in areas of higher risk (i.e., an ideal preemptive settlement pattern, Pulliam and Danielson 1991). Because habitat selection is influenced by numerous factors, we evaluated the relative effects of perceived risk, vegetation, distance to edge, and philopatry on Acadian flycatcher settlement patterns.

METHODS

Study Area

We established a 56-ha study area within the Delta National Forest (32˚41’ N, 90˚49’ W), which encompasses >24,000 ha of contiguous, bottomland hardwood forest approximately 40 km north of Vicksburg, Mississippi, USA. One edge of the study area ran along a slough and gravel road bordering regenerating forest planted 5 years before initiation of the study. With colored flagging, we marked grid points at 50-m intervals (Figure 3.1), with additional flagging at half-way points to improve mapping accuracy in the field. We produced detailed field maps of the study area using geographic coordinates recorded with a GPS (Geographic Positioning System) receiver at a systematic sample of 191 of these points. We estimate mean positional accuracy at ~15-m.

The study site was subject to seasonal flooding, and was dominated by overcup oak (*Quercus lyrata*) and sugarberry (*Celtis laevigata*). Other common canopy trees included sweetgum (*Liquidambar styraciflua*), green ash (*Fraxinus pennsylvanicus*), and water hickory (*Carya aquatica*). Deciduous holly (*Ilex decidua*), swamp forestiera (*Forestiera acuminata*) and saplings of canopy species were common in the midstory. Poison ivy (*Toxicodendron radicans*) dominated the shrub layer, but was also a common vine along with grape (*Vitis* spp.), trumpet creeper (*Campsis radicans*), greenbriar (*Smilax* spp.), and peppervine (*Ampelopsis arborea*). Ground cover was generally sparse, but dominated by prostrate vines.

Study Species

Acadian flycatchers are Nearctic-Neotropical migratory songbirds that typically nest in the lower canopy of mature eastern forests (Whitehead and Taylor 2002). They are one of the most common passerines in bottomland forests in this area (Twedt et al. 1999). Acadian flycatchers began arriving at our study site during the second week of April with settlement of males continuing for several weeks. Most females arrived after most males had established territories.

Red-bellied woodpeckers are opportunistic foragers (Shackelford et al. 2000) and depredate nests of other birds, including Acadian flycatchers (Hazler et al. 2004). Acadian flycatchers are among the host species commonly parasitized by brown-headed cowbirds (Wilson and Cooper 1998). Red-bellied woodpeckers and brown-headed cowbirds are year-round residents in our study area. Both woodpeckers and cowbirds are vocal and conspicuous, so that spatial patterns of perceived risk can be readily mapped using standard avian survey techniques. In addition, there is evidence that Acadian flycatchers recognize both woodpeckers (Hazler et al. 2004) and cowbirds (T. Ford, pers. comm. cited in Whitehead and Taylor 2002) as a threat.

Field Surveys

During spring of 2001 and 2002, we conducted surveys by walking (or canoeing when the area was flooded) along transects 100 m apart (Figure 3.1) and recording the locations of all birds detected on field maps. Each year, we conducted daily surveys (weather permitting) throughout the territory settlement period (April), starting before the first arrival of Acadian flycatchers. We conducted additional surveys during May and

June (2 in 2001, 11 in 2002) after territory settlement. We commenced surveys approximately 0.5 h after first light and continued until the entire plot was covered (usually 3.5 - 4 h). Two observers were required for timely completion of surveys, with each observer covering half of the study area. To avoid bias due to observer ability and temporal changes in vocalizations, we varied starting points and switched observers within sub-areas surveyed.

We recorded Acadian flycatchers as males if they vocalized with the typical territorial song “peet-sah,” and as females if they vocalized with “peet” or “peer” calls (Whitehead and Taylor 2002). Although both males and females may give all of these calls, “peet-sah” is only rarely given by females (Whitehead and Taylor 2002), and males do not appear to give the “peet” and “peer” calls unless in association with a female (Whitehead and Taylor 2002, KRH, pers. obs.). If two birds in close proximity ($\leq$ 15 m) were observed together making “peet” or “peer” calls or otherwise behaving like mates, we marked their location as the midpoint between them and recorded them as a pair. If two or more males were recorded countersinging, we marked lines between them on the map to indicate that their locations were on confirmed separate territories. In addition to Acadian flycatchers, we recorded the locations of cowbirds and red-bellied woodpeckers. The vast majority of detections of all species were auditory only. We digitized bird locations and instances of countersinging marked on field maps into a Geographic Information System (GIS), ArcView v. 3.2 (ESRI 1999). Further GIS manipulations of spatial data were conducted in ArcGIS v. 9.2 (ESRI 2006) unless otherwise indicated.

Territories

We delineated territories of Acadian flycatcher males using standard territory mapping techniques (Robbins 1970, Bibby et al. 1992). After assigning individual detections to territories, we used the Jenrich-Turner method in the ArcView® Animal Movements extension (Hooge and Eichenlaub 2000) to determine the centroid for each territory. We assumed that territory settlement date was the date of the first registered detection within the territory. As a proxy measure of philopatry between years, we calculated the distance from territory centroids (both occupied and vacant) in 2002 to the nearest occupied territory centroids in 2001.

We partitioned the entire study area into occupied (observed) and available but vacant territories. To do this, we generated 50 random points within the study area including the 50-m outer buffer zone, constrained so that no points were closer than 55-m (the minimum separation distance between observed territory centroids; see Results). For each year separately, we culled all random points within 55-m of observed territory centroids, and the remaining points were treated as the centroids of vacant territories. The observed and randomly generated centroids were combined into a single spatial layer, from which we generated Thiessen (= Voronoi) polygons (ESRI 2006, de Smith et al. 2008) representing occupied and vacant territories (Figure 3.2).

Perceived Risk

We used the Kernel method with a 5-m cell size and a 100-m search radius to generate "perceived risk" maps (raster datasets), representing the density of detections (per ha) of red-bellied woodpeckers and brown-headed cowbirds. We used point locations from 30 survey days each year to generate the risk maps. We assumed that risk perceived by Acadian flycatchers was proportional to density of detections of woodpeckers and cowbirds. Although we did not attempt to correct for detection probability, we feel that the frequency and thoroughness of field surveys minimized bias. Moreover, the density of detections should be a valid measure of *perceived* risk even if not strictly proportional to actual density and actual risk.

Habitat

We sampled vegetation at 129 grid points systematically located across the study area (Figure 3.1), and at 218 Acadian flycatcher nest locations (located as part of a companion study). Vegetation sampling was conducted over 3 summers (2001-2003), using a modification of the methods of James and Shugart (1970). At each sampling point, we mapped, measured diameter-at-breast-height (dbh), and identified all trees and snags ≥ 10 cm dbh within an 11.3 m radius (0.04 ha) circle. We also counted all saplings and small trees (< 10 cm dbh, ≥ 2.5 m high) within a 5 m radius circle. We used a 50 cm x 50 cm coverboard, divided into 25 equal squares, to estimate vegetative cover at ground level, 2.5 m, and 5 m above the ground (a variation on the coverboard method described by Nudds (1977). We ranked (0 to 5) the amount of vines (in climbing, not prostrate form) in each cardinal direction. From these measurements, we derived 6 basic quantitative measures of vegetation structure for potential inclusion in statistical analyses: basal area, tree density, sapling density, snag density, vine abundance, and midstory cover.

We used our tree samples to derive an additional quantitative variable representing the floristic composition along the wetland gradient. To each tree species, we assigned a wetland rank ranging from 1 (characteristic of sites flooded 3 months per year or more) to 12 (characteristic of sites flooded 2 weeks to 1 month per year or less). For most trees, these ranks were obtained directly from Dale and Ware (2004). For the remaining trees, we obtained the U.S. Fish and Wildlife Service (USFWS) wetland indicator status from the online PLANTS database (USDA-NRCS 2006). We translated these to the ranking system of Dale and Ware (2004) by calibrating against trees for which we knew the assigned values from both ranking systems. We calculated an overall wetland gradient index for each plot as:

$$WG = \frac{1}{2}\left[\frac{\sum_{1}^{T}(C_t \times W_t)}{C_{sum}} + \frac{\sum_{1}^{T}(B_t \times W_t)}{B_{sum}}\right]$$

where T is the total number of tree species and the subscript t refers to each individual species; C_t and B_t are the counts and basal area, respectively, for species t; C_{sum} and B_{sum} are the counts and basal area summed over all species in the plot; and W_t is the wetland rank of species t on the scale of Dale and Ware (2004).

All grid point and nest vegetation sampling points were georeferenced with a GPS. We generated raster maps of each vegetation variable by interpolation using the Natural Neighbor method (ESRI 2006, de Smith et al. 2008) with a 5-m output cell size. The input dataset for the interpolation consisted of all vegetation samples except the nests found in 2001, which were used as a validation dataset. To assess performance of the interpolation, we regressed interpolated values against directly measured values in the validation dataset. We eliminated variables for which the interpolation performed poorly (linear regression: $R^2 < 0.15$, $p > 0.05$), and thus were left with 4 vegetation characteristics: tree density, sapling density, basal area, and wetland gradient (Table 3.1). We also calculated the distance to the nearest non-forest edge (in this case, a gravel road) for every 5-m cell in the study area.

Statistical Analysis

Perceived risk values in the buffer zone of the study area (Figure 3.1) are biased low. This is because the density of detections at any given point is based on a 100-m search radius, but we reliably recorded detections only out to ~50-m beyond the study area boundary. Therefore, in the analyses described, we completely excluded territories with centroids falling within buffer zone (Figure 3.2). Other peripheral territory polygons were truncated to exclude the portions falling within the buffer zone (Figure 3.3). For each habitat and risk variable, we overlaid the territory layer on the corresponding raster map and extracted the mean value of cells contained within each territory polygon.

We used analysis of variance and comparisons of least squares means to test the hypothesis that occupied territories were located in areas of lower perceived woodpecker and cowbird risk than vacant territories . The analyses were implemented with the MIXED procedure in SAS (SAS Institute Inc. 2004), with year as a random effect, selection status (occupied vs. vacant) as a fixed effect, and woodpecker risk and cowbird risk, respectively, as response variables.

If settlement is non-random with respect to perceived risk, it could arise from direct assessment of predator and parasite cues (e.g., vocalizations), indirect avoidance via correlated habitat cues, or both. We used proportional hazards (Cox) regression

(Allison 1995) to model the effects of explanatory variables on territory settlement by Acadian flycatchers. This model is appropriate for estimating a resource selection function when resources are depleted over time (Manly et al. 1993), in this case accounting for increasingly limited settlement choices as more individuals select sites. Proportional hazards regression analyses were implemented using the PHREG procedure in SAS, with ties in settlement handled by the exact method (Allison 1995). The response variable SELECTED was coded as an event (value = 1 for occupied territories) or as a censored observation (value = 0 for vacant territories). The associated event time was the date of the first registered detection on an occupied territory; for vacant territories it was the latest of all observed territory settlement dates.

We used Aikaike's Information Criterion for small samples (AICc) and weights of evidence (w_i) within an information-theoretic framework (Burnham and Anderson 2002) to compare sets of candidate regression models representing different causal mechanisms. To avoid overparameterization and consideration of an excessive number of candidate models, we first screened the four vegetation variables with a preliminary set of vegetation-only models, and identified only one (the wetland gradient index) that warranted inclusion in subsequent analyses (see Results). The global model thus included a vegetation variable, an edge variable, and two perceived risk variables. The candidate set of models included all possible combinations of these variables, as well as a null model representing random settlement for comparison. To evaluate the relative influence of perceived risk, edge avoidance, and vegetation, we compared effect sizes (ES), calculated as the model-averaged parameter estimates divided by their respective standard errors, as well as sums of weights (Σw_i) of the models including each variable.

In gauging the importance of variables, we note that a variable with $|ES| \geq 1.64$ has a 90% confidence interval that does not overlap zero.

We hypothesized that, if flycatchers use habitat cues to minimize risk, then they should avoid habitat factors associated with risk. To evaluate this hypothesis, we fit a set of simple linear regression models of perceived risk against vegetation and edge variables. We controlled for year effects by first regressing perceived risk on year, then using the residuals as the response variable. We compared the effects of these predictor variables on woodpeckers, cowbirds, and flycatchers.

Site fidelity plays an important role in territory settlement (Whitehead and Taylor 2002) but could not be incorporated in the analyses combining both years because we had no data on territory locations in 2000 as baseline for 2001. Therefore, for 2002 only, we fit a set of post-hoc proportional hazards regression model of territory settlement including the explanatory variables deemed reasonable based on the results of the earlier analysis as well as a proxy variable for philopatry. Because most individuals were not banded, we used the distance from the centroid of each territory (occupied or vacant) in 2002 to the centroid of the nearest occupied territory in 2001 as the proxy variable.

If spatial patterns of risk are consistent between years, then strong site fidelity could reinforce risk avoidance over time. Conversely, if risk is spatially variable among years, site fidelity could counteract risk avoidance. Using 2002 territory footprints as the sample unit, we regressed perceived risk in 2002 against perceived risk in 2001 as a general assessment of the constancy of spatial pattern. A positive relationship with a high coefficient of determination (R^2) would indicate that certain areas are consistently safe or risky, whereas a low R^2 value would indicate a spatial pattern that varies substantially between years.

For those territories that were occupied in both years, we fit a linear regression model of settlement date in 2002 against settlement date in 2001 to determine whether territories were settled in a consistent time sequence. Because this was not the case (see Results), we explored whether the change in settlement dates could be explained in part by changes in perceived risk. Given that territory footprints shifted between years, we calculated 3 indices of change in risk that could be relevant predictors of the change in settlement date, and compared the 3 competing linear regression models against a null model. No global model was included in the candidate set because we considered the 3 indices of change to be exclusive alternatives, and it makes no biological sense to include them in the same model. The three predictor variables we considered were:

1) Δ-abs = [2002 risk in 2002 territory] – [2001 risk in 2001 territory]

This is the absolute change in perceived risk, between years, that would be experienced by a returning settler in 2002 that shifted his territory from its footprint in 2001.

2) Δ-stay = [2002 risk in 2001 territory] – [2001 risk in 2001 territory]

This is the change in perceived risk, between years, that a returning settler would experience if the territory footprint remained exactly the same in 2002 as in 2001.

3) Δ-shift = [2002 risk in 2002 territory] – [2002 risk in 2001 territory]

Unlike the other two indices, this is a within-year comparison. It is the difference in perceived risk, in 2002, between the footprint of the territory actually occupied and the footprint that would have been occupied had the territory not shifted.

To ensure valid inferences from the various candidate sets of regression models described above, we assessed goodness of fit for the global model (where applicable) by plotting deviance residuals against the linear predictor and against each covariate. For proportional hazards regression models, we examined plots of Schoenfeld residuals against time to evaluate whether the proportionality assumption of the global model was met (Allison 1995). We also examined correlation matrices of the predictor variables to determine to what extent multicollinearity was an issue. All analyses were implemented in SAS v. 9.1 (SAS Institute Inc. 2004).

RESULTS

Earliest territory settlement was on 9 April, with the last territories settled on 1 May. The minimum distance between territory centroids was 55 m. We delineated 25 occupied and 15 vacant (random) territories within the study area in 2001; in 2002 we delineated 34 occupied and 9 vacant territories (Figure 3.2). Overall perceived risk differed substantially between years, with more woodpecker detections in 2001 (mean difference = 2.01, SE = 0.45) and more cowbird detections in 2002 (mean difference = 5.85, SE = 0.46). Vacant territories had higher perceived risk from cowbirds than occupied territories in both years, and higher perceived risk from woodpeckers in 2001 only (Figures 3.3-3.4).

Correlations between the vegetation variables were mild ($0.06 \leq |r| \leq 0.20$), so it is unlikely that important effects were obscured due to multicollinearity in the initial variable screening. Of the four vegetation variables considered, only the wetland gradient index appeared to have a measurable effect on settlement. Thus, our global model included four explanatory variables: the wetland gradient, distance to edge, and perceived risk from cowbirds and woodpeckers. There was substantial correlation among some of these variables ($0.14 \leq |r| \leq 0.58$), reinforcing the need for an information-theoretic approach to model selection and parameter estimation.

Based on weights of evidence (w_i), there was no overwhelmingly superior model in the set of candidate models (Table 3.2). The top three models included cowbird risk and vegetation ($w_i = 0.25$), cowbird risk only ($w_i = 0.17$), and both cowbird and woodpecker risk ($w_i = 0.13$). Perceived risk from cowbirds was the most influential variable ($\Sigma w_i = 0.89$, ES = -2.46; Table 3.3), and was included in all of the top-ranked models (Table 3.2). For each 1-unit increase in perceived cowbird risk (detections/ha), the likelihood of selecting a territory was predicted to be reduced by 17.5%. Vegetation was also important ($\Sigma w_i = 0.57$, ES = 1.63). For each 0.1-unit increase in the wetland gradient index, the likelihood of selecting a territory was predicted to increase by 7.7%. There was little evidence for an effect of perceived woodpecker risk ($\Sigma w_i = 0.37$, ES = -0.98), although the effect was in the hypothesized negative direction. There was no support for an edge effect ($\Sigma w_i = 0.27$, ES = -0.05). In summary, flycatchers avoided cowbirds (and possibly woodpeckers), and selected drier areas along the wetland gradient.

Controlling for year effects, perceived risk from both cowbirds and woodpeckers was related to both of the habitat variables we tested (Tables 3.4-3.5, Figure 3.5). Although Acadian flycatchers showed no response to the forest edge, perceived risk decreased with increasing distance from the edge (woodpeckers: $\Sigma w_i = 1.00$, ES = -6.44; cowbirds: ($\Sigma w_i = 0.71$, ES = -2.01). Both woodpeckers and cowbirds were more frequently detected in wetter areas along the wetland gradient (woodpeckers: $\Sigma w_i = 0.88$, ES = -2.53; cowbirds: ($\Sigma w_i = 0.60$, ES = -1.73), in direct contrast to Acadian flycatchers, which were more likely to select territories in drier areas (Figure 3.5). Based on partial regression analysis, the wetland gradient accounted for 4.1 – 17.9% of the variation in perceived woodpecker risk, depending on whether the shared contribution of the correlated explanatory variables is attributable (Graham 2003) to the effect of edge or to the effect of wetland gradient. The wetland gradient accounted for only 2.7 – 5.8% of the variation in perceived cowbird risk.

For the data from 2002 only, we fit a post-hoc set of flycatcher territory selection models including the following predictor variables: distance to the nearest occupied territory centroid in 2001 (proxy variable for philopatry), wetland gradient, and perceived risk from cowbirds and woodpeckers (Tables 3.6-3.7). The top-ranked model (w_i = 0.32) included both philopatry and cowbird risk. Philopatry had the strongest effect (ES = -2.58). For each 10-m increase in distance from the nearest territory centroid occupied in 2001, flycatchers were predicted to be 18.3% less likely to select a territory. After accounting for philopatry, the estimated effect of cowbird avoidance was less than estimated in the previous analysis, but still important (ES = -1.66); for each 1-unit increase in perceived risk, the predicted likelihood of selecting a territory was reduced by 14.6%. There was, however, no evidence for woodpecker avoidance (ES = 0.10), and little support for an additional effect of wetland gradient (ES = -0.90) after accounting for philopatry.

Perceived risk in 2002 was positively related to perceived risk in 2001 (Figure 3.6). However, this relationship accounted for a relatively small proportion of the variability ($R^2 = 0.16$ for cowbirds, $R^2 = 0.13$ for woodpeckers). Thus, although certain areas appeared to be consistently "risky" (e.g., the upper left corner of the study area, which was conspicuously avoided by flycatchers), the spatial pattern of perceived risk varied substantially between years, as can be seen in Figure 3.3.

For territories occupied in both years, we found no relationship between settlement dates in 2002 and 2001 (linear regression, $R^2 < 0.01$, n = 24). The mean difference in settlement date was 1.2 days later, but ranged from 12 days earlier to 13 days later. We examined the explanatory value of changes in perceived cowbird risk only, based on the results above which indicated little or no effect of woodpecker risk on settlement. Neither Δ-abs nor Δ-stay (see Methods) had any explanatory value for the difference in settlement date ($R^2 < 0.09$); both of these models performed worse than the null model (Table 3.8). There was, however, substantial support ($w_i = 0.73$) for a positive effect of Δ-shift (Figure 3.7). The mean shift in the location of territory centroids between years was 26-m, but ranged from 8-m to 59-m. Where perceived risk was reduced (within, not between years) by the territory shift, settlement on that territory tended to be earlier than the previous year. Where perceived risk was increased by the territory shift, settlement was later in all but one case.

DISCUSSION

In an interesting theoretical paper, Brown et al. (1999) examined the connection between predator and prey behaviours, and explored their population- and community-level consequences. They noted that traditional models of predator-prey population dynamics focus on the lethal effects of predators, and usually do not incorporate the antipredator behavior of prey. They argued for the importance of non-lethal effects of predators and risk avoidance behaviour by prey – the "ecology of fear." In this study, we sought to weigh the empirical evidence for risk avoidance behavior in avian territory settlement.

As predicted, we found that occupied flycatcher territories were, on average, located in areas with lower perceived cowbird risk than vacant territories. Occupied territories also had lower perceived woodpecker risk, but only in one of the two years. Songbirds may be able to avoid settling in risky areas by assessing the prevalence of predators or brood parasites through direct cues such as vocalizations. An alternative, not necessarily mutually exclusive mechanism for risk avoidance is the preference for habitat features negatively correlated with risk. Smith and Shugart (1987) demonstrated the importance of habitat structure as a proximate cue for evaluating food resources, and it is reasonable to expect that vegetation could serve as a proximate cue for risk as well. Over generations, predation or parasitism is likely to be a selective force that reinforces adaptive habitat preferences.

Like most songbirds, Acadian flycatchers often return to the same breeding sites between years (Whitehead and Taylor 2002). Survival estimates based on banding returns from constant-effort mist-netting in the southeastern and the south-central United States suggest that 48 – 58% of Acadian flycathers return between years (Michel et al. 2005). We only banded a few of our study animals, so we are unable to say how many birds returned each year, but 13 of 34 (38%) territory centroids in 2002 were within 25 m of a centroid from the previous year. Strong site fidelity could help or hinder optimal territory selection, depending on how consistent spatial patterns of risks and resources are over time, and the degree to which philopatric behavior is flexible. Site fidelity has been shown to be contingent on reproductive success the previous year (Haas 1998, Hakkarainen et al. 2001) as well as changing spatial patterns of risk between years (Roos and Pärt 2004). Lanyon & Thompson's (1986) study of painted buntings (*Passerina ciris*) indicated that site fidelity is tempered by preference for higher quality; some birds would "upgrade" to better territories when they were vacated by previous occupants. We surmise that the observed patterns of flycatcher territory occupancy in our study area arose in part from a combination of habitat preferences leading indirectly to avoidance of cowbirds and woodpeckers, flexible site fidelity, and direct avoidance of cowbirds based on perceived risk (Figure 3.8).

We analyzed the responses of woodpeckers, cowbirds, and flycatchers to two habitat variables: the wetland gradient and distance to the nearest edge. We recorded more detections of cowbirds and woodpeckers near the forest edge. The association between edge and woodpecker detections was especially strong. Although proximity to edge had the potential to serve as an effective habitat cue for minimizing risk from both woodpeckers and cowbirds, we found no evidence of edge avoidance by Acadian flycatchers, even though this species is frequently referred to as a "forest interior" species (Whitcomb et al. 1981, Hamel et al. 1982). In contrast, all three species appeared to respond to the wetland gradient. Acadian flycatchers tended to select somewhat drier sites, while woodpeckers and cowbirds were associated with somewhat wetter sites. Thus, this habitat preference could account for some of the observed difference in perceived risk (especially woodpecker risk) between occupied and vacant territories.

Settlement patterns are undoubtedly influenced by myriad habitat characteristics that we did not measure. One might contend that the apparent influence of perceived cowbird risk on flycatcher settlement would disappear if we had been able to account for all important habitat features. However, site fidelity subsumes the suite of long-term habitat associations. Thus it is not surprising that once we accounted for philopatry, the effect of the wetland gradient became negligible. The fact that perceived cowbird risk was measurably, negatively associated with territory settlement even after accounting for philopatry provides substantial support for the idea that flycatchers avoid cowbirds directly. In contrast, the already negligible effect of perceived woodpecker risk in the initial analysis all but disappeared once we accounted for philopatry. This argues strongly against spatial avoidance of woodpeckers by flycatchers.

There are several possible reasons why flycatchers did not actively avoid woodpeckers. It may simply be that woodpeckers have a fairly negligible effect as nest predators since they are generalist foragers. Also, there are many other nest predator species in the study area, so avoiding one particular species of predator may not be possible without increasing risk from another. Even if woodpeckers do have a substantial effect on nesting success, it may be that flycatchers only respond if densities are above a certain threshold level that was not met during the years of our study. Or, flycatchers may have an alternative behavioural mechanism for dealing with woodpecker risk, rather than shifting the footprints of their territories. For example, Forstmeier and Weiss (2004) demonstrated shifts in dusky warbler (*Phylloscopus fuscatus*) nest height in response to changing predation risk. This type of microhabitat shift warrants further investigation.

