NEST PREDATION ECOLOGY OF THE NORTHERN BOBWHITE IN THE SOUTHEASTERN USA

by

SUSAN N. ELLIS FELEGE

(Under the Direction of John P. Carroll and Michael J. Conroy)

ABSTRACT

Predation is a natural process in ecosystem ecology; however, many ecosystems have undergone tremendous alterations as a result of human impacts. Thus, the process of predation is often altered greatly and requires extensive reevaluation in light of modern landscapes and societal values. Nest predation is considered the leading cause of nest failure for most avian species, including the Northern Bobwhites (*Colinus virginianus*), and may have the potential to limit bobwhite populations. Understanding these predator-prey dynamics requires knowledge of the interactions among predators, prey, and the environments at which they coexist. I report a portion of the findings of a large-scale collaborative study conducted in the southeastern United States to examine the influence of predators on bobwhites population demographics. The objective of this study was to assess the complex nest predation processes through simultaneous study of the meso-mammalian predators and bobwhite nesting. My results suggest that sources of nest mortality by different predators are at least partially compensatory. As nest predation by one guild decreases, other failure causes increase to fill the void. Landscape features appear to influence the predation process more at larger scales (> 50 ha) than smaller scales (< 20 ha) with fallow and annually disked fields being important features of the landscape decreasing nest failures. I found nest predation to be incidental and that fate of a nest was independent of the fate of neighboring nests. My results demonstrate the influences of the first extensive study on quantifying the influence of intensive meso-mammal predator control on predator demographics. Predator control, as done in this study, was intensive enough to meet management objectives of reducing predator use at the local scale, while maintaining predator presence on the greater landscape. Extensive reevaluation of predators, prey, and alternative prey interactions with the modern landscape will be required in order to better understand the predation process in the future.

INDEX WORDS: *Colinus virginianus*, meso-mammal, near-infrared nest camera, Northern Bobwhite, occupancy, predation, predation management, radio-telemetry, scent stations

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DEDICATION

This is dedicated to my loving and supportive husband, Chris, and to my wonderful parents, Bruce and Rose. Without all of you, none of this would have been possible.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW OF BOBWHITE NEST PREDATION ECOLOGY

Predator-prey interactions are one of the most challenging, yet interesting, aspects of gamebird management and ecology. Much debate exists about the extent to which predators can limit avian populations. Research suggests that predators do have the potential to limit gamebird populations (Newton 1998). This topic is of particular interest in the management of Northern Bobwhite (*Colinus virginianus*; hereafter bobwhite), an important gamebird which is extremely vulnerable to predation. Populations, however, have been declining throughout their range since the 1960s (Church et al. 1993, Brennan 1999). The bobwhite decline is thought to be primarily due to a loss in habitat associated with land use changes (Brennan 1991, Fies et al. 1992, Brennan 1993b, Rollins and Carroll 2001). However, it has also been suggested that low quality habitats may predispose bobwhites to high rates of predation (Rollins 1999, Rollins and Carroll 2001) or increased predator populations (Newton 1998) resulting in accelerated rates of population decline. Predators may have some of the strongest influences on distribution, density, and dynamics of prey (Ormerod 2002) and may shape bobwhite populations at the local scale (Errington and Stoddard 1938). Meso-mammalian (medium-size carnivores) predators are known to be one major guild of predators on bobwhites and their nests (Rollins and Carroll 2001). Decreases in mammalian hunting due to declining fur markets, extinction or suppression of top predators, fragmentation, continual land use changes, and societal changes have caused increased meso-predator populations resulting in historically high densities across the southeastern region and other portions of the United States (Palomares et al. 1995, Peoples et al. 1995, Heske et al. 1999).

Long-standing paradigms in quail management do not focus on direct control of predators, rather suggesting that predators should be controlled indirectly through habitat manipulation (Errington 1934). Recently, this paradigm has come under scrutiny by quail managers and other gamebird biologists across North America, with evidence that nest predation may be a limiting factor for bobwhites and other gamebirds (Stoddard 1931, Nelson 2001). The response of predators to habitat manipulations is unknown, but bobwhite populations and predator communities may both benefit from intensive habitat manipulations (Taylor and Burger 1997). The use of predator removal as a tool in wildlife, and specifically bobwhite management, has become an increasingly important, but controversial issue (Messmer and Rohwer 1996, Burger 2002). The state of Georgia now issues permits to private landowners for nuisance wildlife damage control, and many plantations (e.g. private properties intensively managing for bobwhites) have received such permits to control mammalian predators when managing for bobwhites. However, predator removal studies have shown contradictory results on the benefits for target species being managed, and it is unclear if predator removal results in increasing breeding bird populations (Côté and Sutherland 1997, Newton 1998). There is little empirical evidence available on bobwhite responses to predator removal (Brennan 1999, Rollins and Carroll 2001). Additionally, reducing top predators or specific predator guilds may create a cascade effect within the community, and result in increases in other predator guilds and unpredictable results for prey species within the ecosystem (Greenwood et al. 1995, Palomares et al. 1995, Reynolds and Tapper 1996, Riley and Schulz 2001, Treves and Naughton-Treves 2005). Effective management of species such as bobwhite requires an understanding of the predator community, how each species fits in the complex network, and how the community affects demographic responses of bobwhites (Burger 2002).

NEST ECOLOGY OF BOBWHITES

Northern Bobwhites, within the order Galliformes, offer a unique system with which to study nest predation. Bobwhitse are widely distributed throughout the eastern United States and west to the Great Plains, as well as south to Mexico (Brennan 1999), are popular gamebirds, with socio-economic importance (Burger et al. 1999). These non-migratory, social birds are a cryptic, ground-nesting species with complex mating systems (Curtis et al. 1993, Faircloth 2008). Pair formation in the Southeast may begin as early as February with nesting activities continuing from April to October (Stoddard 1931). Bobwhites are indeterminant layers and persistent renesters, often providing multiple opportunities to observe nesting activities within a breeding season. Burger et al. (1995) reported up to 40% of bobwhite females laying multiple clutches in a single breeding season. Incubation is not initiated until the last egg is laid, allowing for the synchronous hatch of precocial young after 23 days of incubation (Stoddard 1931, Brennan 1999).

BOBWHITE PREDATORS

Bobwhites are susceptible to predation at all stages in their life, including the breeding season. Brennan (1999) reported that most opportunistic, terrestrial predators with distributions overlapping those of bobwhites, will consume bobwhite adults, juveniles, and/or eggs. There are

≥ 20 predator species in the Southeast which will prey upon bobwhites or their nests. The predator community includes, but is not limited to, raccoons (*Procyon lotor*), Virginia opossums (*Didelphis virginianus*), bobcats (*Lynx rufus*), nine-banded armadillos (*Dasypus novemcinctus*), red and gray foxes (*Vulpes vulpes* and *Urocyon cinereoargenteus*), coyotes (*Canis latrans*), skunks (*Mephitis mephitis*), snakes [particularly rat snakes (*Elaphus* spp.) and kingsnakes (*Lampropeltis getulus*)], and fire ants (*Solenopsis* spp.), (Hernandez et al. 1997, Fies and Puckett 2000, Staller et al. 2005, Rader et al. 2007), as well as a variety of incidental predator species (Staller et al. 2005, Ellis-Felege et al. 2008, Martin et al. 2008, Terhune et al. 2008).

Medium-sized mammalian predators (e.g., raccoon, opossum, bobcat, armadillo, fox, coyotes, and skunks), often referred to as meso-mammals within the quail literature (Rollins and Carroll 2001, Tewes et al. 2002, Staller et al. 2005), have been considered important nest predators of bobwhites (DeVos and Mueller 1993, Taylor and Burger 1997, Fies and Puckett 2000, Staller et al. 2005). Many of these predator species have reached historically high densities across their range (Peoples et al. 1995, Lovell et al. 1998). Most of these species demonstrate nocturnal or crepuscular activity during the summer months overlapping the bobwhite nesting season (Reid et al. 2006). Meso-mammals can exploit a variety of habitats including mixed habitats with patches of forested area, shrub land, old fields, agricultural areas, wetlands, and suburban areas (Reid et al. 2006). It has been suggested that agricultural field edges, roads, human trails, and other linear edges may serve as travel corridors (Heske et al. 1999, Chalfoun et al. 2002, Kuehl and Clark 2002, Phillips et al. 2003, Frey and Conover 2006). However, other studies have demonstrated conflicting results on generalist predator movement (Pasitschniak-Arts et al. 1998) and densities (Lahti 2001) with respect to habitat edges.

Snakes have been documented as important nest predators of bobwhites (Staller et al. 2005). Recent studies using miniature nest cameras have revealed that snake predation is more important to many avian species than originally thought (Weatherhead and Blouin-Demers 2004). The southeastern United States has the highest reptile species densities in North America (Kiester 1971). Rat snakes (*Elaphus* spp.) and kingsnakes (*Lampropeltis getulus*) are the predominant snake predators on bobwhite nests in this region (Staller et al. 2005). These snakes serve a unique role as both predator and prey within the complex trophic hierarchy. They function as prey to raptors and meso-mammals (Ernst and Ernst 2003, Gibbons and Dorcas 2005), but also, compete with these same species for food items lower in the trophic hierarchy (Stapleton 2005). Both rat snakes and kingsnakes are generalist predators that efficiently prey upon of small mammals, birds, nestlings, and eggs (Hamilton and Pollack 1956, Fitch 1963, Fendley 1980, Ernst and Ernst 2003, Thompson and Burhans 2004, Gibbons and Dorcas 2005, Staller et al. 2005, Stapleton et al. 2008). Generally, rat snakes and kingsnakes are active from spring to fall with two peaks in season activity, April-May and September- October (Ernst and Ernst 2003). Rat snakes are predominantly diurnal species, but may engage in crepuscular or nocturnal activities in the heat of the summer (Ernst and Ernst 2003). Diurnal activities are typical for kingsnakes during fall, winter, and spring, but crepuscular and nocturnal activities are more common during the summer months (Ernst and Ernst 2003). Both types of snakes can be found in a variety of wooded and shrub habitats, including deciduous hardwood forests and scrub-mixed pine. However, rat snakes may be more commonly found along swamp edges than kingsnakes (Ernst and Ernst 2003). Additionally, in the Southeast there is evidence of habitat partitioning among corn snakes which prefer the upland pines and gray rat snakes which are more commonly associated with hardwood drains (Stapleton 2005). Studies in northern regions have found rat snakes prefer field and forest ecotones, particularly during the summer months that coincide with bird breeding (Weatherhead and Charland 1985).

Ants, including the imported red and black fire ants, are other potential nest predators of bobwhites in the southeastern United States. Ants have been documented as nest predators of bobwhites in Texas (Rader et al. 2007), Georgia, and Florida (Staller et al. 2005). In the Southeast, Stoddard (1931) reported bobwhite nest losses by ants to be about 4% of nest failures, while Staller et al. (2005) identified ants as the cause of 12% of nest losses. There exists much controversy over whether the imported ants have contributed to the decline in bobwhites (Allen et al. 1993, Brennan 1993a, Mueller et al. 1999, Burger 2002), but it appears the decline is mostly likely a result of the interaction of a changing landscape and complex predator community including fire ants. Mixed results have been found relative to imported fire ant response to prescribed fire and other bobwhite habitat management (Forbes et al. 2002, Williamson et al. 2002). Imported fire ants are thought to prefer open and semi-open vegetation, such as that provided in early successional habitat maintained for bobwhites (Porter and Tschinkel 1987); however, little else is known about habitat characteristics for fire ants.

Research is needed to study the relationship between nest predation predator diversity, abundance, and activity, as well as management directed at reducing predation (Chalfoun et al. 2002, Stephens et al. 2003, Weatherhead and Blouin-Demers 2004, Sperry et al. 2008). A lack of such studies leaves a weakness in the understanding of predator-prey dynamics and the role specific predators play in limiting avian populations.

PREDATOR CONTROL AS A MANAGEMENT TOOL

Predator control is a controversial topic in wildlife management. This controversy surrounds two opposing demands from the public. The first is to mitigate damage caused by predators (e.g. agriculture and livestock production, abundance of game or imperiled species). The other demand surrounds protection of wildlife from people because of their value to society and the ecosystem (Treves and Naughton-Treves 2005). Many predator control programs have been directed increasing gamebird reproductive success and abundance, but with little understanding of the predator-prey complex and the predation process. Typically, evaluations of the effectiveness of removal programs focus exclusively on the response of the targeted gamebird species. These studies reveal conflicting results on the effectiveness of actually increasing gamebird reproduction and abundance (Côté and Sutherland 1997, Newton 1998). Côté and Sutherland (1997) conducted a meta-analysis on predator control studies and found generally increased hatching success and increased post-breeding populations were observed, but no overall increase in subsequent breeding populations occurred when predators were removed. The effectiveness of predator control may depend on the objectives. Objectives of increased post-breeding season populations are more often achieved through predator control than meeting objectives of increasing the spring population (i.e. breeding population) size (Treves and Naughton-Treves 2005).

Additionally, there has been very little standardization of definitions of predator removal in research or management. The impact of predator removal on predator populations is often unmeasured which lends uncertainty to making inferences on the relationships among predator and prey populations (Treves and Naughton-Treves 2005). Furthermore, important issues of cost-effectiveness, scale, and movement of predators back on to study areas are more difficult to understand when predator population responses are ignored in predator removal studies.

Limited empirical evidence of the impact of predator management on quail breeding success exists in the literature, and no study in the Southeast has ever examined extensive meso-mammal predator removal on bobwhites in good quality habitat. In southern Texas, no treatment effect from mammalian predator removal efforts was observed for bobwhite or scaled quail during a study conducted on a study area of approximately six-square miles (Guthery and Beasom 1977). On 12 farms in North Carolina, predator removals had no effect on bobwhite populations, unless habitat improvements were incorporated. Although predator removals increased the response of bobwhite populations to habitat improvements, habitat was the most limiting factor on the modern farmed landscape (Palmer et al. 2005).

Europe has a history of predator removal as a means of game management that can be traced back to the early 19th century when predators were removed on large, privately owned sporting estates (Reynolds and Tapper 1996). Several studies of the gray partridge (*Perdix perdix*) reported increased production as a result of predator removals (Potts 1986, Tapper et al. 1996). In particular, Tapper et al. (1996) found that predators play a key role in limiting both production and breeding density of partridges; they observed increases in nesting success, average brood sizes, and subsequent breeding densities in areas that received predator control. In Great Britain, red grouse (*Lagopus lagopus*) shooting estates have observed sharp declines in their populations when no predator management was conducted, but estates with active predator control have not seen these same declines (Reynolds and Tapper 1996, Redpath and Thirgood 1999). In fact, estates with predator removal have maintained populations with consistently high grouse densities (Reynolds and Tapper 1996). Thus, European studies suggest predator removal is an effective management tool to increase a fall population and even the subsequent breeding population.

Within the United States, regional differences in bobwhite response to predator control may exist. Early studies of bobwhite populations in Georgia, Florida, and other southeastern states suggest that predators may limit population size, especially during the summer months (Stoddard 1931). However, predation on bobwhites during winter in Wisconsin and Iowa seems to demonstrate a density–dependent relationship where severe weather and food limitations might act in combination with predation to limit abundance (Errington and Stoddard 1938, Newton 1998).

When assessing the potential impacts of predator control on gamebird abundance, there is an obvious bias in where and in what types of ecosystems most studies have been undertaken. For example, the studies by Marctröm et al. (1988), Sovada et al. (1995), Tapper et al. (1996), and Redpath and Thirgood (1999), which represent some of the best research on gamebird-predator interactions relative to predator control, were all conducted in northern temperate ecosystems. All of these systems can be characterized as having relatively simple predator and prey communities. In addition, habitat complexity was simpler and in most cases dominated by agriculture. Translations of these results to more complex ecosystems found in warmer climates might be limited. Only a few key predators are critical to understanding population behaviors in those areas with simpler ecosystems, and thus capable of being controlled with minimal potential interaction with non-target species. In contrast, the Southeastern ecosystems have a large number of mammalian, avian, ant, and snake species that are all known bobwhite predators.

Most predator studies on bird populations do not examine the predators themselves or the factors that account for how they affect nesting birds (Weatherhead and Blouin-Demers 2004).

Changes in the predator community from predator control over the course of the breeding season could alter risk factors associated with nest survival. There are a large number of complex relationships that exist among predator communities and removal of one species of predator could result in increased populations of other smaller predators, the "cascade effect" (Closs et al. 1999, Snyder and Wise 2001). This could potentially contribute to higher levels of mortality on the target species than the predators being reduced. Predation that occurs among predator guilds is important in the shaping of predator communities (Reynolds and Tapper 1996). Snakes serve a unique role as both predators of bobwhites and prey for meso-mmamals (e.g. bobcats; Howze 2009, Schoch 2003). Therefore, snakes may increase as a result of reducing meso-mammal predator populations (Sovada et al. 1995).

It is important to consider alternative prey sources. Crabtree and Wolfe (1988) observed shifts in predators responsible for failures at waterfowl nests when alternative foods resources were supplied to skunks. Population cycling of rodents could potentially provide some reprieve for bobwhites, allowing them an opportunity for population gains. Recent studies demonstrate dramatic shifts in annual survival of bobwhites which are positively related to alternative prey abundance (Palmer and Wellendorf 2007). A positive correlation was observed between tetranoid reproductive success and vole abundance (Marcström et al. 1988). These studies suggest that regional and temporal shifts in the predator community may help explain bobwhite population dynamics, but also, indicate the complexity of predator prey relationships with respect to alterative to prey.

Like all management systems, we should not think about predator removal and how it might affect a single prey or predator species, but instead focus on the predation process and the community effects. In bobwhite management, the traditional objective is to minimize the interaction of predators with bobwhites and their nests during the breeding season, not eradication of the predators. Thus, predation management is a more representative description of the desired management. Predation management involves both direct (e.g. predator reduction) and indirect (e.g. habitat modification, addition of alternative food sources) management of predators. Such management places the emphasis on understanding and manipulating the predation process, rather than solely focusing on reducing the predators.

ASSESSING SHIFTS IN PREDATION RISK

It is well established that predation plays an important role in bobwhite nesting, as well as many other avian species. However, little is known about the role different predators within the community have upon bobwhites or if management geared towards reducing one suite of predators will have an impact upon nest predation by another suite of predators. This idea of intercompensatory factors has long been recognized (Errington 1946, 1956, 1967). We most often think of compensation in wildlife biology in terms of "compensatory mortality," an extension of Errington's theory that includes the effects of harvest (Allen 1954, Anderson and Burnham 1976, Clark 1987). Compensatory mechanisms within nest failures often is overlooked, but has been discussed by Errington (1967) with respect to removal of specific predators at waterfowl nests. He noted that total nest mortality appeared to remain constant each year, even as specific nest predators were reduced. However, the factors responsible for failures appeared to shift. As previously mentioned, Crabtree and Wolfe (1988) also observed shifts in predators responsible for failures at waterfowl nests, but this was with respect to alternative foods resources supplied to skunks. Another way compensation has been examined is in terms of compensatory reproduction (i.e. compensatory releases) following a period of decreased survival for a population (Boyce et al. 1999). Understanding the intercompensations occurring will provide great insight into the predation process and a better understanding of predator-prey community dynamics.

METHODOLOGY

Video technology has become a popular tool in understanding predation events and nesting behavior for many avian species. Recent evidence using camera studies suggest that diagnostic sign at the nest is not a good indicator for identifying predators (Lariviere 1999, Williams and Wood 2002, Staller et al. 2005, Lusk et al. 2006). Through the use of nest cameras, identification of predators can be confirmed and failures can be partitioned among different predators. Camera technology has opened the door to new questions in predator management, specifically in the southeast regarding bobwhites nest predation. Some predator populations can be reduced (e.g. meso-mammals) while others are protected or logistically impossible to reduce from the system (e.g. raptors, snakes, fire ants).

Geo-databases, Geographical Information System (GIS), and spatial software tools (e.g. ArcGIS) are enabling researchers to examine spatial relationships. Coupling these spatial tools with video technology provides an opportunity to attribute nesting events to features of the greater landscape. The identification of predators allows simultaneous spatial analysis of both bobwhite nesting and predator activity. Understanding the connection of predators, prey (e.g. bobwhites and their nests), and the habitats with which they coexist provides a more holistic perspective of the predation process.

Scent stations are a common way to survey mammalian species (Roughton and Sweeny 1982, Conner et al. 1983, Diefenbach et al. 1994). Traditional analysis of this data only provides relative indices of population abundance (Linhart and Knowlton 1975). These indices are commonly used by managers to assess management options relative to meso-mammalian predators to bobwhites. However, the relationship of indices to actual population dynamics has received considerable scrutiny in recent years and findings challenge the reliability of such indices (Diefenbach et al. 1994, Anderson 2001, Anderson 2003, Conroy and Carroll 2009). When scent stations are conducted over several consecutive days and even multiple seasons, occupancy modeling offers a convenient and appropriate analytical methodology to assess scent station techniques to monitor predator population use across a study area (Stanley and Royle 2005, MacKenzie 2006). Imperfect detection is inherent to the sampling process in wildlife, and occupancy provides a technique to account for this challenge. Information on the ability to detect individuals when they are present is obtained through consecutive observations at a specific location, thereby allowing the evaluation of sampling methodology.

STUDY OBJECTIVES

Predation is a natural part of the ecosystem; however, ecosystems have been dramatically altered by human actions. Therefore, in many areas the predation process is now in a transformed state. Despite the extensive studies that have been conducted on bobwhites (Stoddard 1931, Guthery 1997, Williams et al. 2004), many questions exist about detailed predator-prey interactions of bobwhites in modern landscapes. The goal of this study was to examine bobwhite nest predation with respect to meso-mammalian predator management in order to gain a better understanding of the nest predation process. The questions explored were: (1) Do changes in nest predation risk from different predators occur as a result of meso-mammalian reduction on sites managed for bobwhites; (2) What landscape features with respect to failed nests are associated with the different predators responsible for depredations; and (3) How does meso-mammal predator use change as a result of predator trapping? Each of these specific questions is addressed in the subsequent three chapters. Although independently discussed, these questions have an overarching theme of gaining more holistic perspective of the predator-prey community and are summarized in the final chapter with suggestions relative to the management implications of these findings.

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CHAPTER 2

COMPENSATORY SHIFTS IN PREDATION RISK OF NORTHERN BOBWHITE NESTS IN RESPONSE TO PREDATOR REDUCTION[1]

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[1] S. N. Ellis-Felege, M. J. Conroy, D. C. Sisson, W. E. Palmer, and J. P. Carroll. To be submitted to Ecological Applications.

ABSTRACT

Avian nest failure can be caused by many different sources of mortality varying from parasitism, adverse weather, and a variety of predators. Recent interest has emerged in partitioning nest failures among specific causes and being able to quantify these mortality rates among competing risks which may not be independent. Of particular interest to many ecologists and wildlife managers is the allocation of predation risk among the different predator species or guilds responsible for nest failures. Video technology has become a popular tool in avian nest studies and offers the opportunity to accurately identify predators and exact failure times minimizing common issues in nest studies associated with discovery bias. As part of a larger study examining meso-mammal predator control, we monitored 746 Northern Bobwhite (*Colinus virginianus*) nests with 24-hour near infrared cameras. We constructed a set of competing Bayesian multinomial logit random effects models to examine shifts in predation risks among three main predator groups: meso-mammals, snakes, and other causes of nest failure. We modeled failures as non-independent (i.e. compensatory model) by constraining total annual mortality to be a constant while models with independence allowed total mortality to vary each year. Nest mortality by different predator groups was best described by site-specific compensation models. Our results suggest that nest failure causes are not independent of one another, and that shifts in predation risk by one predator guild can lead to compensation by other predator guilds.

INTRODUCTION

The key factors leading to avian nest failure are pivotal for understanding annual recruitment. There are many potential causes of avian nest failure including parasitism, adverse weather, abandonment, egg failure, and a variety of predator species (Etterson et al. 2007). Among the ornithological community, great interest exists in identification and quantification of cause-specific failures at avian nests which may not be independent of one another (Etterson et al. 2007). Specifically, there is a growing interest among wildlife managers in partitioning nest failures due to specific predators or guilds of predators for both theoretical and applied reasons for gamebirds and imperiled bird species. Partitioning failures among predator guilds would provide insight into predator-prey dynamics within a system, as well as, permit estimation of shifts in predation risk as a result of annual changes or manipulation of predator abundance. This information, in turn, would allow prediction about the impacts of community dynamics to better assist managers in decision making directed at increasing avian reproduction.

Accurate identification of specific nest predators would enhance understanding to mechanisms associated with predation events (Soderstrom et al. 1998). Until recently, though, identification of specific fates of nests classified by signs of nest remains after nest failure has been unreliable (Lariviere 1999, Williams and Wood 2002, Weatherhead and Blouin-Demers 2004, Staller et al. 2005, Lusk et al. 2006). Another common technique used to identify nest predators is placing artificial eggs in artificial nests and examining the marks left on the eggs by predators. Potential biases exist in this method since predators at artificial nests have been found not to be representative of predators at real nests (Major and Kendal 1998, Part and Wretenberg 2002, Thompson and Burhands 2004).