Relative levels of perceived woodpecker and cowbird risk in the second year of our study were positively related to relative risk levels the previous year; i.e. there was a tendency for risky areas tended to stay risky, and safe areas safe. The relationship was not particularly strong, however, so spatial patterns of perceived risk varied substantially between the two years. Therefore, for a returning settler, simply re-occupying a territory that was relatively safe and productive the previous year is not optimal. A better strategy would be to return to the general location but then shift the territory footprint depending on current conditions. We found that, for re-occupied territories that had shifted to a footprint that was “safer” in terms of perceived cowbird risk, the settlement date was typically earlier than it had been the previous year. Territories that had shifted to a “riskier” footprint were settled later. We speculate that a shift to a riskier footprint may have been forced by dominant neighbors, or by other dynamic factors that changed the balance of costs and benefits, making the territory less desirable and hence settled later than previously.

Our study has several limitations. First, we could not possibly assess all of the factors that may be important in territory selection. We did not directly measure food and other resources important to flycatchers, nor did we measure other risk factors, such as snakes and mammalian nest predators. Thus, we do not have a full understanding of all the trade-offs faced by flycatchers in selecting breeding sites. Second, our research was confined to a single study area over a relatively short time period. Spatial and temporal replication would be highly desirable. Finally, a banded population would have given more insight into territory re-occupancy and turnover. Despite these limitations, our study provides some empirical evidence for risk avoidance behaviour in avian territory settlement, and yields new insights into the possible dynamics between cowbirds and their hosts.

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Table 3.1. Habitat measurements considered as explanatory variables in models of Acadian flycatcher territory settlement.

Variable	Variable Description	Justification for Inclusion
BA	Basal area of live trees (m^2/ha). Range 21 – 35[a].	Acadian flycatchers are associated with mature forests (Dickson et al. 1993), and thus are likely to be associated with greater basal area at the territory scale.
TR	Trees > 10 cm dbh (number/ha). Range 297 - 934.	Flycatchers are tree nesters, and may prefer territories with a higher density of trees because they provide a greater number of potential nest sites (Martin & Roper 1988)
ST	Number of saplings and small trees < 10 cm dbh and ≥ 2.5-m high (number/ha). Range 259 - 1405.	Cowbirds may be more active in areas with more saplings (Gates & Evans 1998)
HG	Hydrologic gradient index[b]. Range 6.3 – 7.9. $HG = \frac{1}{2}\left[\frac{\sum_{1}^{T}(C_t \times W_t)}{C_{sum}} + \frac{\sum_{1}^{T}(B_t \times W_t)}{B_{sum}}\right]$	This index encapsulates the floristic composition of the forest along the wetland continuum and as such could serve as an indicator of the relative abundance of preferred nesting substrates.
DE	Distance (m) to the nearest forest edge. Range 100 - 717.	Flycatchers have been classified as a forest-interior species (Whitcomb et al. 1981), and may avoid edges because of differences in microclimate, vegetation structure, and food resources near edges, and/or because of higher risk from nest predators or brood parasites (McCollin 1998)

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[a] Ranges given are the values calculated as zonal means for individual territories after interpolation across the study area from the original sample points.

[b] In the formula, T is the total number of tree species and the subscript t refers to each individual species; C_t and B_t are the counts and basal area, respectively, for species t; C_{sum} and B_{sum} are the counts and basal area summed over all species in the plot; and W_t is the wetland rank of species t on the scale of Dale and Ware (2004). The index ranges from 1 (characteristic of sites flooded 3 months per year or more) to 12 (characteristic of sites flooded 2 weeks to 1 month per year or less). See Methods for details.

Table 3.2. Comparison of proportional hazards regression models to evaluate the relative influence of perceived risk, vegetation, and distance to edge on territory settlement by male Acadian flycatchers in 2001-2002.

Variables included[a]	-2 log L[b]	K[c]	AIC_c[d]	Δ_i[e]	w_i[f]
CB HG	288.92	2	293.07	0.00	0.25
CB	291.75	1	293.80	0.73	0.17
WP CB	290.28	2	294.43	1.36	0.13
WP CB HG	288.45	3	294.76	1.69	0.11
CB HG DE	288.92	3	295.22	2.15	0.08
CB DE	291.59	2	295.74	2.66	0.07
WP CB DE	290.12	3	296.43	3.36	0.05
WP CB HG DE[g]	288.22	4	296.73	3.66	0.04
HG	294.78	1	296.83	3.76	0.04
WP HG	293.50	2	297.65	4.58	0.03
HG DE	294.60	2	298.75	5.68	0.01
WP	297.21	1	299.26	6.19	0.01
WP HG DE	293.44	3	299.75	6.68	0.01
Null Model	301.07	0	301.07	8.00	0.00
WP DE	297.21	2	301.36	8.29	0.00
DE	299.52	1	301.57	8.50	0.00

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[a] WP = perceived woodpecker risk, CB = perceived cowbird risk. See Table 3.1 for other variables.
[b] Minus twice the log-likelihood of the model
[c] Number of parameters in the model
[d] Aikaike's Information Criterion, corrected for small sample size
[e] Delta-AIC_c value (difference between the model AIC_c and the minimum AIC_c)
[f] Aikaike weight of evidence for the model, relative to others in the model set.
[g] The generalized coefficient of determination for the global model was $R^2 = 0.14$. Inspection of deviance residuals indicated adequate fit. Inspection of Schoenfeld residuals indicated that the proportionality assumption was met for all predictor variables.

Table 3.3. Relative effects of explantatory variables on Acadian flycatcher territory settlement, 2001-2002, based on models evaluated in Table 3.2. Model-averaged estimates are shown.

Variable[a]	Parameter Estimate	Standard Error	Hazard Ratio	Effect Size	Σw_i[b]
CB	-0.192	0.078	0.825	-2.46	0.89
HG	0.573	0.352	1.774	1.63	0.57
WP	-0.089	0.090	0.915	-0.98	0.37
DE	-0.00005	0.00096	1.000	-0.05	0.27

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[a] Explanatory variables: WP = perceived woodpecker risk, CB = perceived cowbird risk HG = hydrologic gradient index, DE = distance to nearest edge

[b] Sum of Aikaike weights of the models in which the variable was included.

Table 3.4. Comparison of linear regression models of habitat effects on perceived woodpecker and cowbird risk, 2001-2002.

		Perceived Woodpecker Risk[a]				Perceived Cowbird Risk[a]			
Variables included[b]	K[c]	-2 log L[d]	AIC_c[e]	Δ_i[f]	w_i[g]	-2 log L	AIC_c	Δ_i	w_i
HG DE[h]	4	283.83	292.34	0.00	0.88	336.39	344.90	0.00	0.36
DE	3	289.99	296.29	3.95	0.12	338.70	345.00	0.10	0.35
HG	3	318.54	324.85	32.50	0.00	339.46	345.76	0.86	0.24
Null Model	2	334.88	339.03	46.68	0.00	344.49	348.64	3.74	0.06

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[a] Between-year effects were removed by first regressing perceived risk on year, then using the residuals as the response variable.
[b] Explanatory variables: HG = hydrologic gradient index, DE = Distance to edge
[c] Number of parameters in the model
[d] Minus twice the log-likelihood of the model
[e] Aikaike's Information Criterion, corrected for small sample size
[f] Delta-AIC_c value (difference between the model AIC_c and the minimum AIC_c)
[g] Aikaike weight of evidence for the model, relative to others in the model set.
[h] The generalized coefficient of determination for the global model was $R^2 = 0.46$ for the woodpecker model and $R^2 = 0.09$ for the cowbird model. Inspection of residuals indicated adequate fit.

Table 3.5. Relative effects of explanatory variables on perceived woodpecker and cowbird risk, 2001-2002, based on models evaluated in Table 4. Model-averaged estimates are shown.

Variable[a]	Perceived Woodpecker Risk				Perceived Cowbird Risk			
	Parameter Estimate	Standard Error	Effect Size	Σw_i[b]	Parameter Estimate	Standard Error	Effect Size	Σw_i[b]
DE	-0.00638	0.00099	-6.44	1.00	-0.00267	0.00133	-2.01	0.71
HG	-0.968	0.383	-2.53	0.88	-0.935	0.540	-1.73	0.60

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[a] Explanatory variables: HG = hydrologic gradient index, DE = distance to nearest edge
[b] Sum of Aikaike weights of the models in which the variable was included.

Table 3.6. Comparison of post-hoc proportional hazards regression models to evaluate the relative influence of perceived risk, vegetation, and philopatry on Acadian flycatcher territory settlement, 2002.

Variables included[a]	-2 log L[b]	K[c]	AIC_c[d]	Δ_i[e]	w_i[f]
PH CB	149.07	2	153.37	0.00	0.32
PH	151.75	1	153.85	0.48	0.25
PH HG CB	148.08	3	154.69	1.32	0.17
PH HG	151.21	2	155.51	2.14	0.11
PH CB WP	149.01	3	155.63	2.26	0.10
PH HG CB WP[g]	148.05	4	157.10	3.73	0.05

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[a] Explanatory variables: WP = perceived risk from woodpeckers, CB = perceived risk from cowbirds, HG = hydrologic gradient index, PH = distance to nearest occupied territory centroid from previous year, a proxy variable for philopatry

[b] Minus twice the log-likelihood of the model

[c] Number of parameters in the model

[d] Aikaike's Information Criterion, corrected for small sample size

[e] Delta-AIC_c value (difference between the model AIC_c and the minimum AIC_c)

[f] Aikaike weight of evidence for the model, relative to others in the model set.

[g] The generalized coefficient of determination for the global model was $R^2 = 0.26$. Inspection of deviance residuals indicated adequate fit. Inspection of Schoenfeld residuals indicated that the proportionality assumption was met for all predictor variables.

Table 3.7. Relative effects of explanatory variables on Acadian flycatcher territory in 2002, based on post-hoc models evaluated in Table 3.6. Model-averaged estimates are shown. Sums of model weights are not shown for each variable because the variables were not evenly balanced in the set of candidate models.

Variable[a]	Parameter Estimate	Standard Error	Hazard Ratio	Effect Size
PH	-0.018	0.007	0.982	-2.58
CB	-0.158	0.095	0.854	-1.66
HG	-0.511	0.570	0.600	-0.90
WP	0.015	0.155	1.015	0.10

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[a] Explanatory variables: WP = perceived risk from woodpeckers, CB = perceived risk from cowbirds, HG = hydrologic gradient index, PH = proxy variable for philopatry.

Table 3.8. Alternative linear regression models of the effect of changes in perceived cowbird risk on changes in settlement date on territories occupied in both years (n = 24). No global model was included in the candidate set because we considered Δ-abs, Δ-stay, and Δ-shift to be exclusive alternatives and it makes no biological sense to include them in the same model.

Explanatory variable[a]	-2 log L[b]	K[c]	AIC_c[d]	Δ_i[e]	w_i[f]	R^2	Param. Est.	Std. Err.	Effect Size
Δ-shift	151.96	2	159.16	0.00	0.73	0.23	4.050	1.532	2.64
Null model	158.10	1	162.67	3.50	0.13	0.00	n/a	n/a	n/a
Δ-stay	155.91	2	163.11	3.95	0.10	0.09	-0.917	0.607	-1.51
Δ-abs	157.76	2	164.96	5.79	0.04	0.01	-0.359	0.614	-0.59

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[a] Variables: Δ-shift = [2002 risk in 2002 territory] – [2002 risk in 2001 territory], Δ-stay = [2002 risk in 2001 territory] – [2001 risk in 2001 territory], Δ-abs = [2002 risk in 2002 territory] – [2001 risk in 2001 territory]. See Methods for further explanation.

[b] Minus twice the log-likelihood of the model

[c] Number of parameters in the model

[d] Aikaike's Information Criterion, corrected for small sample size

[e] Delta-AIC_c value (difference between the model AIC_c and the minimum AIC_c)

[f] Aikaike weight of evidence for the model, relative to others in the model set.

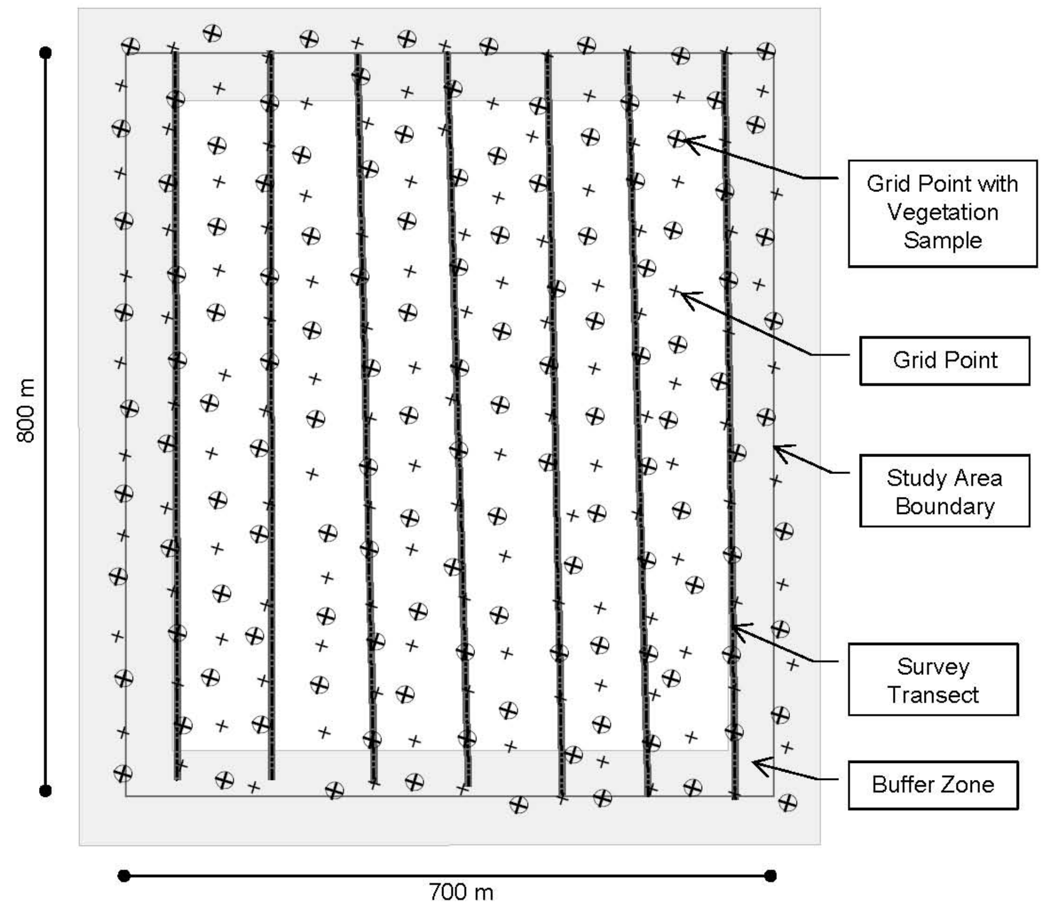

Figure 3.1. Layout of the 56-ha study area in Delta National Forest, Mississippi.

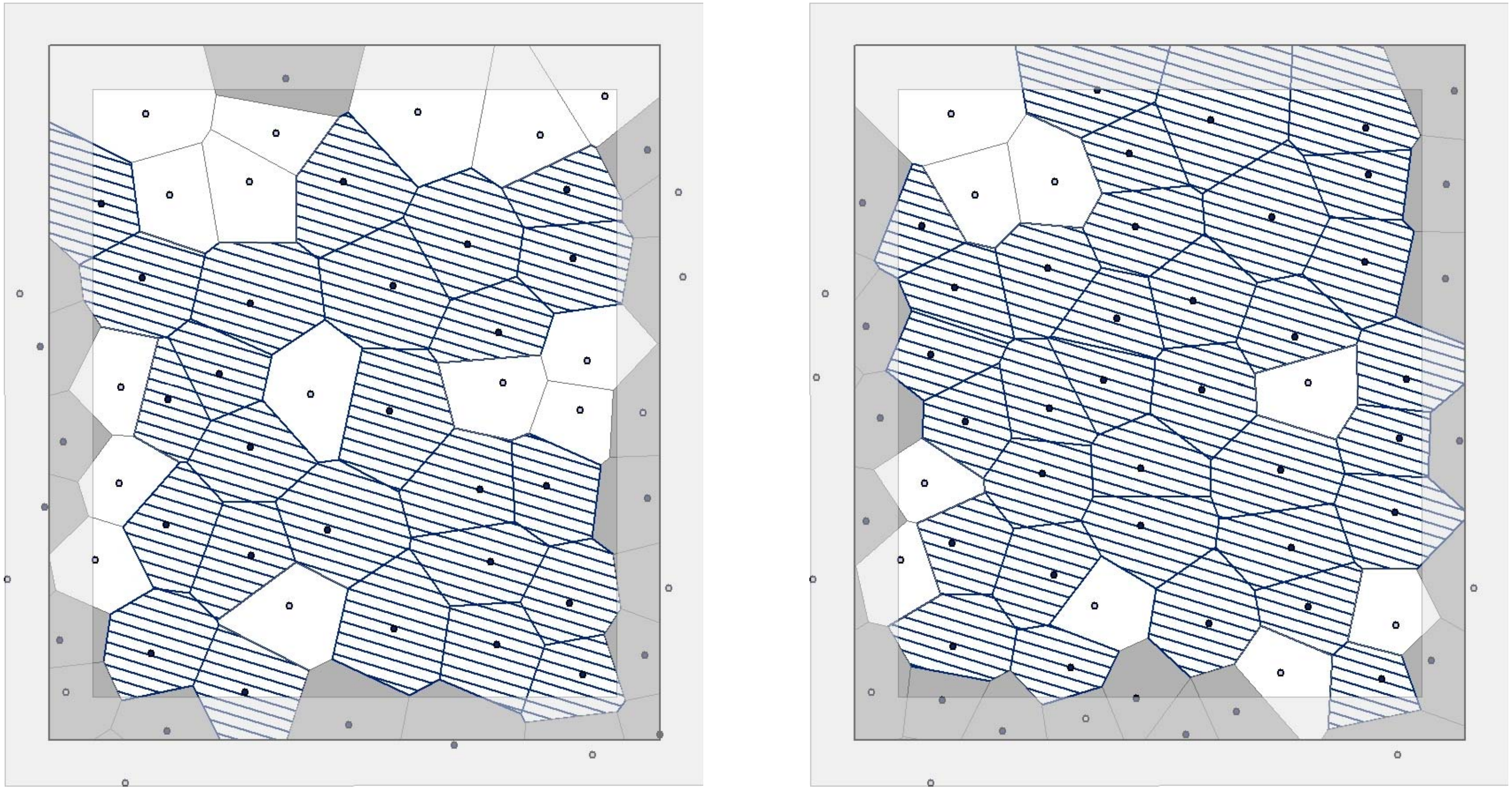

Figure 3.2. The study area subdivided into Thiessen polygons representing Acadian flycatcher territories in 2001 (left) and 2002 (right). Hatched polygons represent occupied territories, and corresponding territory centroids are shown as dark circles. White polygons represent vacant territories, with territory centroids shown as light circles. Grey polygons are territories excluded from analyses because centroids were located within the buffer zone.

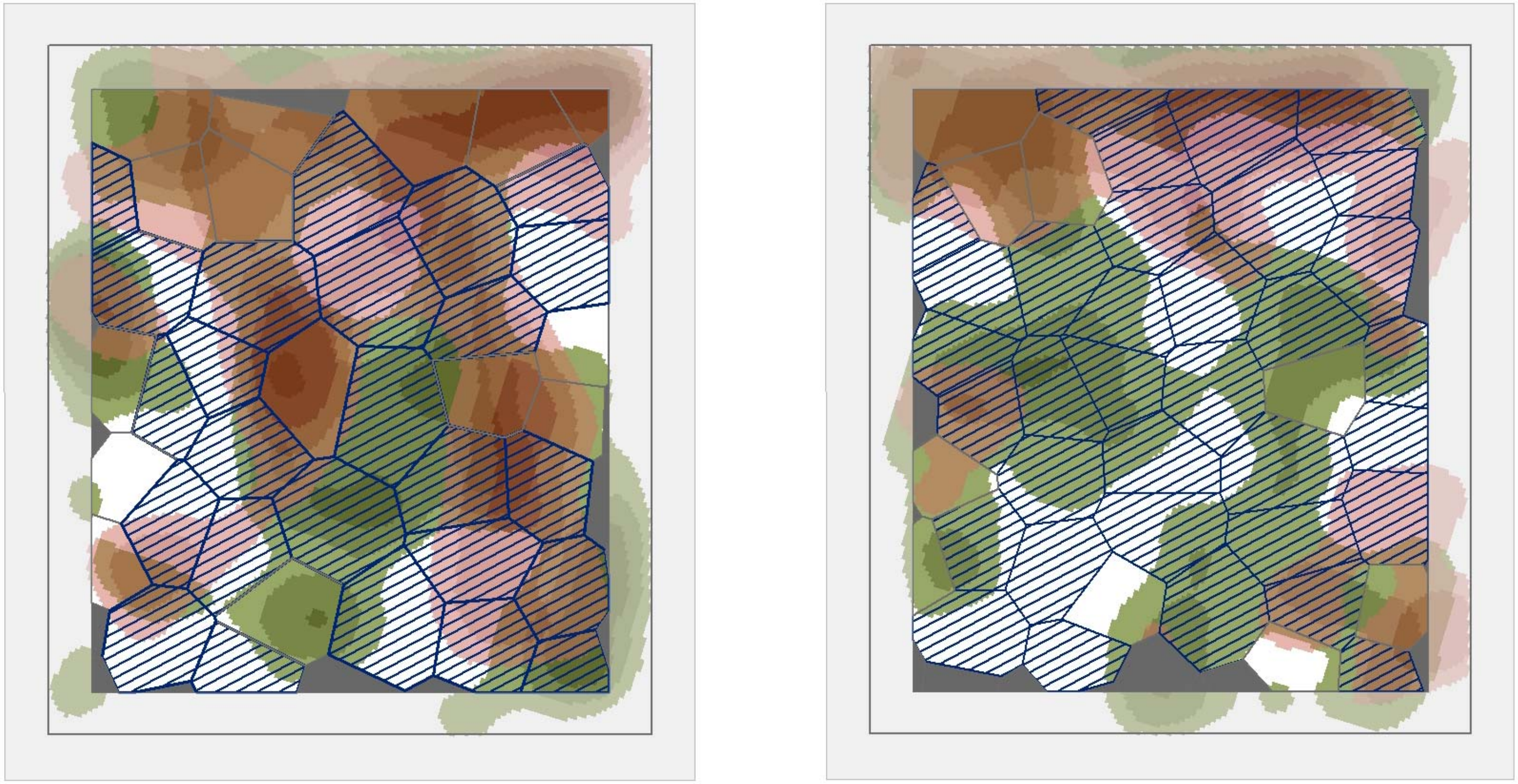

Figure 3.3. Acadian flycatcher territories in 2001 (left) and 2002 (right), superimposed over perceived risk. Territories are represented as in Figure 2 (hatched = occupied, clear = vacant, opaque grey = excluded from analyses), but they are truncated at the buffer zone. Perceived risk is represented in shades of red (woodpeckers) and green (cowbirds), with areas of overlap in shades of brown. More intense colors represent higher perceived risk based on density of detections recorded over a 30-day survey period.

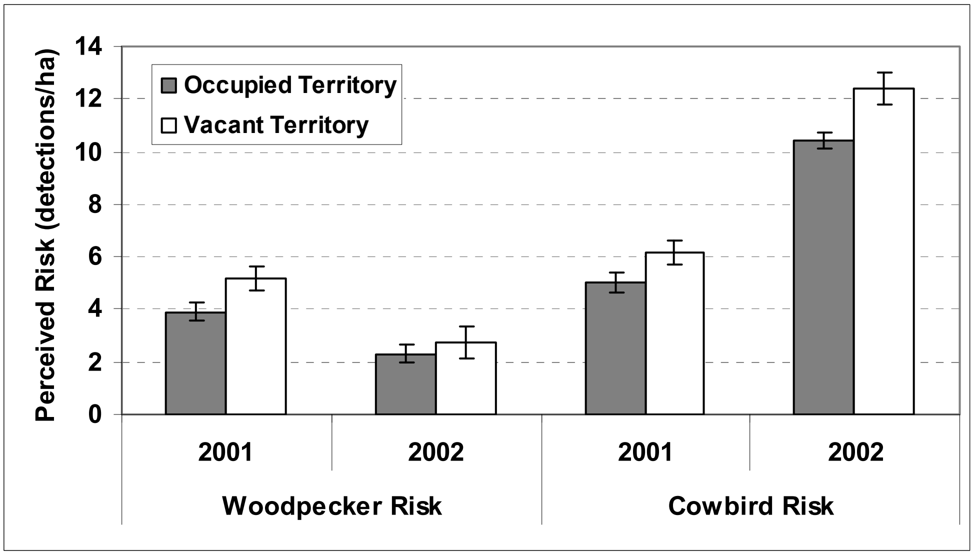

Figure 3.4. Differences in perceived risk (detections/ha ± SE), from woodpeckers and cowbirds, between occupied and vacant territories. Selection status (occupied or vacant) and year were the main effects in an analysis of variance, with perceived woodpecker or cowbird risk as the response variable. Perceived risk from cowbirds was greater on vacant territories in both years (2001 mean difference = 1.15, SE = 0.60; 2002 mean difference = 1.97, SE = 0.69). Perceived risk from woodpeckers was measurably greater on vacant territories in 2001 only (2001 mean difference = 1.27, SE = 0.59; 2002 mean difference = 0.42, SE = 0.68). Sample sizes were 25 occupied and 15 vacant territories in 2001, 34 occupied and 9 vacant territories in 2002.