Video monitoring of nest activities reduces biases associated with predation events, nest parasite events, and use of artificial nests (King et al. 2001). Continuous video monitoring of all activities at the nest allows researchers to confirm the identity of the nest predators and thereby enable the appropriate partitioning of nest failures to occur. From video monitoring, the actual date of nest failure or success also can be observed, reducing bias associated with determining fate dates from intermittent nest checks. This technology allows us to address questions related to estimating cause-specific nest failures, and determine shifts in predation risk with changes in the predator community.

The idea of non-independence among mortality factors is not new to the wildlife field (Errington 1946, Errington 1956, Errington 1967). Errington's ideas of interactions among mortality factors have been extended to include harvest. Traditionally, the focus of such interaction is on the compensatory relationship between hunting and natural mortality factors (i.e. compensatory mortality; Allen 1954, Anderson and Burnham 1976, Clark 1987). Specifically, density-dependent mechanisms are thought to cause reduced per-capita mortality risk when populations are reduced through harvest, and vice versa, up to a threshold limit set by mortality in the absence of harvest (Anderson and Burnham 1976). Compensatory mechanisms associated with nest failures are less frequently considered, but have been discussed by Errington (1967) with respect to removal of specific predators to enhance success of waterfowl nests. He noted that total nest mortality appeared to remain constant each year, even as specific nest predators were reduced. However, predators responsible for failures appeared to shift. This poses an interesting question for nesting birds in complex ecosystems where specific predator guilds are removed in an attempt to increase productivity. For example, in the management of Northern Bobwhite (*Colinus virginianus*; hereafter bobwhite) in the southeastern USA, only middle-sized mammal (hereafter meso-mammalian) predators can legally and logistically be removed during the bobwhite breeding season. These species include raccoon (*Procyon lotor*), Virginia opossum (*Didelphis virginianus*), bobcat (*Lynx rufus*), nine-banded armadillo (*Dasypus novemcinctus*), red and gray fox (*Vulpes vulpes* and *Urocyon cinereoargenteus*), coyotes (*Canis* *latrans*) and skunks (*Mephitis mephitis*; Hernandez et al. 1997, Fies and Puckett 2000, Staller et al. 2005, Rader et al. 2007). However, there are several other predator species that exist within the community, such as snakes [particularly rat snakes (*Elaphus* spp.) and kingsnakes (*Lampropeltis getulus*)], fire ants (*Solenopsis* spp.), and a variety of incidental predator species (Staller et al. 2005, Ellis-Felege et al. 2008, Terhune et al. 2008). Some of these species, such as snakes, serve roles as both bobwhite predators and as prey items to the meso-mammals being reduced (Lang 2008, Howze 2009). Therefore, reduction of certain species or predator guilds may result in releases of other predator groups with unintended consequences on predation events at nests (Henke and Bryant 1999, Tewes et al. 2002). This leads to the question of whether nest mortality factors shift as a result of changes in the predator community dynamics. Studies regarding predator control and nesting success demonstrate mixed results on benefits to the targeted avian species (Côté and Sutherland 1997, Newton 1998), possibly due to compensatory interactions between predation risk from different predator groups. Biologists need to understand the underlying biological processes and complex interactions involved in nest predation to better manage avian reproduction (Burger 2002).

The objective of this study is to gain a better understanding of interactions among competing sources of nest predation. To do this, we monitored bobwhite nests with 24-hour near infrared nest cameras in northern Florida and southern Georgia during 2000-2006 in conjunction with meso-mammal predator control. Bobwhites are an appropriate study species since they exist in an ecosystem with several predator guilds preying upon nests (i.e. meso-mammals, snakes, ant, and incidental species; Stoddard 1931, Hernandez et al. 1997, Fies and Pucket 2000, Staller et al. 2005, Rader et al. 2007). We examined potential shifts in predation by different predator guilds at bobwhites nests as a result of reducing mesopredator populations, as well as annual and site variation among the predator guilds responsible for nest failure. We hypothesized that nest failures caused by the different predator guilds may not be independent and may lead to compensations, at least in part, by other predators species as one species was reduced. Thus, as the meso-mammal predators were reduced, other species such as snakes and ants would “compensate” for these nest losses, and overall nest success would remain relatively constant. Alternatively, independence among the failure cause could occur, and total mortality could vary annually.

METHODS

Study Area and Field Methods

We studied components of bobwhite nest predation at three properties in southern Georgia and northern Florida during 2000-2006. Tall Timbers Research Station (Leon County, FL; 84º 13’ 35” W, 30º 39’ 39” N; hereafter TTRS) and Pebble Hill Plantation (Thomas and Grady County, GA; 84º 5’ 48” W, 30º 46’ 13” N; hereafter PH) were located in the Red Hills physiographic region. Pinebloom Plantation (Baker County, GA; 31° 24’ 42” N, 84° 22’ 45” W) is located in the Upper Coastal Plain physiographic region. Pinebloom was divided into two 1400-ha study plots (hereafter PB East and PB West) with a cypress (*Taxodium distichum*) swamp buffer approximately 607 ha in size between the two sections. Detailed site descriptions can be found in Staller et al. (2005), and for Pinebloom in Sisson et al. (2000, 2009). All three sites are managed for bobwhite with frequent fire, disking, roller-chopping, and mowing to maintain an open, low density pine forest structure. Sites are dominated by loblolly pine (*Pinus taeda*) and shortleaf pine (*Pinus echinata*) with associated “old-field” ground cover vegetation and areas of longleaf pine (*Pinus palustris*) with associated wiregrass (*Aristida stricta*) ground cover. Hardwood drains, hammocks, and fallow fields are interspersed across the landscape.

Field Methods

Each year between January and April, we captured approximately 100 bobwhites on each site using baited funnel traps (Stoddard 1931), and fit them with 6.5g (~4% body-weight) collar-style radio-transmitters (Staller et al. 2005). Trapping, handling, and marking followed University of Georgia procedures (Institutional Animal Care and Use Committee permit #A2004-10109-c1 and A3437-0). We used radio signals to located bobwhites ≥5 days/ week from 15 April to 1 October of each year in order to monitor nesting behavior and determine nest fates. Bobwhites found in the same location on two consecutive days were assumed to be incubating a nest. Flagging was placed near the nest site to mark its location in order to locate the nest when the incubating bobwhite was away foraging. We were able to find nests and begin monitoring within the first few days of incubation. Thus, nests were discovered at approximately the same stage and only included incubation, not the egg-laying phase of nesting (Taylor et al. 1999).

During absences from the nest of the incubating bobwhite, we installed small continuously recording cameras (Furhman Diversified, Seabrook, TX) 1-1.5 m from the nest (Staller et al. 2005). A near-infrared lighting source (950 nm) was attached with the camera to provide lighting for nighttime recording. The camera and light source was supported on an articulating arm that was camouflaged with surrounding vegetation. A 25-m cord linked the camera and lighting unit to a time-lapse VHS recorder and 225-reserve capacity deep cycle battery. Camera batteries and VHS tapes were changed every 24 hours. Unlike many nesting studies, we checked nests daily via telemetry until failure or hatch, minimizing errors in failure dates common to nesting studies. Additionally, we viewed videos to confirm nest fate and identify nest predators in the event of a depredation. Failures were partitioned into successful hatch and three main failure categories including meso-mammals, snakes, and other (e.g. fire ants, incubating adult killed, and incidental predators such as white-tailed deer (*Odocoileus virginianus*), owls (*Bubo virginaianus* and *Strix varia*), and squirrels (*Sciurus* spp.)). We excluded from subsequent analysis nest failures due to abandonment resulting from researcher activities (primarily camera installation), and failures not captured due to camera failure.

Predators were removed from two pairs of study sites, the Red Hills Region and the Albany Region. In each study region we established a treatment and a control plot of approximately 1,300-1,400 ha in size. In 2000, a year of baseline data was collected on bobwhite nesting activities. From 1 March to 30 September in 2001 to 2003, one plot in the Red Hills Region (PH) and one in Albany (PB East) received intensive predator removal by personnel from Georgia USDA Wildlife Services, while predators were not removed at the other plot. During 2004 to 2006, the treatments were reversed (i.e. TTRS and PB West trapped). The experiment follows a blocked, repeated-measures cross-over design.

Statistical Analysis

3-Failure Cause Model

In addition to meso-mammals, snakes are also more important avian nest predators than originally thought (Weatherhead and Blouin-Demers 2004, Staller et al. 2005); therefore, we first examined the 3-failure causes of meso-mammals, snakes, and all other factors. We constructed a multinomial logit random effects model within a Bayesian framework using Markov chain Monte Carlo (MCMC) algorithms to examine predator-specific mortality rates during incubation. We built and ran the model in Python (Version 2.5) and the module PyMC (Version 2.0;

http://code.google.com/p/pymc). The model was developed in a hierarchical fashion conditioned on nest failure. The number of nest failures due to cause (X_i) in each year resulted in a multinomial distribution (Eq. 1)

$$X_i \mid N, p_1, p_2, p_3 \sim \mathrm{Mult}(N, p_1, p_2, p_3) \qquad (1)$$

where $p_3 = 1 - p_1 - p_2$. The probability of each failure cause was modeled as multinomial logit random effects model (Eq. 2).

$$\mathrm{Mult.logit}(\mathrm{p_{ijk}}) = \beta_{0i} + \beta_{1i} w_{jk} + u_j + z_k \qquad (2)$$

where the $\mathrm{Mult.logit}(\mathrm{p_{ijk}}) = \log\left(\frac{p_i}{p_3}\right)$ and third source of mortality serves as the baseline (in our case meso-mammals acted as the baseline for comparisons). β_0 is the intercept, β_1 is the effect of the binary covariate for trapping (w), u is the random effect for site (j = 1,2,3,4) , and z_k is the random effect for year (k = 1,2, …,7), and i represents the mortality cause (1-3). Using varying standard errors drawn from a half-normal distribution ($\tau = 0.001$), we modeled random effects for site and year, where $\tau = \frac{1}{\sigma^2}$. The model included an intercept (β_0) and trap effect (β_1) with prior distributions specified as a normal distribution ($\mu=0$, $\tau = 0.001$).

Total mortality had a prior distribution specified as a beta ($\alpha = 1$, $\beta = 1$) in three distinct models: 1) full compensation model where total mortality was a single constant across all sites and years, 2) site-specific mortality where total mortality was constant across years, but different among sites, and 3) no compensation where totality mortality varied over all years and sites. Absolute mortality for each predator failure cause was derived from total mortality and the predator-specific failure causes. The compensation models (i.e. models 1 and 2 above) were constrained such that the third source of mortality (M_3) was found from subtracting the first two failure causes (M_1 and M_2, respectively) from total mortality (M_{tot}); therefore, modeling dependence among the failure causes (Eq. 3).

$$M_{3,t} = M_{tot} - M_{1,t} - M_{2,t} \qquad (3)$$

In models without compensation, each mortality factor was independent of the others, and total mortality was based simply upon the sum of the three mortality sources each year (Eq. 4).

$$M_{tot,t} = M_{1,t} + M_{2,t} + M_{3,t} \qquad (4)$$

Six models were developed based upon the 3 mechanisms to describe mortality factors and the inclusion of the covariate for meso-mammal trapping mortality. We ran MCMC algorithms for 1,000,000 iterations with a burn-in of 800,000 and thinned every 50 to insure convergence and minimize autocorrelation.

Models were evaluated using a deviance information criteria (DIC), analogous to Akaike Information Criterion (AIC), to find the most parsimonious model explaining bobwhite nest mortality (Spiegelhatler et al. 2002). Thus, smaller DIC values indicate the best approximating and most parsimonious model. Bayesian goodness-of-fit (GOF) was assessed by comparison of deviance from simulated data to that of the observed data. A perfectly fit model would have a GOF = 0.5 which indicates that half of the simulated data deviances exceeded the deviances of the observed data. Much debate exists about the appropriate methods for model-averaging (Link and Barker 2010); we chose instead to focus inference on the best DIC-supported models, and reported the median and 95% credibility intervals (95% CI) of the posterior distribution.

2-Failure Cause Model

We simplified the above model to accommodate a new question of the relationship between managed (i.e. meso-mammals) and unmanaged failure causes (i.e. snakes, ants, and incidental causes) by adjusting the previously described multinomial logit random effects model to only 2 failure causes (i.e. binary logistic model, Eq. 5).

$$\mathrm{logit}(p_{jk}) = \beta_0 + \beta_1 w_{jk} + u_j + z_k \qquad (5)$$

where the $\mathrm{logit}(p_{jk}) = \dfrac{1}{1+\exp(-p_{jk})}$. These included meso-mammals and all other failure causes. The same six competing models were constructed, run for 1,000,000 iterations (burn-in of 800,000, thinned every 50), and assessed using DIC and GOF as previously described.

RESULTS

During 6-years for all study areas combined we removed, 5,161 meso-mammalian predators. We monitored 746 bobwhite nests with nest cameras. Of these, 30 (4.0%) fates were unknown due to thick vegetation, 8 (1.1%) had camera failures, and 32 (4.3%) resulted in abandonment due research activities (primarily as a result of camera installation), leaving 676 (90.6%) total nests with known failure causes. Of the 676 nests where fates could be determined, 429 (63.5 %) hatched at least one egg, and 247 (36.5%) nests failed. Failure causes included 98 (39.7% of total depredated nests with known causes) meso-mammals predation events, 79 (32.0 %) snake depredations, and 70 (28.3%) failed due to other causes (fire ants (13.4%), incidental predator species (1.6%), or mortality of the incubating bobwhite (13.4%)). Failures classified as unknowns were not meso-mammals predators because these predators were apparent even in thick vegetation. These unknown failures were incorporated into the 2-failure model since our best evidence suggested they were snakes (Staller et al. 2005), but could only be confirmed as not meso-mammals and could not be determined whether they were snakes or smaller incidental predators from camera footage.

3-Failure Cause Model

We first examined the role of compensation with respect to 3-failure causes (i.e. meso-mammals, snakes, and other failures) and obtained posterior statistics, goodness-of-fit, and information theoretic statistics for the 6 alternative models (Appendix A.2.1). We did not incorporate the 29 nests that could not be confirmed as snakes or other failure causes (i.e. unknown) in this model. Goodness-of-fit was adequate for all models, but lower for the 2 full compensation models (Table 2.1). The best approximating model, based upon DIC values, for this data was the site-specific compensation model with the meso-mammal trap effect covariate included (Table 2.1). This model had 77.2% of the model weight and was 3.9 times more likely than the next best-fitting model, which described site-specific compensation without the trap effect included.

Total mortality varied among the 4 sites. The largest differences existed between PB West and TTRS. We found credibility intervals overlapped for 3 of the 4 sites, indicating similar mortality among all sites except PB West (Figure 2.1). Meso-mammal depredations decreased with trap efforts, whereas snakes and other failure causes increased during this period (Figure 2.2). Based upon the top model, the effect of trapping efforts made snake depredations 2.80 times more likely (95% CI: 1.44 - 5.61) than meso-mammal predation events. Other depredations were 3.58 times more likely (95% CI: 1.84 – 7.24) than meso-mammals nest failure events.

2-Failure Cause Model

The 2-failure cause model allowed us to incorporate the 29 nest failures that were known not to be meso-mammals, but could not be positively identified as snakes. This increased the sample size to 706 total nests examined, of which, there were 277 nests to fail (39.9%). Like the

3-failure cause models, we obtained posterior estimates, goodness-of-fit, and information theoretic statistics for the 6 alternative models (Appendix A.2.2). All models exhibited adequate fit (Table 2.2). The best approximating model, based upon DIC values, for the 2-failure cause data was also the site-specific compensation model with the meso-mammal trap effect included as a covariate (Table 2.2). This model had 92.9% of the model weight and was >17 times more likely than the second best fitting model describing full compensation with the trap effect covariate included. The top model for the 2-failure causes had a similar pattern in total mortality with PB West exhibiting higher annual total mortality than other sites (Figure 2.1). The effect of trapping made meso-mammal depredations 2.73 times less likely (95% CI: 1.51 – 4.86) than other types of nest failure (Figure 2.3).

DISCUSSION AND MANAGEMENT IMPLICATIONS

These results suggest that a dependency exists among bobwhite nest mortality factors once incubation has been initiated. Total mortality at bobwhite nests appears relatively constant from year to year; however, each site has its own specific failure rate. As Errington (1967) observed with waterfowl nests, shifts in the predators responsible for the failures appear to occur with respect to trapping efforts. Crabtree and Wolfe (1988) also observed similar shifts in predators responsible for mortality of waterfowl nests when alternative foods were supplied for skunks. We observed decreased depredations by meso-mammals as result of trapping while other predator guild depredations increased. Studies examining the effects of predator control programs on increasing avian productivity have demonstrated mixed results (Côté and Sutherland 1997, Newton 1998). Most of these studies have examined nest success, which is simply the result of subtracting total mortality from one. Additional evaluation of bobwhite productivity found increased chicks/hen with respect to meso-mammalian predator control, despite the findings of this study where total mortality (and thus, nest success) was relatively constant (J.P. Carroll and W.E. Palmer, unpublished data). In fact, nest success is considered only an index to annual fecundity and likely does not accurately reflect actual production (Etterson et al. *In Review*). Therefore, increases in productivity as the result of meso-mammal predator reduction may not be observed as raw increases in nesting success.

In ecosystems with few nest predators and relatively simple community dynamics, such as those of northern temperature regions and portions of Europe, predator reduction efforts have demonstrated increased nesting success of gamebirds (Chesness et al. 1968, Schranck 1972, Duebbert and Lokemoen 1980, Sargeant et al. 1995, Tapper et al. 1996). These simple ecosystem dynamics with fewer predators may not demonstrate compensations as strongly as complex systems, such as those of the southeastern USA. Additionally, bobwhites across the Southeast have a long nesting season, and thus are persistent renesters and frequently have multiple clutches (Burger et al. 1995, Brennan 1999). Although our results only examine nests once incubation has begun, they suggest that nest survival may not be sensitive enough to detect the underlying processes occurring and therefore unable to detect the actual effect predator control efforts have upon reproduction and community dynamics.

Although there is clear dependence among the failure causes, it is unclear whether the meso-mammal manipulations in the predator community resulted in compensatory releases of other predators within the community (e.g. snakes) or if by removing the more efficient meso-mammal nest predators, other less efficient predators or predators with different foraging behaviors (e.g. ants) now have the opportunity to prey upon the nest. Henke and Bryant (1999) conducted coyote removal and found shifts in populations of other members of the predator community, primarily to other meso-predators. They suggested that predator reduction efforts may lead to unintended consequences within the community dynamics, requiring a deeper understanding of the predator-prey complex of interactions. Tewes et al. (2002) also suspected that bobcats and other meso-predators could have unpredictable effects upon the community dynamics. Reduction of one or more of these species may have indirect effects on the population sizes and distribution of other predators which may be a more serious threat to quail nests.

The broader implications of this study extend to the challenges of identifying and understanding community interactions, particularly when generalist predators are a part of the community. One way of understanding community dynamics is through modeling food-web dynamics; however, this has been found to very complex and challenging (Closs et al. 1999, Stouffer et al. 2005). There has been considerable debate about how best to incorporate the role of generalist predators (Closs et al. 1999). There appears to be spatial and temporal considerations, as well as complexity in the number of species in the system, the number of links among the different species, and the strength of the interaction of these links (Closs et al. 1999).

Diet of meso-mammal predators, such as bobcats (Neale and Sacks 2001, Godbois et al. 2003, Schoch 2003, Lang 2008, Howze 2009), coyotes (Litvaitis 1981, Neale and Sacks 2001), fox (Neale and Sacks 2001), and opossum (Reynolds 1945, Llewellyn and Uhler 1952) have documented snakes being a component of the diet. However, these interactions do not necessarily have to focus on predators preying upon other predators. For example, predators such as ants generally do not depredate nests until eggs are hatching since they are unable to directly access eggs until after hatching has commenced (Staller et al. 2005). Thus, if nests are available on the landscape longer as the result of reduced meso-mammal depredations, then these nests are now susceptible to depredations by other predators, such as ants, that have different foraging techniques.

Shifts in the predators responsible for nest failure will likely require a better understanding of the underlying predator community dynamics at each site (see Chapter 4). To fully understand the predation process, we must first understand the initial predator community present and the behaviors of these predators. For bobwhites, partial depredation events, where some of the eggs are left intact and capable of being hatched, appear to be caused by only certain predator species (Ellis-Felege et al. *In Press*). Thus, shifts in full depredation events may also reflect shifts in partial depredations that could have large implications for annual productivity.

Previous attempts at understanding competing sources of nest mortality have frequently suffered from inadequate information on the specific failure causes (King et al. 2001). Video cameras have enabled us to confirm the predators responsible for the nest failure. Other issues associated with quantifying cause-specific nest mortality are associated with discovery bias of nests, as well as actual dates of nest failure (Etterson et al. 2007). Through the use of radio-telemetry, we were able to monitor almost the entire 23-day incubation period for our nests. However, the expense of video equipment, as well as coupling nest monitoring with radio-telemetry makes comprehensive studies such as these uncommon and financially challenging to obtain adequate sample sizes. Additionally, quantifying dependence among the failure causes has been problematic for avian species with discovery bias. Challenges still exist in models for examining competing risks. Many still examine the failure causes as independent risks for situations with discovery bias, creating an area for future research efforts (Etterson et al. 2007).

Nesting success does not appear to be sensitive enough to detect the underlying biological processes occurring and the potential impacts of management actions. This study can be extended beyond the scope of predation management. Other researchers have found a lack in correlation between nesting success and other reproductive metrics (Murray 2000). Our study supports a potential reason for the decoupling of these reproductive measures. The complex bobwhites breeding system has many factors, such as being persistent renesters, multiple clutches, and male incubation and brooding (Burger et al. 1995) that could influence overall fecundity. Partial depredations also are common occurrences for bobwhites (Ellis-Felege et al. *In Press*). As such, all of these factors make estimation of seasonal productivity more challenging and requiring additional information about reproductive processes for not only bobwhites, but for many other avian species.

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Table 2.1: Goodness-of-fit (GOF) statistics and model selection statistics using DIC (Deviance Information Criterion) to assess best-approximating model for 3-nest failure causes (meso-mammals, snakes, other incidental failures) at Northern Bobwhite nests on 4 study sites over 7 years in northern Florida and southern Georgia.

Model	**GOF**	**DIC**	**ΔDIC**	**W_i**
Site-Specific Compensation[1], Trap Effect[2]	0.64	332.9	0	0.772
Site-Specific Compensation[1]	0.61	335.6	2.7	0.200
Not Compensatory[3], Trap Effect[2]	0.64	341.2	8.3	0.012
Full Compensation[4], Trap Effect[2]	0.71	341.3	8.4	0.012
Not Compensatory[3]	0.61	343.5	10.6	0.004
Full Compensation[4]	0.71	353.3	20.4	0.000

[1] Site-specific compensation refers to compensation being site-specific.

[2] Trapping effect refers to meso-mammal predator removal or not.

[3] Not compensatory refers to independence among nest failure causes.

[4] Full compensation refers to total mortality being constant across all sites, rather than site-specific.

Table 2.2: Goodness-of-fit (GOF) statistics and model selection statistics using DIC (Deviance Information Criterion) to assess best-approximating model for 2-nest failure causes (meso-mammals and all other failures) at Northern Bobwhite nests on 4 study sites over 7 years in northern Florida and southern Georgia.

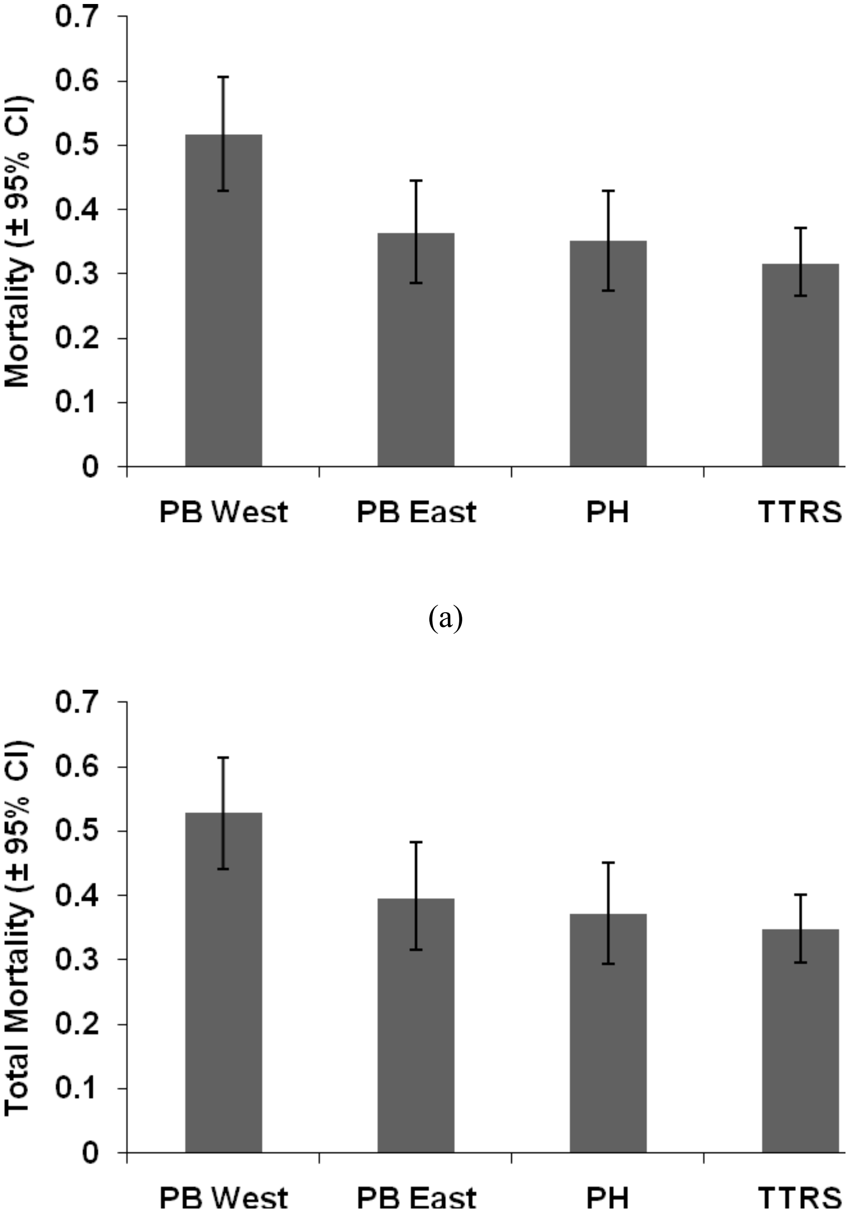
Model	**GOF**	**DIC**	**ΔDIC**	**W_i**
Site-Specific Compensation[1], Trap Effect[2]	0.53	236.7	0	0.9292
Full Compensation[4], Trap Effect[2]	0.61	242.4	5.7	0.0537
Site-Specific Compensation[1]	0.54	244.8	8.1	0.0162
Full Compensation[4]	0.61	250.6	13.9	0.0009
Not Compensatory[3]	0.68	280.7	44	0.0000
Not Compensatory[3], Trap Effect[2]	0.68	281.4	44.7	0.0000

[1] Site-specific compensation refers to compensation being site-specific.

[2] Trapping effect refers to meso-mammal predator removal or not.

[3] Not compensatory refers to independence among nest failure causes.

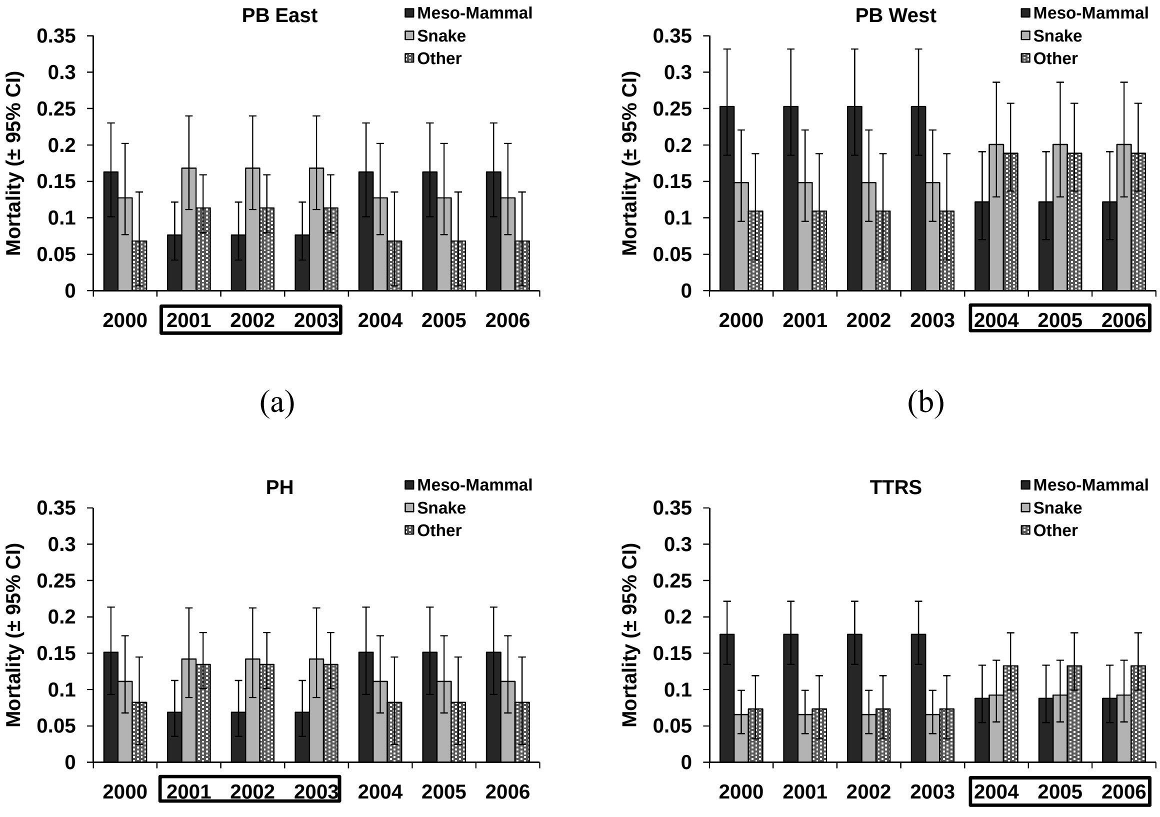
[4] Full compensation refers to total mortality being constant across all sites, rather than site-specific.



(a)

(b)

Figure 2.1: Median bobwhite total nest mortality (± 95 % Bayesian credibility interval) from our top model with site-specific compensation and a covariate for trap effect at 4 study sites in northern Florida and southern Georgia when examining mortality (a) among 3-specific nest failure causes and (b) the 2-failure cause model.



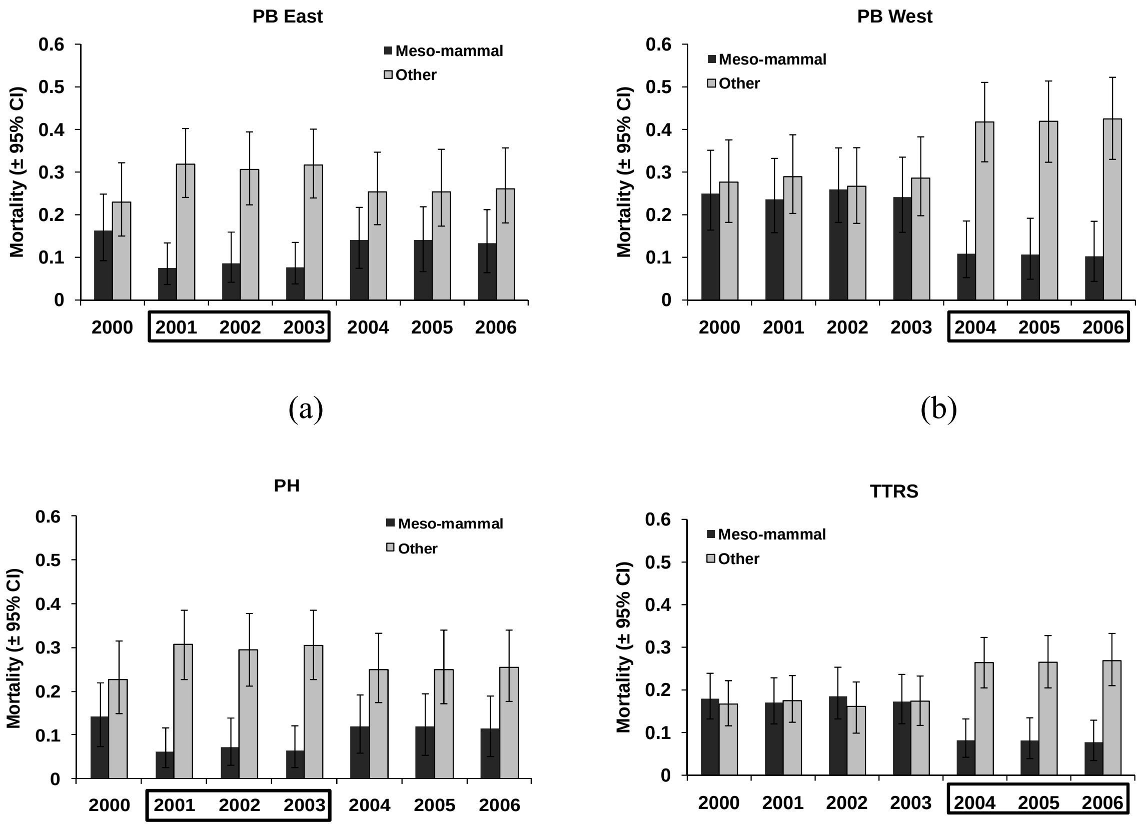
(a)

(b)

(c)

(d)

Figure 2.2: Median predator-specific rates of mortality (± 95% Bayesian credibility interval) when examining 3-failure causes from our top model with site-specific compensation and a covariate for trap effect at bobwhite nests in northern Florida and southern Georgia. Years of meso-mammal trapping for each site are highlighted by the box.



(a) (b)

(c) (d)

Figure 2.3: Median predator-specific rates of mortality (± 95 % Bayesian credibility interval) when examining 2-failure causes from our top model with site-specific compensation and a covariate for trap effect at bobwhite nests in northern Florida and southern Georgia. Years of meso-mammal trapping for each site are highlighted by the box.

CHAPTER 3

LANDSCAPE FEATURES AFFECTING NORTHERN BOBWHITE PREDATOR-SPECIFIC NEST FAILURES IN THE SOUTHEASTERN USA[1]

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[1] S. N. Ellis-Felege, S. E. Albeke, N. P. Nibbelink, D. C. Sisson, S. D. Wellendorf, M. J. Conroy, W. E. Palmer, and J. P. Carroll. To be submitted to Landscape Ecology.

ABSTRACT

Nest predation is a critical component in avian productivity and typically is the leading cause of nest failure for most birds. Habitat use and selection by both predator and prey are of paramount importance to understanding the predation process. Several landscape features are thought to drive the behavioral interaction between bobwhites (e.g. nest placement) and their predators (e.g. search methods for food acquisition). In order to understand habitat characteristics influencing predation, we studied Northern Bobwhite (*Colinus virginianus*) nests using 24-hour near-infrared cameras. We installed cameras at 675 bobwhite nests on 3 properties in northern Florida and southern Georgia from 2000-2006. We checked nests daily until hatch or failure occurred. Video footage confirmed the fate and identity of predators in the event of nest failure. To test the association between nest failures and specific failure causes with landscape structure, we calculated a suite of landscape metrics and examined these at 4 spatial scales (3.1-ha, 19.6-ha, 50.3-ha, 176.7-ha). We did not find landscape metrics to be important predictors of bobwhite nest failures at small scale (< 20 ha), but percent composition and proximity to fallow and annually disked fields at larger scales (< 50 ha) increased the probability of nest success. Fields may provide alternative prey items important in buffering nest predation. For predator-specific failures, we observed increases in field composition to decrease incidental nest failure causes relative to meso-mammals at the smallest scale (3.1-ha). Increased distance between nests and supplemental feed lines slightly increased the probability of nest failure due to ant predation relative to meso-mammal predation events at the 3 larger spatial scales. Interestingly, the fate of a nest was independent of the fate of neighboring nests, suggesting bobwhite nest predation is primarily incidental. Although bobwhite management is often undertaken at fine (stand) scales, our analysis demonstrates the need to incorporate more

landscape scale metrics, such as habitat composition at larger spatial scales in management programs.

INTRODUCTION

Predation is a process that relies on the interactions among predators, prey, and the habitat where they coexist. Nest predation is considered the leading cause of nest failure for most avian species (Ricklefs 1969). Effective management to enhance breeding success of an avian species requires accurate identification of the predators responsible for failures, as well as, knowledge of predator and prey distribution, abundance, diversity, and habitat use. Nest predation is likely to be in part the result of incidental encounters of predators with nests (Vickery et al. 1992, Jones et al. 2004). Therefore, management that reduces the probability of these interactions may result in increased reproductive success. Frequently, predator control is used mitigate nest losses for many gamebirds and imperiled bird species; however, many conflicting results exist about its effectiveness to enhance avian reproductive success and abundance (Côté and Sutherland 1997, Newton 1998). The Northern Bobwhite (*Colinus virginianus*) is a declining grassland- and early successional-dependent species. Bobwhites are particularly vulnerable to predation since they nest on the ground with large clutches and relatively long nest exposure periods. It has long been thought that habitat management is the most effective tool at enhancing their populations (Stoddard 1931) based on the premise that predator populations can be manipulated indirectly through habitat modifications (Errington 1934). This non-lethal method has been suggested as the first tool that should be implemented to offset predation losses (Rollins and Carroll 2001). In order to increase bobwhite reproductive output, biologists need to first understand the complex relationship among the predators, bobwhite nests, and the habitats which lead to increased interactions between nests and predators.

Relatively little is known about nest predation and macrohabitat composition for bobwhites (Staller et al. 2002), and specifically what spatial scales might be most important to bobwhite reproductive success (Roseberry and Klimstra 1984, Taylor et al. 1999b, White et al. 2005). Radio-telemetry technology has greatly enhanced our understanding of bobwhite nest selection; yet identification of the predators responsible for nest predation events is rarely known since signs at the nest may be misleading (Lariviere 1999, Staller et al. 2005, Lusk et al. 2006). Traditional studies of bobwhite nesting relative to habitat features have focused on the influence of habitat on nest site selection or nest success (Taylor et al. 1999a, Taylor et al. 1999b, White et al. 2005, Collins et al. 2009). Only one study to date has examined the specific predator species responsible for nest failures, and their interactions with habitat characteristics (Staller et al. 2002). Advances in camera technology have enabled biologists to accurately identify nest predators, and cameras have become a popular tool in studying avian nest predation (Pietz and Granfors 2000, Staller et al. 2005). This technology coupled with measuring habitat characteristics can assist in managing habitat to reduce nest predation and target the predominant predator species responsible for nest failure.

Common bobwhite nest predators include raccoons (*Procyon lotor*), nine-banded armadillos (*Dasypus novemcinctus*), opossums (*Didelphis marsupialis*), bobcats (*Lynx rufus*), red and gray foxes (*Vulpes vulpes* and *Urocyon cinereoargenteus*), coyotes (*Canis latrans*), skunks (*Mephitis mephitis*), snakes (*Elaphe* spp. and *Lampropeltis getula*), and fire ants (*Solenopsis* spp.) (Hernandez et al. 1997, Fies and Puckett 2000, Staller et al. 2005). These predators have broad diet and habitat needs, and are thought to opportunistically feed on nests. Therefore, understanding how features on the landscape determine predator behaviors, such as foraging, has substantial value in managing not just bobwhites, but also entire avian communities (Kuehl and Clark 2002).

Habitat edges may serve as travel corridors for many wildlife species, particularly medium-sized mammals (Heske et al. 1999, Chalfoun et al. 2002, Kuehl and Clark 2002, Phillips et al. 2003). However, some studies contradict the role linear edges may play in mammalian predator movement (Pasitschniak-Arts et al. 1998). Ecotones and other edges are frequently found to be preferred by some snake species, particularly in northern regions (Weatherhead and Charland 1985). Edges may be important to predators particularly where habitat patches are small with relatively little “core” area to be searched (Temple 1986). For some species, such as fox, activity is greater in smaller patches (Sovada et al. 2000) and is likely the result of a fragmented landscape with many edges that enable the predator to search the area with greater efficiency. Edges may attract avian nesting, but these abrupt transition zones may serve as ecological trap (Gates and Gysel 1978). Gates and Gysel (1978) further proposed that the low quality habitat surrounding a narrow strip of suitable nesting habitat made the nests more vulnerable to predation.

Although many bobwhite predators are generalists, little research has focused on the habitat composition and configuration preferences which might influence the ability of these predators to find avian nests (Phillips et al. 2003). These generalist meso-mammals frequently exploit a variety of habitats including mixed habitats with forested area, shrub land, old fields, agricultural areas, wetlands, and suburban areas (Reid et al. 2006). However, some meso-mammalian predators were found to prefer specific habitat cover types in the Prairie Pothole Region of North America (Phillips et al. 2003). In addition, edge use was dependent upon the types of surrounding land cover, with wetlands being more attractive edges for meso-mammals (Phillips et al. 2003). Snake species utilize a variety of habitats including wooded and shrub areas with both hardwood and pine forests and wetland edges. Within the snake community used habitats often are different even among closely related species. For example, in our study areas, corn snakes most often use upland pine areas, whereas gray rat snakes are most often found in hardwood drains (Stapleton 2005). Thus, wildlife managers could benefit in understanding whether specific habitat composition and configuration of land cover types might increase predation risk to avian nests by certain predator guilds.

The objectives of this study were to determine the landscape composition and configuration features important to 1) the failure of bobwhite nests and 2) to the specific predators responsible for nest failures across 4 different spatial scales. This was conducted by coupling radio-telemetry, nest camera technology, and spatial analysis tools (e.g. geographical information systems (GIS), ArcMap). The findings of this study provide insight on spatial scales at which nest predation processes are occurring, underlying spatial relationships relevant to predation processes, and potential management that may minimize nest predation.

METHODS

Study Area

We studied bobwhite nesting at 3 sites in southern Georgia and northern Florida during 2000-2006. Located in Red Hills physiographic region are Tall Timbers Research Station and Land Conservancy, Inc. (Leon County, FL; 84º 13’ 35” W, 30º 39’ 39” N) and Pebble Hill Plantation (Thomas and Grady County, GA; 84º 5’ 48” W, 30º 46’ 13” N). Pinebloom Plantation (Baker County, GA; 31° 24’ 42” N, 84° 22’ 45” W) is located in the Upper Coastal

Plain physiographic region. Detailed site description for the Red Hills sites can be found in Staller et al. (2005), and for Pinebloom in Sisson et al. (2000, 2009). Sites are dominated by loblolly (*Pinus taeda*) and shortleaf pine (*P. echinata*) with associated "old-field" ground cover vegetation and areas of longleaf pine (*P. palustris*) with associated wiregrass (*Aristida stricta*) ground cover. All 3 sites use frequent fire (1-3 year rotations), disking, roller-chopping, and mowing to maintain an open, low density pine forest structure. Hardwood drains, hammocks, fallow fields, and wetlands are interspersed across the landscape. On the greater landscape, the adjacent land to Pinebloom Plantation includes some row crop agriculture predominantly for cotton and peanuts. Supplemental feeding of bobwhites occurred on all 3 properties. Every 2 to 3 weeks throughout most of the year, sorghum was spread at a rate of approximately 6 bushels per 1.6 km on specified trails (feed lines).

Bobwhite Nesting

On each study site, we captured approximately 100 bobwhites each year between January and April, 2000-2006, using baited funnel traps (Stoddard 1931). We classified captured bobwhites by age and sex, and fitted each with 6.5g (~4% body-weight) collar-style radio-transmitters (Staller et al. 2005). Trapping, handling, and marking methods followed those required in our University of Georgia Institutional Animal Care and Use Committee permit #A2004-10109-c1 and A3437-0. Using radio-telemetry homing techniques (White and Garrott 1990), we located bobwhites ≥ 5 days/week to monitor nesting behavior between 15 April and 1 October of each year. Bobwhites found in the same location on two consecutive days and did not have the mortality sensor activated were assumed nesting. We placed flagging near the nest site location so the location could be found when the incubating bobwhite was away foraging. The nest location was recorded into a geo-database using GIS and ArcGIS software

(Environmental Systems Research Institute, Inc.). We were able to find nests and begin monitoring within the first few days of incubation. Nests were discovered at approximately the same stage and our monitoring only included incubation, not the egg-laying phase of nesting (Taylor et al. 1999b).

When the incubating bobwhite was away from the nest, a continuous-recording, near-infrared camera (Furhman Diversified, Seabrook, TX) was installed at the nest. The small camera with a near-infrared (950nm) lighting source was placed about 1-1.5 m from the nest opening (Staller et al. 2005). We camouflaged the cameras using surrounding vegetation. Cameras and lighting sources were linked via a 25 m cable to VHS recorders and 225-reserve capacity deep cycle battery. The recorders were modified to operate at 1/3 speed, allowing an 8-hour tape to last 24 hours. We replaced tapes and batteries daily. Unlike many nesting studies, we checked nests daily via telemetry until failure or hatch, thus minimizing errors in failure dates common to nesting studies. We viewed videos to confirm fate of the nest and identify the nest predator if the nest failed. Nests were categorized first as successful (i.e. hatched ≥ 1 egg) or failed. From camera monitoring, failed nests were further classified as failed due to meso-mammals, snakes, ants, and other factors (e.g. incidental predators or bobwhites killed away from the nest).

Land Cover

We digitized land cover types at 1:1,500 m scale using 1999 Digital Orthophoto Quarter Quardrangles in ArcMap (version 9.2). Additionally, knowledge of the study area, remote imagery and ground-truthing specific areas using handheld GPS units were used to update the land cover polygons representative of the study years, 2000-2006. We delineated 10-land cover types. These included pine (i.e. open pine savannah), planted pine (i.e. densely planted pine stands), agriculture (i.e. row crops), ragweed and fallow fields, hardwood drains, roads, feed lines, wetland, open water, other (i.e. predominantly urban).

Landscape Metrics

We were most interested in spatial relationships of nest fates relative to the composition of the landscape at different scales, proximity of specific landscape features to the nest, and amount of edge near nests at the different scales. We constructed a circular buffer around each nest site with radii of 100 m (3.14 ha), 250 m (19.6 ha), 400 m (50.3 ha), and 750 m (176.7 ha). Buffer sizes were selected based upon the variety of home range sizes in the predator community. These scales also encompassed bobwhite home ranges on the study areas (Sisson et al. 2000, Wellendorf and Palmer 2009), scales representative of home ranges in other areas of Georgia (Parnell et al. 2001), and scales comparable to previous studies examining bobwhite nesting relative to landscape characteristics (Staller et al. 2002, White et al. 2005). We intersected each buffer size with the land cover layer of the study areas using ArcMap intersect tools. Within each buffer size, percent composition of the habitat cover types was calculated. We calculated Euclidean distance between nests to landscape features of interest (e.g. roads, feedlines, hardwood drains). Using Fragstats (Version 3.3; McGarigal et al. 2002), we created grid layers with the landscape metric for edge density (total length of edge in the landscape divided by total area of landscape) at the varying scales. Although, there are many metrics which can be calculated, we focused on edge density since edges are thought to be primary travel corridors for predators. These values were extracted to the nest point using the Spatial Analyst Tool "Extract Values to Point" in ArcMAP.

Statistical Analysis

First, we assessed the probability nest failures relative to specific landscape metrics using a logistic regression. We initially examined models at each of the 4 spatial scales to determine which models were most important at the individual scales. To avoid multicollinearity, we conducted Pearson correlations on all pairs of predictor variables. We considered $r^2 > 0.3$ to be a conservative estimate of correlated variables and thus, did not use them in the same regression model. We selected 9 metrics to use as predictors variables including percent of hardwood composition within each buffer, percent of wetland composition within each buffer, percent of annually disked fields composition within each buffer, edge density at each buffer size, distance to hardwoods, distance to fields, distance to wetlands, distance to roads, and distance to feedlines (Table 3.1). We examined $\hat{c}$ of the global model to determine if the data were overdispersed (Lebreton et al. 1992). We ran a Hosmer-Lemeshow goodness-of-fit (GOF) test on the global model, where an adequate fit is observed if the $P > 0.05$ (Hosmer and Lemeshow 1989). We used model selection approaches (Akaike's Information Criterion adjusted for small sample sizes; AIC_c) to determine the models which described the data best (Burnham and Anderson 2002). The top two best-fitting models at each scale (based upon AIC weight) were then used in a subsequent multi-scale analysis to determine which scale described the probability of nest failures best. Model-averaged estimates from the entire candidate model set were calculated for the coefficients of the predictor variables (Burnham and Anderson 2002, Anderson 2008). The model-averaged odds ratios were calculated for the parameter estimates and scaled to biologically significant values important for management at each of the 4 spatial scales and for a multi-scale model which examined the top two models from each individual scale.