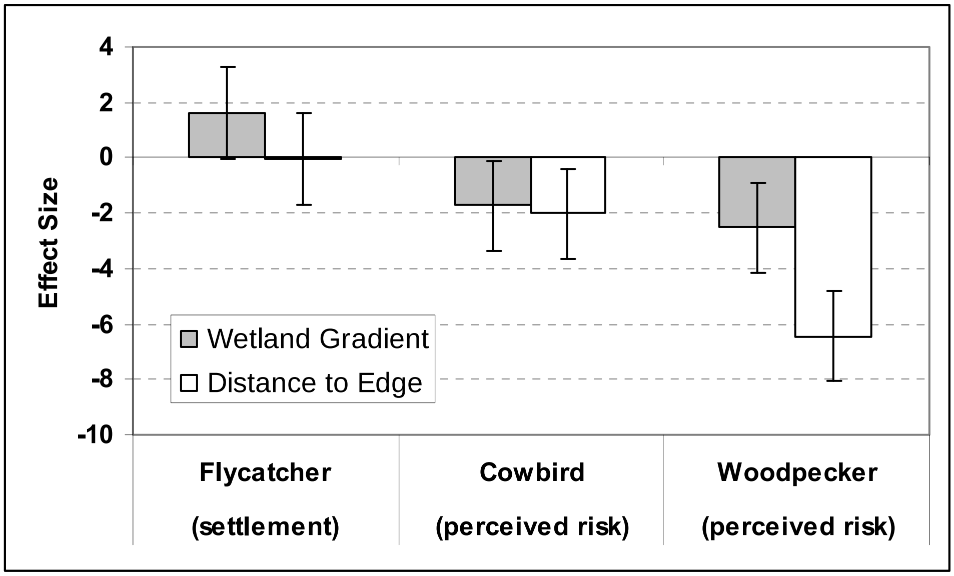

Figure 3.5. Effects of habitat variables on flycatcher settlement (proportional hazards regression) and perceived risk from cowbirds and woodpeckers (linear regression), 2001-2002. Effect size for each variable is calculated as the model-averaged parameter estimate divided by the standard error. Error bars are 90% confidence intervals.

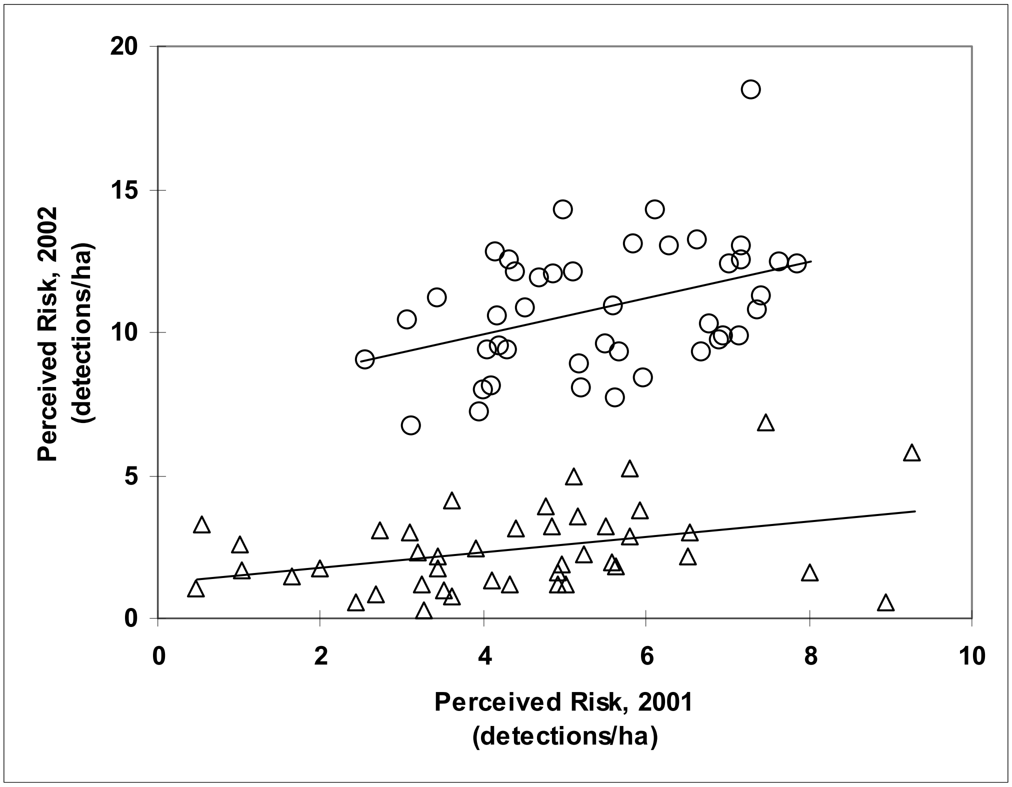

Figure 3.6. Relationship between perceived risk in 2001 and 2002. Woodpecker risk (triangles): linear regression slope = 0.26, SE = 0.10, $R^2 = 0.13$. Cowbird risk (circles): linear regression slope = 0.64, SE = 0.23, $R^2 = 0.16$.

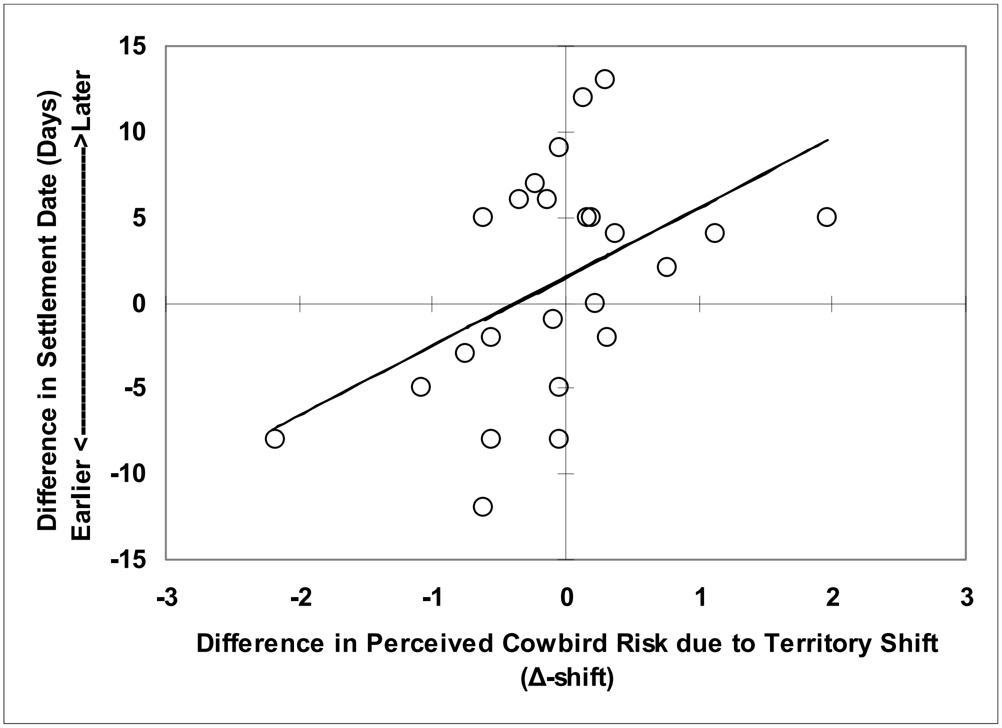

Figure 3.7. Relationship between the difference in perceived cowbird risk due to territory shift (Δ-shift) and the difference in territory settlement date (linear regression slope = 4.05, SE = 1.60, $R^2 = 0.23$, n = 24). Where perceived risk was reduced by the territory shift, settlement on that territory tended to be earlier than the previous year. Where perceived risk was increased by the territory shift, settlement was later in 8 of 10 cases.

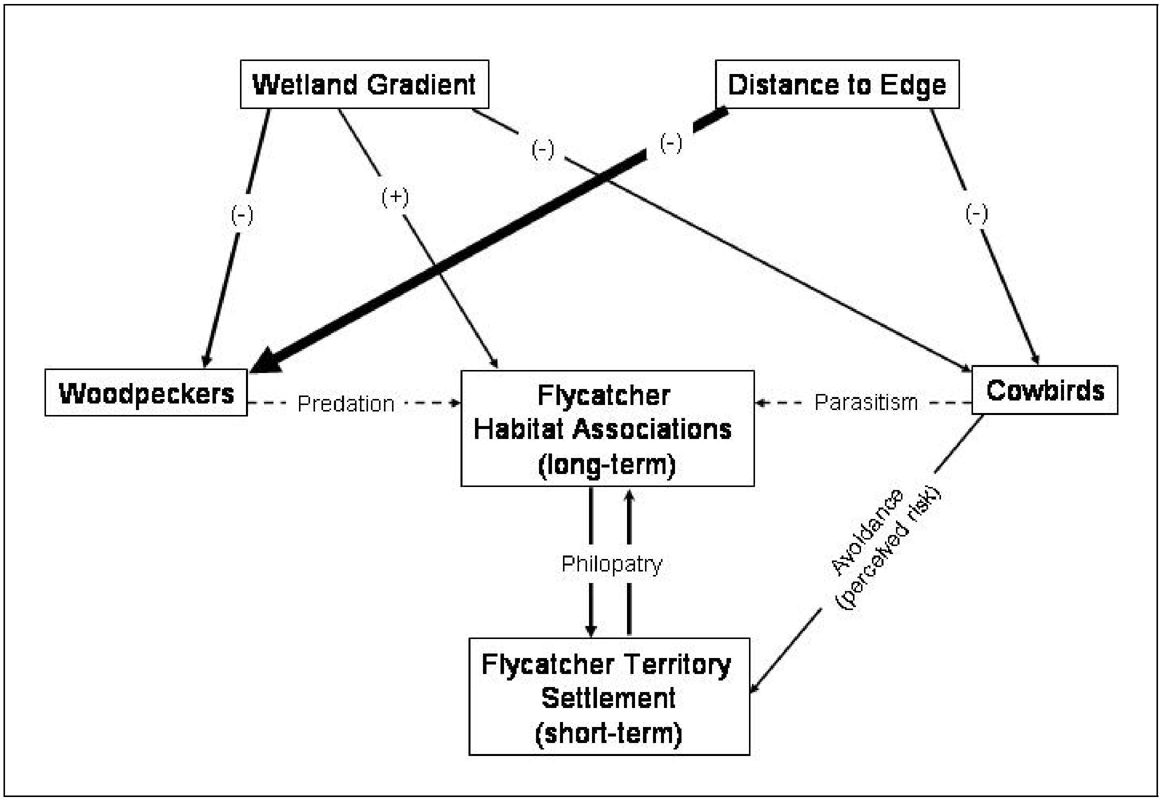

Figure 3.8. Conceptual model of the ecological relationships between habitat factors (wetland gradient and distance to edge), risks (woodpecker and cowbird activity), and flycatcher territory settlement in Delta National Forest. The relative strength of effects estimated in this study is represented by the thickness of connecting arrows; dashed lines indicate that the effect was not estimated in this study. For simplicity, many other influencing factors, such as unmeasured habitat features and the abundance of food resources, are not shown.

CHAPTER 4

EFFECTS OF FOREST RESTORATION AND LANDSCAPE CONTEXT ON ACADIAN FLYCATCHER NEST SUCCESS IN THE MISSISSIPPI ALLUVIAL VALLEY[1]

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[1] K.R. Hazler, D.J. Twedt, and R.J. Cooper. To be submitted to Landscape Ecology

ABSTRACT

In the Mississippi Alluvial Valley, bottomland hardwood forest is considered the habitat of greatest concern for avian conservation. Conservation planners emphasize reforestation adjacent to large tracts of extant forest, thereby increasing forest "core" area and improving both quantity and quality of habitat for forest-interior birds and other wildlife. However, it is not clear at what seral stage reforested stands effectively increase forest core from the perspective of mature forest specialists. We assessed the impact of increasing forest cover on Acadian flycatcher (*Empidonax virescens*) reproductive success, based on a 1-km radius around each nest, while controlling for other landscape and nest-level variables. We defined "forest cover" in alternate ways, depending on whether or not early successional stages were included. In a sample of 182 nests, nest survival was positively related to forest cover defined to include all successional stages. Models in which forest cover was defined to include only mature forest had little support. This implies that even prior to maturity, reforested tracts have a positive impact in the landscape in terms of improving nest survival in extant stands. In contrast, in a sample of 58 nests, brood parasitism was much more strongly related to mature forest cover than to forest cover defined to include all successional stages. Although the parameter estimate for the effect of mature forest cover did not differ statistically from zero, the trend suggests that brood parasitism decreased as mature forest cover increased. If this trend is real, then reforested tracts will need to mature before they can provide the benefit of reduced parasitism. Brood parasitism also decreased with increasing distance from interior forest disturbances, suggesting that forest harvest operations may increase the incidence of brood parasitism within extant forests.

INTRODUCTION

In the Mississippi Alluvial Valley (MAV), bottomland hardwood forest is considered the habitat of greatest concern for avian conservation (Twedt and Loesch 1999, Mueller et al. 2000). Formerly dominating the region, these bottomland forests have been largely converted to, and fragmented by, agriculture (Hamel et al. 2001). However, over the past few decades thousands of hectares of agricultural land have been reforested, with an ultimate restoration goal of 800,000 ha (King and Keeland 1999, Haynes 2004). In addition to increasing the quantity of mature bottomland hardwood habitat in the future, it is hoped that reforestation in the MAV will also improve the quality of extant forests in the short term by making the landscape context more favorable for forest-interior and area-sensitive birds.

Twedt et al. (2006) developed a spatially explicit decision support model for the restoration of forest bird habitat in the MAV. The model emphasizes a strategic approach to maximize the amount of forest “core”, defined as interior forest at least 1-km from a “hostile” edge (e.g., agricultural fields). Hence, reforestation adjacent to large tracts of extant forest is prioritized over reforestation of isolated tracts. However, it is not immediately clear at what seral stage reforested tracts effectively increase forest core area from the perspective of mature forest specialists.

Avian fecundity depends, in part, on nest survival and brood parasitism rates (Pease and Grzybowski 1995). These are likely influenced by processes operating at multiple spatial scales (Martin and Roper 1988, Chalfoun et al. 2002, Gannon 2005). At broad scales, landscape composition and juxtaposition of habitats drive patterns of predator and parasite abundance, while finer-scale habitat conditions can influence the vulnerability of individual nests.

Responses of nest predators to landscape patterns are complex, and can vary widely among taxa in different regions (Chalfoun et al. 2002). As a result, relationships between nest success and landscape structure cannot necessarily be extrapolated from one region to another. Context-specific data are necessary for conservation planning. Brood-parasitic Brown-headed Cowbirds (*Molothrus ater*) are likely to be most abundant in areas where feeding sites (e.g., agricultural fields and feedlots) are near host breeding sites (e.g., forests and shrublands). However, they are known to commute several km to use spatially distinct habitats for feeding, breeding, and roosting (Rothstein et al. 1984, Thompson 1994, Gates and Evans 1998, Raim 2000, Thompson and Dijak 2000). By converting agricultural fields back to forest, it is expected that the incidence of cowbird parasitism, and possibly nest depredation, should decrease in the region. Management of existing forests is likely to be a factor as well. Thinnings, patch cuts, and other disturbances create interior openings within the forest, which could affect the distribution of cowbirds and other predators. Forest disturbance in the form of patch cut harvests was associated with higher parasitism and nest depredation rates in another study within the MAV (Gannon 2005).

At local scales, several features of the habitat can affect nesting success. The availability of a large number of potential nest sites may dilute risk from predators and brood parasites (Martin and Roper 1988, Schmidt and Whelan 1999). For tree-nesting species, we expect that tree density or basal area could be an important predictor of nest survival. Floristic composition of potential nest substrates may be important as well. For some species, risk of nest predation and brood parasitism may be reduced by dense vegetation concealing the nest (Kelly 1993, Murphy et al. 1997, Hoover and Brittingham 1998). For other species, such as flycatchers, aggressive nest defense is often more important than nest crypticity, and open vegetation can reduce risk by increasing visibility and facilitating defensive maneuvers around the nest (Murphy et al. 1997).

We examined the influence of landscape context on the reproductive success of Acadian flyatchers (*Empidonax virescens*), a mature forest specialist that has been classified as a forest-interior, area-sensitive species (Whitcomb et al. 1981, Hamel 1992). Our primary objective was to quantify the impact of increasing forest cover, which we defined in two alternative ways depending on whether younger seral stages (i.e., reforested tracts and patch cuts) were included in the concept. We weighed the evidence to determine which measure of forest cover was a better predictor of nest survival and brood parasitism. As a third alternative, we considered the possibility that distance to agriculture was a better predictor than forest cover *per se*. A secondary objective was to determine whether the successional stage of reforested stands was a relevant factor. A third objective was to assess the impact of interior forest openings due to harvesting operations and other disturbances. In addition to addressing these main objectives, we also controlled for potentially important nest-level characteristics.

METHODS

Study Sites

We located and monitored nests on 30 study sites in northeast Louisiana and west-central Mississippi within 60-km of Vicksburg, Mississippi. From 2000 to 2002, we surveyed 10 different 14- to 28-ha study sites per year on Tensas National Wildlife Refuge, Delta National Forest, Twin Oaks Wildlife Management Area, Mahannah Wildlife Management Area, and adjacent private lands (Table 4.1, Figure 4.1); none of these sites were revisited between years. Each study site was located within mature bottomland hardwood forest adjacent to either an agricultural field or a field that had been reforested. The surveyed area extended 400-m into the forest interior.

Nests

We located and monitored nests within each study site from mid-April through the end of July, checking nests every 2-3 days to determine their fates. We used a mirror mounted on an extendable pole (maximum reach ~9 m) to monitor nest contents. However, because many nests were beyond reach of this pole, we also relied on behavioral observations to determine nest status. If parents were not in attendance, observers monitored nests until a parent returned or for ≥15 min. A nesting attempt was declared finished if no parent was observed near the nest for two consecutive 15-min checks, an obvious renest was found nearby, and/or there were obvious signs of fledging or failure.

We assigned nest fates based on evidence as recommended by Manolis et al. (2000). We assigned the fate of "fledged" if one or more chicks were last observed sitting high up or on the edge of the nest, stretching wings, or otherwise visibly ready to fledge; if fresh droppings were found directly below the nest; or if fledglings were found nearby. We assigned the fate of "failed" if a nest became inactive prior to the date at which fledging could potentially have occurred. Fate was declared "unknown" if a nest was found inactive after reaching the potential fledging window, or if monitoring was discontinued for some reason not related to nest fate.

For nest survival analysis using proportional hazards regression (see Statistical Analysis), we had to estimate nest age at the beginning of the statistical observation period. Nest age was counted from 0 (zero) on the day the first egg was laid. Nests found during building or laying could be aged precisely. For nests found later in the cycle, we assumed that the third and last egg was laid at nest age = 2, chicks hatched at nest age = 15, and fledged at nest age = 29. We used hatch and fledge dates (if known) to age the nest accordingly. Nests found during and surviving through the incubation phase were aged at (15 – [# observation days until hatch]). Nests found and terminated during the incubation phase were aged at (8.5 – 0.5*[# obs. days until last active]). Nests found during the hatchling stage and surviving to the potential fledge stage were aged at (29 – [# obs. days until last active]). Nests found during the hatchling stage but not surviving to fledge were aged at (0.5*(15 + (29 – [# obs. days until last check])). For successful nests and those of unknown fate, nest age at termination (= censoring time in survival analysis) was assumed to be the age when last active; for failed nests it was the mean of the ages when last active and last checked.

For the estimation of parasitism rates, we included only those nests found prior to the nestling stage in which we could reliably distinguish flycatcher from cowbird eggs. Although a few nests were parasitized with more than one cowbird egg, we designated nests simply as either “parasitized” or “not parasitized”.

Vegetation

Once a nest was terminated, we sampled vegetation using a modification of the methods of James and Shugart (1970), from which 5 variables were derived to describe the habitat immediately surrounding each nest (Table 4.2). Within 11.3-m radius (0.04 ha) of the nest, we identified and measured diameter at breast height (dbh) of all trees ≥10 cm dbh. From these data, we calculated tree density and basal area. We used our tree samples to derive an additional quantitative variable representing the floristic composition along the hydrologic gradient, ranging from 1 (characteristic of sites flooded 3 months per year or more) to 12 (characteristic of sites flooded 2 weeks to 1 month per year or less). This hydrologic gradient index was calculated as:

$$HG = \frac{1}{2}\left[\frac{\sum_{1}^{T}(C_t \times W_t)}{C_{sum}} + \frac{\sum_{1}^{T}(B_t \times W_t)}{B_{sum}}\right]$$

where T is the total number of tree species and the subscript t refers to each individual species; C_t and B_t are the counts and basal area, respectively, for species t; C_{sum} and B_{sum} are the counts and basal area summed over all species in the plot; and W_t is the wetland rank of species t on the scale of Dale and Ware (2004). See Chapter 3 for more details. As a measure of understory density, we used a 50 cm x 50 cm coverboard, divided into 25 equal squares, to estimate vegetative cover at 2.5-m and 5-m above the ground – a variation on the coverboard method described by Nudds (1977). Our measure of understory cover was the mean of coverboard readings in 4 cardinal directions, reported as a proportion of total possible squares covered. As an alternate measure of understory density, we counted the number of stems of saplings and small trees (< 10-cm dbh) within a 5-m radius of the nest.

Landscape

We used Erdas Imagine (Leica Geosystems 2003) to conduct a supervised classification of Landsat imagery (30-m resolution) from September 2001. We initially derived 6 land cover classes: MF (mature forest), RF2 (reforestation at sapling - tall shrub stage), RF1 (reforestation at grass - low shrub stage), AGR (agriculture or pasture), BARE (roads and other barren land), and H2O (water). We used a number of geographic data sources from the Mississippi Alluvial Valley Conservation Planning Atlas (MAV-CPA, LMVJV 2002), as well as our own knowledge of conditions on and adjacent to our study sites, to choose suitable training sites for the classification. We iteratively added training sites until a satisfactory classification was obtained. We considered the classification satisfactory once >90% of RF1 and RF2 training sites were correctly identified as reforested, and >70% were identified to the correct reforestation stage. This resulted in >95% correct classification of MF, AGR, and H2O training sites. The percentage of BARE classed pixels was minimal in the vicinity of our study areas and was not evaluated.

We converted the classified image to GRID format for further processing in ArcView (ESRI 1999) and ArcGIS (ESRI 2006). Harvested patches and other openings within the mature forest matrix were typically classified as RF1 or RF2. To distinguish these forest interior disturbances from former agricultural tracts that had been reforested, we masked the classified grid with a forest/non-forest classification based on 1992 imagery from the MAV-CPA (LMVJV 2002). All pixels classified as forest in the MAV-CPA but classified as reforestation based on the 2001 imagery were reclassifed as HARV (harvest or other interior forest disturbance). A landcover map obtained from the

Mississippi Gap Analysis Program (R. Minnis, personal communication) was used to further refine the final classification.

We subjected the classified image to one pass of a majority filter to reduce speckling, which was a problem in the reforested stands where some pixels were misclassified as AGR. We expanded the MF class by one pixel to clean up the mature forest-agriculture and mature forest-reforestation edges. However, this resulted in the loss of much of the HARV and H2O classes in the forest interior, so we ran a map query to return those pixels to their original classification.

We ran the Euclidean distance tool to determine the distance of each pixel from the AGR and HARV classes, and extracted these values for each nest location, which had been recorded in the field using a GPS receiver. We then buffered each nest with a 1-km radius, and tabulated the areas of each cover class within the buffer for each nest. We derived 4 landscape metrics based on the amount of forest cover of different seral stages within 1-km of nest locations, and additional 2 metrics measuring the distance to agriculture, and the distance to patch cuts and/or other interior forest disturbances (Table 4.2).

Statistical analysis

We used proportional hazards regression to model the effects of landscape context and vegetation variables (Table 4.2) on nest survival, and logistic regression to model the effects on the incidence of brood parasitism. All analyses were conducted using the PHREG procedure in conjunction with other macros and procedures in the SAS statistical package (Allison 1995, SAS 2004). We stratified by sub-region (Delta, Mahannah, and Tensas) to account for some of the spatio-temporal variation.

We evaluated competing models within an information-theoretic framework (Burnham and Anderson 2002), ranking models by Aikaike's Information Criterion for small samples (AIC_c) and weights of evidence (w_i). The set of 10 candidate models was developed to (1) weigh the evidence in favor of several primary hypotheses relating landscape context to reproductive success, (2) control for nest initiation date and/or important vegetation characteristics at the nest, if applicable, and (3) minimize correlations between predictor variables (Graham 2003) included in individual models. To compare the relative importance of different predictor variables, we calculated model-averaged effect sizes (ES; parameter estimate divided by standard error), noting that $|ES| \geq 1.64$ is equivalent to a 90% confidence interval that does not include zero. We also generated model-averaged predictions of the probabilities of brood parasitism and of a nest surviving the full nesting cycle (30 days) under varying conditions.

To evaluate the effect of increasing forest cover on reproductive success, we estimated the responses to the predictor variables PFOR1 (proportion of mature forest in the landscape) and PFOR2 (proportion of forest of any successional stage in the landscape). If increasing mature forest cover in the landscape improves reproductive success, but earlier successional forests (e.g., reforested tracts and harvested areas) do not contribute to this effect, then nest survival and/or brood parasitism should be more strongly related to the variable PFOR1 than to PFOR2. Alternatively, if increasing forest cover in the landscape improves reproductive success regardless of successional stage, then nest survival and/or brood parasitism should be more strongly related to PFOR2 than to PFOR1. A third alternative is that simply increasing the distance from agriculture improves reproductive success, regardless of landscape composition. If this is the case, then nest survival and/or brood parasitism should be more strongly related to DAGR than to PFOR2 or PFOR1.

We hypothesized that reforestation in the grass-short shrub stage might be of less value to improving reproductive success than reforestation in the tall shrub-sapling stage, and evaluated this by testing the response to the variable PRF1 (early-stage reforestation as a proportion of all reforestation). We also hypothesized that openings in the mature forest interior would reduce reproductive success by attracting nest predators and/or cowbirds. We evaluated this by measuring the response to the variables PHARV (proportion of disturbed interior forest) and DHARV (distance to nearest interior forest disturbance).

In addition to addressing the above hypotheses, we sought to control for potentially important nest-level characteristics. Since these variables were not of primary interest in this study, we only included a subset deemed most appropriate based on an initial screening. After eliminating highly correlated nest-level variables (see below), we screened the remaining variables by fitting all possible 2-variable models, then examining model weights and model-averaged parameter estimates. We retained only those variables that had 90% confidence intervals not spanning zero and/or had greater weight of evidence (in a single-variable model) than the null model. The retained subset of nest-level variables was then included in all landscape-level candidate models to reduce nuisance variation and improve precision of parameter estimates.

We examined the correlation matrix of the predictor variables and sought to minimize statistical problems associated with multicollinearity (Graham 2003) by carefully selecting appropriate variable combinations. We decided *a priori* to include at most one measure of overstory structure (either TREES or BASAL) and one measure of understory structure (STEMS or UCOV). We also considered floristic composition along the hydrologic gradient (HG) and nest initiation date (NI) as predictor variables. By their nature, PFOR1, PFOR2, and DAGR are inevitably highly correlated and it made no biological sense to include any combination of them in the same model. Hence, there is no global model in the candidate set within which all other models are nested. PHARV and DHARV are also directly related, so only one would be included in any given model, with the decision made to minimize correlation with the other landscape factors.

Because there was no global model, we instead assessed the fit of a “proxy” global model, which was one of the most highly parameterized models in the candidate set. We plotted deviance residuals against the linear predictor, against each predictor variable, against study sites, and against geographic coordinates to see if there were any patterns indicating a lack of model fit due to spatial autocorrelation or misspecification of the relationship with one or more covariates. For the proportional hazards model, we also examined plots of Schoenfeld residuals for each predictor variable against time to evaluate whether the proportionality assumption was met.

Additional post-hoc analyses are described in the Results section, since they were not planned as part of the original analytical approach, instead arising from unexpected results.

RESULTS

Variable Screening

As expected, there was a relatively high correlation between TREES and BASAL ($r = 0.46$) and between STEMS and UCOV ($r = 0.51$). We chose TREES and STEMS to represent overstory and understory structure, respectively, because these were less correlated with other variables of interest (Table 4.3). After eliminating BASAL and UCOV, the remaining nest-level variables TREES, STEMS, HG, and NI had low pairwise correlations ($|r| < 18$). After variable screening and elimination with preliminary regression analyses, TREES was the only nest-level variable retained for inclusion in the nest survival models, and NI (nest initiation date) was the only variable retained for inclusion in the brood parasitism models.

Nest Survival

We included 182 nests in the survival analysis, of which 89 failed and 93 were censored (primarily due to fledging, but some due to truncated monitoring or unknown fates). Average nest height was 8.2 m but ranged from 2.8 to 18.3 m. Thus, nearly half of the nests were out of reach of an extendable pole and relied on behavioral observations for monitoring. Regardless of sub-region, a nest had a 38.4% probability (90% confidence interval = [32.4% , 45.4%]) of surviving until the potential fledging stage, which we considered to be 3 days before the fledge date of a “typical” nest (nest age = 26).

Inspection of deviance and Schoenfeld residuals from the model with predictors PFOR2, PRF1, PHARV, and TREES revealed no notable patterns, and we concluded that model fit was adequate and that the proportionality assumption was satisfied.

The 3 top-ranked models (Table 4.4) all contained the variable PFOR2, and the model-averaged parameter estimate (Table 4.5) supported the hypothesis that the probability of nest survival increased with increasing forest cover of all successional stages (Figure 4.2). The alternative hypotheses represented by the variables PFOR1 (proportion of mature forest cover) and DAGR (distance to agriculture) had less support. Excluding models 1, 2, 7, and 8 to put the alternatives on equal footing, the relative weights of evidence for PFOR2, DAGR, and PFOR1 were 1.00, 0.34, and 0.23, respectively. In addition, the parameter estimates for DAGR and PFOR1 were not statistically different from zero, although they were in the hypothesized direction.

There was equivocal evidence for an effect of interior disturbances in mature forest, as measured by PHARV (proportion) and DHARV (distance). There was essentially no difference in the weight of evidence in favor of models with either PHARV or DHARV (models 1, 3, 5, 7, and 10; $\sum w_i = 0.49$) versus models without either of these variables (models 2, 4, 6, 8, and 9; $\sum w_i = 0.51$), and neither of their effect sizes (-1.425 and 1.351, respectively) were statistically different from zero at the 90% confidence level. We had hypothesized that PHARV would increase and DHARV would decrease the hazard of nest failure, but if anything the opposite would be indicated, since our parameter estimates were of opposite sign (Table 4.5).

There was even less support for an effect of PRF1 (early-stage reforestation as a proportion of all reforestation). Excluding the PFOR1 models (to balance the models considered), the support for models with PRF1 as a covariate was 0.38 relative to models without it. The parameter estimate was opposite in sign from what we had hypothesized, but was not statistically different from zero. At the scale of the nest site, increasing tree density (TREES) had a positive effect on nest survival (Table 4.5, Figure 4.3).

Brood parasitism

We included 74 nests in the analysis of brood parasitism. The overall parasitism rate [90% C.L.] was 0.446 [0.370, 0.512], but varied substantially between sub-regions. We documented only one nest parasitized out of 16 in the Tensas sub-region, with a corresponding parasitism rate of 0.063 [0, 0.154]. The parasitism rate was 0.595 [0.501, 0.671] in the Delta sub-region, and 0.476 [0.329, 0.591] in the Mahannah sub-region. It was important to control for a seasonal effect, because incidence of brood parasitism declined with later nest initiation dates (Table 4.7).

Inspection of deviance residuals plotted against geographic coordinates revealed poor fit of the proxy global model, due to the lack of brood parasitism in the Tensas sub-region. Plots of the residuals against predictor variables revealed no pattern, however. Without adding undue complexity to the models (e.g., interaction terms between sub-region and predictor variables), we felt that the only way to rectify the problem was to eliminate the Tensas nests from the dataset. This reduced sample size to 58, but improved model fit and our confidence in model selection and parameter estimatation, applicable to the Delta and Mahannah sub-regions. We report here the results from this reduced dataset, but note that the same qualitative conclusions were reached by analyzing the full dataset.

There was some evidence that the probability of brood parasitism decreased with increasing mature forest cover. The top-ranked model ($w_i = 0.49$; Table 4.6) included the variables PFOR1, DHARV, and NI. There was greater support for an effect of PFOR1 than for DAGR or PFOR2, with relative weights of evidence of 1.00, 0.36, and 0.11, respectively (excluding models 1, 2, 7, and 8 to keep models on equal footing). None of these parameter estimates were statistically different from zero at the 90% confidence level, but PFOR1 came closest with an effect size of -1.405 (Table 4.7). In contrast, both PFOR2 and DAGR had standard errors that exceeded the parameter estimates. There also was essentially no support for an impact of PRF1, which is consistent with the lack of effect of PFOR2.

Brood parasitism decreased with increasing distance to the nearest interior forest disturbance (Table 4.7, Figure 4.4). Models including either DHARV or PHARV had a combined weight of evidence of 0.78, as compared to 0.22 (a ratio of 3.55 to 1) for models not including either variable (Tables 4.6).

In an attempt to elucidate why there was such a difference in parasitism rates between Tensas and the other two sub-regions, we inspected the distributions of predictor variables by sub-region and conducted analyses of variance to see if there were any notable differences. Only two variables, basal area and the hydrological gradient, differed significantly (Tukey pairwise comparisons, $p < 0.05$) between Tensas and both other sub-regions (Figures 4.5-4.6). We fit an additional set of post-hoc models (again excluding the Tensas nests) which included DHARV and NI, plus all combinations of PFOR1, BASAL, and HG (Table 4.8). Since values of BASAL and HG were higher in Tensas, where parasitism was low, we hypothesized that parasitism was negatively associated with these variables. However, the opposite was the case (Table 4.9). Both variables had positive coefficients, although the coefficient for BASAL was not statistically different from zero. We also found that the evidence in favor of dropping PFOR1 as a covariate was 3 to 2. Its estimated effect size was somewhat reduced compared to the estimate in the a priori analysis. It trended negative, but was not statistically different from zero. The estimated effects of DHARV and NI remained similar to the previous estimates, increasing confidence in their importance.

DISCUSSION

Forest Cover and Reforestation

In the long term, reforestation efforts in the Mississippi Alluvial Valley will increase the availability of bottomland hardwood habitat, but it may take 60 years or more (King and Keeland 1999) for these tracts to become suitable for mature forest specialists, such as Acadian flycatchers. In the short term, our study demonstrates that reforested tracts can act as habitat buffers, effectively increasing forest core area by improving nest survival in adjacent mature forests. It is consistent with other studies that have documented a positive relationship between forest cover and nesting success (e.g., Robinson et al. 1995, Hartley and Hunter 1998), but opposing examples exist as well (e.g., Tewksbury et al. 1998), emphasizing the need for region-specific data.

Using a 1-km radius to define landscapes surrounding each nest, we explicitly evaluated whether nest survival was most closely related to the distance to agriculture (DAGR), to the proportion of mature forest only (PFOR1), or to the proportion of forest regardless of successional stages (PFOR2). We found the latter to be the case. All else being equal, our models predicted that the probability of nest survival to the potential fledging stage would increase from about 0.24 at 40% forest cover, to about 0.37 at 80%

forest cover (Figure 4.2). More demographic data are needed for full evaluation, but this difference in nest success could mean the difference between a population source and a sink (Donovan and Thompson 2001). The ratio of earlier-stage reforestation to all reforestation appeared to have little or no effect on nesting success. Thus, the widespread replacement of agriculture with reforestation, even in the early stages, is likely to have a positive impact on the nesting success of forest songbirds in the region.

The influence of forest cover on the incidence of brood parasitism was more equivocal, because neither measure of forest cover had a parameter estimate statistically different from zero. However, the weight of evidence in favor of PFOR1 over PFOR2 was nearly 9 to 1. Furthermore, while the confidence interval for PFOR2 was nearly symmetrical about zero, the confidence interval for PFOR1 trended to the negative, suggesting a decrease in brood parasitism with increasing mature forest cover. In our post hoc analysis, in which models were evenly balanced so that half included PFOR1 and half did not, the evidence in favor of dropping PFOR1 was 3 to 2. The model-averaged effect size was similar in the two analyses: -1.405 in the a priori analysis and -1.232 in the post hoc analysis. A larger sample size likely would have clarified the relationship. We do not feel confident in proclaiming the importance or unimportance of this variable based on the current study. However, other studies have shown decreased parasitism rates with increasing forest cover (e.g., Petit and Petit 2000, Thompson et al. 2000), and we suspect that the trend we observed, although weak, was real. If the observed trend is real, it is possible that as reforested tracts mature, the incidence of brood parasitism in the region could decline over time. In the successional stages at which we observed them, however, reforested tracts do not appear to have any impact on reducing cowbird parasitism in adjacent forests.

Forest Disturbance

We found no evidence that interior forest disturbances, as measured by DHARV or PHARV, caused increased nest failure. In fact, if anything, nest survival was higher closer to interior forest openings, or in areas with a greater proportion of interior openings. The effect sizes were not statistically different from zero, but the trends were apparent and in opposition to our expectations. In another study in the region, uneven-aged group selection timber harvest reduced nest success of species nesting in the forest midstory and canopy, including Acadian flycatchers (Twedt et al. 2001). Gannon (2005) observed that interior forest roads were associated with increased nest predation, but patch cuts were not. Our image classification based on LandSat imagery was too crude to distinguish between different types of forest openings, and we also did not account for size of the openings. This may be relevant and probably warrants further investigation.

Our data strongly supported the hypothesis of a positive association between interior forest disturbance and brood parasitism. Our a priori models predicted ~58% chance of parasitism at 50-m from an interior opening, as compared to ~18% chance of parasitism at 450-m from an opening (Figure 4.4). The estimated effect size was similar and even somewhat stronger in our set of post hoc models. Our result is consistent with Gannon's (2005), who found that proximity to patch cuts increased the probability of brood parasitism for both Acadian Flycatchers and Prothonotary Warblers. Likewise, Robinson and Robinson (2001) reported higher parasitism rates on Acadian Flycatchers and Kentucky Warblers in selectively harvested forest, as compared with less disturbed forest.

Most hardwood forests of the major alluvial floodplains in the southern United States have been logged one to several times in the past (Kellison et al. 1998, Wigley and Lancia 1998). Given land ownership patterns and economic realities, timber harvesting is likely to continue shaping the ecology of present and future forests in the LMAV (Hamel et al. 2001). Small clearcuts or selective harvests can mimic treefall gaps and provide habitat conditions suitable for bird species associated with early-successional and forest understory habitat. Several such species are considered high priority for management in the LMAV, and active forest management is viewed as compatible with bird conservation (Twedt et al. 1999). However, the potential benefits of forest management for early-successional birds must be weighed against the potential detrimental impacts on species depending on mature forests (Hagan et al. 1997, Wigley and Lancia 1998, Twedt et al. 1999).

Nest-level Characteristics

We found a positive influence of tree density on nest survival. Although vegetation measurements directly at the nest are not necessarily typical of the stand in which the nest is located (Wilson and Cooper 1998a), they are probably at least correlated at the scale of our study. This finding suggests that efforts to achieve higher stem densities in reforested tracts may be beneficial. We recorded a range of stem densities (including only trees > 10 cm dbh) from 3 to 33 per 0.04-ha plot, which equates to 75 to 825 trees/ha. Twedt et al. (in review) recommended achieving stem densities of > 1000 stems/ha in reforestation plantings.

The hydrologic gradient can have a significant influence on habitat use by many bird species (Robbins et al. 1989, Wakeley and Roberts 1996, Wigley and Lancia 1998, Inman et al. 2002). However, the importance of the hydrologic gradient to Acadian flycatcher reproduction is unclear. Our post hoc analysis revealed a positive correlation between HG and brood parasitism, indicating that nests on drier sites were more likely to be parasitized. Yet parasitism rate was extremely low in Tensas, where nest sites were typically drier than in the other sub-regions.

Nests inititated later in the season were less prone to brood parasitism, corresponding with the cowbird breeding cycle (Lowther 1993). This highlights the importance of renesting. Some birds renested at least 5 times (personal observation). Acadian flycatchers were also likely to double-brood if the first nest fledged, and the second nest would be less likely to be parasitized due to the seasonal effect. Because parasitism rates were high, and clutch size is typically reduced in parasitized nests, renesting may be critical for achieving seasonal fecundity sufficient to offset annual adult mortality (Dececco et al. 2000). Other species with less propensity to renest may not do as well in these conditions, especially those that fledge only cowbirds and then do not attempt a second brood (Pease and Grzybowski 1995).

Sub-regional Differences

Among our three study sub-regions, nest survival was similar. We reported a 38% chance of survival to the potential fledging window, which equates to approximately

33% nest success. This compares favorably with estimates from other researchers working with Acadian flycatchers in the Mississippi Alluvial Valley. In the White River National Wildlife Refuge, Wilson and Cooper (1998b) reported success rates of 10% - 25%, and Gannon (2005) reported success rates of 8% - 46%. Twedt et al. (2001) reported nest success rates of 14% -35% in the Tensas National Wildlife Refuge.

Brood parasitism varied substantially between our sub-regions. We found extremely high parasitism rates in Mahannah (48%) and Delta (60%), as compared with 21% - 29% reported from other studies in the MAV (Wilson and Cooper 1998b, Gannon 2005). In stark contrast, out of 16 nests with sufficient data there was only 1 documented case of brood parasitism in the Tensas sub-region, leading us to eliminate the Tensas nests from the parasitism dataset prior to analysis. Since years and sub-regions were confounded, it is impossible to know whether spatial or temporal factors were responsible for the large discrepancy. We conducted point counts at each study site during the same years in which nests were monitored, and cowbirds were detected with similar frequency in all 3 sub-regions (see Chapter 4). Thus it is unlikely that population levels could account for the drastically lower parasitism rate in Tensas. Besides cowbird density, various interacting factors can influence brood parasitism rates, including availability of preferred and alternative hosts; juxtaposition of and distance between distinct feeding, breeding, and roosting areas; host-parasite behavioral interactions; and habitat characteristics at various scales (Smith et al. 2000).

Our post hoc analyses failed to elucidate possible habitat features that could have been associated with the sub-regional difference. Basal area and the hydrologic gradient were higher at nests in Tensas than in the other two sub-regions, suggesting that brood parasitism might decrease with higher basal area and/or drier sites. However, the opposite was the case: post-hoc logistic regression models of parasitism (excluding the Tensas nests) revealed a positive response to the hydrologic gradient, that is, nests on drier sites were more likely to be parasitized. There was also a possible (statistically uncertain) positive response to basal area. Adding to the confusion we found that, at the scale of a single 56-ha plot, cowbird activity was associated with wetter areas along the hydrologic gradient (Chapter 3). Cowbirds, and their interactions with hosts, may be responding to the hydrologic gradient differently depending on the scale of reference. Further study is warranted to determine whether parasitism rates in the year 2000 were uncharacteristically low, or whether there is a true sub-regional difference. If the latter is the case, discovery of the driving factors responsible could assist in finding strategies to reduce brood parasitism across the region.

Bottomland hardwood forest restoration in the Missisippi Alluvial Valley is an ambitious undertaking, with a stated goal of converting circa 800,000 ha of agricultural land back to forest (Haynes 2004). In the past, reforestation efforts have been somewhat opportunistic, focused on maximizing the area restored but with little consideration for landscape context (King and Keeland 1999). Yet, as demonstrated in this and other studies, landscape context can have a profound impact on habitat quality for breeding birds. By prioritizing reforestation adjacent to extant forest tracts (Llewellyn et al. 1996, Twedt et al. 1999, Twedt et al. 2006), current conservation efforts are increasing habitat quality as well as quantity for forest birds, now and into the future.

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Table 4.1. Study areas in the Mississippi Alluvial Valley.

Site Acronym	Sub-Region	Year Studied	Adjacent habitat[a]	Area (ha)	N_s[b]	N_p[c]
CHEC	Tensas[d]	2000	AGR	20	6	1
MCLE	Tensas	2000	AGR	20	5	3
TEND[e]	Tensas	2000	AGR	20	0	0
WAVE[f]	Tensas	2000	AGR	20	0	0
WORD	Tensas	2000	AGR	20	11	4
DOOD	Tensas	2000	RF1	19	3	1
MADD	Tensas	2000	RF1	20	4	1
CHAP	Tensas	2000	RF2	20	6	2
GOSS	Tensas	2000	RF2	20	11	3
NOLA	Tensas	2000	RF2	20	3	1
DELT	Delta[g]	2001	AGR	28	3	1
OAKS	Delta	2001	AGR	14	5	5
SPAN	Delta	2001	AGR	28	8	5
DAVI	Delta	2001	AGR/RF1	28	8	3
LONG	Delta	2001	RF1	28	8	2
SNAK	Delta	2001	RF1	30	10	5
WILL	Delta	2001	RF1	28	11	4
HUFF	Delta	2001	RF2	28	5	3
MANA	Delta	2001	RF2	28	6	2
TWIN	Delta	2001	RF2	14	6	3
UGLY	Delta	2002	AGR	27	12	4
JARV	Mahannah[h]	2002	AGR	28	5	3
MART	Mahannah	2002	AGR	28	4	1
ATWO	Mahannah	2002	RF1	25	10	1
HOLE	Mahannah	2002	RF1	14	9	6
NEWM	Mahannah	2002	RF1	28	6	1
COLE	Mahannah	2002	RF2	14	5	2
CYPR	Mahannah	2002	RF2	25	4	2
JOLL	Mahannah	2002	RF2	28	7	5
MIMS	Mahannah	2002	RF2	26	1	0
TOTAL					**182**	**74**

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[a] AGR = agriculture, RF1 = reforestation in the grass/low shrub stage, RF2 = reforestation in the sapling/tall shrub stage.

[b] Sample size of nests used in survival analysis

[c] Sample size of nests used in parasitism analysis. Sample size is smaller than for survival analysis because nests had to be found early in the nesting cycle and be accessible with a mirror pole.

[d] Sites within or near Tensas National Wildlife Refuge

[e] Only one active nest was found at this site, but vegetation data are missing so it was excluded from analysis.

[f] Although 8 active nests were found and monitored at this site, harvest operations prior to the end of the field season precluded vegetation sampling so they were excluded from analysis.

[g] Sites within or near Delta National Forest or Twin Oaks Wildlife Management Area

[h] Sites within or near Mahannah National Wildlife Refuge

Table 4.2. Predictor variables considered in analyses of Acadian flycatcher nest survival and brood parasitism.

Variable	Variable Description	Formula (if applicable)[a]	Range	Mean
	Landscape Context Variables			
PFOR1	Proportion of forest in the landscape[b], including only mature forest	$\frac{MF}{TOT}$	0.30 – 0.84 (proportion)	0.60
PFOR2	Proportion of forest in the landscape, including all successional stages	$\frac{MF + PCUT + RF2 + RF1}{TOT}$	0.37 – 1.00 (proportion)	0.84
PRF1	Area of early-stage reforestation as a proportion of total reforestation	$\frac{RF1}{RF2 + RF1}$	0.00 – 1.00 (proportion)	0.43
PHARV	Area of patch cuts and other interior forest disturbance as a proportion of all extant (non-reforestation) forest	$\frac{PCUT}{MF + PCUT}$	0.01 – 0.41 (proportion)	0.10
DHARV	Distance to nearest patch cut or other interior forest disturbance		0 – 524 m	148
DAGR	Distance to nearest agriculture		0 – 859 m	315
	Nest-level Variables			
TREES	Number of trees > 10-cm dbh within 11-m radius		3 – 33 trees/0.04 ha	16
BASAL	Basal area of trees > 10-cm dbh		5.5 – 64.9 m^2/ha	26.02
STEMS	Density of saplings and small trees < 10-cm dbh within 5-m radius		0 – 55 stems/0.008 ha	7
UCOV	Understory cover at 2.5-m and 5.0-m		0.00 – 0.97 (proportion)	0.28
HG	Hydrologic gradient index: a quantification of floristic composition along the hydrologic gradient[c]	$\frac{1}{2}\left[\frac{\sum_{1}^{T}(C_t \times W_t)}{C_{sum}} + \frac{\sum_{1}^{T}(B_t \times W_t)}{B_{sum}}\right]$	1.28 – 10. 89 (scale 1 – 12)	8.27
NI	Nest initiation date		3May – 9Jul	30May

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[a] TOT = total area in the landscape, minus pixels classified as water (H2O) or barren (BARE); MF = mature forest area; HARV = area of patch cuts or other interior forest disturbance; RF2 = later-stage reforestation (tall shrub – sapling stage); RF21 = earlier-stage reforestation (grass – short shrub stage)

[b] Landscape is defined as a 1-km radius circle around each nest.

[c] See Methods for details

Table 4.3. Correlation matrix of potential predictor variables. Correlations with |r| > 0.20 are in boldface; |r| > 30 are also underlined.