Second, conditioned on nest failure, we examined the specific cause of nest failure relative to landscape metrics using a multinomial logistic regression at the 4 spatial scales. We selected uncorrelated metrics as described above in the nest success models, and evaluated GOF using a likelihood ratio test, where adequate fit is observed if $P > 0.05$ (Menard 2002). Models were evaluated at each of the 4 spatial scales using AIC model selection approaches (Burnham and Anderson 2002) described above for the logistic models. We present model-averaged estimates for each of the coefficients of the predictor variables with odds ratios scaled to biologically significant values important to management for interpretation. All odds ratios presented describe the effect of the predictor on cause-specific nest mortality by ants, snakes, and other causes relative to meso-mammals.

Additionally, we examined the residuals of the top regression models and calculated Moran's I to determine if any spatial structure was not accounted for by the predictor variables based upon the distances among nests within each study area (Overmars et al. 2003) using program Spatial Analysis in Macroecology (SAM; version 3.1; Rangel et al. 2006). We also explored spatial structure within our response variables by plotting correlograms and examining average Moran's I to determine if any spatial structure might exist in the underlying nest failure process among nests in close proximity to one another. A Moran's I value near 0 indicates no spatial autocorrelation where values near 1 and -1 indicate clustering and randomness, respectively.

RESULTS

During the 7-year study, cameras were installed at 675 bobwhite nests. We excluded 29 nests from subsequent analysis because these nests were abandoned due to research activities (primarily a result of camera installation). Of the remaining 646 nests, 394 (61.0%) succeeded and 252 (39.0%) failed. The specific failures were attributed to meso-mammals (92 nests: 36.5% of failures), snakes (67 nests: 26.6% of failures), ants (28 nests: 11.1% of failures), and other incidental causes (30: 11.9% of failed nests). At 35 nests (13.9% of failed nests), the exact failure causes could not be determined from the camera footage because dense vegetation often limited visibility for small species (e.g. snakes). Failures classified as unknowns were not meso-mammals predators, as these predators were easily identified even in thick vegetation, but were suspected to be snakes (Staller et al. 2005). Unknown failures were included in the logistic failure models only.

Nest Failures Relative to Landscape Features

Global models at all scales demonstrated adequate fit ($P > 0.05$) and no overdispersion was observed in the data ($\hat{c} = 1.01$). The best-fitting models included hardwood distance only and an additive model of distance to hardwoods and to fields for both the 3.14- and the 19.6-ha models (Table 3.2, Appendices B.3.1 and B.3.3). However, no predictors strongly influenced the probability of nest failures at the 2 smaller scales (3.1- and 19.6-ha scales). Model-averaged parameter estimates for these predictors had estimates close to 0 and many had broad 95% CIs indicating no strong trend for a positive or negative relationship with nest failures (Appendices B.3.2 and B.3.4). Therefore, nest failure did not appear to be much more or less likely based upon these predictor variables. At the 50.3-ha scale, the best-fitting model describing the probability of nest failures was percent field composition and distance to fields. This model possessed 45.5% model weight (Appendix B.3.5). Within the 50.3-ha buffered area, the probability of nest failure was 1.6 times less likely with each 10% increase in field composition (Appendix B.3.6.). Probability of nest failure was 1.1 times less likely with each 50-m increase in distance toward a field (Appendix B.3.6.). Similar results were found at the 176.7-ha scale (Appendix B.3.7) with the probability of nest failure being 1.8 times less likely with each 10% increase in percent field composition in the buffered area and 1.1 times less likely for each 50-m increase in proximity to fields (Appendix B.3.8).

The top two models at each scale were then examined as a candidate model set to determine which scale described the probability of failure best. The top model was an additive model of percent field composition at the 50.3-ha scale and distance to fields (Table 3.3). This model had 40.5% of the model weight and was 1.3 times more likely than the next best-fitting model of distance to hardwood patches. At the 50.3-ha and 176.7-ha buffer areas, the probability of nest failure was 1.7 and 1.8 times less likely, respectively, with every 10% increase in field composition (Table 3.4). For every 50-m increase in distance between nests and fields, the probability of nest failure was 1.1 times less likely (Table 3.4).

We found no spatial autocorrelation in the residuals of the overall top model for the probability of nest failure (Moran's $I_{avg} = -0.008$; Figure 3.1), therefore no modification to the modeling structure was necessary (Cliff and Ord 1981). We examined the correlogram for the response variable of nest success/failure with respect to the proximity of nests from one another and found overall no spatial pattern (Moran's $I_{avg} = -0.009$). We hypothesized that predation at neighboring nests would be more likely related to nests within the same year, so we further examined the spatial relationship of the response variable by year. Generally, we found very little spatial relationship in nest fate relative to the nest fate of neighboring nests (Figure 3.2), with the exception of 2002 and 2005 where there appeared to be slight clustering in the fate of nests within 200 m of one another (Moran's I = 0.36 and 0.42, respectively).

Specific Failure Causes Relative to Landscape Features

Global models at each scale indicated adequate fit for the multinomial models (P > 0.05). Predator-specific failure causes were influenced differently by landscape metrics at the 3.1-ha scale compared to the 3 larger scales. Percentage of fields described the data best at the 3.1-ha scale, whereas the best-fitting models included distance to feed lines for the 3 larger spatial scales (Table 3.5; Appendices B.3.9, B.3.11, B.3.13, B.3.15). Most of the model-averaged parameter estimates were near 0 and had broad 95% confidence intervals which encompassed 0 (Appendices B.3.10, B.3.12, B.3.14, B.3.16). When we examined the top 2 models from each the 4 spatial scales as a multi-scale model, we found the smallest scale predictor of percentage of field composition described the probability of predator-specific failure causes best (Table 3.6). At the 3.1-ha scale, for every 10% increase in field composition, other predation events were 2.2 times less likely than meso-mammal predation events (Table 3.7). With every 10% increase in field composition, we found ant predation to be 1.3 times more likely than meso-mammal predation events and snake predation events to be 1.1 times more likely than meso-mammal events at the smallest scale (Table 3.7). For every 50-m increase in distance between nests and supplemental feed lines, ant depredations were 1.04 times more likely than meso-mammal predation events (Table 3.7). We also found that each 10% increase in hardwood composition at the 50.3-ha scale increased the probability of ant predation by 1.3 times that of meso-mammals failures (Table 3.7).

We examined spatial structure in the response variable by comparing meso-mammals first to all other failure causes collectively (i.e. snakes, ants, and other). Then, we compared meso-mammals to each of the other 3 failure causes individually. Similar to the success-failure model, we observed little spatial autocorrelations among the nest failure cause of neighboring nests when meso-mammals were compared to all other failure causes collectively or individually (Moran's $I_{avg} < 0.2$).

DISCUSSION AND MANAGEMENT IMPLICATIONS

We found that the relationship between fate of bobwhite nests and landscape attributes was dependent upon the spatial scale at which the landscape metrics were evaluated. At the small scale (<20 ha), metrics were not particularly informative for explaining nest fate, and models describing the failure process best were scale-independent metrics of proximity. Failures at nests can result from a large suite of different predator species, each with their own foraging methods and relationship with the habitat features we explored. These smaller scales correspond to some of the predominant predator species, such as armadillos (Layne and Glover 1977) and gray rat snakes (Stapleton 2005) which have home ranges less than 20 ha. However, many of the predators, such as raccoons (Urban 1970, Chamberlain et al. 2003a), have large home ranges that exceed 20 ha. Top predators such as bobcats and coyotes have home ranges that even can exceed our largest scale of 176.7-ha (Chamberlain et al. 2003b).

At larger scales (>50 ha), we found increased percent field composition decreased nest failure probabilities. In other words, the higher the percent field composition the more likely the nest was to succeed. Our results suggest that the nest predation process is likely operating at scales related to the larger predator home range sizes. Annually disked fields, ragweed fields, and fallow fields provide sources of food to bobwhites that would be valuable during the nesting season. Having these habitats readily available may minimize bobwhite foraging time or number of daily foraging trips that may leave a nest more vulnerable to predation. In addition, ragweed and annually disked fields produce large amounts of biomass important to alternative to prey.

Cotton rats (*Sigmodon hispidus*) are a common alternative prey item for many bobwhite predators (Schoch 2003), and fallow fields are preferred habitat by this species (Hannon 2006). Cotton rats also may use the ragweed fields as important sources of seeds, while heavily utilizing the adjacent upland pine as primary habitat. Thus, a higher abundance of cotton rats might equate to a higher abundance of alternative prey options for predators. Nesting studies examining alternative prey have found increased availability of alternative prey to be correlated with higher nesting success for waterfowl (Byers 1974, Weller 1979, Crabtree and Wolfe 1988, Vander Lee et al. 1999). Although this might be directly related to alternative prey availability, this might also be a function of diversion of predators to habitats for foraging where bobwhites do not commonly nests. Potentially there is an interaction effect of alternative prey and foraging diversion.

When examining predator-specific failures, we found that at the smallest scale (3.1-ha), field composition was also important. At this scale, percent field composition described the data best for incidental failures compared to meso-mammals predation events at the nest. Many of the incidental failure causes were the result of mortality of the incubating bobwhite while it was away foraging. Given the likely value of fields as a source of alternative prey, it is probable that increased fields harboring abundant cotton rat populations could offset predation on adult bobwhites. From a management perspective, there is still the potential for renesting when the nest fails due to meso-mammals as long as the bobwhite survives.

There is relatively little understood about the how fire ants interact with habitat management. Distance to feed lines was important in ant depredations relative to meso-mammals at the 3 larger scales. Habitat disturbances such as burning and mowing appear to enhance ant populations (Williamson et al. 2002), but supplemental feeding practices have not been examined relative to ants. However, the imported red fire ants can be attracted to seeds and are known to disperse seeds of native plant species (Zettler et al. 2001, Stuble et al. 2009), but this did not appear to be occuring in our study since ant depredations were slightly more likely than meso-mammals with increasing distance between the nest and the feed line. Other studies have documented trends that supplemental feed lines attract bobcats (Godbois et al. 2004) and avian predators (Haines et al. 2004). Feed lines may attract alternative prey attractive to meso-mammals and snakes. However, our findings suggest that meso-mammals predation events were only slightly more likely than ants the closer the nest was to the feed line and no more likely than snake predation. In addition, we observed ants were 1.3 times more likely to depredate nests than meso-mammals with increasing percent composition of fallow and ragweed fields at the 3.1-ha scale and increasing percentage of hardwoods at the 50.3-ha scale. There is much interest in these findings since ants tend to depredate nests late in incubation when the chicks are beginning to hatch (Ellis-Felege et al. *In Press*). This is doubly important for persistent renesters because the parent invested a considerable amount into this nest and may not have sufficient time to renest following nest depredation. Conversely, ants only contributed to about 11% of nest failures. They are more likely to only destroy part of the clutch therefore some chicks may successfully hatch, whereas meso-mammals usually will destroy the entire clutch (Ellis-Felege et al. *In Press*). We only examined full depredation events in this study, but incorporation of partial clutch loss, particularly due to ants may be of interest in the future to examine this association between ants with feed lines, percentage of landscape in fields, and hardwood composition.

We observed no differences between landscape features that strongly influence snake predation differently than meso-mammals. Only percent field composition appeared to slightly increase snake predation relative to meso-mammals at our smallest scale, but decreased snake predation relative to meso-mammals at the 19.6-ha scale. These predator guilds are generalists and thus have very broad habitat and diet requirements, as well as potentially species-specific habitat preferences. By pooling snakes into one category, we may have obscured habitat characteristics influential to specific snake species. For example, gray rat snakes in the area of this study frequently used hardwoods and wetlands more than corn snakes which predominantly used upland pine habitat (Stapleton 2005). Furthermore, kingsnakes may be more likely in the uplands than rat snakes (Ernst and Ernst 2003). Staller et al. (2002) recommended bobwhite nesting cover be promoted away from drain edges to reduce snake predation, but gray rat snakes were the predominant snake species in that study. However, in our study, this would only partially mitigate snake predation. On one of our study sites, Pinebloom, kingsnakes were the primary snake predators, whereas both species of rat snakes were the predominant snake predators in the Red Hills Region. Unfortunately, it was not always possible to identify snakes to species from our camera data. Future examination of species-specific failures may uncover stronger trends in relationship to habitat characteristics and nest failures.

Of particular interest in our study is our observation that the fate of an individual nest appeared to be spatially independent of the fate of neighboring nests during most years. Frequently, predators are thought to search for prey items in a directed manner such that they might return to an area where they have successfully found a food source previously. However, learning and foraging theory suggests that animals may not return to locations where they successfully obtained prey items (Real 1994). This could be the result of predators selecting among patches with varying resource availability. It also could be that predators are trying to search an area efficiently; therefore, they might not return to an area previously exploited because they have already searched it. Angelstam (1986) also found predators did not appear to develop a memory for the location of artificial nests. For generalist predators, it may be that random foraging modified by some selection of high alternative food source habitats, such as fields, is the most efficient search method since they have broad dietary requirements which can easily be met within our landscape.

The years (2002, 2005) for which we observed a slight spatial pattern in nest fate, were years when production was very high, and many bobwhites on our study areas had second nests. We observed renests by individual birds to be fairly close to one another and thus, the spatial relationship between close nests may have been the result of the same bobwhite renesting close to their first nest. Nest fate may have been explained more by the successfulness of an individual bird than the predation process. In other words, bobwhites having successful first nests may be more likely to have successful second nests or vice versa. In addition, microhabitat features selected by the bobwhite may have influenced the fate of the nest. Amount of litter cover, vegetative height, and presence of specific plant species may camouflage nests better than others (Taylor et al. 1999a) and certain bobwhites might be better at microhabitat nest site selection than others.

In general, our results suggest predators are likely not directing their search for bobwhite nests, but rather that bobwhite nests are probably incidental prey items for many of the generalist predator species. Other grassland bird nests have been found to be incidental prey for mammal species such as the striped skunk (Vickery et al. 1992). This also suggests that if nest predation is incidental, then bobwhite nest fate is likely related to other prey items that are being more actively searched as a prey item (Vickery et al. 1992). Therefore, our findings suggest that habitat important to alternative prey or that is more challenging for the nest to be found (e.g. dense nesting vegetation) might reduce incidental occurrences of predator-bobwhite interactions.

Studies have found edges to be important (Heske et al. 1999, Chalfoun et al. 2002, Kuehl and Clark 2002, Phillips et al. 2003), but we did not find edge density or distance to edges to strongly influence the probability of nest failures with the exception of field edges. Although models at smaller scales indicated distance to edges of hardwoods described the data best from our model selection approaches, this predictor was no more or less likely to influence nest fate. Distance to field edge, however, was negatively related to the success of a nest and may have been related to attributes of the field which attracted predators to these sources of abundant alternative prey. Therefore, increased probability of nest encounter by a predator would be more likely. These results seem to contradict our findings of increased field composition benefiting bobwhite nesting. There is a definite tradeoff, but in most cases, the percentage of these fallow or annually disked ragweed fields on the larger landscapes is generally small. For example, our observed ranges were 0 – 25% field composition at the 50.3-ha scale and less than 15% at the 176-ha scale.

One caveat of our study is that we monitored bobwhites in habitat which is managed to sustain high bobwhite densities; therefore, influences of many potential factors that could drive the predation process may have been diluted relative to their effects in more degraded habitats typical of the modern landscape. Future work needs to focus on extending our study toward understanding predation in areas with intensive agriculture, forestry practices, and more fragmented habitats to understand landscape characteristics that may assist biologists in minimizing predator-bobwhite interactions during the breeding season.

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Table 3.1: Landscape metrics potentially influencing Northern Bobwhite nest failures in northern Florida and southern Georgia, their range of values within our data, and their description.

Parameter	**Range of Values**	**Description**
Hardwood_Comp	3.1-ha: 0-88.5% 19.6-ha: 0-65.8% 50.3-ha: 0-55.3% 176.7-ha: 0-40.7%	Percent hardwood composition within the buffered scale around the nest.
Wetland_Comp	3.1-ha: 0-82.3% 19.6-ha: 0-76.8% 50.3-ha: 0-75.1% 176.7-ha: 0-60.7%	Percent wetland composition within the buffered scale around the nest.
Field_Comp	3.1-ha: 0-81.0% 19.6-ha: 0-37.0% 50.3-ha: 0-24.5% 176.7-ha: 0.1-14.2%	Percent annually disked field composition within the buffered scale around the nest.

Parameter	Range of Values	Description
Edge Density	3.1-ha: 0-833.7 m/ha 19.6-ha: 79.8-482.6 m/ha 50.3-ha: 109.1-442.7 m/ha 176.7-ha: 131.7-421.4 m/ha	Total edge length divided by total area.
Hardwood_Dist[1]	0-2442 m	Euclidean distance to the nearest hardwood drain.
Field_Dist[2]	0 - 476 m	Euclidean distance to nearest field.
Wetland_Dist[3]	0 - 1701 m	Euclidean distance to nearest wetland.
Road_Dist	0 - 425 m	Euclidean distance to nearest road.
Feed_Dist	0 - 2179 m	Euclidean distance to nearest feedline.

[1] Due to multicolinearity with other predictors, this predictor was evaluated in models at scales except the 176.7-ha models.

[2] Due to multicolinearity with other predictors, this predictor was only evaluated in the 50.3- and 176.7-ha models.

[3] Due to multicolinearity with other predictors, this predictor was only examined in the 3.1- and 19.6-ha models.

Table 3.2: AIC_c model selection and model weights for the top two models from each of the 4 spatial scales (3.1-ha, 19.6-ha, 50.3-ha, and 176.7-ha) examining the probability of Northern Bobwhites nest failure relative to landscape metrics in northern Florida and southern Georgia, 2000-2006.

Scale	**Model**	**AICc**	**Weight**
3.1-ha	Int + Hardwood_Dist	915.05	0.557
	Int + Hardwood_Dist + Field_Dist	916.96	0.215
19.6-ha	Int + Hardwood_Dist	915.05	0.549
	Int + Hardwood_Dist + Field_Dist	916.96	0.212
50.3-ha	Int + Field_Comp + Field_Dist	914.52	0.455
	Int + Hardwood_Dist	915.05	0.349
176.7-ha	Int + Field_Dist + Field_Comp	916.97	0.367
	Int + Field_Comp	918.88	0.141

Table 3.3: Model selection using AIC_c weights of the top two models from each of the 4 spatial scales incorporated into a multi-scale model examining the relationship between the probability of Northern Bobwhite nest failure and landscape metrics in northern Florida and southern Georgia, 2000-2006.

Model	**K**	**AIC_c**	**ΔAIC_c**	**Weight**
Int + Field_Dist + Field_50.3ha	3	914.52	0.00	0.405
Int + Hardwood_Dist	2	915.05	0.53	0.311
Int + Wetland_Dist + Hardwood_Dist	3	916.96	2.44	0.120
Int + Field_Dist + Field_176ha	3	916.97	2.45	0.119
Int + Field_176ha	2	918.88	4.36	0.046

Table 3.4: Model-averaged parameter estimates for coefficients of the landscape metrics potentially influencing the probability of Northern Bobwhite nest failures in northern Florida and southern Georiga, 2000-2006.

Parameter	**Estimate**	**SE**	**95% LCI**	**95% UCI**	**Unit Scalar**	**Scaled Odds Ratio**	**Scaled LCI**	**95% CI UCI**
Intercept	-0.0713	0.4055	-0.8662	0.7235				
Field_Dist	-0.0022	0.0009	-0.0040	-0.0003	50	0.8980	0.8200	0.9831
Field_50.3ha	-0.0529	0.0182	-0.0886	-0.0173	10	0.5890	0.4123	0.8416
Wetland_Dist	-0.0001	0.0003	-0.0006	0.0005	50	0.9953	0.9685	1.0228
Hardwood_Dist	0.0004	0.0002	0.0001	0.0007	50	1.0215	1.0055	1.0372
Field_176ha	-0.0576	0.0255	-0.1076	-0.0076	10	0.5621	0.3410	0.9265

Table 3.5: AIC_c model selection and weights for the top two models from each of the 4 spatial scales examining the probability of Northern Bobwhite nest failure due to meso-mammal, snakes, ants, and other causes relative to landscape metrics in northern Florida and southern Georgia, 2000-2006.

Scale	**Model**	**AICc**	**Weight**
3.1-ha	Int + Field_Comp	549.75	0.66
	Int + Field_Comp + Feed_Dist	551.97	0.22
19.6-ha	Int + Feed_Dist	556.30	0.24
	Int + Field_Comp	556.57	0.21
50.3-ha	Int + Feed_Dist	556.30	0.27
	Int + Hardwood_Comp	556.91	0.20
176.7-ha	Int + Feed_Dist	556.30	0.34
	Int + EdgeDensity	558.52	0.11

Table 3.6: AIC model selection for the top two models from each of the individual 4 spatial scale evaluations incorporated into a multi-scale model examining the relationship between the probability of specific failure causes (meso-mammals, snakes, ants, and other) at Northern Bobwhite nests and landscape metrics in northern Florida and southern Georgia, 2000-2006.

Model	**AIC**	**ΔAIC**	**Weight**
Int + % Field_3.1ha[1]	549.75	0.00	0.694
Int + % Field_3.1ha[1] + Feed_Dist[2]	551.97	2.22	0.229
Int + Feed_Dist[2]	556.30	6.55	0.026
Int + % Field_19.6ha[3]	556.57	6.82	0.023
Int + % Hardwood_50.3ha[4]	556.91	7.16	0.019
Int + EdgeDensity176ha[5]	558.52	8.77	0.009

[1] Represents the percent field composition within the 3.1-ha buffer.

[2] Represents the scale independent variable for Euclidean distance to feed lines.

[3] Represents the percent field composition within the 19.6-ha buffer.

[4] Represents the percent hardwood drain composition within the 50.3-ha buffer.

[5] Represents the edge density within the 176.7-ha buffer.

Table 3.7: Model-averaged parameter estimates for the coefficients of landscape metrics influencing the probability of Northern Bobwhite nest failures due to specific predators (meso-mammals, snakes, ants, and other failures) in northern Florida and southern Georiga, 2000-2006.

Parameter	Estimate	SE	LCI	UCI	Unit Scaler	Scaled Odds Ratio	Scaled LCI	95% UCI
Intercept[1]	-0.781	3.104	-6.865	5.303				
Intercept[2]	-1.485	4.036	-9.395	6.426				
Intercept[3]	-0.390	2.305	-4.908	4.127				
Field_3.1ha[1]	-0.077	0.074	-0.222	0.068	10	0.462	0.108	1.970
Field_3.1ha[2]	0.026	0.037	-0.047	0.100	10	1.302	0.625	2.714
Field_3.1ha[3]	0.010	0.031	-0.050	0.070	10	1.105	0.605	2.017
Feedline Distance[1]	0.000	0.001	-0.002	0.002	50	1.002	0.920	1.091
Feedline Distance[2]	0.001	0.001	-0.001	0.002	50	1.036	0.964	1.113
Feedline Distance[3]	0.000	0.001	-0.001	0.001	50	1.000	0.938	1.067
Field_19.6ha[1]	-0.058	0.040	-0.137	0.021	10	0.559	0.254	1.232

Field_19.6ha[2]	0.028	0.032	-0.035	0.091	10	1.323	0.708	2.473
Field_19.6ha[3]	-0.018	0.027	-0.070	0.035	10	0.839	0.497	1.417
Hardwood_50.3ha[1]	-0.003	0.020	-0.042	0.036	10	0.967	0.654	1.428
Hardwood_50.3ha[2]	0.030	0.017	-0.004	0.063	10	1.343	0.961	1.878
Hardwood_50.3ha[3]	-0.005	0.015	-0.034	0.025	10	0.955	0.709	1.286
EdgeDensity_176ha[1]	-0.004	0.005	-0.013	0.005	1	0.996	0.987	1.005
EdgeDensity_176ha[2]	-0.007	0.005	-0.016	0.003	1	0.993	0.984	1.003
EdgeDensity_176ha[3]	-0.002	0.003	-0.009	0.005	1	0.998	0.991	1.005

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[1] Other nest failure causes relative to meso-mammals depredations.

[2] Nest failures due to ants relative to meso-mammals depredations.

[3] Nest failures due to snakes relative to meso-mammal depredations.

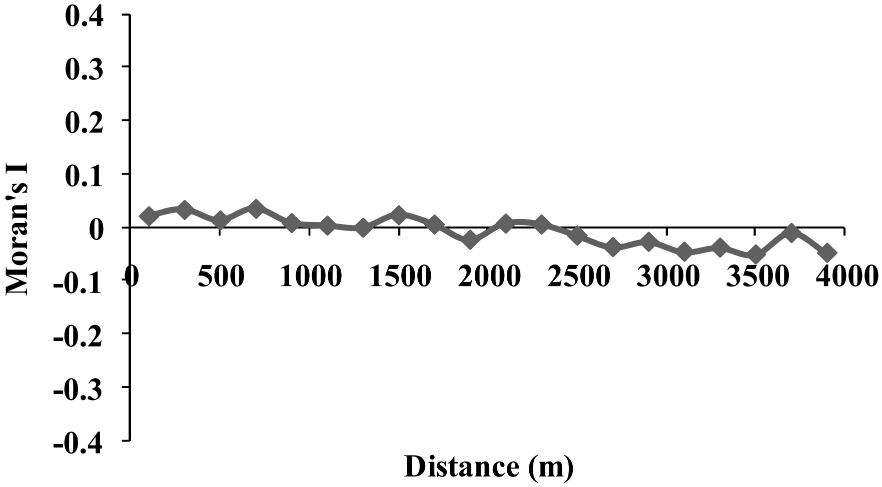

Figure 3.1: Correlogram of Moran’s I for the spatial structure of the residuals of the top model for the probability of bobwhite nest failure (Percent Field Composition at 50.3-ha scale + Distance to Fields) where values of Moran’s I close to 0 indicate no spatial autorcorrelation.