	TREES	BASAL	STEMS	UCOV	HG	NI	PFOR1	PFOR2	PRF1	PHARV	DHARV	DAGR
TREES		**0.46**	-0.17	**-0.29**	0.09	-0.13	0.11	**0.23**	-0.15	0.02	0.00	**0.21**
BASAL	**0.46**		-0.07	**-0.24**	**0.33**	0.01	**0.21**	0.03	-0.10	**-0.24**	**0.28**	**0.23**
STEMS	-0.17	-0.07		**0.51**	-0.14	0.01	-0.02	-0.01	-0.11	-0.05	-0.02	0.00
UCOV	**-0.29**	**-0.24**	**0.51**		-0.13	0.03	**-0.21**	-0.13	-0.14	0.06	-0.12	-0.17
HG	0.09	**0.33**	-0.14	-0.13		0.00	-0.03	**-0.26**	0.01	**-0.27**	**0.45**	-0.09
NINIT	-0.13	0.01	0.01	0.03	0.00		0.00	0.08	-0.06	0.01	-0.05	0.09
PFOR1	0.11	**0.21**	-0.02	**-0.21**	-0.03	0.00		**0.50**	0.08	**-0.61**	**0.24**	**0.59**
PFOR2	**0.23**	0.03	-0.01	-0.13	**-0.26**	0.08	**0.50**		-0.05	0.06	**-0.31**	**0.60**
PRF1	-0.15	-0.10	-0.11	-0.14	0.01	-0.06	0.08	-0.05		-0.12	0.15	-0.12
PHARV	0.02	**-0.24**	-0.05	0.06	**-0.27**	0.01	**-0.61**	0.06	-0.12		**-0.53**	**-0.23**
DHARV	0.00	**0.28**	-0.02	-0.12	**0.45**	-0.05	**0.24**	**-0.31**	0.15	**-0.53**		0.07
DAGR	**0.21**	**0.23**	0.00	-0.17	-0.09	0.09	**0.59**	**0.60**	-0.12	-0.23	0.07	

Table 4.4. Comparison of proportional hazards regression models to evaluate the influence of landscape context on Acadian flycatcher nest survival.

Explanatory variables[a]	Model #	-2 log L[b]	K[c]	AIC_c[d]	Δ_i[e]	w_i[f]
PFOR2 TREES	4	560.01	2	564.16	0.00	0.25
PFOR2 PHARV TREES	3	557.93	3	564.24	0.08	0.24
PFOR2 PRF1 PHARV TREES[g]	1	557.39	4	565.91	1.75	0.10
DAGR TREES	9	561.99	2	566.14	1.97	0.09
PFOR2 PRF1 TREES	2	559.98	3	566.29	2.12	0.08
DDAGR DHARV TREES	10	560.34	3	566.65	2.48	0.07
PFOR1 TREES	6	562.84	2	566.99	2.83	0.06
PFOR1 DHARV TREES	5	560.96	3	567.27	3.11	0.05
DAGR PRF1 TREES	8	561.99	3	568.29	4.13	0.03
DAGR DHARV PRF1 TREES	7	560.09	4	568.61	4.45	0.03

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[a] See Table 2 for explanation of variables.

[b] Minus twice the log-likelihood of the model

[c] Number of parameters in the model

[d] Aikaike's Information Criterion, corrected for small sample size

[e] Delta-AIC_c value (difference between the model AIC_c and the minimum AIC_c

[f] Aikaike weight of evidence for the model, relative to others in the model set.

[g] Because there was no global model, we chose this model to perform a qualitative assessment of goodness-of-fit by inspecting patterns of deviance and Schoenfeld residuals. The generalized R^2 was 0.06.

Table 4.5. Relative effects of explanatory variables on Acadian flycatcher nest survival. Model-averaged estimates are from proportional hazards models shown in Table 4. Effect sizes shown in bold differ from zero at the 90% confidence level. Sums of model weights are not shown for each variable because the variables were not evenly balanced in the set of candidate models.

Variable[a]	Parameter Estimate[b]	Standard Error	Hazard Ratio	Effect Size
PFOR1	-0.968	0.978	0.380	-0.990
PFOR2	**-1.417**	**0.711**	**0.242**	**-1.993**
PRF1	-0.194	0.463	0.824	-0.419
PHARV	-2.590	1.818	0.075	-1.425
DHARV[c]	0.013	0.010	1.013	1.351
DAGR[b]	-0.009	0.007	0.991	-1.302
TREES	**-0.043**	**0.021**	**0.958**	**-2.021**

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[a] See Table 2 for explanation of variables.

[b] Note that a negative parameter estimate equates to a positive relationship with nest survival.

[c] Variable was first transformed by dividing by 10 obtain these estimates

Table 4.6. Comparison of logistic regression models to evaluate the influence of landscape context on the incidence of brood parasitism of Acadian flycatcher nests. Nests in the Tensas region were eliminated from the dataset prior to this analysis due to the exceedingly low incidence of parasitism in that region.

Explanatory variables[a]	Model #	-2 log L[b]	K[c]	AIC_c[d]	Δ_i[e]	w_i[f]
PFOR1 DHARV NI	5	59.41	3	66.14	0.00	0.49
DAGR DHARV NI	10	61.33	3	68.06	1.92	0.19
PFOR1 NI	6	64.48	2	68.84	2.70	0.13
DAGR DHARV PRF1 NI	7	61.30	4	70.55	4.41	0.05
PFOR2 PHARV NI	3	64.41	3	71.14	5.00	0.04
DAGR NI	9	66.88	2	71.23	5.10	0.04
PFOR2 NI	4	67.14	2	71.49	5.36	0.03
PFOR2 PRF1 PHARV NI[g]	1	64.31	4	73.56	7.42	0.01
DAGR PRF1 NI	8	66.87	3	73.60	7.46	0.01
PFOR2 PRF1 NI	2	67.14	3	73.87	7.73	0.01

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[a] See Table 2 for explanation of variables.
[b] Minus twice the log-likelihood of the model
[c] Number of parameters in the model
[d] Aikaike's Information Criterion, corrected for small sample size
[e] Delta-AIC_c value (difference between the model AIC_c and the minimum AIC_c
[f] Aikaike weight of evidence for the model, relative to others in the model set.
[g] Because there was no global model, we chose this model to perform a qualitative assessment of model fit by inspecting patterns of deviance residuals. The generalized R^2 was 0.12.

Table 4.7. Relative effects of explanatory variables on the incidence of brood parasitism of Acadian flycatcher nests. Model-averaged estimates are from logistic regression models shown in Table 6. Nests in the Tensas region were eliminated from the dataset prior to this analysis due to the exceedingly low incidence of parasitism in that region. Effect sizes shown in bold differ from zero at the 90% confidence level. Sums of model weights are not shown for each variable because the variables were not evenly balanced in the set of candidate models.

Variable[a]	Parameter Estimate	Standard Error	Hazard Ratio	Effect Size
PFOR1	-3.661	2.606	0.026	-1.405
PFOR2	-0.285	1.813	0.752	-0.157
PRF1	0.180	1.108	1.197	0.162
PHARV	7.544	4.846	1888.815	1.557
DHARV[b]	**-0.067**	**0.031**	**0.935**	**-2.136**
DAGR[b]	0.004	0.018	1.004	0.244
NI	**-0.056**	**0.025**	**0.946**	**-2.257**

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[a] See Table 2 for explanation of variables.

[b] Variable was first transformed by dividing by 10 obtain these estimates

Table 4.8. Comparison of post-hoc logistic regression models to evaluate the influence of landscape context and nest-level variables on the incidence of brood parasitism of Acadian flycatcher nests. Nests in the Tensas region were eliminated from the dataset prior to this analysis due to the exceedingly low incidence of parasitism in that region.

Explanatory variables[a]	-2 log L[b]	K[c]	AIC_c[d]	Δ_i[e]	w_i[f]
DHARV NI HG	57.45	3.00	64.18	0.00	0.23
DHARV NI BASAL HG	55.39	4.00	64.64	0.46	0.18
PFOR1 DHARV NI BASAL HG	53.77	5.00	65.70	1.52	0.11
DHARV NI	61.36	2.00	65.72	1.54	0.11
PFOR1 DHARV NI BASAL	56.48	4.00	65.73	1.55	0.11
PFOR1 DHARV NI HG	56.75	4.00	66.00	1.82	0.09
PFOR1 DHARV NI	59.41	3.00	66.14	1.96	0.09
DHARV NI BASAL	59.65	3.00	66.38	2.20	0.08

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[a] See Table 2 for explanation of variables.

[b] Minus twice the log-likelihood of the model

[c] Number of parameters in the model

[d] Aikaike's Information Criterion, corrected for small sample size

[e] Delta-AIC_c value (difference between the model AIC_c and the minimum AIC_c

[f] Aikaike weight of evidence for the model, relative to others in the model set.

Table 4.9. Relative effects of explanatory variables on the incidence of brood parasitism of Acadian flycatcher nests. Model-averaged estimates are from post-hoc logistic regression models shown in Table 8. Nests in the Tensas region were eliminated from the dataset prior to this analysis due to the exceedingly low incidence of parasitism in that region. Effect sizes shown in bold differ from zero at the 90% confidence level.

Variable[a]	Parameter Estimate	Standard Error	Hazard Ratio	Effect Size
PFOR1	-3.725	3.024	0.024	-1.232
DHARV[b]	**-0.097**	**0.042**	**0.908**	**-2.303**
NI	**-0.061**	**0.026**	**0.940**	**-2.383**
BASAL	0.063	0.043	1.065	1.453
HG	**0.747**	**0.422**	**2.110**	**1.770**

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[a] See Table 2 for explanation of variables.

[b] Variable was first transformed by dividing by 10 obtain these estimates

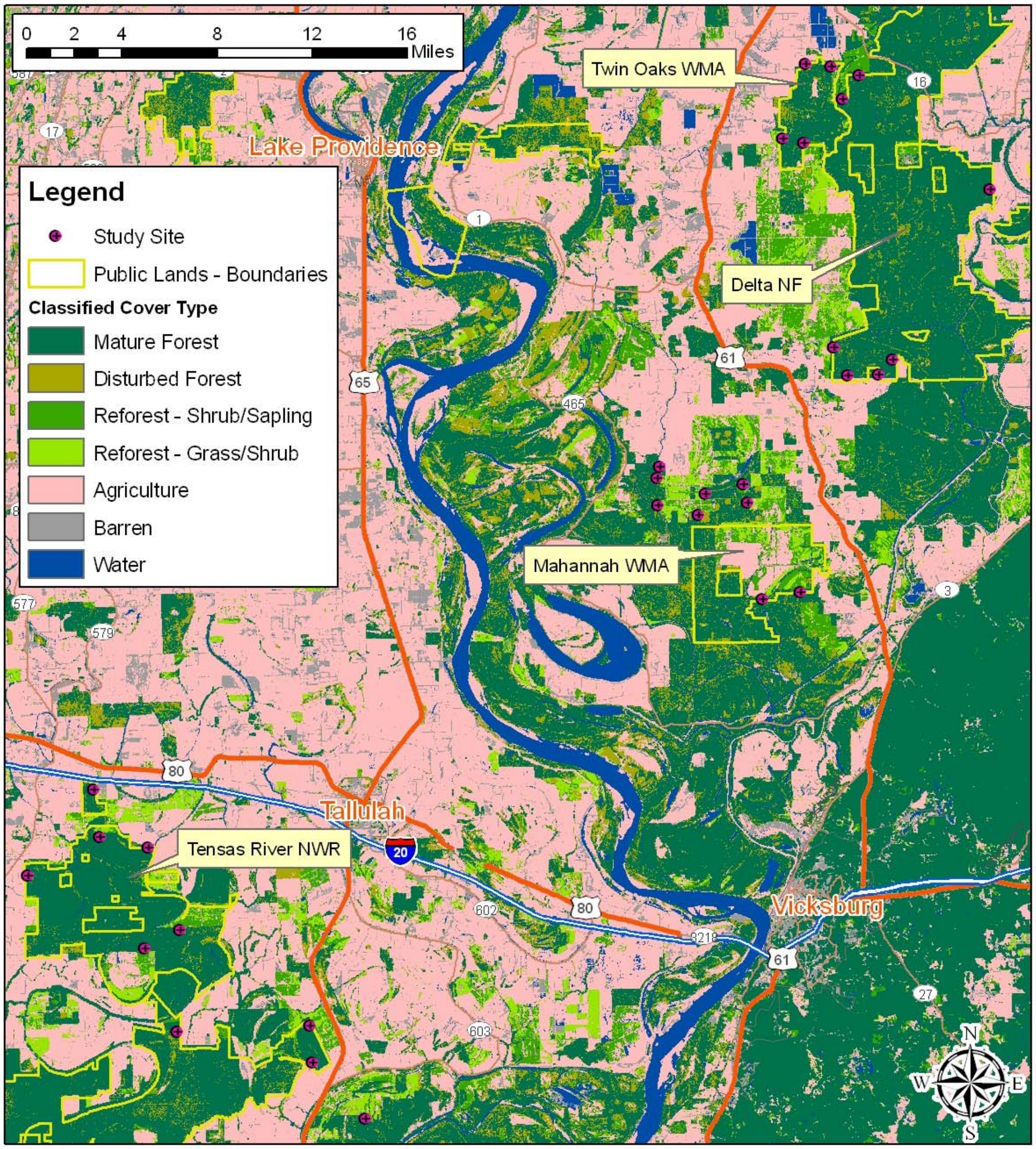

Figure 4.1. Study sites in the Mississippi Alluvial Valley, near Vicksburg, MS and Tallulah, LA.

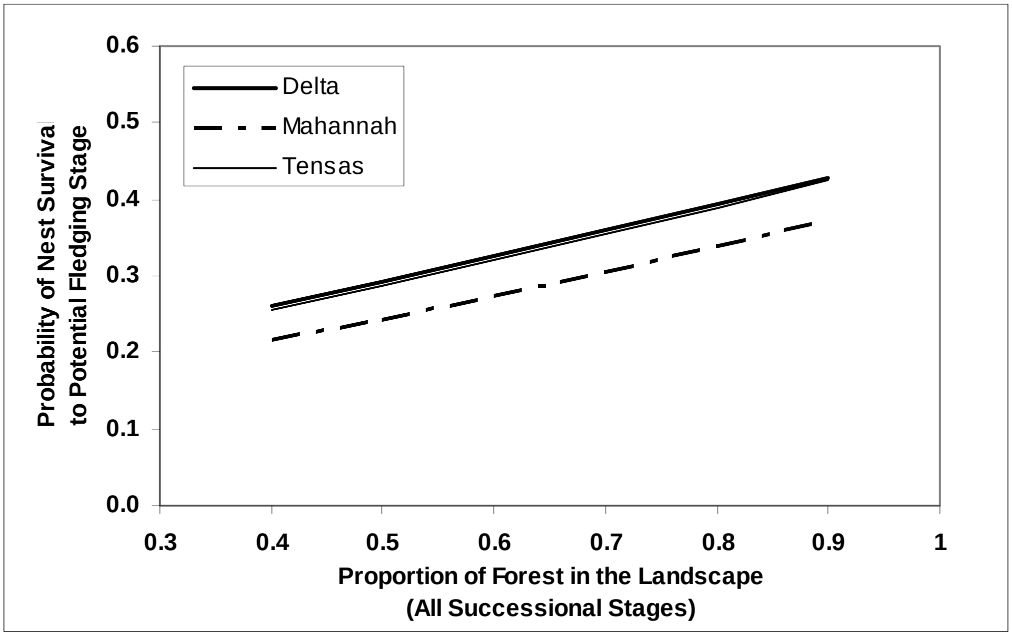

Figure 4.2. The probability of an Acadian flycatcher nest surviving through the potential fledging stage increased with the amount of forest cover in the landscape (1-km radius around the nest). Forest cover is here defined to include all successional stages, including reforested tracts and interior forest disturbances. The relationship shown here is based on model-averaged predictions with all covariates except PFOR2 set to their mean values.

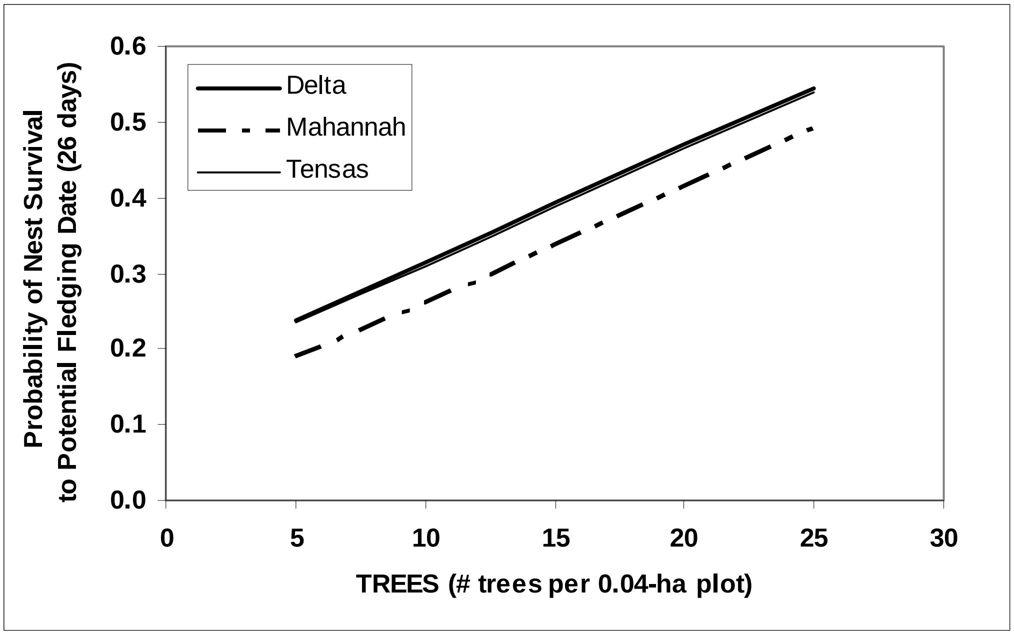

Figure 4.3. The probability of an Acadian flycatcher nest surviving through the potential fledging stage increased with the density of trees directly surrounding the nest (0.04-ha plot). The relationship shown here is based on model-averaged predictions with all covariates except TREES set to their mean values.

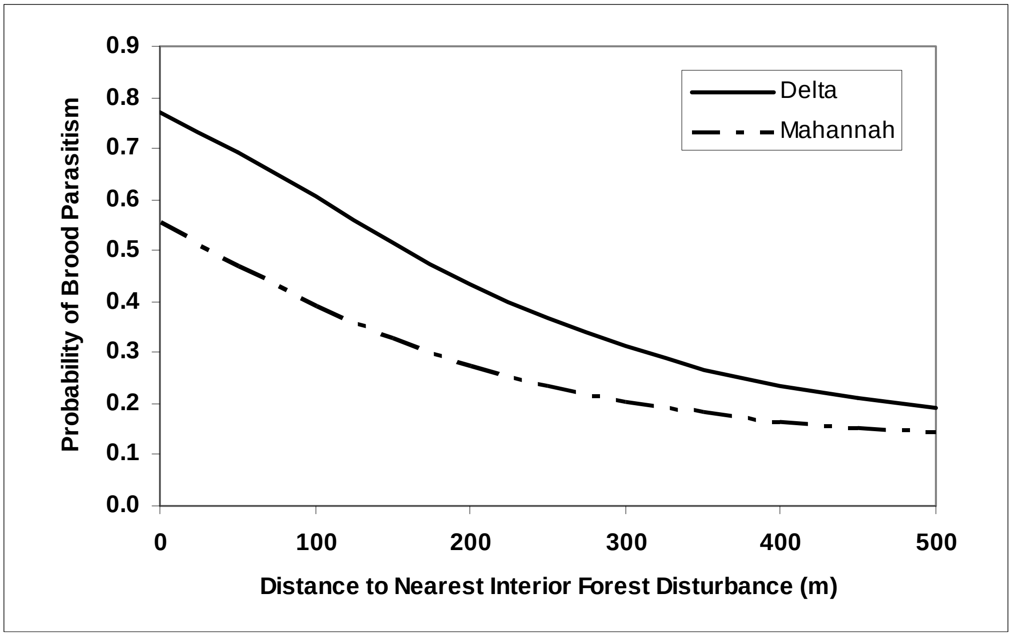

Figure 4.4. The probability of an Acadian flycatcher nest being parasitized decreased with increasing distance from an interior forest disturbance. The relationship shown here is based on model-averaged predictions with all covariates except DHARV set to their mean values. Nests in the Tensas region were eliminated from the dataset prior to this analysis due to the exceedingly low incidence of parasitism in that region.

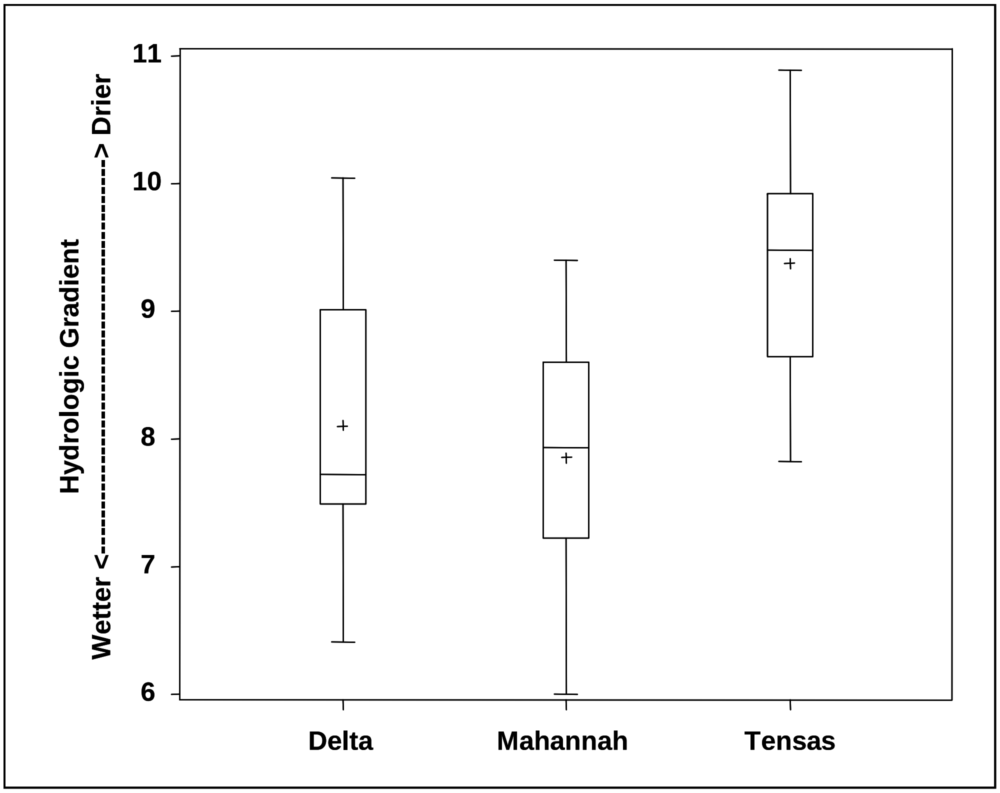

Figure 4.5. Difference in hydrologic gradient at nests in Tensas vs. Delta and Mahannah regions.

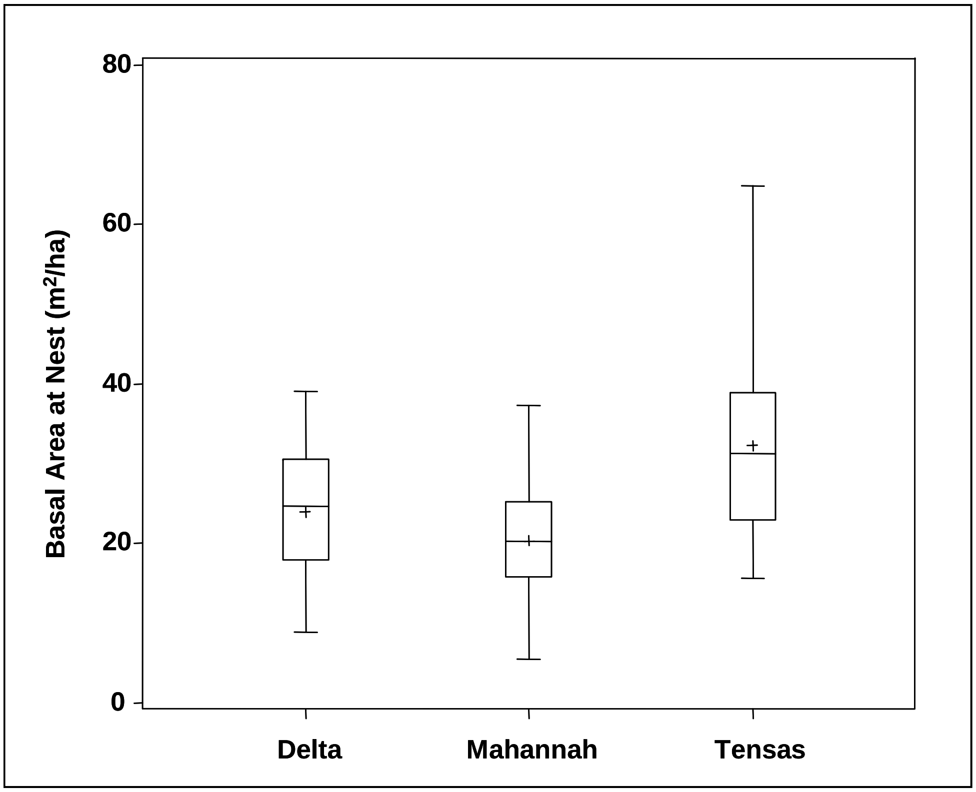

Figure 4.6. Difference in basal area at nests in Tensas vs. Delta and Mahannah regions.