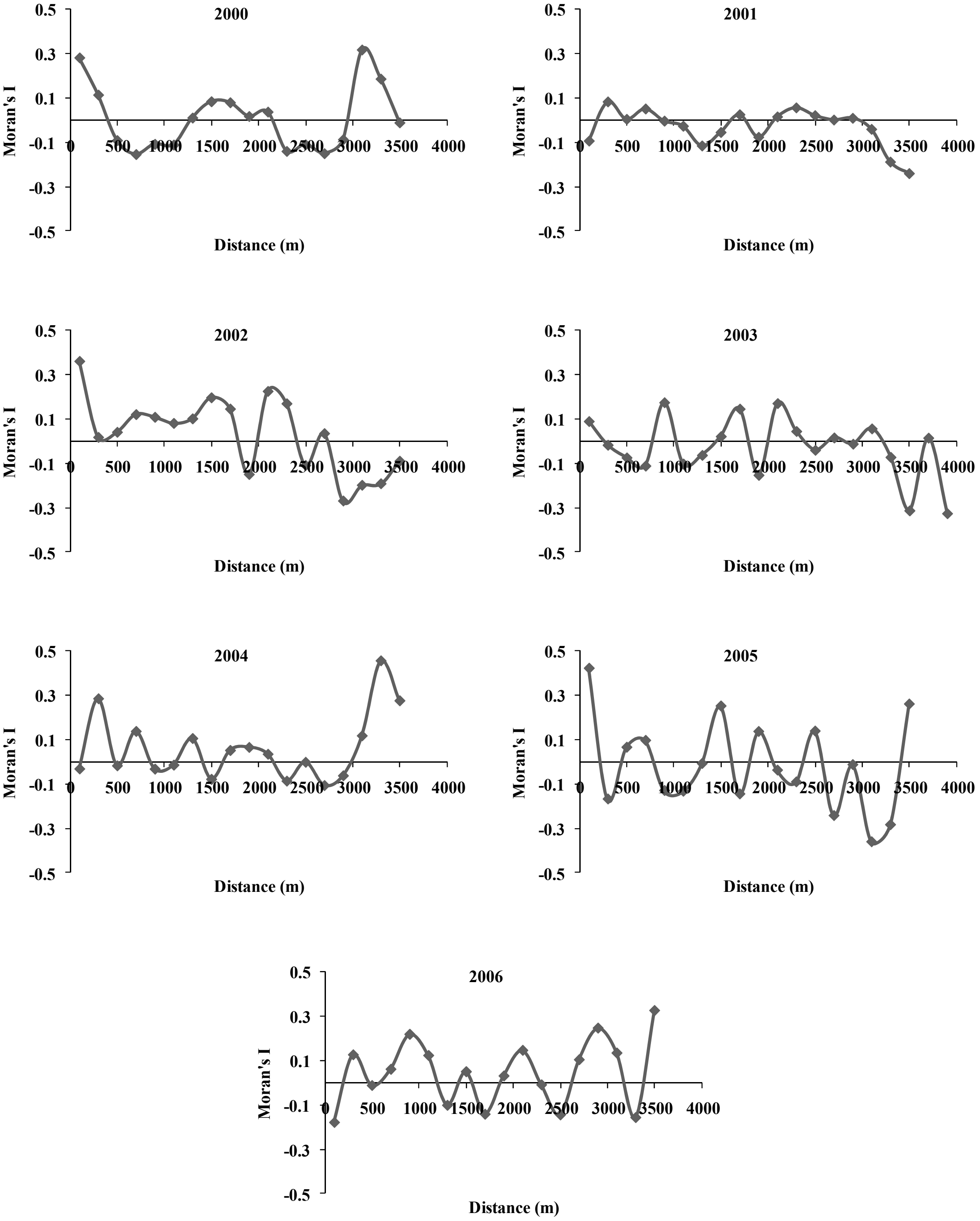

Figure 3.2: Correlogram of Moran’s I for the binary response variable of success/failure of bobwhite nests during 2000-2006 showing the spatial autocorrelation between nests, where I-values close to 0 indicate no relationship in nest fate to the fate of neighboring nests.

CHAPTER 4

PREDATION MANAGEMENT AND GAMEBIRD NESTING: UNDERSTANDING DYNAMICS OF PREDATOR REMOVAL[1]

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[1] S. N. Ellis-Felege, M. J. Conroy, D. C. Sisson, S. D. Wellendorf, W. E. Palmer, and J. P. Carroll. To be submitted to Journal of Wildlife Management.

ABSTRACT

When examining the role of predation on avian reproductive success, rarely do researchers simultaneously examine predator demographics. Medium-sized, generalist mammals (i.e. meso-mammals) are important nest predators of the ground-nesting gamebird, the Northern Bobwhite (*Colinus virginianus*) and have been subjected to predator removal programs. In order to determine the effect of predator control on the meso-mammal population, we monitored six species using scent stations on 4 study sites (1300-1400 ha each) in northern Florida and southern Georgia during 2000-2006. We collected baseline data in 2000 for all study sites, and during 2001-2003, two sites received meso-mammal predator reduction for seven months of the year while the other two sites served as controls with no reduction occurring. We reversed the treatments in 2004-2006. A total of 5,161 meso-mammals was removed from our study areas over the 6 years of treatment. Using predator detection at scent stations, we modeled the probability that predators used 25-ha sample patches across the study sites via a community-level robust design occupancy model in program MARK. Model selection indicated the best approximating model from the candidate set was where occupancy was influenced by the additive effects of trapping and region; local extinction was based upon trapping and region; and detection was different among primary periods (years) and region- and species-specific. Predator patch use was 2.5 times less likely on trapped sites than non-removal sites, but the effects of predator reduction did not carry across years. We found that rapid recolonization occurred following discontinuation of predator trapping. This suggests our predator control methods could achieve management goals of reducing predator-prey interactions at the local scale without eliminating meso-mammal predators from the ecosystem.

INTRODUCTION

Predator control is one of the most controversial topics in wildlife management (Messmer and Rohwer 1996). Debate continues over the value of predator control as a tool to increase prey populations, as well as implications associated with societal values (Messmer and Rohwer 1996, Messmer et al. 1999). As part of a predation management program, predator control aimed at enhancing gamebirds populations is one area that has received considerable attention. Gamebird populations have reported varying results of the effectiveness of predator control at increasing predator production, fall population, or breeding season populations (Côté and Sutherland 1997, Newton 1998, Valkama et al. 2005). There are many factors which influence a prey population's response to predator control, including the intensity and effectiveness of altering the predator community being targeted for reduction. Unfortunately, predator population responses to intensive removal efforts are rarely examined during studies investigating predator reduction programs (Burger 2002, Treves and Naughton-Treves 2005, Berger 2006). Furthermore, during avian nesting studies with emphasis on nest predation, rarely are predator population dynamics or activity simultaneously monitored with nesting activities (Sperry et al. 2009).

Over time, human perspective relative to predator values has shifted from predators being competition for food resources to predators being important components of the ecosystem and biodiversity (Messmer and Rohwer 1996). This shifting viewpoint equates to the need for validating the effectiveness of predator control programs for enhancing a target species, while maintaining biodiversity within the community. The objective shifts away from extirpation to one that manages predator populations that can sustain high rates of mortality induced by predator management programs, and be reduced enough to elicit a population response from the species of interest. Generally, predator reduction efforts are thought to have little effect upon long-term densities of meso-mammals (Treves and Naughton-Treves 2005). However, few studies investigating predator control for avian species or predator-livestock conflicts have examined predator population dynamics or ecosystem and community effects, despite the long history of such programs (Burger 2002, Berger 2006). If predator control efficacy is to be evaluated thoroughly, it is important to understand the effects this tool has on the targeted predator community and to quantify the demographic response to reduction efforts.

Medium-sized mammalian predators, often referred to as meso-mammals, are thought to be important predators of Northern Bobwhites (*Colinus virginianus*; hereafter bobwhites) and their nests (Stoddard 1931, DeVos and Mueller 1993, Fies and Puckett 2000, Staller et al. 2005), and may limit bobwhite populations (Errington and Stoddard 1938, Newton 1998). These mammalian species include raccoons (*Procyon lotor*), Virginia opossums (*Didelphis virginianus*), bobcats (*Lynx rufus*), nine-banded armadillos (*Dasypus novemcinctus*), red and gray foxes (*Vulpes vulpes* and *Urocyon cinereoargenteus*), coyotes (*Canis latrans*), and skunks (*Mephitis mephitis*) (Fies and Puckett 2000, Staller et al. 2005, Rader et al. 2007). Meso-mammals, considered generalist predators, have great flexibility in their diet and habitat requirements. They can exploit a variety of habitats including mixed habitats with patches of forested area, shrub land, old fields, agricultural areas, wetlands, and suburban areas (Reid et al. 2006). Furthermore, these mammalian predator species have reached historically high densities all across the southeastern region and other portions of their range in the United States. The increased predator abundance may be the result of decreased mammalian hunting with the decline in fur markets, extinction or suppression of top predators, habitat alteration, and potentially beneficial land use changes (Palomares et al. 1995, Peoples et al. 1995, Heske et al. 1999).

Scent stations are a common method for monitoring mammalian species (Roughton and Sweeny 1982, Conner et al. 1983, Diefenbach et al. 1994); however, traditional analysis of these data only provides relative indices of population abundance (Linhart and Knowlton 1975) and is subject to possible bias and high variability (Diefenbach et al. 1994, Williams et al. 2002). Frequently, managers of game species, such as bobwhites, utilize raw scent station indices to assess predator use in order to determine if predator reduction might be a beneficial management tool. These indices have been used to assess activity patterns of meso-predators of waterfowl, and found to be influenced by year, location, and patch size (Sovada et al. 2000). Questions, though, remain about the relationship of indices to population abundance since these indices may not be proportionally related to actual abundance (Diefenbach et al. 1994, Anderson 2001, Williams et al. 2002, Anderson 2003, Conroy and Carroll 2009). Therefore, evaluation of indices should be assessed to determine if the simple index is sufficient to reflect actual demographic changes of mammalian populations. Of paramount importance to the reliability of an index using scent station methodology is an understanding of issues related to detection rates. This becomes even more of an issue when we attempt to apply scent station techniques to multiple predator species. In this case, there are issues of individual detection, individual species behavior, and abundance interacting within the system.

When scent stations are conducted over several consecutive days and even multiple seasons, occupancy modeling offers a convenient and appropriate analytical methodology to assess scent stations techniques to monitor predator population use across a study area (Stanley and Royle 2005, MacKenzie 2006). Since imperfect detection occurs during the sampling process, multiple observations on consecutive days (or over a period when the population is considered to be closed) provide information on the ability to detect individuals when they are present. With much debate about the reflection of indices to true population dynamics, calculating the probability of detection allows us to evaluate the effectiveness of techniques such as scent stations at determining population demographics. Additionally, continued use, discontinued use, and new use of an area can be evaluated with respect to habitat changes or population manipulation when monitored over multiple seasons using robust occupancy modeling (MacKenzie 2006).

Understanding the influence of predators on nesting birds requires knowledge of the species responsible for nest failures. Miniature video cameras have become a popular tool for monitoring nest predation events and allow for cause-specific nest failures to be assessed. Comparison of predation rates from camera-monitoring can be coupled with monitoring of predator abundance and activity to determine if a relationships between predator community demographics and nest predation occurs.

In this study, we examined three aspects of meso-mammal predators of bobwhite nests in southern Georgia and northern Florida. First, we construct a community occupancy model based upon presence-absence of individual predator species at scent stations to determine if meso-mammal predator control, as done in our study, was intensive enough to reduce predator use across our 4 study sites. Second, we compare raw scent station indices to occupancy rates to determine if incorporation of imperfect detection reflects different inferences made about predator population dynamics across our 4 study sites during the 7-year period. Finally, we compare predator-specific nest mortality to changes in meso-mammal predator occupancy rates. The findings of this study mark the first extensive analysis of quantifying the effects of predator control on the predator community, and this study is one of the few studies to simultaneously monitor both predator and prey dynamics.

METHODS

Study Area

We studied meso-mammal predators at 3 properties in southern Georgia and northern Florida during 2000-2006. Pinebloom Plantation (PB East and PB West; Baker County, GA; 31° 24’ 42” N, 84° 22’ 45” W) is located in the Upper Coastal Plain physiographic region. Pinebloom was divided into two 1,400-ha study sites with a cypress (*Taxodium distichum*) swamp buffer approximately 607 ha in size between the two sections. Tall Timbers Research Station and Land Conservancy, Inc. (TTRS; Leon County, FL; 84º 13’ 35” W, 30º 39’ 39” N) and Pebble Hill Plantation (PH; Thomas and Grady County, GA; 84º 5’ 48” W, 30º 46’ 13” N) are located in the Red Hills physiographic region. Detailed site description for the Red Hills sites can be found in Staller et al. (2005), and for Pinebloom in Sisson et al. (2000, 2009). All of these sites are dominated by loblolly pine (*Pinus taeda*) and shortleaf pine (*Pinus echinata*) with associated “old-field” ground cover vegetation, as well as areas of longleaf pine (*Pinus palustris*) with associated wiregrass (*Aristida stricta*) ground cover. Fallow fields, hardwood drains, and hammocks are interspersed across the landscape. All sites maintain an open, low density pine forest structure through use of frequent fire, disking, roller chopping, and mowing.

Predator reduction and scent station monitoring

Predator control was conducted at the two pairs of study areas, the Thomasville Region and the Albany Region. Each study region had a treatment and a control site of approximately 1,300-1,400 hectares in size. One year of baseline data was collected in 2000. During 2001 – 2003, one site in the Thomasville Region (PH) and one in Albany (PB East) received intensive predator removal from 1 March to 30 September of each year by USDA Wildlife Services’ personnel, while predators were not removed at the other sites. We reversed the treatments during 2004 – 2006 (i.e. TTRS and PB West trapped). The experiment followed a blocked, repeated measures cross-over design (Table 4.1).

Meso-mammal predator use was examined using 30-40 scent stations at each site. Stations were located ≥ 500 m apart next to unimproved roads, fire breaks, and other potential travel lanes which resulted in 1 station per 25 ha. A station consisted of a 1-m circle cleared of all vegetation and covered in fine, sifted sand. A fatty-acid tablet acted as scent lure and was placed in the center of the circular station to attract predators. Scent stations were checked on 5 consecutive mornings during the first week of October. Each day we identified predator tracks, raked the sand, and replaced scent lures as needed.

Bobwhite Nest Monitoring

Each year between January and April, we captured approximately 100 bobwhites on each site using baited funnel traps (Stoddard 1931). Bobwhites were fitted with 6.5g (~4% body-weight) collar-style radio-transmitters (Staller et al. 2005). Trapping, handling, and marking followed University of Georgia procedures (Institutional Animal Care and Use Committee permit #A2004-10109-c1 and A3437-0). Using homing techniques (White and Garrott 1990), we located bobwhites ≥5 days/ week from 15 April to 1 October of each year to monitor nesting behavior. Birds found in the same location on two consecutive days with radio-collars not emitting a mortality signal were assumed incubating a nest. Flagging was placed near the nest site to mark its location so the nest could be found when the incubating bobwhite was away foraging. We were able to find nests and begin monitoring within the first few days of incubation. Therefore, nests were discovered at approximately the same stage and only included incubation, not the egg-laying phase of nesting (Taylor et al. 1999). When the incubating bobwhite was away from the area, researchers found the exact nest position and installed small continuously recording cameras equipped with a near-infrared lighting source (Furhman Diversified, Seabrook, TX) 1-1.5 m from the nest (Staller et al. 2005). We camouflaged the camera with surrounding vegetation. A 25-m cord linked the camera and lighting unit to a time-lapse VHS recorder and 225-reserve capacity deep cycle battery. Camera batteries and VHS tapes were changed every 24 hours. Unlike many nesting studies, nests were checked daily via telemetry until failure or hatch. Videos were viewed to confirm nest fate and identify nest predators in the event of a depredation. Nest failures due to abandonment resulting from researcher activities (primarily a result of camera installation) and failures not captured due to camera failure were not included in the subsequent analysis.

Statistical Analysis

Occupancy Analysis

We constructed a community occupancy model for the six intensively trapped, meso-mammal predators of bobwhites (e.g. raccoon, opossum, bobcat, armadillo, fox, and coyotes) based upon the presence/absence of tracks at scent stations. Competing models were constructed in program MARK (White and Burnham 1999) using the robust occupancy design (MacKenzie et al. 2003). The robust occupancy design is similar to the robust design of capture-recapture methods where closure is assumed within each primary period and assumed open among primary periods (Pollock 1982). We considered each year a primary period, while the 5-days of sampling within a year was defined as a secondary period. We were most interested in how trapping directly influenced occupancy rates, as well as the probability of discontinued sample patch use. Therefore, we used the parameterization for directly examining occupancy over each year or primary period (Ψ_t), the probability of local extinction (ε_t; the probability that an occupied site will become unoccupied in the following primary sampling period), and detection (p; the probability of detecting an individual species given it is present). Using estimates from Ψ_t, ε_t, and p, derived estimates of recolonization (γ_t; the probability of an unoccupied site becoming occupied in the following primary sampling period) and the finite rate of change (λ_t) could be calculated (MacKenzie 2006) within program MARK.

Probability of detection was first explored by fitting different models for each primary season. Detection was examined to determine if it varied by time within primary periods (t), by study site (site), by species (sp), constant (.), and additive combinations of predictor variables. Additionally, models were built to explore if detection probabilities varied among primary periods. Dummy variables were used to explore the influence of site and species using *n*-1 categories. Next, we fit predictors for the probability of local extinction. The predictors we examined were study site, species, time, trapping (trap), constant, and additive relationships of these predictors. Since extinction describes a relationship between years, we modeled trap effect as dummy variables representing a year of no trapping to continued no trapping (N-N), no trapping to trapping (N-T), trapping to continued trapping (T-T), and trapping to discontinued trapping (T-N). Finally, we modeled occupancy each year by examining whether occupancy was constant, differed by site or region (Thomasville vs. Albany), differed by species, differed by trapping treatment, or differed by additive combinations of these predictors. Trap effect was modeled as a binary variable, and dummy variables were used to assess the influence of site, region, and species for *n*-1 categorical groups.

In total, we constructed 41 models and compared them using Akaike's Information Criterion (AIC) within program MARK (Akaike 1973, Burnham and Anderson 2002). In order to account for model uncertainty, model-averaged estimates were calculated for the real, beta, and derived parameters within program MARK. No formal procedures currently exist for adequately assessing model fit of robust occupancy, particularly with missing values (MacKenzie and Bailey 2004, Nicholson and Van Manen 2009). However, we examined the Pearson X^2 statistic divided by the degrees of freedom (ĉ) of a fully parameterized model (i.e. global) similar to goodness-of-fit procedures for single-season occupancy modeling (MacKenzie and Bailey 2004). If lack of fit occurred, overdispersion would be observed as ĉ > 1 and could be adjusted within MARK.

Raw Index Comparison

Simple indices were calculated for each year on each study site similar to Linhart and Knowlton (1975). The total number of different predators visiting scent stations divided by total scent station days provides a crude index of overall nest predator activity of the study sites. Scent station days were calculated by multiplying the number of stations by the number of days. We calculated this index by individual species and as a community, including all 6 species in a single index. Since managers often use the raw scent station index to assess predator use and to help them decide if predators should be reduced, we compared occupancy with raw scent station visitation rates by calculating the Pearson correlation coefficient (r), as well as graphical examination to assess the reliability of the index as a management tool.

Cause-specific Nest Failures Relative to Occupancy

We calculated apparent cause-specific rates of nest mortality conditioned on failure by site for each of the 7-year study period. Apparent rates were used since nest monitoring was initiated at approximately the same stage for most nests (Taylor et al. 1999). We calculated Pearson correlation coefficients and graphically explored if relationships existed between predator use and cause-specific nest failures. We used mortality rates conditioned on failure instead of hatch rates because we were interested in assessing mortality factors rather than factors contributing to nest success.

RESULTS

A total of 5,161 meso-mammals were removed during the study period across the 4 study sites, ranging from 243 – 737 predators at a site in a single year (Table 4.2). Most of the meso-mammals removed were opossums (44.4%) and raccoons (29.0%), and the fewest were foxes (<1%). We conducted 5,002 station-days (averaged 178 scent station-days each year on each study site) with 953 unique tracks identified for the 6 species. Most of the meso-mammal tracks were identified as raccoons (45.6%), and the fewest recorded were from foxes (4.6%).

Occupancy Modeling and Predator Response to Trapping

Goodness-of-fit assessment for the models constructed in MARK indicated adequate fit and no overdispersion for the global model ($\hat{c} = 0.71$). Thus, no adjustments were made for underdispersion since estimates would be more conservative, and there is no underlying biological reasoning for underdispersion. Of the 41 models evaluated, only 11 had any AIC weight (Table 4.3; Appendix C.4.1). Our model selection approach indicated the best-approximating model from the candidate set was where Ψ_t (occupancy) was influenced by the additive effects of trap and region; ε (local extinction) was based upon trap and region; and detection was different among primary periods (years) and region- and species-specific (Table 4.3). This model had 22.0% of the model weight and was 1.2 times more likely than the second best model [Ψ_t(trap+region+sp), ε(trap+region), p_1, p_2, p_3, p_4, p_5, p_6, p_7(sp+region)].

Model-averaged parameter estimates for occupancy (Ψ_t) were similar among species, but some noticeable differences in the variability surrounded the estimates (Figures 4.1, 4.2).

Estimates of occupancy were predominantly driven by trapping effect and region; however, there was substantial variability surrounding the estimates of the trapping effect and region on the probability of occupancy (Table 4.4). The probability of predator use was 2.5 times less likely on trapped sites than those which were not. Predator use on the Thomasville sites was 1.46 times less likely than on the Albany sites.

Probability of discontinued use (i.e. ε, local extinction) of a scent station sample was greatest when a site received no trapping in one year and trapping in the following year, and lowest probability of discontinued use was observed when a site received 2 consecutive years without trapping (Figure 4.3). Although there was considerable variability around our estimate of the effect of the different trapping regimes, generally it was more likely for discontinued predator use when a site moved from no trapping to trapping relative to years without trapping in 2 consecutive years (Table 4.5). In general, the probability of discontinued sample patch use was more likely in the Thomasville region than Albany (Table 4.5).

The probability of recolonization was similar, but not identical among predator species (Appendix 4.2). The highest probability of recolonization by predators was between trapped and no trap years during 2003-2004 for PB East and PH (Figure 3.4; Appendix C.4.2).

Predator detection differed among years, by species, and by region (Figure 4.5). Estimates of detection were highest for raccoons (range 0.1 – 0.3) and mostly < 0.1 for all predator species (Figure 4.5). We used armadillos as our baseline for species-specific comparisons for detection. Generally, detection was more likely for raccoons compared to armadillos; however, there was little difference in detection among the other 4 species relative to armadillos (Appendices C.4.3-C.4.9).

A ratio of consecutive occupancy rates or a rate-of-change estimate in occupancy can be derived from the occupancy parameter estimates. The rate-of-change in predator use was close to 1.0 in most years for all species. The exceptions were during 2000-2001 when trapping was initiated in 2001 on PB East and PH and during 2003-2004 when treatments were reversed and trapping was initiated on PB West and TTRS (Figure 4.6). The rate-of-change of predator use was similar among species, but small differences existed in the variability surrounding the estimates (Appendix C.4.10).

Comparison of Raw Scent Station Indices and Occupancy Estimates

Raw indices for each site demonstrated the influence of different predator community compositions among sites visiting scent stations. Albany sites' raw indices were influenced primarily by raccoon visitations, whereas Thomasville sites were not consistently influenced by any single predator species (Figures 4.7-4.8). Generally, visitation rates were low for each species with the exception of raccoons. We found the Pearson correlation coefficient (r) by each species and site ranged from -0.164 – 0.877. The raw scent station index was correlated most with raccoon species and more specifically raccoons at the Albany sites (Figure 4.9, Appendix C.4.11).

Meso-Mammal Nest Mortality Relative to Predator Occupancy

We monitored 746 nests during the 7-year study using the 24-hour nest cameras. Of these, 32 (4.3%) were abandoned due to research activities and 8 (1.1%) had camera failures during predation events so predators could not be identified. These 40 nests were subsequently removed from the analysis. In the 706 nests remaining, we observed 277 (39.2%) nest failures via camera. Meso-mammals, when combined as a guild rather than by species, were the predominant failure cause (99, 35.7% of failures). Remaining failures included snakes (*Elaphe* spp. and *Lampropeltis getula*; 79, 28.5% of failures), fire ants (*Solenopsis* spp.; 33, 11.9% of failures), and incidental predators or the incubating adult was killed away from the nest (38, 13.7% of failures). Thick vegetation at the nest site, common across all the study sites, precluded identification of the specific failure cause at 29 (10.5%) nests, where all that could be confirmed was that the predator was not a meso-mammal.

Of the meso-mammal predation events, we observed nest failures caused by 31 armadillos, 28 raccoons, 20 opossum, 17 bobcats, and 2 coyotes. No nest predation by red or gray fox was observed via camera. The correlation coefficient indicated a relationship existed between raccoon predation events at nests and occupancy rates ($r = 0.725$). Relative to trapping, we observed apparent predation by raccoons to decrease on all study sites with predator trapping, paralleling decreased observed occupancy (Figures 4.10-4.13). Patterns between apparent failures rates and occupancy were less clear for other species when examined across all 4 study sites with correlation coefficients ranging from -0.283 to 0.197 (Figures 4.10-4.13).

DISCUSSION AND MANAGEMENT IMPLICATIONS

Effectiveness of Reducing Predator Use across the Landscape

Predator control efforts, as done in our study, were sufficient enough to reduce predator use of our sample patches. The influence of trapping was most noticeable (non-overlapping confidence intervals) in species with smaller home ranges (raccoons, armadillos, and opossum) and weakest in the wide ranging species (foxes, coyotes, and bobcats). Occupancy increased in subsequent years immediately after discontinued trapping efforts, demonstrating that breeding season predator reduction resulted in only temporary reductions of predators. We observed the highest probabilities of sampling patch extinction following the first year of trapping. Additional local extinction in subsequent trapped years declined slightly, but always remained higher than in years without trapping. This suggests a slight multi-year additive effect. After discontinued trapping, increases in recolonization demonstrated that predators are likely filling the vacant patches from the surrounding landscape. Other studies have observed similar results of rapid recolonization and essentially short-lived effectiveness of predator culling programs (Treves and Naughton-Treves 2005). For example, control efforts on red foxes in the United Kingdom exhibited replacement of vacant territories, which often occurred within the same season (Reynolds et al. 1993). These authors suggested, as we found in our study, to have effective predator management, control efforts must continue through the end of the avian breeding season. It has been suggested that heavily exploited populations where mortality rates are high may exhibit compensatory reproduction when populations is below carrying capacity (Knowlton 1972, Knowlton et al. 1999). In other research on one of our study areas, armadillo populations from Tall Timbers Research Station were examined using genetic sampling mark-recapture to assess the intensive predator control efforts during the 3-year portion of reduction (McDonough et al. 2007). From their findings, these researchers also concluded that individuals from the surrounding landscape were moving into replace those removed, but they did not believe the armadillo population was exhibiting compensatory reproduction.

In general, we observed regional differences playing a role in occupancy, probability of discontinued use, as well as detection probabilities. As such, regional differences within the predator context (i.e. who are the predators and how much of the community do they comprise) may translate into different effects of predator removal on the predator community. Generally, occupancy rates were higher in Albany compared to Thomasville, regardless of whether it was trapped or not trapped, indicating some regional differences in predator populations.

We assumed our sampling patches were independent from one another and that occupancy was closed during the 5-day sampling period. However, we recognize these assumptions may have been violated given home ranges of some predators in our study are ≥ 25 ha. In addition, scent stations were placed along roads which act as travel corridors and may result in some spatial autocorrelation along these linear routes. However, our focus was directed towards determining the area across the landscape the predators were using. These independence issues are more problematic in direct abundance estimation. Future studies should consider different sampling scales to account for variation in predator home range to determine if scent station protocols should be adjusted.

Comparison of Scent Station Indices to Occupancy

We observed year to year variation in detection rates of predators that suggests raw indices are not directly comparable across years. Occupancy modeling provided a means of handling sampling issues associated with variable detection and is recommended when possible over raw scent station indices. However, raw scent station indices were at least somewhat correlated with occupancy and did provide similar trends to occupancy rates on some of our study sites. As long as these limitations are realized, these indices can provide some useful information for management purposes, particularly when the predator community has a high proportion of raccoons relative to other species.

In general, we observed low detection probabilities (<10%), and more generally low visitation rates, for most species with the exception of raccoons. Kuhn (2007) monitored predator activity of several species using scent stations in North Dakota and also found low visitation rates by all the species monitored except raccoons. Higher abundance or behavioral differences (e.g. curiosity) may be the reason for observing increased visitation rates by raccoons

(Sargeant et al. 1993). Detection rates below 10% indicate that changes in monitoring technique or scent station protocols may be in order. For example, increasing the number of days monitored to more than 5 consecutive days could increase detection probabilities. Coupling camera technology with scent stations may provide a better means of gauging whether predators are visiting stations, but without leaving tracks within the established area where they can be detected. Cameras may reveal rates of visitations by groups of individuals, which may provide additional information on the relationship between visitation and abundance. In short, this technology or other forms of double-sampling can assist in determining whether other field methods may be better at reflecting population changes. For example, Sumner and Hill (1980) found bobcats were detected more often using predator calling than scent stations.

Meso-mammal Nest Predation Relative to Predator Use

Raccoon predation did appear to fluctuate with some consistency to occupancy rates. However, we did not observe clear patterns among all meso-mammals and apparent rates of predation by each of those species. Despite tremendous physical and financial effort, we had limited sample nest sizes when examining cause-specific nest mortality by year and site. This may have created the false appearance of a decoupled linkage between predator occupancy rates and predation rates at the nest. However, this is one of the few studies to compare relationships of predator activity to nest predation rates. Some studies have found a relationship between predator activity and nest predation (Cain et al. 2003, Cain et al. 2006) whereas Peterson et al. (2004) did not observe similar patterns. Sperry et al. (2008) found Texas rat snake (*Elaphe obsolete*) activity was negatively related to nest predation of Black-capped Vireos (*Vireo atricapilla*), but a less pronounced relationship existed with Golden-cheeked Warbler (*Dendroica chrysoparia*) nests.

Conclusions and Future Directions

Nest predation is considered the primary cause of nest failure for most bird species (Ricklefs 1969, Martin 1993). However, rarely do studies focused on understanding avian nest predation or the influences of predator activity on avian reproductive success through simultaneously studying the predator population dynamics (Sperry et al. 2008). Most predator control studies direct their efforts to monitoring only the targeted avian species of interest; therefore, they have no certainty that the intensity of the predator control is sufficient to influence the predator population. Our results demonstrate that predator removal is not a binary treatment of trapped and not trapped, but rather can span a continuum on the influence it plays on the predator population. As a result, it is not surprising that a variety of outcomes ranging from large increases to no effect in avian reproduction have been observed with respect to predator control (Côté and Sutherland 1997, Newton 1998). Measuring predator population demographics before, during, and after predator reduction is of paramount importance if researchers and managers are to understand the influence predators have on avian populations and specifically reproduction.

Presently, culling programs are assumed to have little to no impact on population viability of target species as a whole (Treves and Naughton-Treves 2005), but this is rarely examined. Our study showed that intensive control can influence predator use of the study area (i.e. local scale), but this is only temporary and these induced high mortality rates are counteracted by the greater regional population. However, no studies have examined long-term effects of intensive control on the predator population.

Without studying community dynamics, we do not know the impact of changes one predator guild may have within the ecosystem, another area of predator control rarely examined and in need of future research efforts (Berger 2006). Despite being a very extensive study over a relatively long time horizon and with replication of treatments, this is just one snap-shot of a much larger issue. Many questions still need to be addressed relative to how these results translate to different predators within the community, particularly those who may serve as both predators and prey. In addition, predator control efforts focused in other ecosystems or in more fragmented habitats may see different responses of predators and prey within the community.

From a historical perspective, predator removal has generally had implications that elimination of predators from the landscape might be a positive objective (Treves and Naughton-Treves 2005). Predator control as part of predation management in support of a game species is a more representative description. The objective becomes one of minimizing interactions of meso-mammal predators with game species, such as bobwhites, during the breeding season, rather than eradication of the predators from landscape. With the shifting perspective of societal value of predators, it is likely more scrutiny will be placed on predator management programs. Monitoring the impacts of such programs on both predator and prey will be required to justify their use as a tool for enhancing game species, imperiled species, or reducing wildlife-livestock conflicts. Our study demonstrates that intensive predator reduction of meso-mammal species achieves management objectives of reducing predator activities during nesting season at a local scale, but these targeted predator species remain on the greater landscape and appear to function within the ecosystem.

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Table 4.1: Representation of trapping (T) and no trapping (N) treatments of meso-mammalian predators at 4 sites located within two regions (block) of northern Florida and southern Georgia during a 7-year predator control study.

Block/Region	**Site**	**Baseline** **2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
Thomasville	TTRS	N	N	N	N	T	T	T
	PH	N	T	T	T	N	N	N
Albany	PB West	N	N	N	N	T	T	T
	PB East	N	T	T	T	N	N	N

Table 4.2: Number of meso-mammalian predators removed by species for each of the 4 study sites in southern Georgia and northern Florida, 2001-2006.

	PB East			**PB West**			**PH**			**TTRS**			
Predator	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**Total**
Raccoon	193	236	104	175	140	169	90	47	57	104	87	95	1497
Opossum	60	179	276	406	164	174	106	186	140	246	153	203	2293
Armadillo	43	45	51	119	61	47	61	44	31	150	149	153	954
Bobcat	20	40	22	26	9	8	14	5	9	20	13	16	202
Coyote	9	14	6	4	7	14	13	13	4	12	12	12	120
Fox	4	8	7	1	2	3	6	0	1	0	6	5	43
Feral	8	6	8	6	3	2	6	2	1	0	4	6	52
Total	337	528	474	737	386	417	296	297	243	532	424	490	5161

Table 4.3: Summary of model selection results examining meso-mammal community occupancy (Ψ), local extinction (ε), and detection probability (p_t) for t =1 - 7 with respect to trapping efforts during 2000-2006 in southern Georgia and northern Florida with any Akaike's Information Criteria (AIC_c) model weight (W_i). Table includes number of parameters (K), likelihood (L_i), and deviance. Predictor variables include predator trapping (trap), physiographic region (region), study site (site), species (sp), year, and constant (.).

Model	**K**	**AICc**	**Δ AICc**	**W_i**	**L_i**	**Deviance**
Ψ(trap+region), ε(trap+region), p_t(sp + region)	57	7590.62	0.00	0.22	1.00	7475.54
Ψ(trap+region+sp), ε(trap+region), p_t(sp + region)	60	7590.98	0.36	0.19	0.84	7469.78
Ψ(trap), ε(trap), p_t(sp + region)	55	7591.39	0.76	0.15	0.68	7480.37
Ψ(trap+site), ε(trap), p_t(sp + region)	58	7592.08	1.46	0.11	0.48	7474.96
Ψ(trap+year), ε(trap+region), p_t(sp + region)	62	7592.47	1.85	0.09	0.40	7467.19
Ψ(trap+region+year), ε(trap+region), p_t(sp + region)	63	7592.74	2.12	0.08	0.35	7465.41
Ψ(trap), ε(trap+region), p_t(sp + region)	56	7592.82	2.20	0.07	0.33	7479.78
Ψ(trap+region), ε(trap+site), p_t(sp + region)	59	7594.41	3.78	0.03	0.15	7475.24
Ψ(trap+region), ε(trap), p_t(sp)	49	7594.65	4.03	0.03	0.13	7495.85
Ψ(trap), ε(trap+site), p_t(sp + region)	58	7596.59	5.97	0.01	0.05	7479.46
Ψ(trap+site), ε(trap), p_t(sp)	51	7597.33	6.71	0.01	0.04	7494.46

Table 4.4: Model-averaged beta estimates for the probability of predator use (i.e. occupancy) including the estimate, standard error (SE), 95% confidence intervals of the estimate (LCI, UCI), the odds ratio, and the 95% confidence intervals of the odds ratio.

Parameter	**Estimate**	**SE**	**LCI**	**UCI**	**Odds Ratio**	**95% LCI Odds Ratio**	**95% UCI Odds Ratio**
Intercept	0.305	2.047	-3.707	4.317			
Trap[1]	-0.922	1.370	-3.607	1.763	0.398	0.027	5.832
Region[2]	-0.378	1.202	-2.734	1.978	0.685	0.065	7.229
PB East[3]	-0.187	0.344	-0.860	0.487	0.830	0.423	1.627
TTRS[3]	-0.419	0.382	-1.167	0.328	0.657	0.311	1.389
PH[3]	-0.507	0.399	-1.289	0.275	0.602	0.276	1.316
2001[4]	-0.382	0.529	-1.419	0.656	0.683	0.242	1.926
2002[4]	0.058	0.612	-1.142	1.258	1.060	0.319	3.517
2003[4]	0.262	0.708	-1.126	1.651	1.300	0.324	5.210
2004[4]	0.327	0.762	-1.167	1.821	1.386	0.311	6.176
2005[4]	-0.366	0.647	-1.633	0.902	0.694	0.195	2.464
2006[4]	-0.115	0.645	-1.380	1.150	0.891	0.252	3.157

[1] Trap relative to no trapping

[2] Thomasville region is relative to Albany region

[3] Sites are relative to Pinebloom West

[4] Years are relative to 2000

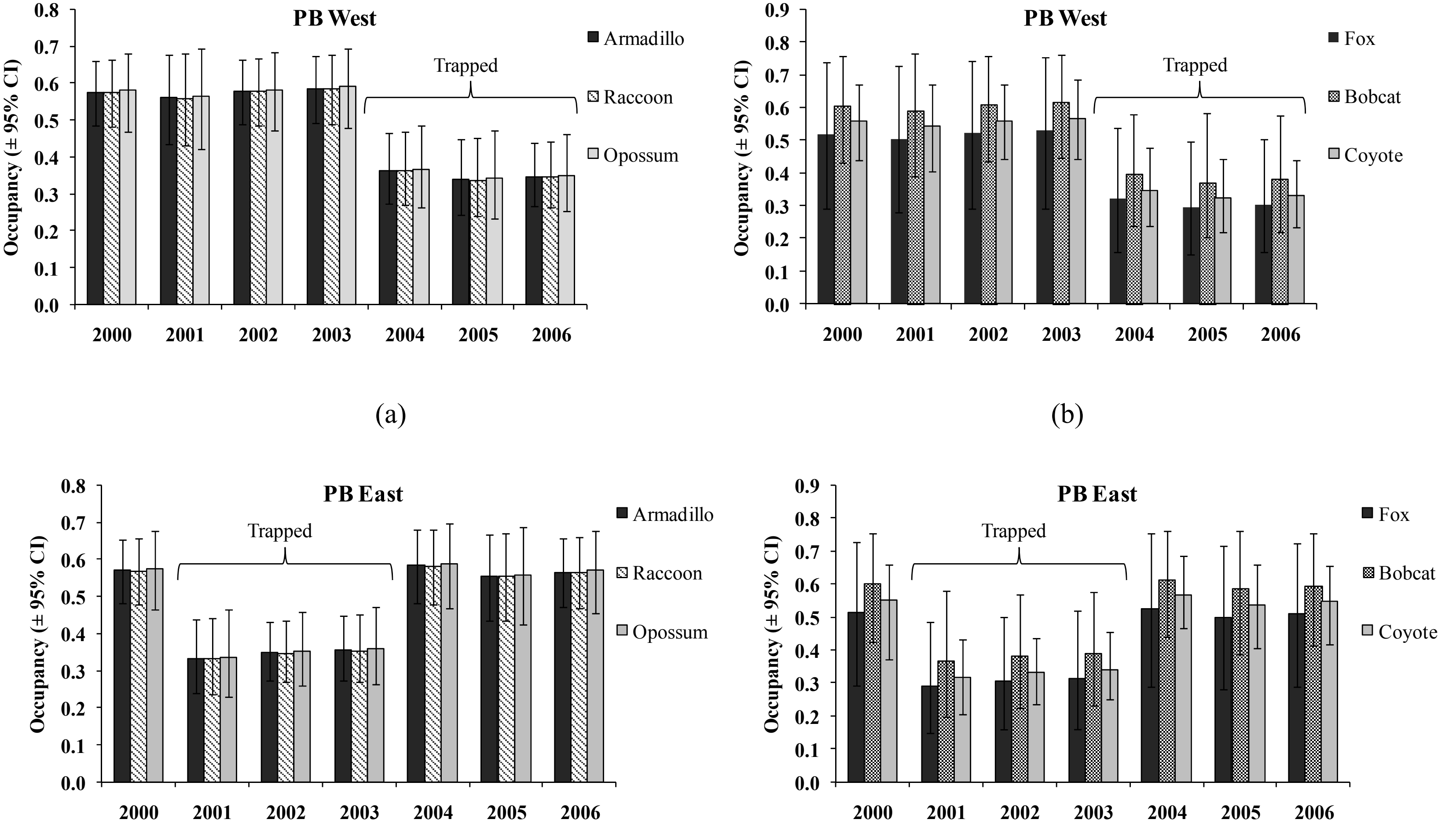
Table 4.5: Model-averaged beta estimates for the probability of discontinued use (i.e. local extinction) including the predictor, estimate, standard error, 95% confidence intervales of the estimate (LCI, UCI), the odds ratio, and the 95% confidence intervals of the odds ratio.

Parameter	**Estimate**	**SE**	**LCI**	**UCI**	**Odds Ratio**	**95% LCI Odds Ratio**	**95% UCI Odds Ratio**
Intercept	-1.186	3.085	-7.232	4.861			
Trap (N-T)[1]	1.571	3.988	-6.245	9.388	4.813	0.002	11944.129
Trap (T-T)[1]	1.043	4.780	-8.325	10.412	2.839	0.000	33265.856
Trap (T-N)[1]	0.841	5.913	-10.749	12.431	2.319	0.000	250491.687
Region[2]	0.288	2.416	-4.447	5.023	1.333	0.012	151.821
PB East[3]	-0.189	0.719	-1.597	1.220	0.828	0.203	3.386
TTRS[3]	0.179	1.146	-2.068	2.425	1.196	0.127	11.303
PH[3]	0.113	1.359	-2.551	2.777	1.120	0.078	16.066

[1] Trap regimes relative to 2 consecutive years of no trapping (N-N)

[2] Thomasville region is relative to Albany region

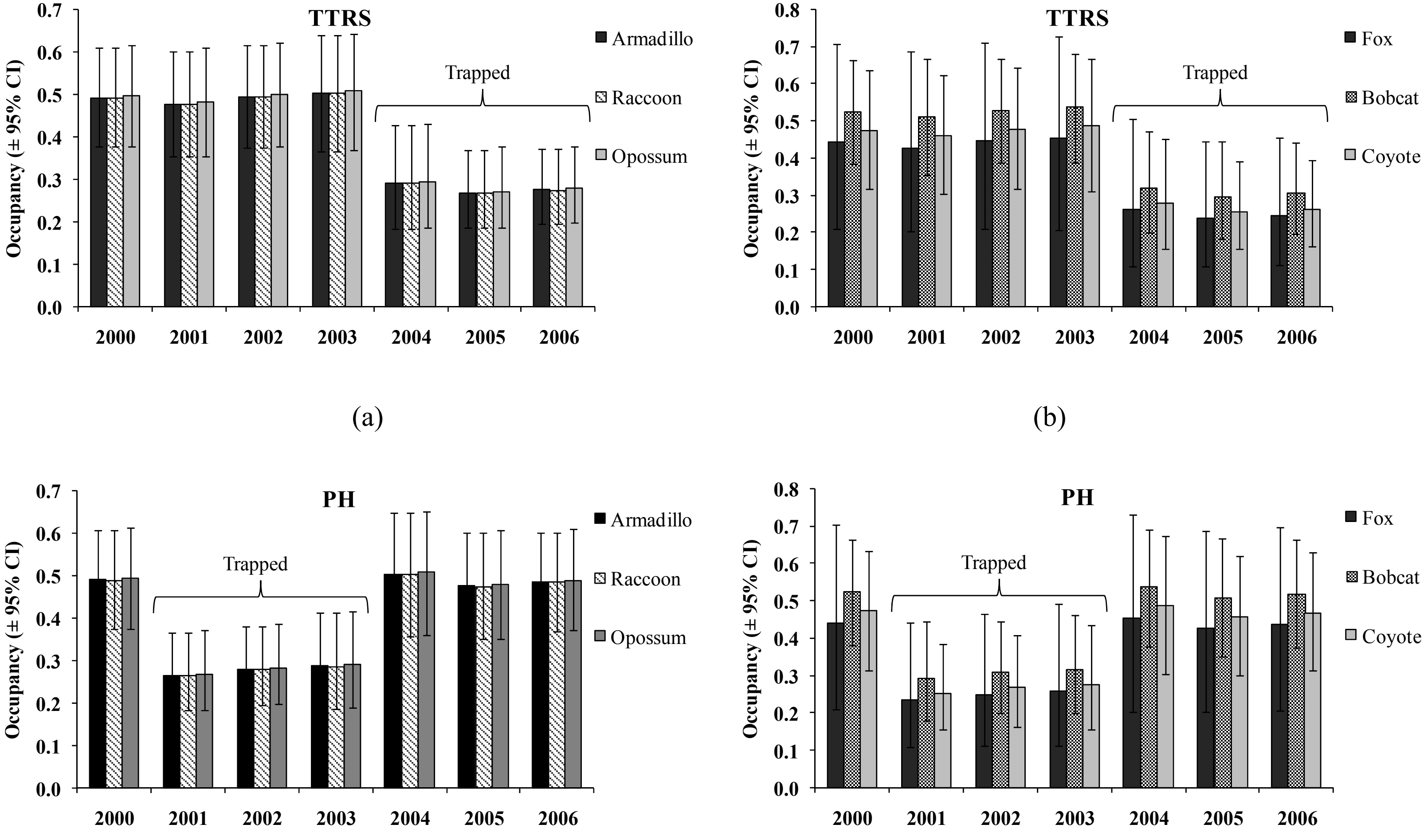
[3] Sites are relative to Pinebloom West



(a) (b)

(c) (d)

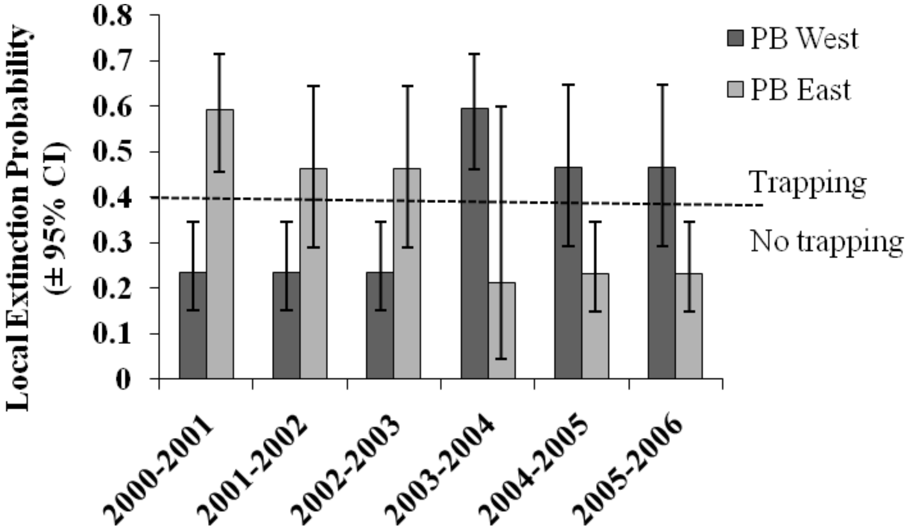
Figure 4.1: Model-averaged estimates (± 95% CI) for the probability of occupancy (or use) of sites (± 95 CI) by species in the Albany region for (a,b) PB West and (c,d) PB East, 2000-2006.