CHAPTER 5

LANDSCAPE AND LOCAL EFFECTS ON AVIAN ABUNDANCE IN BOTTOMLAND HARDWOOD FORESTS[1]

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[1] Hazler, K.R., D.J. Twedt, and R.J. Cooper. To be submitted (in abbreviated format) to The Auk.

ABSTRACT

We examined the effects of landscape context, local vegetation, and biotic interactions on density or relative abundance of 5 migratory bird species, a brood parasite (brown-headed cowbird, *Molothrus ater*), and an avian nest predator (red-bellied woodpecker, *Melanerpes carolinus*) breeding in bottomland hardwood forests in the Mississippi Alluvial Valley. Both vegetation and landscape effects were influential and varied among species. Acadian flycatcher (*Empidonax virescens*), considered a "forest interior" species, responded positively to the amount of mature forest cover in the landscape, but this appeared to be driven more by sensitivity to interior forest openings from harvesting and other disturbances, with which mature forest cover was negatively correlated. This is likely related to the fact that relative abundance of brown-headed cowbirds increased with forest disturbance and successional habitat in general. Among sites adjacent to reforested tracts, shrub-nesting indigo bunting (*Passerina cyanea*) responded positively to forest disturbance, but this trend appeared to be reversed among sites adjacent to agricultural fields. We speculate that generalist nests predators may have caused this interactive effect. After controlling for landscape context and vegetation, both cowbird and flycatcher abundance decreased with increasing red-bellied woodpecker abundance, which lends support to the idea that woodpeckers are influential nest predators. Surprisingly, density of 3 of the 5 migratory species appeared to increase with cowbird abundance, controlling for landscape and vegetation features. It seems biologically unreasonable that these species would be attracted to cowbirds, so we infer that they were cueing on an unmeasured habitat correlate, possibly related to safety from nest depredation.

INTRODUCTION

Historically, bottomland hardwood forests dominated the Mississippi Alluvial Valley (Putnam et al. 1960, MacDonald et al. 1979). The landscape has since been drastically altered, with disruption of the natural hydrology for flood control and large-scale conversion of forests to cash crops such as cotton, soybeans, rice, corn, and catfish (Hamel et al. 2001). Only 20% of the original 10 million hectares of forested wetlands remain (Hefner and Brown 1985, Schoenholtz et al. 2001). Much of the extant forest is highly fragmented (Rudis 1995, Twedt and Loesch 1999), although there are some notable exceptions, such as Delta National Forest (> 24,000 ha) in Mississippi. Because higher, drier sites were preferentially cleared for agriculture, large forest remnants typically represent community types prone to permanent or semipermanent flooding, whereas drier forest types are more likely to occur as small patches (Rudis 1993, 1995, Twedt and Loesch 1999). Most hardwood forests of the major alluvial floodplains in the southern United States have been harvested one to several times (Kellison et al. 1998, Wigley and Lancia 1998).

Environmental concerns and changes in the economic climate have led to widespread reforestation in the Mississippi Alluvial Valley (MAV) over the past few decades (King and Keeland 1999, King et al. 2006), with an ultimate restoration goal of 800,000 ha (Haynes 2004). One of several objectives for forest restoration is to provide habitat for birds and other wildlife associated with mature bottomland forests. About 70 bird species breed regularly in bottomland hardwood forests of the southeastern United States, including about 30 species of Neotropical migrants (Pashley and Barrow 1993). Bottomland hardwoods are also important wintering grounds for short-distance migrants and provide stopover habitat for long-distance migrants in transit (Twedt et al. 1999a). A large-scale bird conservation plan for the MAV developed by the conservation group Partners in Flight identifies bottomland hardwood forest as the habitat of greatest concern (Twedt et al. 1999a, Mueller et al. 2000).

Many bird species, especially migrants, respond not only to patch-level conditions, but also to characteristics of the surrounding landscape (Freemark et al. 1995, Mazerolle and Villard 1999, Dunford and Freemark 2005). Biotic interactions between species, with concomitant impacts on the fundamental population processes of natality and mortality, are influenced by the prevalence and juxtaposition of different habitat elements within the landscape (Dunning et al. 1992, Wiens 1995, Pickett and Rogers 1997). For example, forest fragmentation is often associated with lower reproductive success for songbirds due to increased nest depredation and/or brood parasitism near habitat edges, particularly in agricultural settings (Donovan et al. 1995, Robinson et al. 1995, Stephens et al. 2004). Lower densities of populations sensitive to fragmentation probably occur not only due to reduced reproductive output, but also due to preferential selection of more suitable, less risky habitats (Suhonen et al. 1994, Roos and Pärt 2004, Thomson et al. 2006, also see Chapter 3). Landscape composition and configuration are likely to affect dispersal and colonization (Pulliam and Danielson 1991, Doak et al. 1992, Belisle et al. 2001, Belisle and Desrochers 2002, Russell et al. 2003), further amplifying population differences between fragmented and more contiguous habitats.

Reforestation in the MAV may impact migratory bird populations in several ways: by increasing the absolute amount of suitable habitat in the landscape, by reducing the absolute amount of "hostile" habitat elements that promote brood parasitism and nest depredation, and/or by acting as a buffer between suitable and hostile habitats. Recognizing the importance of landscape context, Twedt et al. (2006) developed a spatially explicit decision support model for the restoration of forest bird habitat in the MAV to maximize the conservation value of reforested tracts. Restoration adjacent to existing forests has been prioritized to increase the area of forest core, defined as forest > 1 km from hostile habitats such as agricultural fields. Because agricultural fields provide feeding areas for brood parasitic brown-headed cowbirds (*Molothrus ater*) (Donovan et al. 2000), it is assumed that parasitism rates should decline in areas where extant forests are buffered by reforested tracts. This strategy may also reduce the impacts of nest predators that are often common in habitat ecotones (e.g., Gates and Gysel 1978, Robinson 1988).

Although it can take 60 years or more for reforested tracts to provide suitable habitat for some species dependent on mature forests (King and Keeland 1999), it is assumed that even early-successional tracts will increase the effective core area of adjacent forests, resulting in increased reproductive success and higher densities of songbird populations (Twedt et al. 1999a). Successional stage is likely to be important for some shrub-nesting species in terms of direct habitat value (Twedt et al. in revision [Journal of Wildlife Management]), and may also impact the effectiveness of reforested tracts as habitat buffers for species associated with mature forests.

In addition to reforestation, the impacts of interior forest disturbance are worthy of investigation, since timber harvesting is likely to continue shaping the ecology of present and future forests in the MAV (Hamel et al. 2001). Interior forest openings from harvests and other disturbances may be beneficial by promoting understory growth and heterogeneity for shrub-nesting species, as well as a variety of food resources such as insects and fruits. Yet they may also attract cowbirds and generalist predators with concomitant negative impacts on reproductive success and hence population densities. The negative impacts may be exacerbated at sites near agricultural fields due to increased activity of cowbirds and nest predators in these areas.

We sought to quantify the effects of reforestation and landscape context on densities of several avian species breeding in mature bottomland hardwood forests of the Mississippi Alluvial Valley, while controlling for local vegetation characteristics. At study sites within large tracts of extant forest, we estimated densities of 5 migratory songbird species representing different habitat affiliations and nesting guilds (Table 5.1), as well as the relative abundance of a brood parasite, the brown-headed cowbird, and a nest predator, the red-bellied woodpecker (*Melanerpes carolinus*). At the landscape scale, we examined the effects of habitat adjacency (agricultural vs. reforested fields), proportional forest cover and successional stage, and interior forest disturbance. At the local scale, we examined the impacts of several measures of vegetation structure and composition. Finally, after controlling for landscape and vegetation, we weighed the evidence for possible behavioral responses of migrants to red-bellied woodpeckers and/or cowbirds (Chapter 3), and of cowbirds to woodpeckers.

METHODS

Study sites

We established 21 study sites within or adjacent to Delta National Forest, Twin Oaks Wildlife Management Area, and Mahannah Wildlife Management Area, Mississippi (Table 5.2, Figure 5.1). The sites, located within mature bottomland forest habitat, were subject to seasonal flooding to varying degrees. Typical canopy species included overcup oak (*Quercus lyrata*), sugarberry (*Celtis laevigata*), sweetgum (*Liquidambar styraciflua*), green ash (*Fraxinus pennsylvanicus*), and water hickory (*Carya aquatica*). Each site was adjacent to either an agricultural field (n = 7), a reforested field in the grass – short shrub stage (n = 7), or a reforested field in the sapling – tall shrub stage (n = 7). Within each site, we typically established 4 – 6 point count plots that were separated by at least 200-m. One row was 50-m and the other row 300-m from the forest-field edge. At one larger site, which was the focus of a more intensive study, we included a third row of plots at 550-m from the edge, for a total of 9 plots.

Bird surveys

In 2001-2002, we conducted two 5-min counts per point location, but each site was sampled during only one of the two years (Table 5.2). A single observer (K. Hazler) performed 73% of the counts, with the remainder performed by four experienced assistants. We conducted counts between 0600h and 1030h, from 1 May through 18 June, and did not survey during rain or excessive winds.

We recorded the locations and distances of birds detected on circular plot forms with radii marked at 25-m and 50-m, using arrows to keep track of any movements during the sample period. We used different colored pens to record whether individual birds were detected during the first 3-min interval, the second 2-min interval, or both, so that detection probability could be estimated using the time-of-detection method (Alldredge et al. 2007a, see Detection Probability, below).

Vegetation

Within 11.3-m radius (0.04 ha) of each point count plot, we identified and measured all trees and standing snags with diameter at breast height (dbh) ≥ 10 cm. We counted the number of small trees and saplings (< 10 cm dbh, ≥ 2.5 m high) within 5.0-m radius. We used a 25-cm x 25-cm coverboard, divided into 25 equal squares, to estimate understory cover in 3 strata (0.5-m, 2.5-m, and 5.0-m) based on the proportion of the coverboard obscured by vegetation [a variation on the method described by Nudds (1977)]. We used these measurements to derive 6 vegetation variables (Table 5.3).

We used the species composition of trees sampled to derive a seventh vegetation variable, which is an index quantifying the floristic composition along the hydrologic gradient. To each tree species, we assigned a hydrologic rank ranging from 1 (characteristic of sites flooded ≥ 3 months per year) to 12 (characteristic of sites flooded ≤ 1 month per year). For most trees, ranks were obtained directly from Dale and Ware (2004). For the remaining trees, we obtained their wetland indicator status from the online PLANTS database (USDA-NRCS 2006) and assigned ranks by calibrating against trees for which we knew the assigned values from both ranking systems. We calculated an overall hydrologic gradient index (HG) for each plot as:

$$(1) \qquad HG = \frac{1}{2}\left[\frac{\sum_{1}^{T}(C_t \times H_t)}{C_{sum}} + \frac{\sum_{1}^{T}(B_t \times H_t)}{B_{sum}} \right]$$

where T is the total number of tree species and the subscript t refers to each individual species; C_t and B_t are the counts and basal area, respectively, for species t; C_{sum} and B_{sum}

are the counts and basal area summed over all species in the plot; and H_t is the hydrologic rank of species *t* on the scale of Dale and Ware (2004).

Landscape metrics

We used Erdas Imagine (Leica Geosystems 2003) to conduct a supervised classification of Landsat imagery (30-m resolution) from September 2001. We initially derived 6 land cover classes: MF (mature forest), RF2 (reforestation at sapling - tall shrub stage), RF1 (reforestation at grass - low shrub stage), AGR (agriculture or pasture), BARE (roads and other barren land), and H2O (water). We used a number of geographic data sources from the Mississippi Alluvial Valley Conservation Planning Atlas (MAV-CPA, LMVJV 2002), as well as our own knowledge of conditions on and adjacent to our study sites, to choose suitable training sites for the classification. We iteratively added training sites until a satisfactory classification was obtained. We considered the classification satisfactory once >90% of RF1 and RF2 training sites were correctly identified as reforested, and >70% were identified to the correct reforestation stage. This resulted in >95% correct classification of MF, AGR, and H2O training sites. The percentage of BARE classed pixels was minimal in the vicinity of our study areas and was not evaluated.

We converted the classified image to GRID format for further processing in ArcView (ESRI 1999) and ArcGIS (ESRI 2006). Harvested patches and other openings within the mature forest matrix were typically classified as RF1 or RF2. To distinguish these disturbed areas from former agricultural tracts that had been reforested, we masked the classified grid with a forest/non-forest classification based on 1992 imagery from the

MAV-CPA (LMVJV 2002). All pixels classified as forest in the MAV-CPA but classified as reforestation based on the 2001 imagery were reclassifed as HARV (harvest or other interior forest disturbance). A landcover map obtained from the Mississippi Gap Analysis Program (R. Minnis, personal communication) was used to further refine the final classification.

We subjected the classified image to one pass of a majority filter to reduce speckling, which was a problem in the reforested stands where some pixels were misclassified as AGR. We expanded the MF class by one pixel to clean up the mature forest-agriculture and mature forest-reforestation edges. However, this resulted in the loss of much of the HARV and H2O classes in the forest interior, so we ran a map query to return those pixels to their original classification. We buffered each study site with a 1-km radius, and tabulated the areas of each cover class within the buffer. From this we derived 5 landscape metrics to be used as predictor variables in models of avian density, in addition to a dichotomous variable indictating whether each study site was adjacent to an agricultural or reforested field (Table 5.3).

We ran the Euclidean distance tool to determine the distance of each pixel from the AGR and HARV classes. We extracted these values for each point count location, which had been recorded in the field using a GPS receiver. These distance values were used as predictor variables in models of avian detection probability.

Detectability

In our point count samples, the vast majority of birds were detected by ear and were not seen. Therefore, the probability that a bird is detected, given that it is present, depends on two components: (1) the probability that the bird vocalizes during the sampling period, and (2) the probability that it is detected by the observer, given that it vocalizes (Farnsworth et al. 2002, Alldredge et al. 2007a). Although distance sampling methodology has been advocated to model and adjust for detection probability (Rosenstock et al. 2002), this approach does not account for the first detection component. Instead, it requires the assumption that all birds present are available for detection, and that detection probability is influenced only by distance from the observer. In fact, numerous factors influence bird song rates and hence their detectability. For example, unpaired males often sing more frequently than paired males (Gibbs and Wenny 1993), and birds may also vocalize more frequently in response to nearby conspecifics (i.e., at higher densities, Rothstein et al. 2000). For this reason, and the fact that distance estimates for auditory detections are unreliable beyond ~65-m, we subscribe to the view that distance sampling methods are not appropriate for avian point counts (Alldredge et al. 2007c). Instead, we used the time-of-detection method (Alldredge et al. 2007a) to model detectability and adjust bird counts accordingly.

Although we recorded the presence and distance of all birds detected, for the migratory species we restricted the analyses to those birds detected within 50-m of the plot center, which allowed us to estimate a defined sampling area and calculate density from adjusted counts. Based on other studies in which distance sampling methods have been employed, effective detection distances are probably > 50-m (e.g., McGarigal and McComb 1995, Lichstein et al. 2002), so we assumed that distance-related attenuation of detectability was not an issue especially since all counts were conducted in similar habitat. For woodpeckers and cowbirds, we had insufficient data for reliable estimates from the fixed 50-m radius. We therefore included all detections, making the assumption that although detectability declines with distance, this is unrelated to relevant differences among our study areas. Use of an unlimited radius precluded density estimation, so we instead used adjusted counts to calculate relative abundance.

The time-of-detection method (Alldredge et al. 2007a) rests on the premise that by keeping track of individual birds detected during separate time intervals within a point count sample, detections can be treated as “captures”, and detection probability can be modelled using a capture-recapture framework. Because our point count samples included only 2 time intervals, we were unable to employ more complex models advocated by Alldredge et al. (2007a), incorporating elements such as individual heterogeneity or behavioral response. Instead, we were restricted to an analog of the simple Lincoln-Peterson estimator, which allows only for for temporal variation in detection probability between “capture” periods (Williams et al. 2002, pp. 290-292), i.e., between the 2 time intervals.

We estimated detectability using the Huggins closed captures module of program MARK (White 2009). We included several individual covariates that we suspected could influence detection probabilities: sub-region (a dummy variable), day of the season, distance to agriculture, distance to nearest interior forest disturbance, tree density, and hydrologic gradient. For each species, we evaluated 16 candidate models within an information-theoretic framework (Burnham and Anderson 2002), generated model-averaged estimates of detection probability, and derived adjusted counts for each study site.

Density estimation

As discussed above, we did not attempt to estimate density for cowbirds and woodpeckers. Instead, we divided the adjusted counts by the number of samples at each site to obtain measures of relative abundance. For the migratory species, the most straightforward estimator of density at a study site is

$$(2) \qquad \hat{D}_s = \frac{\hat{C}_s}{n_s \pi r^2}$$

where $\hat{C}_s$ is the adjusted count for the site derived from program MARK, n_s is the total number of point counts conducted at the site, and πr^2 is the area of a point count plot of radius *r*. Although the radius of our point count plots was 50-m, the effective sampling radius was larger. Birds can move in and out of the "capture area" from territory centers well beyond the fixed radius of our plots, making the actual area sampled somewhat ambiguous (Johnson 1995).

One approach used to calculate the effective sampling area for standard square or rectangular trapping arrays (e.g., in small mammal studies) is to add a buffer width equal to the average territory radius (Williams et al. 2002, pp. 314-316). We applied the same concept to increase the estimated sampling area of our circular plots. Although this is a rather *ad hoc* approach, we felt that it was better than the alternative of not adjusting the effective sample area at all. As part of a concurrent study (Chapter 3), we had detailed territory data for Acadian flycatchers at one study site (BRAN). The average distance to the nearest neighbor, measured between territory centroids, was approximately 100-m, implying an average territory radius of 50-m. We thus considered the effective sampling radius of our circular plots to be 100-m for flycatchers, and assumed that this was a reasonable estimate for the other migratory species as well.

We applied an additional adjustment to our density estimates based on the habitat affiliations of the individual species (Table 5.1), as follows:

$$(3) \qquad \hat{D}_{s-adj} = \frac{\hat{D}_s}{H_s}$$

where H_s is the proportion of potential habitat within the effective sample area of the study site. We assumed that Acadian flycatchers, prothonotary warblers, and blue-gray gnatcatchers were restricted to mature forest habitat. However, we included interior forest disturbances in the definition of potential habitat because we assumed that some interior disturbances would be included within their territories, even if not actively used. For indigo buntings and white-eyed vireos, we included all successional stages of forest as potential habitat. The proportional adjustment, for each site and each species, was determined by using GIS to buffer the point counts with a 100-m radius and tabulate the areas of different cover classes within the buffer area. As a general evaluation of the performance of our density estimation approach, we compared the density estimates for Acadian flycatchers at the BRAN study site derived from territory mapping and point counts, and found these independent estimates to be nearly identical (see Results).

Modelling approach

We used linear regression to model the effects of landscape context, local vegetation, and biotic interactions (responsed to woodpeckers and cowbirds) on avian density or relative abundance. Pairwise correlations among variables of interest were relatively high (Table 5.4). Therefore careful model development was critical to avoid finding spurious effects or obscuring true effects (Graham 2003). We evaluated sets of competing models within an information-theoretic framework (Burnham and Anderson 2002), ranking models by Aikaike's Information Criterion for small samples (AICc) and weights of evidence (w_i).

For each species, we first fit a global model including all variables of interest. To account for possible differences among sub-regions not accounted for by the predictor variables in the original global model, we included a random intercept (Snijders and Bosker 1999, pp. 38- 52). We used the MIXED procedure in SAS (2004), specifying maximum likelihood as the estimation method and a random intercept with sub-region as the subject. Since the group-level error term was estimated as zero in all global models, we reverted to linear regression without a random effect. We assessed the suitability of the global model by examining patterns of residuals.

After fitting the global model, we fit a model including only the vegetation variables. From this model we obtained the residuals, which were used as the response variable in a set of landscape models (see below). In this way, we could assess the relative merits of each landscape model and variable independent of vegetation effects. Similarly, we fit a model including only the landscape variables, and used the residuals as the response variable in a set of vegetation models (see below). We examined model weights, model-averaged parameter estimates and effect sizes[1], and pairwise correlations

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[1] Effect size (ES) is defined as the parameter estimate divided by its standard error); note that $|ES| \geq 1.64$ is equivalent to a 90% confidence interval that does not include zero.

between variables to identify those landscape and vegetation variables most likely to have significant influence on population levels.

Based on these findings, we constructed a small, final set of reasonable composite models combining landscape and vegetation variables. These are described for each species in the Results, as this was essentially a *post hoc* analysis. For migratory species, we also examined whether behavioral responses (avoidance of woodpeckers and/or cowbirds) might explain residual variation remaining after accounting for landscape and vegetation effects. We crossed the set of composite landscape-vegetation models with a set of 4 behavioral response models that included woodpecker abundance, cowbird abundance, both, or neither as covariates. Similarly, we tested for woodpecker avoidance by cowbirds.

Landscape models

We developed a set of 10 *a priori* landscape models (Tables 5.7, 5.10) representing alternative hypotheses, not all mutually exclusive, relating landscape variables to avian density. If the amount of suitable or preferred habitat in the landscape is an important determinant of local population density for mature forest species, then they should respond positively to mature forest cover, represented by PFOR1. Similarly, shrub-nesting forest generalists and early successional specialists might exhibit a positive response to the the proportional cover of successional forests, represented by PFOR3. Alternatively, if the amount of agricultural cover is more important than the amount of preferred habitat, there should be a stronger response to total forest cover regardless of successional stage (PFOR2). This variable was structured so that an increase in the proportional cover of forest is the same thing as a decrease in the proportional cover of agricuture. A third alternative is that direct proximity to agriculture is more important than the total amount of preferred habitat or agriculture in the landscape; this should be reflected in a stronger response to YAGR (representing adjacency to agriculture as opposed to reforestation).

Impacts of forest harvest and other interior disturbances should be reflected in responses to PHARV. We included an interaction term, YAGR*PHARV to reflect the possibility that cowbirds or generalist predators might be more active in disturbed forests adjacent to agriculture, thereby impacting migrant populations more severely. Finally, we included the variable PRF1 to represent the proportion of reforested tracts in earlier vs. later successional stages.

Vegetation models

Of the vegetation variables in Table 5.3, we decided *a priori* to include at most one measure of overstory structure (either TREES or BASAL) and one measure of understory structure (STEMS or UCOV1 for ACFL, PROW, BGGN, and RBWO; STEMS or UCOV2 for INBU, WEVI, and BHCO) in any model. For PROW and RBWO, we included SNAGS as a possible covariate, since these species use cavities in dead trees for nesting. HG was tested as a possible covariate for all species because the hydrologic condition can have a significant influence on habitat use by many bird species (Robbins et al. 1989, Wakeley and Roberts 1996, Wigley and Lancia 1998, Inman et al. 2002). We fit all possible 2- and 1-variable models (subject to the above restrictions).

RESULTS

Detectability

For all migrants, there was some support for a decline in detection probability over the course of the season, although the effect size did not differ significantly from zero (at the 90% confidence level) for PROW and WEVI. The top-ranked models for ACFL, BGGN, and INBU all yielded remarkably similar coefficient estimates (± SE) for the effect of Day (ACFL: -0.041 ± 0.020; BGGN: -0.040 ± 0.022; INBU: -0.044 ± 0.024). For migrants, there was also some evidence for a sub-regional effect, with detection probabilities higher in the Delta subregion. However, it is possible that this was driven by a temporal effect because subregion and year were almost completely confounded. The effect was significant for PROW (1.381 ± 0.740) and INBU (1.428 ± 0.650) but weak for the others. There was little evidence that the landscape or vegetation variables we considered affected detection probability (Table 5.5).

Overall detection probability was relatively high for migrants, ranging from 0.511 to 0.702 in the 3-minute time interval, and from 0.327 to 0.477 in the 2-minute time interval (Table 5.6). As a result, the probability of detecting an individual bird during an entire 5-minute point count ranged from 0.710 to 0.843. Our estimates of detection probabilities for migrants appeared to be reasonable in comparison with an analysis of simulated point counts, in which detection probabilties for a 3-minute interval ranged from 0.41 to 0.67 at low song rates, and from 0.60 to 0.83 at high song rates (Alldredge et al. 2007b). Detection probabilities for RBWO were also relatively high. In contrast, the detection probability for BHCO was very low, resulting in only 0.259 probability of detection over the duration of a 5-minute point count (Table 5.6).

Adjusted counts, density, and relative abundance

To evaluate the reliability of adjusted counts output by program MARK, we inspected the estimates relative to their standard errors. Although the estimate/SE ratios for BHCO (1.13) and WEVI (1.49) were lower than desirable, we still feel that the point estimates were suitable for deriving density or relative abundance as response variables for regression analyses. For the remaining species, the average ratio of estimates to their standard errors exceeded 2.16.

WEVI was not detected at 4 study sites, all of which were in the Delta sub-region. PROW and BHCO were each not detected at one site. All other species were detected at all sites. Our density estimates (Table 5.6) for the migratory species were in reasonable ranges compared with those reported by Twedt et al. (1999b) and Smith et al. (2001) at other bottomland hardwood forest sites in the region, except that our estimates for ACFL were substantially lower than those of Twedt et al. (1999b). However, we compared the estimates derived from point counts to the estimates derived from territory mapping at the BRAN site. From point counts, we derived an estimate of 4.3 pairs/10-ha. In 2001, when the point counts were conducted, we mapped 25 territories in the 56-ha study area (Chapter 3), equivalent to 4.5 pairs/10-ha. The estimates differed by < 5%, lending credence to our density estimation approach.

Landscape models

For the 4 species of tree- and cavity-nesting birds, none of the *a priori* landscape models was overwhelmingly superior (Table 5.7). Inference is drawn instead from model-averaged effect sizes (Table 5.8). RBWO and PROW exhibited no definitive associations with landscape features, although there was a tendency for PROW to be positively associated with mature forest cover (PFOR1). ACFL was density increased with the amount of mature forest cover, but was even more strongly, negatively associated with interior forest disturbance (PHARV). Because PFOR1 and PHARV were highly correlated (r = -0.59), it is uncertain whether ACFL density was affected by forest disturbance alone, or by both forest disturbance and forest cover. There was some evidence, albeit slight, for a possible interactive effect of PHARV and YAGR (adjacency to agriculture) on ACFL density. BGGN density increased with increasing total forest cover (PFOR2), and also with the proportion of early-stage reforestation (PRF1).

There was a clearly superior landscape model for INBU (model 7), a moderately superior model for BHCO (model 1), and more uncertainty about suitability of models for WEVI (Table 5.10). Adjacency to agriculture (YAGR) and interior forest disturbance (PHARV) had interacting effects on INBU density: at sites adjacent to reforestation, density increased with increasing forest disturbance, but at sites adjacent to agriculture there appeared to be an opposite trend (Figure 5.2). There is inherent uncertainty about the trend for sites adjacent to agriculture, however, because these did not cover the same range of forest disturbance. BHCO density was positively associated with both total successional forest in the landscape (PFOR3) and with increasing interior forest disturbance (PHARV). These variables are highly correlated (r = 0.72) because PHARV is essentially a component of PFOR3; the latter had the stronger effect (Table 5.11). BHCO density decreased with PRF1, implying an affinity for later seral stages of reforested tracts. In contrast, WEVI density increased with PRF1 (Table 5.11).

Vegetation models

At the local scale, neither RBWO (Table 5.9) nor WEVI (Table 5.12) exhibited definitive associations with the vegetation characteristics we measured, although there was a tendency for woodpeckers to be positively associated with understory stem density and/or negatively associated with tree density. For PROW, the top 3 models included BASAL only, BASAL and SNAGS, and SNAGS only, and carried similar weights of evidence (0.13, 0.12, and 0.10, respectively) although they were not clearly superior over several of the other vegetation models. Based on effect sizes, the only definitive habitat association for PROW was a positive relationship with BASAL. However, PROW tended to be positively associated with SNAGS.

For ACFL, the best vegetation model ($w_i = 0.53$) included BASAL and STEMS; density increased with basal area and decreased with understory stem density. UCOV1 also had a strong negative effect, but this was redundant with the inclusion of STEMS as a measure of understory cover. BGGN density decreased with increasing tree density, and the vegetation model including only this variable had the strongest support ($w_i = 0.30$). INBU had a strong positive association with understory cover (UCOV2), and the model including only this variable had the strongest support ($w_i = 0.52$). For BHCO, the best vegetation model ($w_i = 0.37$) included both TREES and STEMS; density decreased with both of these variables (Table 5.12).

Composite models

For Acadian flycatchers, we considered 3 composite landscape-vegetation models. All included PHARV, BASAL, and STEMS, and included either AGR and

PHARV*AGR, PFOR1, or neither of these additional variables. Crossed with the biotic interactions, this resulted in 12 models under consideration. The most parsimonious model ($w_i = 0.65$) implies that flycatchers were positively associated with basal area, negatively associated with forest disturbance and understory stem density, and avoided either red-bellied woodpeckers or some unmeasured correlate of woodpecker abundance (Table 5.13). The model-averaged effect size of woodpecker abundance was -3.183. The model-averaged effect size of PFOR1 for this set of models was only 0.606, supporting our suspicion that the positive response observed in the *a priori* landscape models was due to the correlation between PFOR1 and PHARV rather than a true response of flycatchers to forest cover.

For prothonotary warblers, we considered 4 composite landscape-vegetation models. All included BASAL, and included either PFOR1, SNAGS, both, or neither of these additional variables. Crossed with the 4 biotic interactions models, this yielded 16 models. The highest-ranked ($w_i = 0.29$) of these models included BASAL and BHCO, but the next best model, nearly tied, ($w_i = 0.27$) also included PFOR1 (Table 5.13). The model-averaged effect size for PFOR1 from this *post hoc* set of models was 1.720, lending more support to the hypothesis that density increased with mature forest cover. The relationship with cowbird density, contrary to prediction, was positive, with a model-averaged effect size of 2.570.

For blue-gray gnatcatchers, we constructed a single composite landscape-vegetation model including PFOR2, PRF1, and TREES, and crossed this with the 4 biotic interaction models. The top-ranked model ($w_i = 0.45$) included only the landscape and vegetation variables, but was nearly tied with the next best model ($w_i = 0.43$), which included cowbird density (Table 5.13). As for PROW, the relationship of BGGN density to cowbird density was positive, with a model-averaged effect size of 2.099.

The single composite landscape-vegetation model we considered for indigo buntings included PHARV, YAGR, YAGR*PHARV, and UCOV2. Crossed with the 4 biotic interaction models, there was no support for effects of BHCO or RBWO, as the model without either of these effects was clearly superior ($w_i = 0.79$; Table 5.13).

We did not construct a composite landscape-vegetation model for white-eyed vireos due to the lack of response to vegetation, but we crossed the PRF1 model with the 4 biotic models. Although the best model ($w_i = 0.42$) did not include biotic effects, there was substantial support for a positive relationship with BHCO ($w_i = 0.31$; model-averaged effect size = 1.705).

We constructed 2 composite landscape-vegetation model for brown-headed cowbirds. Both included PFOR3, PRF1, TREES, and STEMS, and one additionally included PHARV. Crossed with models including or not including an effect of woodpecker abundance, this yielded 4 models. There was most support ($w_i = 0.49$) for the model with neither PHARV nor RBWO effects. There was however also some support for a model including RBWO but not PHARV ($w_i = 0.28$; RBWO model-averaged effect size = -2.061). We did not construct a composite model for red-bellied woodpeckers due to our inability to discern any definitive associations with either landscape or vegetation variables.

DISCUSSION

Responses to forest cover and reforestation

Numerous studies have demonstrated that the amount of forest cover in the landscape (or correlates thereof) influences many forest-breeding birds' presence/absence and/or relative abundance (e.g., Robbins et al. 1989, McGarigal and McComb 1995, Trzcinski et al. 1999, Austen et al. 2001). The direction of response to forest cover, if any, depends in part on the species' life history characteristics and habitat associations. For example, Robbins et al. (1989) found that although neotropical migrants more often responded positively to focal patch area and/or forest cover within 2-km, the opposite was true for short-distance migrants and residents. Austen et al. (2001) found that several forest interior species (as classified in the literature) responded positively to forest cover within a 2-km radius, whereas several edge species responded negatively and only one had a significant positive response.

Of the 4 mature forest associates in our study, only the two classified from the literature as forest-interior species (Table 5.1) exhibited increased density with increasing mature forest cover (PFOR1). The result for the prothonotary warbler must be viewed with some caution because the model-averaged coefficient for PFOR1 was only statistically different from zero in the composite set of models (*post hoc*). For the Acadian flycatcher, the effect was uncertain because of the negative correlation between mature forest cover and forest disturbance (PHARV); it appeared that PFOR1 was redundant after accounting for the flycatcher's negative response to PHARV.

The blue-gray gnatcatcher responded positively to total forest cover (PFOR2) rather than to mature forest cover. Even though forests in later seral stages may be preferred and/or support higher densities of this species (Hamel 1992), it can occur in earlier seral stages and is frequently found near forest edges (Ellison 1992). Thus, it is not clear if the observed response reflected a positive association with potential habitat, or a negative association with the amount of agriculture in the landscape. In either case, the result suggests that an increase in forest cover over time due to reforestation will be beneficial for this species.

We expected densities of white-eyed vireos and indigo buntings to increase with increasing amounts of successional forest cover in the landscape (PFOR3). This was not the case for vireos, and was of uncertain or negligible importance for buntings, whose density was much more strongly related to interior forest disturbance (PHARV) as opposed to the properties of the reforested tracts.

Cowbirds exhibited a clear positive response to the total amount of successional forest in the landscape. They did not, as might be expected, exhibit higher densities at sites adjacent to agricultural fields as compared with sites adjacent to reforested tracts. Cowbirds can travel long distances between feeding (e.g., agricultural fields) and breeding areas (e.g., forests) on a daily basis, with reported distances ranging up to almost 7 km (Rothstein et al. 1984). For this reason, adjacent habitat may not be particularly a relevant predictor of cowbird abundance; landscape composition may be more important than the exact juxtaposition of habitats for this species. Yet we did not find evidence that cowbirds were positively associated with the proportional cover of agriculture, either. If greater amounts of agriculture promoted higher cowbird densities, we should have seen a negative response to PFOR2. The effect of PFOR2 was not strong enough to draw weighty conclusions, but if anything, the response was positive, not negative. (Table 5.11).

In Chapter 4, we found no relationship between parasitism of Acadian flycatcher nests and distance to agriculture, nor between parasitism and proportion of total forest cover in the landscape. Based on our findings, we cannot infer that shifting the balance of landscape composition from agriculture to reforestation will reduce cowbird populations or parasitism rates, at least in the short term. It is possible that for cowbirds, reforested tracts provide not only hosts to parasitize, but also feeding opportunies comparable to the agricultural rowcrops being replaced (Thompson and Dijak 2000). More research is needed on this issue to guide bird habitat management in the MAV.

The gnatcatcher and the white-eyed vireo both increased in density with increasing PRF1, the amount of early-stage reforestation as a proportion of all reforestation in the landscape. In terms of habitat use, we would expect vireos, and especially gnatcatchers, to be more associated with later-stage reforestation, so this was an unexpected finding. In contrast, cowbird density increased with decreasing PRF1, implying an affinity for later-stage reforestation. In a concurrent study we found that among reforested stands sampled, cowbirds were more abundant, and nest were more heavily parasitized, on well-developed sites supporting high densities of white-eyed vireos, indigo buntings and other thamnic and silvicolous species (Twedt et al. in revision [Journal of Wildlife Management]). Because of cowbirds' high mobility, they are likely to commute between mature forests and reforested stands. It is possible that there could be a spillover effect resulting in higher parasitism rates for individuals breeding in nearby mature forests. In Chapter 4 we did not find an effect of PRF1 on parasitism of Acadian flycatcher nests, but results may be somewhat species-dependent.

Responses to forest disturbance

Depending on habitat affiliations, clearcuts will have a positive influence on some species, and a negative influence on others (Germaine et al. 1997, Hagan et al. 1997). Acadian flycatcher, a species that is thought to be particularly sensitive to habitat fragmentation and "requires relatively undisturbed mature forest throughout its range" (Whitehead and Taylor 2002), had an unambiguously negative response to our forest disturbance variable, PHARV. In addition to the effects of habitat loss for mature forest obligates, harvesting operations can affect nest predator communities and thus affect reproductive success and recruitment of birds in managed forests. For example, Perison et al. (1997) found that snakes, which commonly depredate nests in bottomlands, were more abundant in clearcuts than in an unharvested area. Although more information is needed on the specific effects of harvesting operations on nest predator communities in bottomland forests, Twedt et al. (2001) showed that Acadian flycatcher nesting success in the LMAV was lower in stands subjected to group-selection timber harvest than in unharvested controls. Others have also reported that reproductive success of Acadian flycatchers is lower in forests with a high density of clearcuts and/or wildlife openings (D. Winslow, P. Doran, pers. comm. cited in Whitehead and Taylor 2002).

Clearcuts and other internal forest openings have been reported to increase levels of cowbird activity in the forest (Brittingham and Temple 1983, Verner and Ritter 1983, Annand and Thompson 1997, Moorman et al. 2002, Gannon 2005). Likewise, we found that cowbird abundance was positively related to forest disturbance (actually, to successional forests in general). Consistent with this result, we showed in Chapter 4 that the probability of an Acadian flycatcher nest being parasitized declined with increasing distance from an interior forest disturbance.

We expected both white-eyed vireos and indigo buntings to respond positively to forest disturbance. White-eyed vireo is strongly associated with successional and edge habitats (Hopp et al. 1995) and has been shown to respond positively to selective harvests that mimic treefall gaps (Barrow 1990, cited in Pashley and Barrow 1993). However. we did not find any influence of PHARV on vireos. Indigo buntings responded positively, but with a caveat: there appeared to be an interaction effect with the habitat (reforestation or agriculture) adjacent to the study site. Presumably, buntings face a tradeoff between preference for successional habitats and risk from generalist nest predators that are attracted to similar habitats. Sites adjacent to agricultural fields may have a higher concentration of such predators, making forest openings in these areas more risky for nesting.

Responses to local vegetation

Mature forest obligates Acadian flycatcher and prothonotary warbler both exhibited higher densities with increasing basal area. Gnatcatchers and cowbirds had higher densities where tree density was lower, and the woodpecker exhibited a similar trend. Neither buntings nor vireos revealed a response to either of these overstory measures. We expected both buntings and vireos to respond positively to shrub cover

(UCOV2), but this was only the case for the bunting. Both flycatchers and cowbirds were negatively associated with density of saplings and small trees.

Behavioral responses

There was relatively strong support for the idea that, after controlling for landscape and vegetation effects, flycatcher and cowbird abundance was negatively affected by red-bellied woodpecker abundance. In chapter 3 we had hypothesized that flycatchers actively avoid both woodpeckers (because of the risk of nest predation) and cowbirds (because of the risk of parasitism). At the territory scale, the apparent avoidance of woodpeckers in one year could be reasonably explained by vegetation factors and philopatry. In this case however, we feel that we identified and controlled the important vegetation and landscape effects, and the impact of woodpeckers on density is convincing. We suspect that either some behavioral mechanism of interspecific avoidance at the stand level is at play, and/or that woodpeckers have a significant effect on the reproductive output of flycatchers and cowbirds. This is a very preliminary finding that warrants further investigation, but is supportive of our original hypothesis (Chapter 2) that red-bellied woodpeckers may have a significant impact as nest predators.

In testing for responses of migrants to cowbirds, we expected, if anything, evidence for avoidance. Instead we found the opposite. Three of the 5 migratory species (prothonotary warbler, blue-gray gnatcatcher, and white-eyed vireo) showed some evidence for a positive association with cowbirds. It seems biologically unlikely that these species would be actively attracted to cowbirds. It is more likely that there is some unmeasured correlate driving these relationships, possibly related to safety from nest depredation.

General conclusions

Based on our results, reforestation efforts may, in the long run, not only provide additional habitat, but also increase population densities for some species such as the blue-gray gnatcatcher, and possibly Acadian flycatchers and prothonotary warblers. Successional stage of reforestation in the vicinity of our study sites appears to be an important factor for some species. We suspect this may be due to cowbirds' affinity for later-stage reforestation and a spillover effect into nearby or adjacent mature forests. Based on our findings, we cannot infer that shifting the balance of landscape composition from agriculture to reforestation will reduce cowbird populations or parasitism rates, at least in the short term.

The impacts of active forest management and harvesting need to be considered in the context of conservation planning. While some species, such as the indigo bunting, are likely to benefit from the heterogeneity created by timber harvesting, others like the Acadian flycatcher will experience lower densities in response to increasing forest disturbance. Possible interaction effects between forest disturbance and habitat adjacency should alson be investigated further. Finally, an understanding of specific biotic interactions between birds and their nest predators and brood parasites may help clarify certain landscape and local habitat relationships.

Since different species respond in different ways to various landscape and local factors, it will never be possible to recommend management options that will universally benefit all species. Probably the biggest limitation of this study is the lack of sufficient data to produce habitat models for a number of species listed by Partners in Flight as high priority for conservation (Twedt et al. 1999a). However, it is hoped that the data presented here will help conservation planners make informed decisions about the relevance of various landscape and local factors to those species of concern for which we had sufficient data, and to draw inferences about other high priority species with similar characteristics and habitat requirements.

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Table 5.1. Bird species codes, names, and habitat associations.

Code	Species Name	Habitat[a]	Interior/Edge[b]	Nesting Guild[c]	Migratory Status[d]
ACFL	Acadian flycatcher (*Empidonax virescens)*	M/O	I	T	M
PROW	prothonotary warbler (*Protonotaria citrea*)	M/O	I	C	M
BGGN	blue-gray gnatcatcher (*Polioptila caerulea*)	M/G	I/E	T	M
WEVI	white-eyed vireo (*Vireo griseus*)	S/S	E	S	M
INBU	indigo bunting (*Passerina cyanea*)	S/G	E	T, S	M
BHCO	brown-headed cowbird (*Molothrus ater*)	G	E	T, S, C[e]	R
RBWO	red-bellied woodpecker (*Melanerpes carolinus*)	M/G	I/E	C	R

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[a] Forest habitat associations: M/O = mature forest obligate; M/G mature forest generalist; S/obligate = successional forest obligate; S/G = successional forest generalist; G = forest generalist. Based on successional stage suitability designations for oak-gum-cypress forests and individual species accounts compiled by Hamel (1992), as well as individual species accounts in the Birds of North America series.

[b] Interior/edge associations: I = preference for forest interior (edge avoidance), E = preference for forest edge (edge affinity), I/E = no particular affinity for edge or interior. Designations are from Freemark and Collins (1992) except WEVI (Hopp et al. 1995).

[c] Nesting guilds: T = trees/saplings; S = shrubs; C = cavities. Generally follows Hamel (1992, Appendix D), but modified according to personal observations at our study sites (Hamel lists indigo buntings as shrub nesters, but we frequently observed them nesting in tall saplings and trees).

[d] M = Neotropical migrant, R = resident, based on designations by Freemark et al. (1995)

[e] Host nesting guilds

Table 5.2. Study sites in the Mississippi Alluvial Valley.

Site Acronym	Sub-Region[a]	Year Sampled	Adjacent habitat[b]	Area (ha)	N[c]
DELT	Delta	2001	AGR	28	6
OAKS	Delta	2001	AGR	14	6
SPAN	Delta	2001	AGR	28	6
DAVI	Delta	2001	AGR/RF1[d]	28	6
BRAN	Delta	2001	RF1	56	9
LONG	Delta	2001	RF1	28	6
SNAK	Delta	2001	RF1	30	6
WILL	Delta	2001	RF1	28	6
HUFF	Delta	2001	RF2	28	6
MANA	Delta	2001	RF2	28	6
TWIN	Delta	2001	RF2	14	4
UGLY	Delta	2002	AGR	27	6
JARV	Mahannah	2002	AGR	28	6
MART	Mahannah	2002	AGR	28	6
ATWO	Mahannah	2002	RF1	25	5
HOLE	Mahannah	2002	RF1	14	4
NEWM	Mahannah	2002	RF1	28	6
COLE	Mahannah	2002	RF2	14	4
CYPR	Mahannah	2002	RF2	25	6
JOLL	Mahannah	2002	RF2	28	6
MIMS	Mahannah	2002	RF2	26	6
TOTAL					**122**

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[a] "Delta" = sites within or near Delta National Forest or Twin Oaks Wildlife Management Area; "Mahannah" = sites within or near Mahannah National Wildlife Refuge

[b] AGR = agriculture, RF1 = reforestation in the grass/low shrub stage, RF2 = reforestation in the sapling/tall shrub stage.

[c] Number of point count stations. Each station was sampled twice.

[d] This site was adjacent to an agricultural field that was partially reforested. It was treated as an AGR site because the predominant context was agriculture.

Table 5.3. Predictor variables considered in analyses of avian density.

Variable	Variable Description	Formula (if applicable)[a]	Range	Mean
	Landscape Context Variables[b]			
PFOR1	Proportion of forest in the landscape, including only mature forest	$\frac{MF}{TOT}$	0.33 – 0.80 (proportion)	0.58
PFOR2	Proportion of forest in the landscape, including all successional stages	$\frac{MF + HARV + RF2 + RF1}{TOT}$	0.56 – 0.99 (proportion)	0.83
PFOR3	Proportion of early successional forest in the landscape	$\frac{HARV + RF2 + RF1}{TOT}$	0.01 – 0.51 (proportion)	0.25
PRF1	Area of early-stage reforestation as a proportion of total reforestation	$\frac{RF1}{RF2 + RF1}$	0.04 – 0.92 (proportion)	0.44
PHARV	Harvested openings and other interior forest disturbances as a proportion of all extant (non-reforestation) forest	$\frac{HARV}{MF + HARV}$	0.01 – 0.28 (proportion)	0.12
YAGR	Dichotomous variable indicating whether study area was adjacent to agricultural field or reforestation		n/a	n/a
	Vegetation Variables[c]			
TREES[d]	Number of live trees > 10-cm dbh		9.00 – 25.84 (trees/0.04 ha)	15.36
SNAGS	Number of dead trees > 10-cm dbh within 11-m radius		0.00 – 6.17 (snags/0.04 ha)	1.57
BASAL	Basal area of trees > 10-cm dbh		14.9 – 33.6 (m^2/ha)	24.09
STEMS	Density of saplings and small trees < 10-cm dbh within 5-m radius		2.33 -16.50 (stems/0.008 ha)	8.08
UCOV1	Understory cover at 2.5-m and 5.0-m; proportion of coverboard covered		0.08 – 0.59 (proportion)	0.32
UCOV2	Understory cover at 0.5-m and 2.5-m; proportion of coverboard covered		0.10 – 0.63 (proportion)	0.35
HG[c]	Hydrologic gradient index: a quantification of floristic composition along the hydrologic gradient[e]	$\frac{1}{2}\left[\frac{\sum_{1}^{T}(C_t \times H_t)}{C_{sum}} + \frac{\sum_{1}^{T}(B_t \times H_t)}{B_{sum}}\right]$	6.33 – 8.83	7.66

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[a] TOT = total area in the landscape, minus pixels classified as water (H2O) or barren (BARE); MF = mature forest area; HARV = area of patch cuts or other interior forest disturbance; RF2 = later-stage reforestation (tall shrub – sapling stage); RF1 = earlier-stage reforestation (grass – short shrub stage)

[b] Landscape is defined as the area within a 1-km radius buffer around the periphery of each study area.

[c] We used the mean of values within each study area as the predictor variable.

[d] Variable also included in models of detection probability. In models of detection probability, this was the value measured at individual count stations rather than the mean for the study area.

[e] See Methods for details

Table 5.4. Correlation matrix of potential predictor variables of avian density. See Table 5.3 for variable descriptions.

	TREES	SNAGS	BASAL	STEMS	UCOV1	UCOV2	HG	PFOR1	PFOR2	PFOR3	PRF1	PHARV	YAGR
TREES		0.07	0.12	-0.38	-0.30	-0.34	-0.47	0.26	0.54	0.33	-0.04	0.11	-0.38
SNAGS	0.07		-0.11	-0.23	-0.08	-0.20	-0.05	-0.15	-0.28	-0.16	-0.31	0.16	0.20
BASAL	0.12	-0.11		0.18	-0.46	-0.47	-0.04	0.34	0.21	-0.07	-0.22	-0.37	-0.20
STEMS	-0.38	-0.23	0.18		0.45	0.16	0.21	0.26	-0.14	-0.34	-0.25	-0.45	0.12
UCOV1	-0.30	-0.08	-0.46	0.45		0.66	0.16	0.10	-0.06	-0.14	-0.03	-0.01	0.10
UCOV2	-0.34	-0.20	-0.47	0.16	0.66		0.27	0.03	-0.35	-0.37	0.22	-0.19	0.49
HG	-0.47	-0.05	-0.04	0.21	0.16	0.27		-0.08	-0.36	-0.30	0.35	-0.13	0.46
PFOR1	0.26	-0.15	0.34	0.26	0.10	0.03	-0.08		0.38	-0.41	0.02	-0.59	-0.06
PFOR2	0.54	-0.28	0.21	-0.14	-0.06	-0.35	-0.36	0.38		0.68	-0.06	0.26	-0.84
PFOR3	0.33	-0.16	-0.07	-0.34	-0.14	-0.37	-0.30	-0.41	0.68		-0.08	0.72	-0.78
PRF1	-0.04	-0.31	-0.22	-0.25	-0.03	0.22	0.35	0.02	-0.06	-0.08		0.03	0.09
PHARV	0.11	0.16	-0.37	-0.45	-0.01	-0.19	-0.13	-0.59	0.26	0.72	0.03		-0.33
YAGR	-0.38	0.20	-0.20	0.12	0.10	0.49	0.46	-0.06	-0.84	-0.78	0.09	-0.33	

Table 5.5. Aikaike weights (w_i) of models of avian detection probabilities[a] in bottomland forest sites in the Mississippi Alluvial Valley. Top-ranked models with Δ-QAIC$_c$[b] < 2.0 are emphasized in bold.