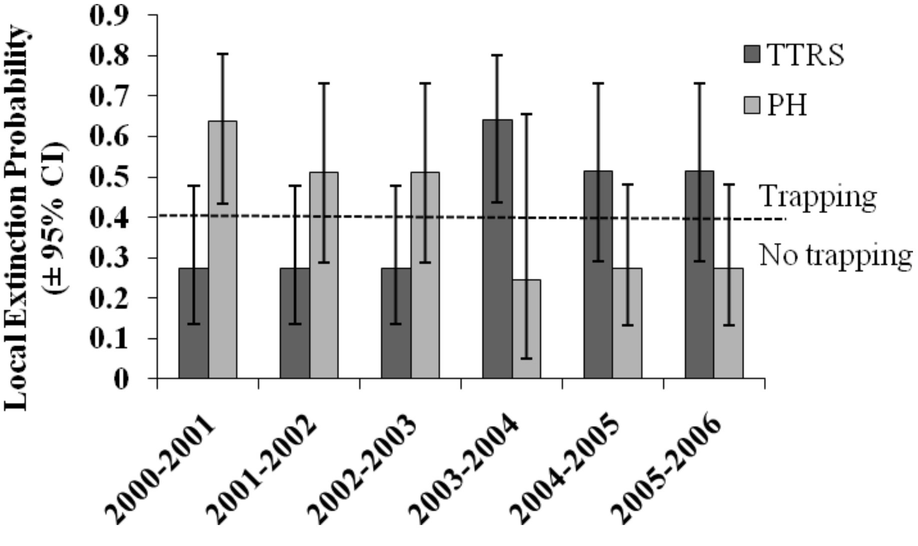
(a) (b)

(c) (d)

Figure 4.2: Model-averaged estimates (± 95% CI) for the probability of occupancy of sites by species in the Thomasville region for (a,b) TTRS and (c,d) PH, 2000-2006.

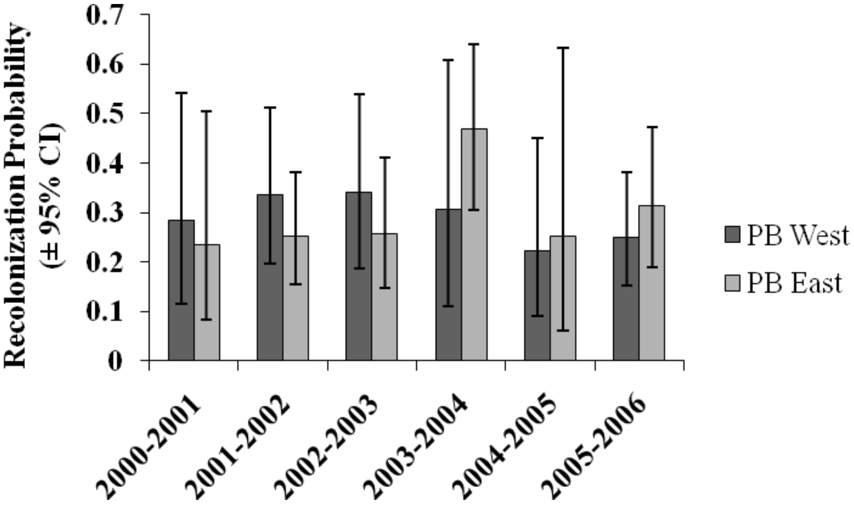


(a)

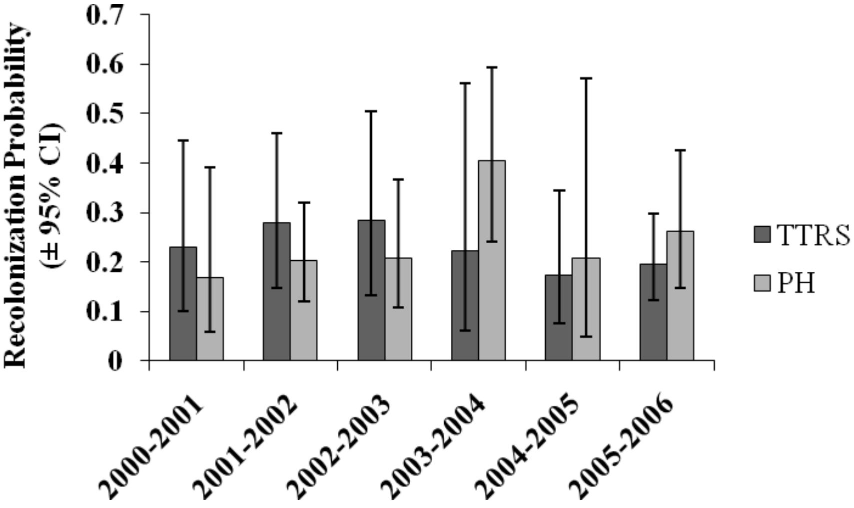


(b)

Figure 4.3: Probability of discontinued use (i.e. local extinction) of a sampling patch between years for (a) Albany sites and (b) Thomasville sites. Above the line trapping occurred (PB East and PH in 2001-2003 and for PB West and TTRS in 2004-2006) and below the line no trapping occurred.

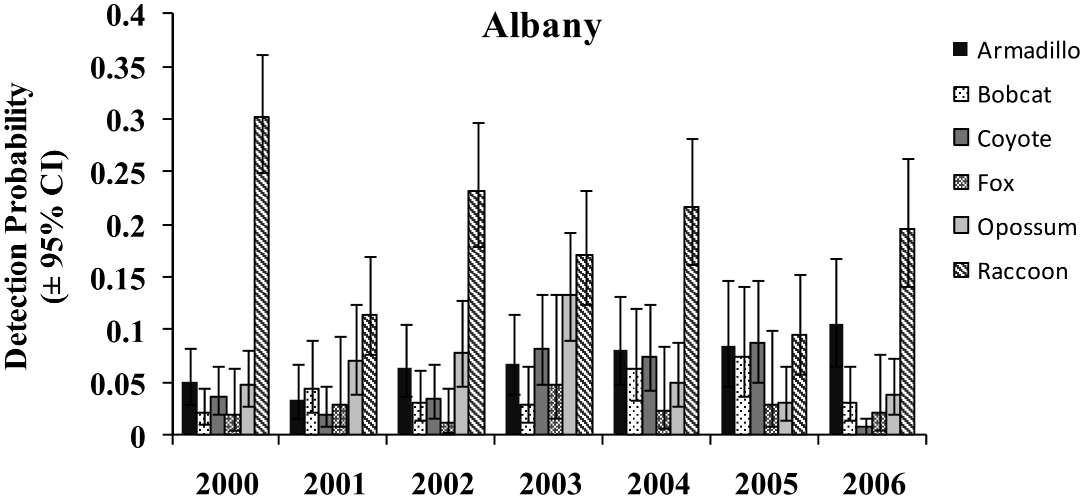


(a)

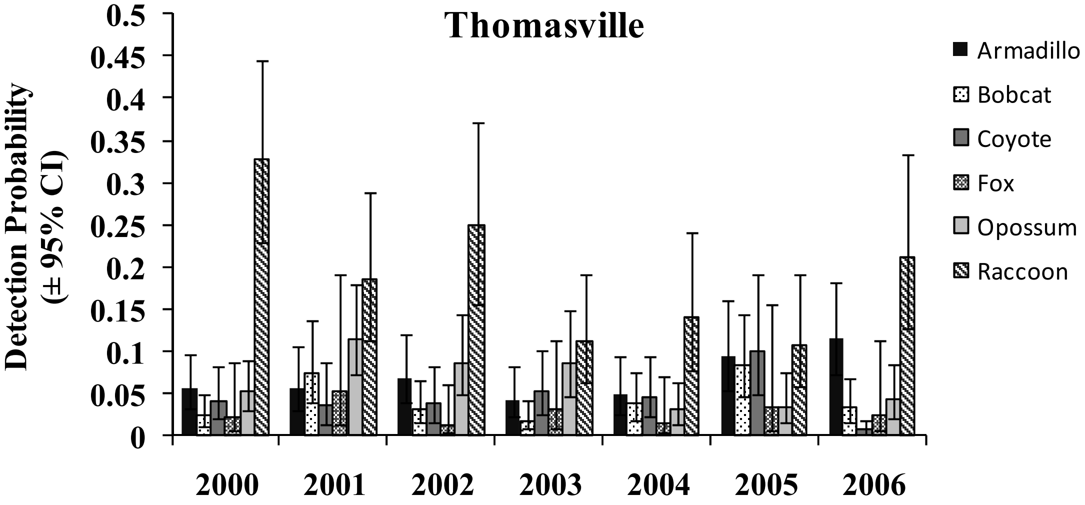


(b)

Figure 4.4: Probability of an unoccupied sampling patch becoming occupied (i.e. recolonization) for raccoons in (a) the Albany region and (b) the Thomasville region. PB East and PH were trapped for meso-mammals from 2001-2003, and PB West and TTRS were trapped from 2004-2006. Note 2003-2004 demonstrates the transition between a trapped year to no trapping year for PB East and PH with increased probability of recolonization by predators between those years.



(a)



(b)

Figure 4.5: Detection probability for 6 meso-mammalian predator species during 7 years of scent station monitoring in the (a) Albany region and (b) Thomasville region.

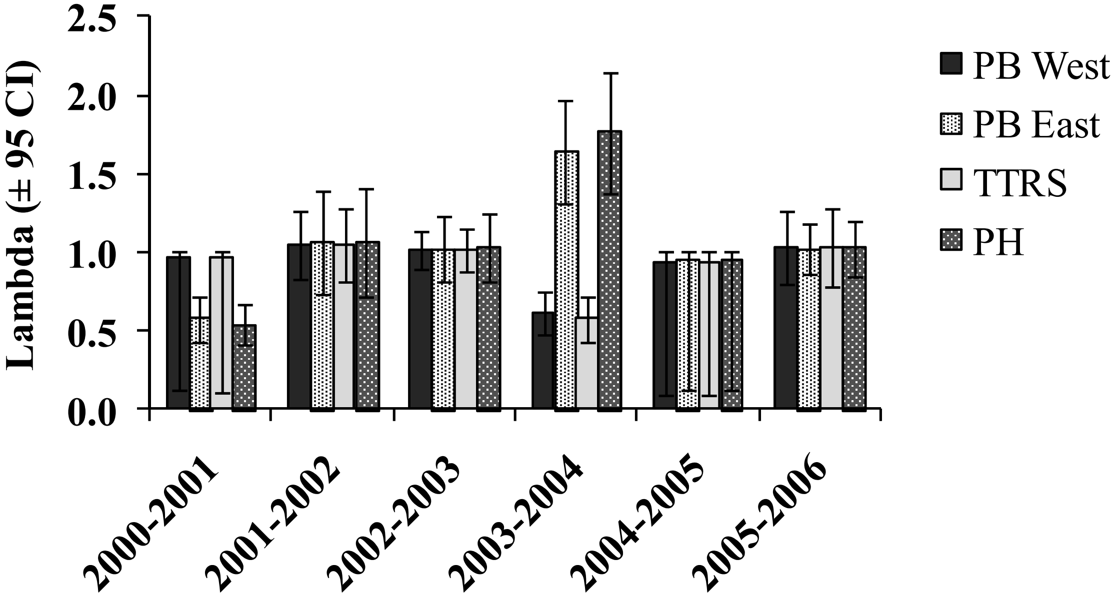
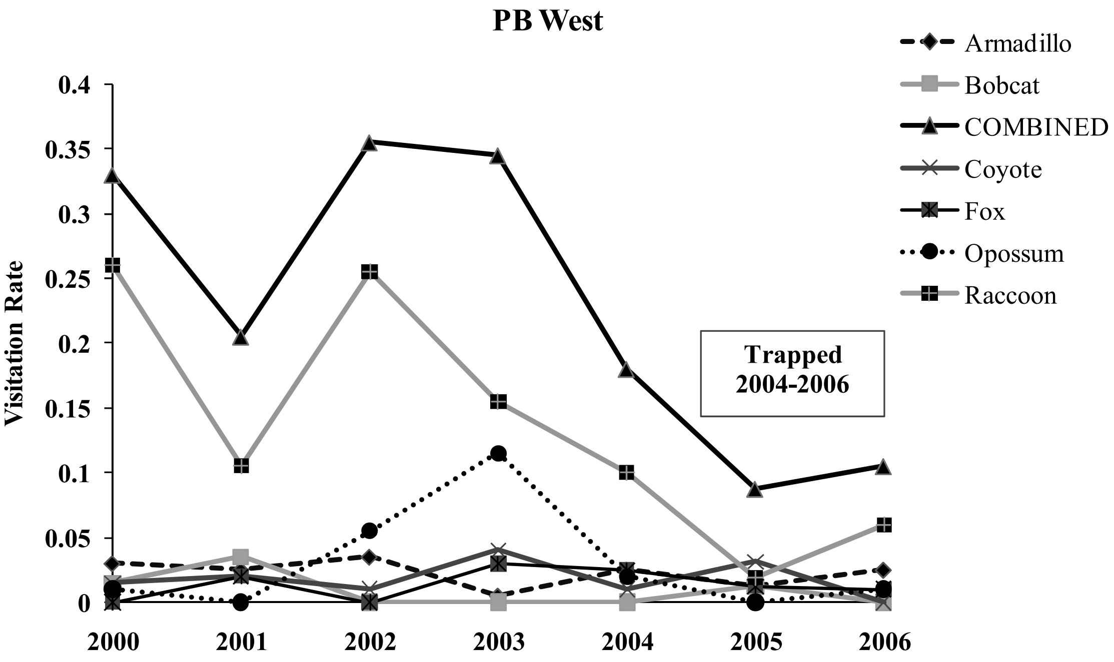
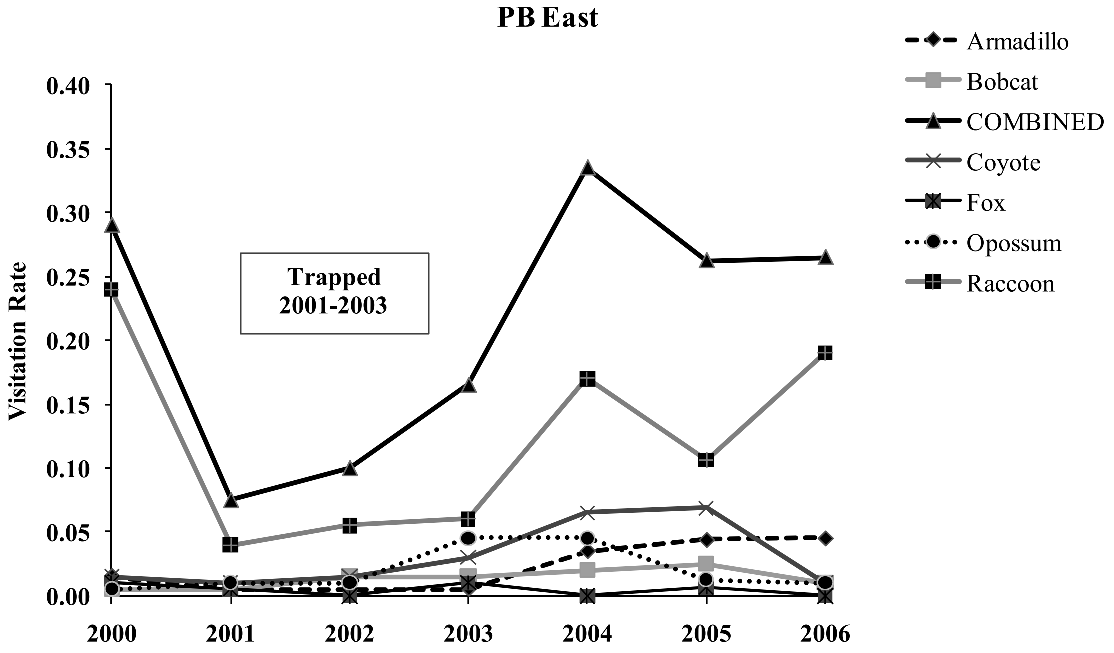


Figure 4.6: Derived estimates for the rate of change of occupancy for raccoons with 95% confidence intervals at 4 study sites in southern Georgia and northern Florida during 2000-2006. Note changes in occupancy during 2000-2001 at the initiation of trapping on PB East and PH and changes during 2003-2004 when trapping treatments were reversed.

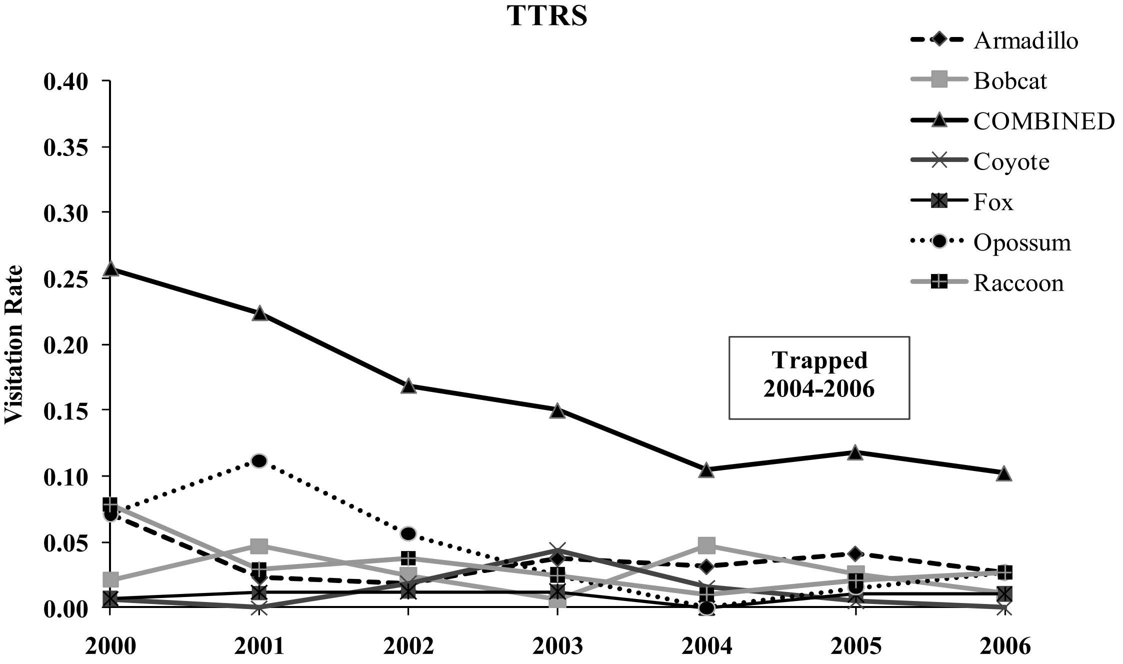


(a)

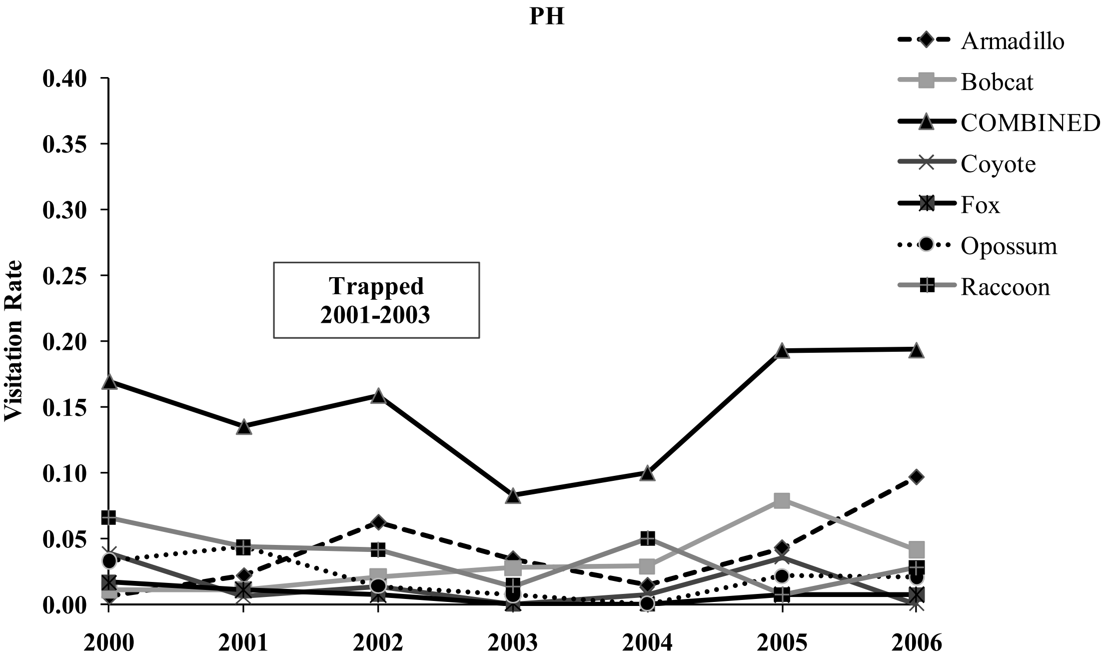


(b)

Figure 4.7: Overall (COMBINED) and individual species crude visitation rates at scent stations for (a) Pineboom West and (b) Pinebloom East, 2000-2006.



(a)



(b)

Figure 4.8: Overall (COMBINED) and individual species crude visitation rates at scent stations for (a) Tall Timbers and (b) Pebble Hill, 2000-2006.

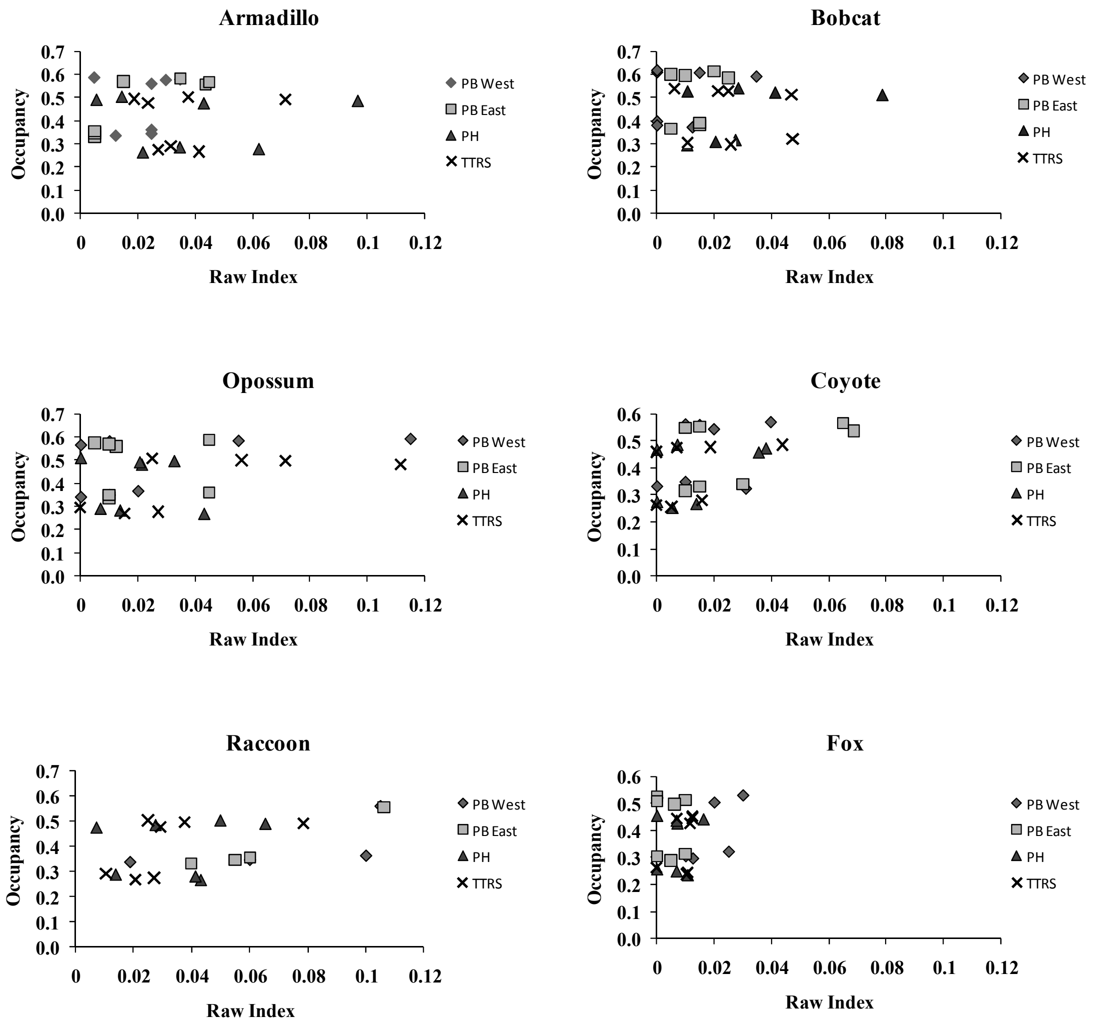


Figure 4.9: Raw scent station indices compared to occupancy rates for each of the 6 predator species monitored on 4 study sites in southern Georgia and northern Florida, 2000-2006, demonstrating litte relationship between scent station indices and occupancy rates.