Model # and variables included	K[c]	ACFL	PROW	BGGN	INBU	WEVI	BHCO	RBWO
1. Global Model: Sub-region[d], Day[e], Landscape[f], Vegetation[g]	8	0.00	0.00	0.00	0.01	0.00	0.00	0.00
2. Day, Landscape, Vegetation	7	0.01	0.00	0.01	0.00	0.01	0.01	0.01
3. Sub-region, Landscape, Veg.	7	0.00	0.01	0.00	0.00	0.00	0.01	0.00
4. Landscape, Vegetation	6	0.00	0.00	0.00	0.00	0.01	0.02	0.00
5. Sub-region, Day, Landscape	6	0.02	0.02	0.02	0.09	0.01	0.01	0.03
6. Day, Landscape	5	0.07	0.02	0.05	0.03	0.04	0.03	0.07
7. Sub-region, Landscape	5	0.01	0.05	0.02	0.04	0.02	0.04	0.00
8. Landscape	4	0.02	0.01	0.02	0.00	0.06	0.07	0.01
9. Sub-region, Day, Vegetation	6	0.02	0.03	0.03	0.06	0.01	0.02	0.03
10. Day, Vegetation	5	0.07	0.02	0.08	0.01	0.03	0.03	0.07
11. Sub-region, Vegetation	5	0.01	0.05	0.02	0.03	0.02	0.05	0.00
12. Vegetation	4	0.02	0.02	0.03	0.00	0.05	0.09	0.01
13. Sub-region, Day	4	0.16	**0.17**	**0.13**	**0.44**	0.07	0.07	**0.21**
14. Day	3	**0.43**	**0.16**	**0.33**	0.08	**0.22**	**0.10**	**0.50**
15. Sub-region	3	0.05	**0.32**	0.11	**0.19**	0.11	**0.19**	0.02
16. Null model (intercepts only)	2	0.11	0.10	**0.14**	0.00	**0.33**	**0.26**	0.04

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[a] Detections were limited to a 50-m fixed radius for migrants (ACFL, BGGN, PROW, INBU, and WEVI). All detections were included for BHCO and RBWO.

[b] Δ-QAIC$_c$ is the difference between the model QAIC$_c$ and the candidate set's minimum QAIC$_c$ (Aikaike's Information Criterion, corrected for small sample size and adjusted for overdispersion).

[c] Number of parameters in model, including 2 intercepts (for the probability of detection in each of 2 intervals). Because models were adjusted for c-hat (the dispersion parameter calculated from the global model #1), the parameter count was increased by 1 in the calculation of QAICc. Values shown reflect the number of parameters in models prior to this adjustment.

[d] Indicator variable denoting whether sample was from the Mahannah or Delta sub-region

[e] Day of the season, counted from April 1.

[f] Includes the variables DAGR (distance to agriculture) and DHARV (distance to nearest interior forest disturbance)

[g] Includes the variables TREES (tree density = number of trees per 0.04-ha sample) and HG (hydrologic gradient index).

Table 5.6. Estimates of avian detection probabilities and density or relative abundance.

Code	Number of Detections[a]	P_1[b] (SE)	P_2[c] (SE)	P_{tot}[d]	Range of Density or Relative Abundance[e]
ACFL	168	0.702 (0.099)	0.472 (0.109)	0.843	0.92 – 4.76
PROW	147	0.569 (0.109)	0.327 (0.091)	0.710	0.00 – 8.08
BGGN	110	0.594 (0.132)	0.374 (0.121)	0.746	0.72 – 5.13
WEVI	59	0.511 (0.160)	0.408 (0.148)	0.711	0.00 – 2.75
INBU	141	0.628 (0.099)	0.477 (0.101)	0.805	0.42 – 6.59
BHCO	123	0.178 (0.098)	0.086 (0.051)	0.259	0.00 – 5.06
RBWO	275	0.556 (0.114)	0.276 (0.089)	0.679	1.15 – 3.68

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[a] From 244 counts (122 stations sampled twice). For migrants (ACFL, BGGN, PROW, INBU, and WEVI) this includes only detections within a fixed 50-m radius. For residents (BHCO and RBWO) this includes all detections (unlimited radius).

[b] Probability of detection during first time interval (3 minutes), based on model-averaged estimates with covariates set to mean values.

[c] Probability of detection during second time interval (2 minutes), based on model-averaged estimates with covariates set to mean values.

[d] Average probablity of detection during full point count period (5 minutes): $P_{tot} = 1 - (1-P_1)(1-P_2)$

[e] For migrants this is density expressed as pairs per 10-ha. For residents this is relative abundance expressed as number per unlimited radius point count sample.

Table 5.7. Aikaike weights (w_i) of linear regression models to evaluate the influence of landscape context on densities of bird species associated with mature forests in the Mississippi Alluvial Valley, after controlling for vegetation[a]. Top-ranked models with Δ-$AIC_c < 2.0$ are emphasized in bold.

Model # and variables included[b]	K[c]	ACFL	PROW	BGGN	RBWO
1. PFOR1 YAGR	4	0.04	0.07	0.04	0.05
2. PFOR1	3	**0.17**	**0.33**	0.07	**0.20**
3. PFOR2 PHARV PRF1	5	0.05	0.01	0.06	0.02
4. PFOR2 PHARV	4	**0.25**	0.06	0.07	0.09
5. PFOR2 PRF1	4	0.01	0.08	**0.28**	0.07
6. PFOR2	3	0.04	**0.26**	**0.27**	**0.24**
7. YAGR PHARV YAGR*PHARV	5	**0.14**	0.01	0.01	0.02
8. YAGR PHARV	4	**0.26**	0.03	0.04	0.08
9. YAGR	4	0.04	**0.15**	**0.17**	**0.22**

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[a] The response variables for the models were the residuals from a model including all the vegetation variables of interest.
[b] See Table 5.3 for variable codes.
[c] Number of parameters in model, including intercept and residual error term.

Table 5.8. Relative effects of landscape variables on densities or relative abundance of tree- or cavity-nesting bird species in the Mississippi Alluvial Valley, after controlling for vegetation. Model-averaged estimates are from linear regression models shown in Table 5.7[a]. Effect sizes emphasized in bold differ from zero at the 90% confidence level.

Variable[b]	Acadian Flycatcher			Prothonotary Warbler			Blue-grey Gnatcatcher			Red-bellied Woodpecker		
	Coeff. Est.	SE	Effect Size	Coeff. Est.	SE	Effect Size	Coeff. Est.	SE	Effect Size	Coeff. Est.	SE	Effect Size
PFOR1	**0.293**	**0.160**	**1.829**	0.278	0.209	1.333	-0.063	0.187	-0.338	-0.403	1.279	-0.315
PFOR2	0.026	0.127	0.208	0.196	0.170	1.154	**0.253**	**0.138**	**1.839**	0.664	1.023	0.649
PRF1	-0.015	0.071	-0.215	0.081	0.098	0.819	**0.143**	**0.077**	**1.847**	0.505	0.586	0.862
YAGR	0.019	0.061	0.311	-0.019	0.055	-0.342	-0.061	0.046	-1.321	-0.185	0.340	-0.544
PHARV	**-0.695**	**0.270**	**-2.576**	-0.123	0.376	-0.326	0.148	0.305	0.486	2.230	2.209	1.010
YAGR*PHARV	-0.975	0.626	-1.559	-0.292	0.979	-0.298	-0.030	0.813	-0.037	4.647	5.522	0.842

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[a] The response variables for the models were the residuals from a model including all the vegetation variables of interest.

[b] See Table 5.3 for variable codes.

Table 5.9. Relative effects of vegetation variables on densities or relative abundance of tree- or cavity-nesting bird species in the Mississippi Alluvial Valley, after controlling for landscape. Model-averaged estimates are from a set of linear regression models[a] with combinations of one or two vegetation variables, not shown. Effect sizes emphasized in bold differ from zero at the 90% confidence level.

Variable[b]	Acadian Flycatcher			Prothonotary Warbler			Blue-grey Gnatcatcher			Red-bellied Woodpecker		
	Coeff. Est.	SE	Effect Size	Coeff. Est.	SE	Effect Size	Coeff. Est.	SE	Effect Size	Coeff. Est.	SE	Effect Size
TREES	0.004	0.004	1.053	-0.003	0.008	-0.448	**-0.009**	**0.005**	**-1.775**	-0.056	0.040	-1.412
BASAL	**0.008**	**0.003**	**2.471**	**0.009**	**0.005**	**1.763**	-0.001	0.004	-0.237	0.023	0.030	0.774
STEMS	**-0.016**	**0.004**	**-3.879**	-0.010	0.008	-1.320	0.006	0.005	1.043	0.056	0.043	1.305
UCOV1	**-0.399**	**0.117**	**-3.428**	-0.180	0.208	-0.864	-0.067	0.143	-0.466	-0.269	1.175	-0.229
HG	0.008	0.021	0.386	0.038	0.035	1.087	0.013	0.027	0.493	0.114	0.209	0.544
SNAGS				0.033	0.021	1.565				-0.009	0.124	-0.073

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[a] The response variables for the models were the residuals from a model including all the landscape variables of interest.

[b] See Table 5.3 for variable codes.

Table 5.10. Aikaike weights (w_i) of linear regression models to evaluate the influence of landscape context on densities of shrub-nesting bird species and a brood parasite in the Mississippi Alluvial Valley, after controlling for vegetation[a]. Top-ranked models with Δ-$AIC_c < 2.0$ are emphasized in bold.

Model # and variables included[b]	K[c]	INBU	WEVI	BHCO
1. PFOR3 PRF1	4	0.04	**0.17**	**0.40**
2. PFOR3	3	0.14	**0.16**	**0.15**
3. PFOR2 PHARV PRF1	5	0.01	0.04	**0.19**
4. PFOR2 PHARV	4	0.05	0.04	0.05
5. PFOR2 PRF1	4	0.01	**0.20**	0.11
6. PFOR2	3	0.05	**0.18**	0.05
7. YAGR PHARV YAGR*PHARV	5	**0.60**	0.01	0.00
8. YAGR PHARV	4	0.05	0.04	0.02
9. YAGR	4	0.05	**0.17**	0.02

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[a] The response variables for the models were the residuals from a model including all the vegetation variables of interest.

[b] See Table 5.3 for variable codes.

[c] Number of parameters in model, including intercept and error term.

Table 5.11. Relative effects of landscape variables on densities or relative abundance of shrub-nesting bird species and a brood parasite in the Mississippi Alluvial Valley, after controlling for vegetation. Model-averaged coefficient estimates are from linear regression models in Table 5.9[a]. Effect sizes emphasized in bold differ from zero at the 90% confidence level.

Variable[c]	Indigo Bunting[b]			White-eyed Vireo			Brown-headed Cowbird		
	Coeff. Est.	SE	Effect Size	Coeff. Est.	SE	Effect Size	Coeff. Est.	SE	Effect Size
PFOR3	0.270	0.187	1.448	0.053	0.092	0.575	**2.791**	**1.182**	**2.361**
PFOR2	-0.051	0.200	-0.256	0.073	0.093	0.788	1.687	1.283	1.315
PRF1	0.063	0.112	0.565	**0.098**	**0.053**	**1.875**	**-1.637**	**0.668**	**-2.452**
YAGR	**0.235**	**0.124**	**1.896**	-0.016	0.031	-0.510	0.257	0.907	0.284
PHARV	**1.154**	**0.413**	**2.796**	-0.045	0.208	-0.219	**5.309**	**2.525**	**2.103**
YAGR*PHARV	**-2.779**	**0.849**	**-3.273**	-0.319	0.539	-0.592	-3.749	6.385	-0.587

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[a] The response variables for the models were the residuals from a model including all the vegetation variables of interest.

[b] Coefficients for INBU are from the single top-ranked model ($w_7 = 0.96$), not model-averaged.

[c] See Table 5.3 for variable codes.

Table 5.12. Relative effects of vegetation variables on densities or relative abundance of shrub-nesting bird species and a brood parasite in the Mississippi Alluvial Valley, after controlling for landscape. Model-averaged estimates are from a set of linear regression models[a] with combinations of one or two vegetation variables, not shown. Effect sizes emphasized in bold differ from zero at the 90% confidence level.

Variable[c]	Indigo Bunting[b]			White-eyed Vireo			Brown-headed Cowbird		
	Coeff. Est.	SE	Effect Size	Coeff. Est.	SE	Effect Size	Coeff. Est.	SE	Effect Size
TREES	-0.001	0.006	-0.207	-0.002	0.004	-0.628	**-0.035**	**0.017**	**-2.020**
BASAL	-0.001	0.005	-0.297	0.001	0.003	0.396	-0.004	0.013	-0.326
STEMS	0.008	0.007	1.038	0.000	0.004	-0.039	**-0.035**	**0.018**	**-1.953**
UCOV2	**0.603**	**0.172**	**3.508**	0.083	0.108	0.768	0.651	0.512	1.271
HG	-0.032	0.028	-1.162	0.015	0.017	0.887	0.087	0.087	0.996

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[a] The response variables for the models were the residuals from a model including all the landscape variables of interest.

[b] Coefficients for INBU are from the single top-ranked model ($w_7 = 0.96$), not model-averaged.

[c] See Table 5.3 for variable codes.

Table 5.13. Final composite models of avian density.

				Explanatory Power (R^2)[a]			
Species	Equation[b]	M[c]	w_i[d]	R^2_{ls}	R^2_{veg}	R^2_{comp}	R^2_{full}
ACFL	Density = 0.338 – 0.803*PHARV + 0.012*BASAL – 0.010*STEMS – 0.064*RBWO	12	0.65	0.30	0.37	0.60	0.74
PROW	Density = -0.103 + 0.013*BASAL + 0.051*BHCO	16	0.29				
	Density = -0.342 + 0.011*BASAL + 0.063*BHCO + 0.466*PFOR1		0.27	0.07	0.09	0.12	0.39
BGGN	Density = 0.147 + 0.214*PFOR2 + 0.233*PRF1 – 0.011*TREES	4	0.45				
	Density = 0.073 + 0.170*PFOR2 + 0.230*PRF1 – 0.009*TREES + 0.031*BHCO		0.43	0.23	0.06	0.34	0.44
INBU	Density = -0.246 + 0.382*YAGR + 1.837*PHARV – 3.371*YAGR*PHARV + 0.873*UCOV2	4	0.79	0.48	0.34	0.76	0.76
WEVI	Density = 0.036 + 0.199*PRF1	4	0.42				
	Density = 0.036 + 0.197*PRF1 + 0.017*BHCO		0.31	0.34	n/a	n/a	0.41
BHCO	RelAbund = 6.566 + 2.432*PFOR3 – 0.725*PRF1 – 0.175*TREES – 0.235*STEMS	4	0.49				
	RelAbund = 8.168 + 2.895*PFOR3 – 0.702*PRF1 – 0.215*TREES – 0.224*STEMS – 0.547*RBWO		0.28	0.10	0.38	0.46	0.54

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[a] R^2 values are given for model subsets including landscape variables only (ls), vegetation variables only (veg), composite of landscape plus vegetation variables, but not including biotic variables (comp), and for the full model (full).

[b] Coefficients are model-specific, not model-averaged.

[c] Number of models considered in the *post hoc* model set.

[d] Aikaike weight of model (in *post hoc* model set).

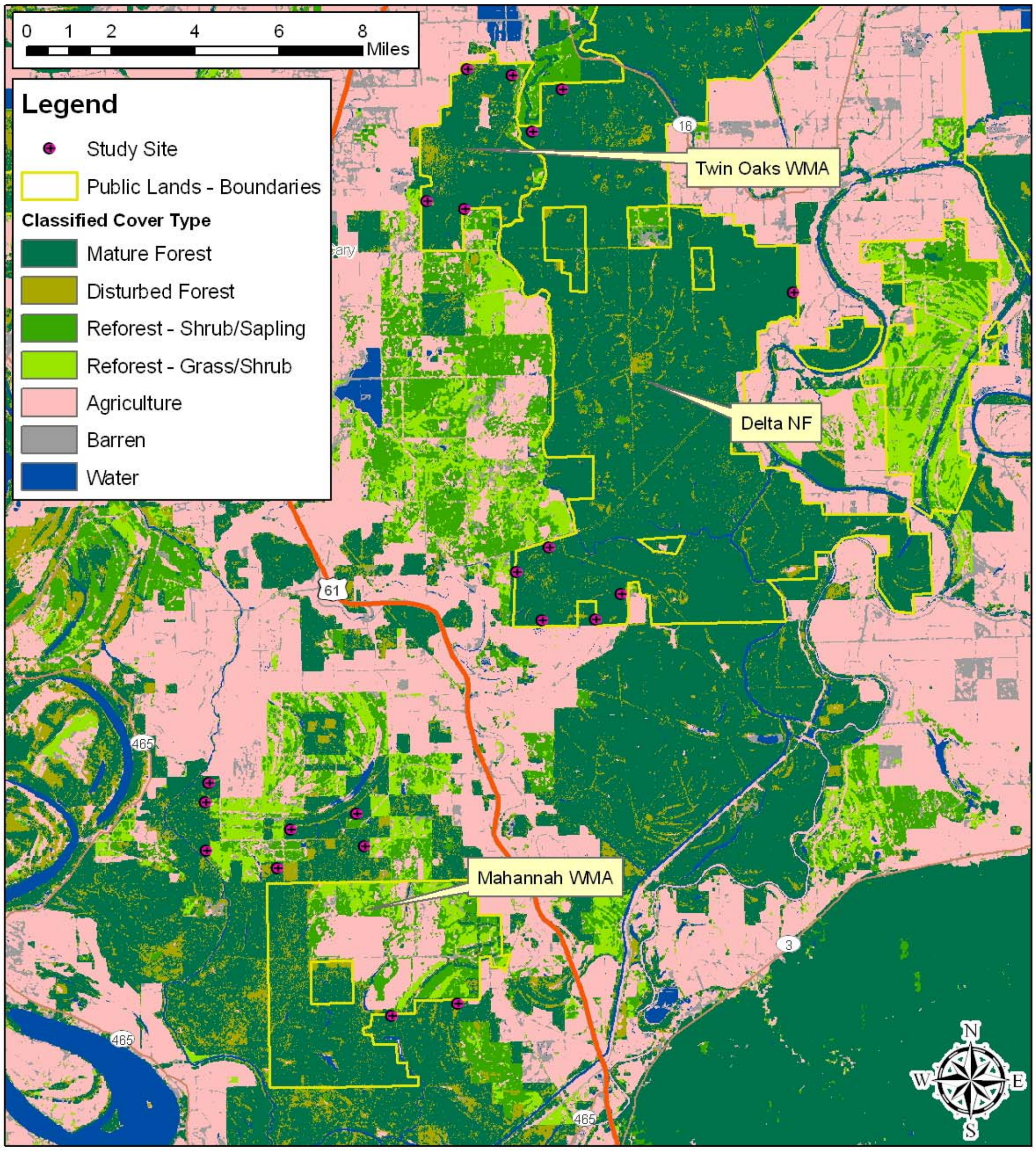

Figure 5.1. Study sites near Vicksburg, MS.

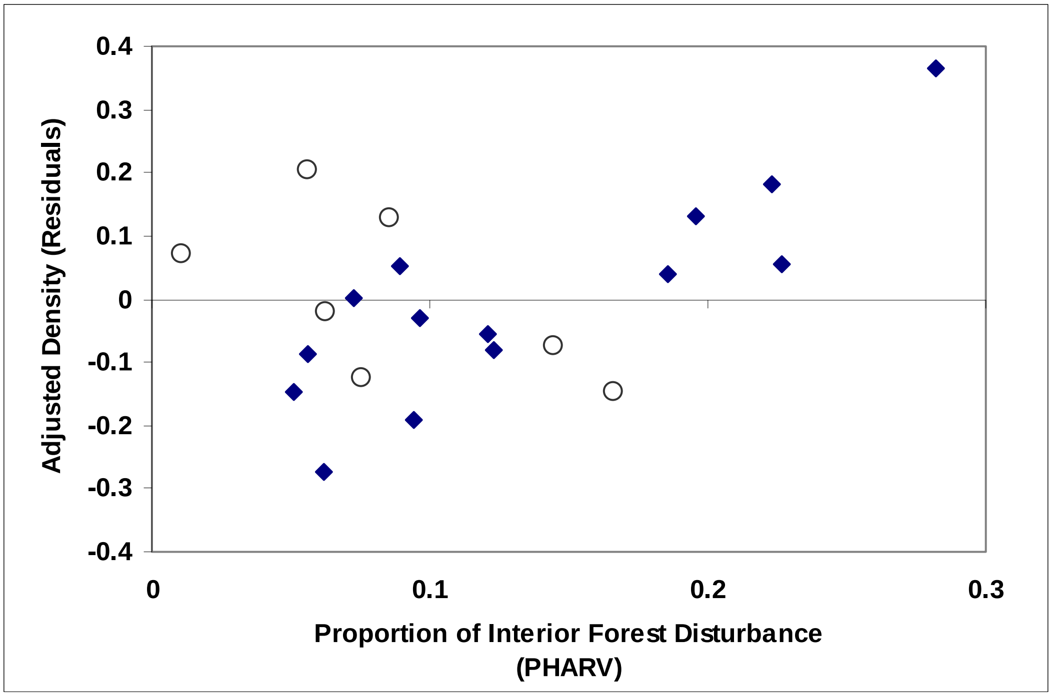

Figure 5.2. Interacting effects of interior forest disturbance (e.g., from selective harvests) and adjacent habitat on density of indigo buntings in mature bottomland forest. Indigo bunting density increases with increasing interior forest disturbance among sites adjacent to reforested fields (dark diamonds). Among sites adjacent to agriculture (open circles), density decreases with increasing forest disturbance. Adjusted density residuals are shown, after controlling for understory cover (UCOV2).

CHAPTER 6

CONCLUDING REMARKS

Theoretical models of habitat settlement (Fretwell and Lucas 1970, Rosenzweig 1981, Pulliam and Danielson 1991, Rodenhouse et al. 1997) typically assume that animals are able to assess habitat quality and preferentially settle in the best habitat patch available. More realistically, however, individuals have only partial knowledge of the components of habitat quality, and may not always choose the best available breeding and/or foraging sites. As a consequence, average fitness and population growth are not fully maximized (Pulliam and Danielson 1991). To understand and predict population dynamics, empirical data are needed to determine how well individuals assess habitat quality when establishing breeding territories. In this dissertation, I explored the connection between habitat use, risk avoidance, and reproductive success in a migratory songbird.

Although some relatively easily measureable features of the habitat are useful predictors of population distribution and productivity, ecologists increasingly recognize the role of the social environment in mediating observed patterns. As reviewed in Chapter 1, competitors, cooperators, predators and parasites all exert an influence on individuals making settlement decisions. Better knowledge of the suite of influential predators in a system, and behavioral responses of prey, will help direct research and inform management decisions. Chapter 2, though anecdotal, fills a knowledge gap because many researchers, especially in North America, are still unaware that woodpeckers are nest predators.

Most frequently, habitat studies report patterns but not processes. If population density is high and patterns of occupancy are documented after the habitat settlement process has already occurred, it may be impossible to infer anything about habitat preferences. Late-arriving individuals are likely to occupy less preferred territories, but these cannot be distinguished without temporal information. In Chapter 3, I specifically set out to document the process of sequential territory settlement by Acadian flycatchers in relation to a measure of perceived risk from the red- bellied woodpecker (nest predator) and brown-headed cowbird (brood parasite). In both years, perceived cowbird risk was higher on vacant than on occupied territories, whereas perceived woodpecker risk was higher on vacant territories in only one year.

Flycatchers selected somewhat drier sites along the wetland continuum, resulting in indirect avoidance of woodpeckers and cowbirds due to their opposing response. However, flycatchers appeared to directly avoid cowbirds as well, even after accounting for habitat effects and philopatry. I found that, for re-occupied territories that had shifted to a footprint that was “safer” in terms of perceived cowbird risk, the settlement date was typically earlier than it had been the previous year. Territories that had shifted to a “riskier” footprint were settled later. I speculate that a shift to a riskier footprint may have been forced by dominant neighbors, or by other dynamic factors that changed the balance of costs and benefits, making the territory less desirable and hence settled later than previously.

In chapters 4 and 5, I turned to the landscape scale, examining both reproductive success and population density. Based on comparisons of population density among study sites, Acadian flycatchers appeared to be particulary sensitive to interior forest openings from patch cuts and other disturbances. This was likely driven by the fact that the incidence of brood parasitism increased with proximity to forest disturbances, and was consistent with our finding that brown-headed cowbirds were positively associated with early successional forest cover in the landscape, including interior forest openings.

At this scale, I found no evidence that Acadian flycatcher density was affected by cowbirds after accounting for landscape context and vegetation. I did find, however, that flycatcher density decreased with increasing woodpecker abundance. I believe that I identified and controlled for the important vegetation and landscape effects, and that the negative correlation between woodpecker and flycatcher density is convincing. Whether the observed correlation was due to behavioral avoidance, direct impacts of predation, or a response to some unmeasured correlate, is unknown. This is a very preliminary finding that warrants further investigation, but is at least consistent with my original hypothesis that red-bellied woodpeckers have a significant impact as nest predators, and that Acadian flycatcher habitat selection is influenced, in part, by an attempt to avoid them.

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