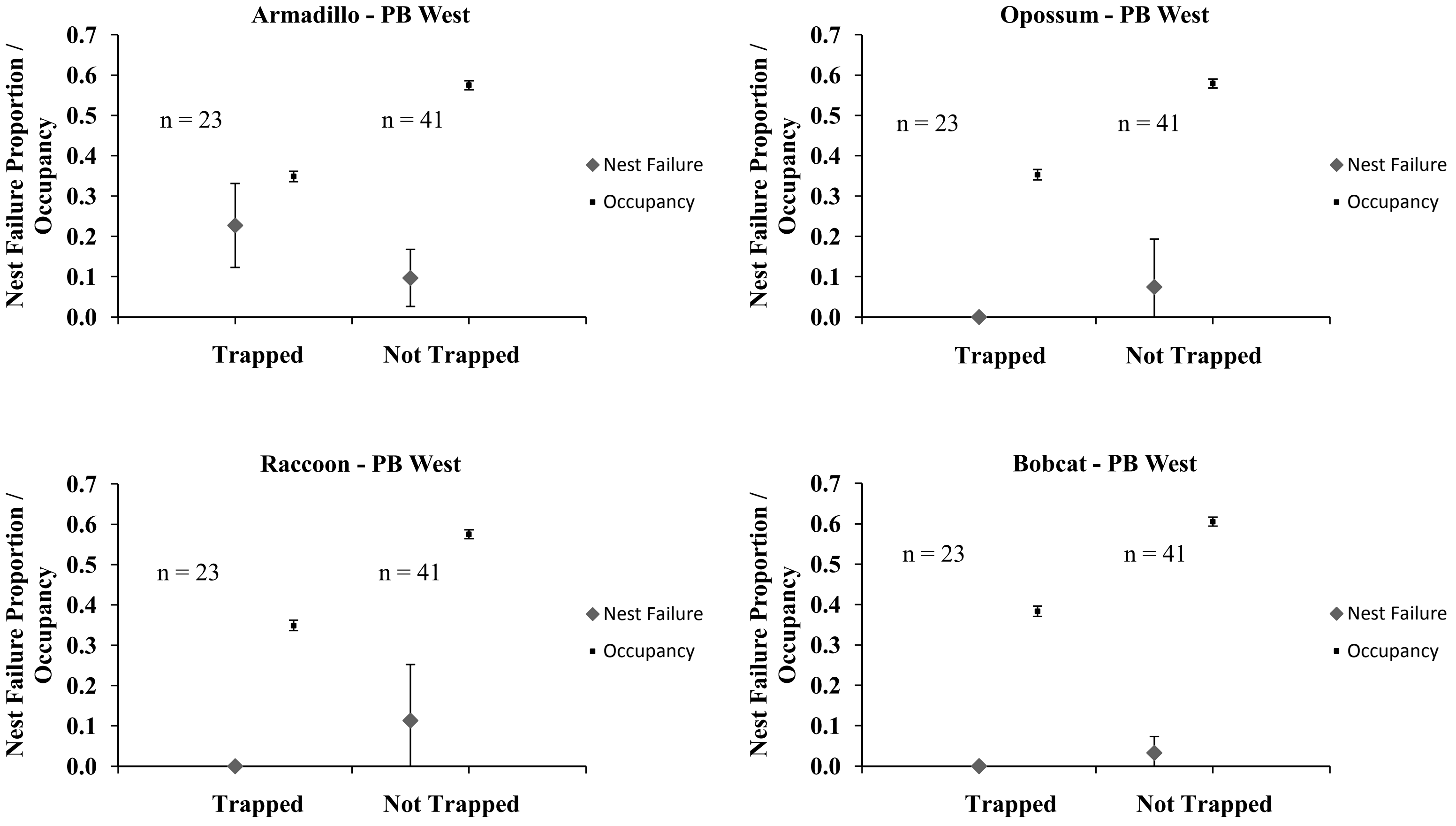


Figure 4.10: Relationship between species-specific average (± SE) nest failures observed via 24-hour nest cameras and average (± SE) predator occupancy rates for trapped and not trapped years at Pinebloom West in southern Georgia, 2000-2006. Numbers above the bars represent total number of nest failures observed during the trapped and not trapped periods. Note no fox predation events and only 2 coyote events were observed on camera on any study site during the study.

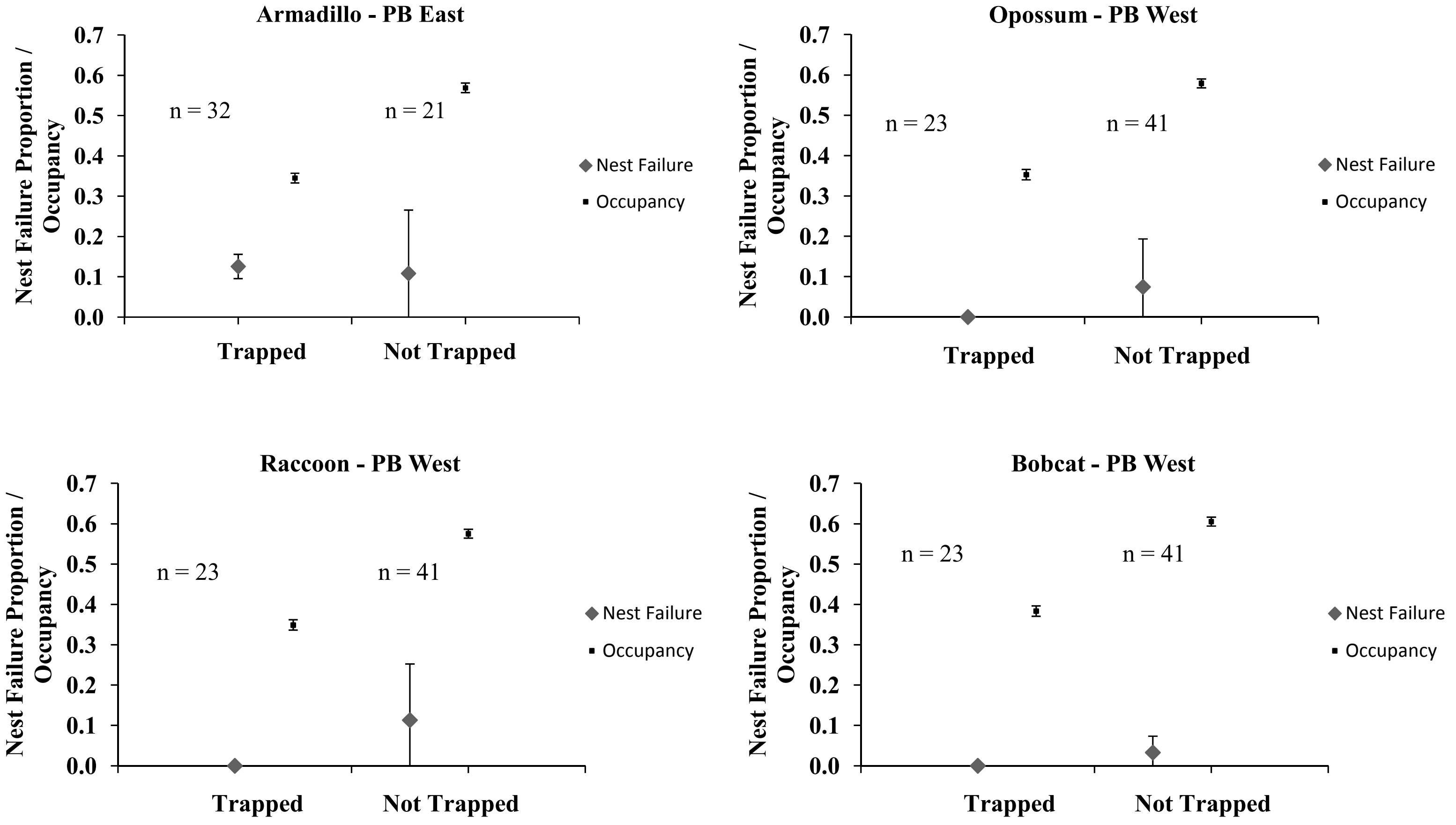


Figure 4.11: Relationship between species-specific average (± SE) nest failures observed via 24-hour nest cameras and average (± SE) predator occupancy rates for trapped and not trapped years at Pinebloom East in southern Georgia, 2000-2006. Numbers above the bars represent total number of nest failures observed during the trapped and not trapped periods. Note no fox predation events and only 2 coyote events were observed on camera on any study site during the study.

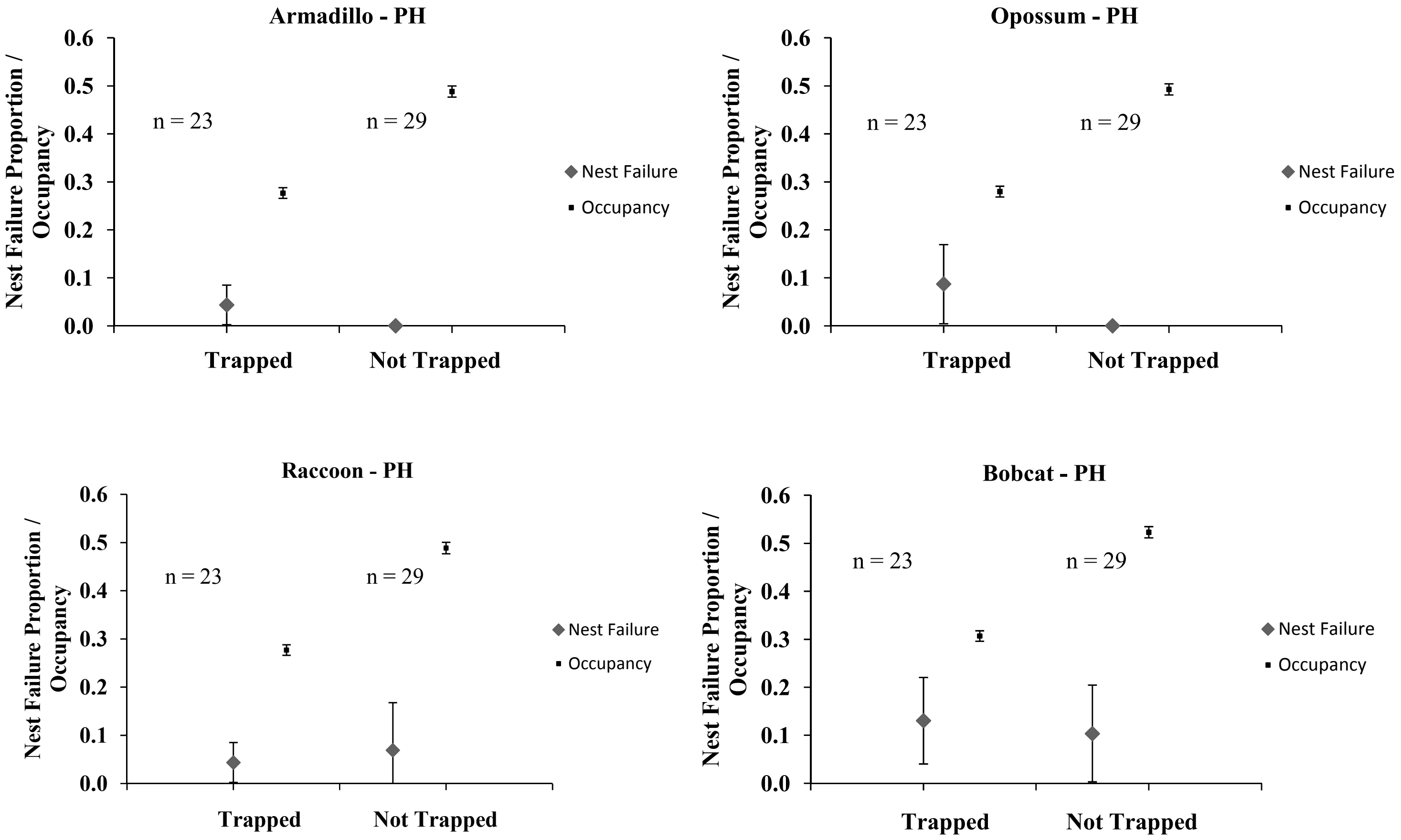


Figure 4.12: Relationship between species-specific average (± SE) nest failures observed via 24-hour nest cameras and average (± SE) predator occupancy rates for trapped and not trapped years at Pebble Hill in southern Georgia, 2000-2006. Numbers above the bars represent total number of nest failures observed during the trapped and not trapped periods. Note no fox predation events and only 2 coyote events were observed on camera on any study site during the study.

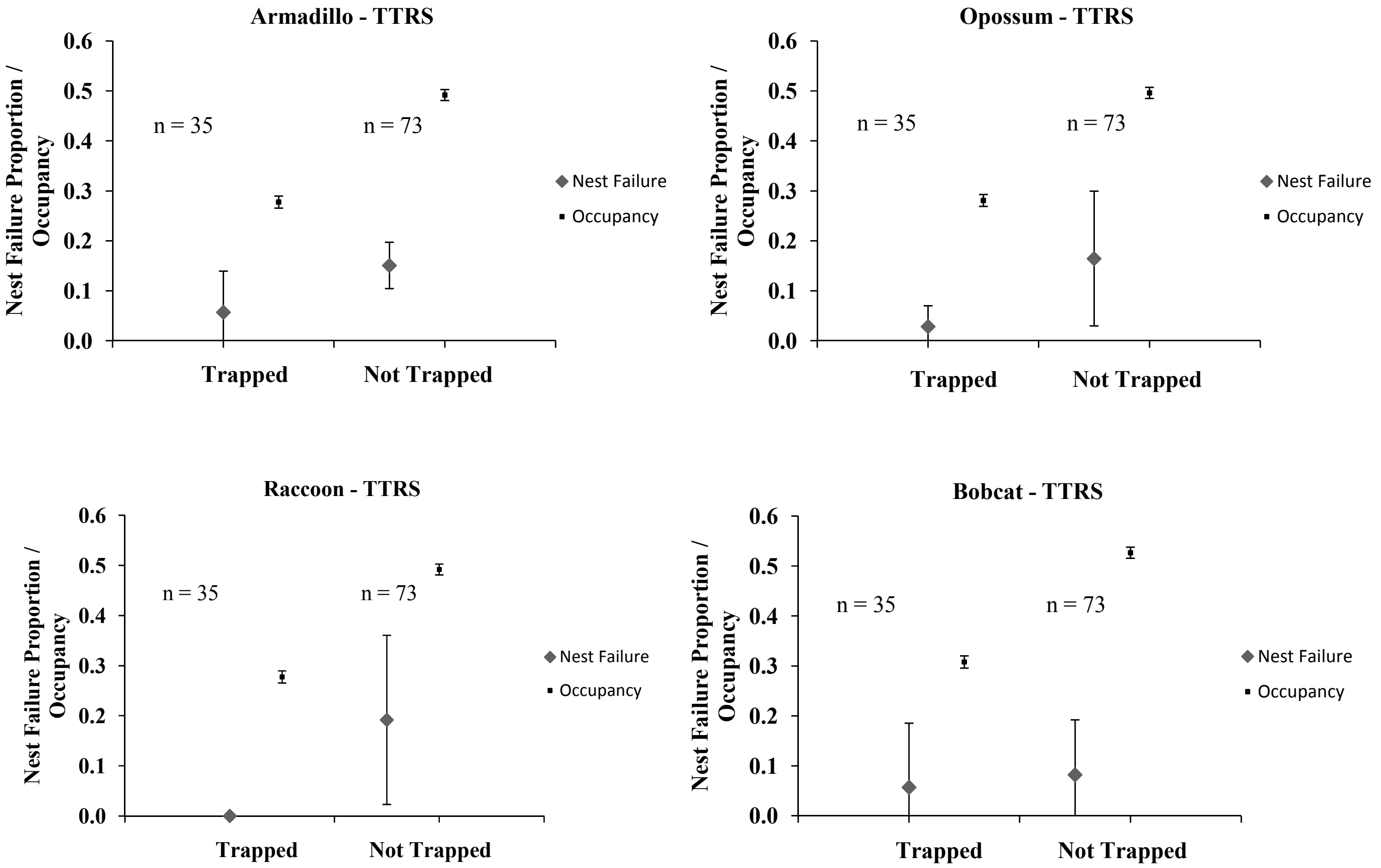


Figure 4.13: Relationship between species-specific average (± SE) nest failures observed via 24-hour nest cameras and average (± SE) predator occupancy rates for trapped and not trapped years at Tall Timbers in northern Florida, 2000-2006. Numbers above the bars represent total number of nest failures observed during the trapped and not trapped periods. Note no fox predation events and only 2 coyote events were observed on camera on any study site during the study.

CHAPTER 5

CHALLENGING PREDATION PARADIGMS: CONCLUSIONS AND FUTURE RESEARCH CONSIDERATIONS

Predation is a natural process (Errington 1967) and is considered to be both a proximate and ultimate driving force in community ecology (Taylor 1984, Sih 1987, Lima and Dill 1990). However, many ecosystems have been dramatically altered across the landscape as a result of human impacts, and with these changes, the process of predation has transformed. The changing landscape and shifting land-use practices have been implicated as the primary cause for the decline of many species, including the Northern Bobwhite (Brennan 1991, Fies et al. 1992). Vast expanses of continuous habitat are now smaller, fragmented blocks. Soil disturbances, as a result of intensive forestry and agricultural practices, have modified the plant communities. Historically high densities of many middle-sized predators, particularly meso-mammals, have been observed across the Southeast (Peoples et al. 1995, Lovell et al. 1998). Reduction or eradication of top predators, limited hunting pressure upon these meso-mammals, as well as potential benefits from the altered landscape matrix are likely contributing factors to their increased abundance. These changes reflect the alteration of an entire ecosystem with extensive loss of early successional plant communities and changing faunal dynamics (Church et al. 1993). As a result of these changes, predation, in its altered form, requires extensive reevaluation to understand the process on the modern landscape (Burger 2002). Ultimately, the results of this study and many recent studies involving nest cameras or predator reduction are challenging the prevailing paradigms set forth by Errington (1934), and predation may be a limiting factor in avian populations (Newton 1998, Burger 2002). As a result, it may be imperative to directly manage predators in order to try to mitigate their effects on imperiled species or popular game species.

Historically, predator removal focused on control of predator populations with the implication that elimination of predators from landscapes might be a positive objective (Treves and Naughton-Treves 2005). Predation management, a more representative description, should not be viewed as eradication of predators from the landscape, but rather reducing the interactions of predators with avian species being targeted for management. This object can be met through direct (e.g. predator control) or indirect manipulation (e.g. habitat modification; providing alternative prey) of predator dynamics (Jimenez and Conover 2001, Carroll et al. 2007); however, the extent to which these methods influence the interaction may vary greatly spatially and temporally. To properly assess the effects of predator management programs aimed at increasing reproductive output, one needs to examine not only the target avian species, but also, the predator community. Proper predation management requires knowledge of the predator context and the extent to which each predator plays in bobwhite nest failures. Reviews of predator control studies have demonstrated conflicted results (Côté and Sutherland 1997, Newton 1998). These discrepancies are likely the result of researchers perceiving removal as a binomial treatment (i.e. control or no control) when in fact it presents as a wide continuum on how it influences predator dynamics and predator-prey interactions. In some studies, predator reduction may not affect predator abundance and use of space even in the short term. Predator population abundance may population demographics directly, but also indirectly through perceived risks. These perceived risks from predators by the prey species may alter behavioral shifts in reproductive decisions (Lima and Steury 2005), such as observations of bobwhite nest defense against certain predators and not others (Burnam 2008).

Reduction of one particularly guild of predators, such as meso-mammals, in a complex ecosystem could result in a "cascade effect" (Closs et al. 1999, Snyder and Wise 2001). Removal of predators can have unintended consequences within the ecosystem, and this potential cascade effect is often overlooked during monitoring efforts conducted with respect to predator reduction programs (Berger et al. 2001, Berger 2006). Community dynamics across predator guilds such as the impacts on the snakes, which serve as both predator and prey in our system, is an area where future research efforts need to be focused. Predation among the predator guilds is critical for shaping the predator community (Reynolds and Tapper 1996). Snakes and other predator populations or behaviors may be altered as a result of meso-mammalian reduction. As can be seen in Chapter 2 of this dissertation, our findings lead to questions about whether bobwhite nests failures due to snakes or fire ants may actually be more detrimental to bobwhite productivity than other causes. These predation events typically occur late in incubation when bobwhites have invested maximum time and energy into a particular clutch and may have limited opportunity to renest. Additionally, the metrics selected to evaluate reproductive success will need to be sensitive enough to detect changes in actual reproduction (Etterson et al. *In Review*). Predator control may not translate to increased nest success, particularly for persistent renesting species like the bobwhite when per capita fecundity rates are increasing.

Understanding the predator community and the predominant nest predators will enable biologists to target habitat management for these specific species. In Chapter 3, we discussed the role of habitat characteristics on the probability of nest failure and even the probability of specific nest failures. This study marked the first extensive study and only the second study to date which coupled nest predator identity found from cameras with landscape features. Our findings suggest that scale is important to the predation process with the probability of failure being influenced by field composition at scales >50 ha surrounding bobwhite nests. However, smaller scales may be more influential at understanding specific predator dynamics. In a companion study (Hannon 2006), fields were found to be important as a potential source of habitat for cotton rats, an alternative prey item for many bobwhite predators. Alternative prey and potentially changes of predator foraging patterns as a result appear to offer some buffering that offsets nest predation from generalist predators and is area where future research efforts should be directed. Supplemental feeding, using grain scattered along lines on the landscape, is common for bobwhite management and has positive impacts on this species (Whitelaw et al. 2009). Interestingly, increasing distance between nests and feed lines appears to make bobwhite nests slightly more vulnerable to ant predation than meso-mammals. In addition, bobwhite nests are more likely to fail due to ant predation than meso-mammals when hardwood composition is increased at approximately the 50-ha scale. The relationship between ants and feed lines and hardwood composition warrants further examination in future research, although ants only contributed to approximately 11% of all nest failures. Bobwhite nest predation, in general, appeared to be primarily opportunistic events since we found very little spatial relationship between the fate of a nest relative to the fate of neighboring nests. Thus, providing abundant sources of alternative food items may be the best way to minimize predator-bobwhite nest interactions.

Public perception of predators has seen dramatic shifts as predators are now more commonly viewed as valuable to society, as well as biodiversity and integrity of the ecosystem. The shifting perspectives about predators will place more emphasis on quantifying the demographic effects of management actions to their populations. Chapter 4 demonstrates the first extensive study quantifying the influence of predator control on meso-mammals during a predator reduction study. We demonstrated the ability to reduce predator use across our study areas, while these predators remained on the greater landscape. Thus, we were able to meet our objectives of reducing potential interactions between a meso-mammal predator and bobwhites during the nesting season. Meso-mammals recolonized habitat patches that were previously vacant in the subsequent year following cessation of trapping efforts, and patch use increased in these years. Thus, predator reduction, as done on our study areas, provides only temporary reduction in bobwhite-predator interactions, but ultimately leaves these meso-predators functioning within the greater ecosystem.

A few key methodological issues associated with scent station monitoring of meso-mammals were uncovered. First, scent stations provided low visitation rates, and ultimately, low rates of detection (i.e. the probability to detect an individual species given it is present). Adoption of longer sampling periods or entirely different techniques (e.g. camera traps) may be required to obtain a better reflection of meso-mammal activity patterns. Additionally, detection rates varied from year to year, suggesting caution should be used when assessing just simple scent station indices. We suggest incorporating imperfect detection (i.e. use of occupancy modeling). However, our raw scent station indices were correlated with occupancy rates, but varied considerably among sites. The raw index may be adequate for managers, but awareness of limitations of the index must be realized.

We have only just started the reevaluation process of predation within the modern landscape. Future work will need to focus on entire communities to understand the predation process. In the southeast, to understand the bobwhite predation process research will have to thoroughly evaluate the community, including alternative prey (e.g. cotton rats, other rodent, and songbirds) and the entire predator community (i.e. meso-mammals, snakes, ants, and raptors) with respect to interactions with the habitat. The key predators for bobwhites and their nests are generalist predators. These predators are not targeting bobwhite nests specifically, but rather in an opportunistic fashion. Studies have demonstrated increased survival and reproductive success of avian species with increased alternative food availability (Crabtree and Wolfe 1988, Marcström et al. 1988, Palmer and Wellendorf 2007). Thus, the role of alternative prey should be a primary focus of future predation studies. Additional focus should be placed on comparing how habitat characteristics in largely fragmented landscapes compare to areas with relatively little fragmentation in the Red Hills and Albany regions of northern Florida and southern Georgia.

The tools we use to manage predation issues for game species, as well as imperiled species, will require an understanding of the transformed predation process within our modern landscape. The bobwhite may serve as an umbrella species with which to understand predation on this landscape, while simultaneously being a species of focus for conservation efforts that could benefit many other species coexisting in these habitats. Our management efforts related to predation may require both direct and indirect manipulations of the predator community to meet landowner and public objectives across the altered landscape. The field of wildlife management has seen many periods of shifting perspectives ranging from overexploitation to restoration to complete environmental protection. The era of human dimensions is upon us, and we will see shifting paradigms in management necessary to mitigate human-wildlife conflicts, requiring adjusting our tools and being able to quantify their influences to mitigate the effects of a human-altered ecosystem on wildlife populations. This era will require extensive reevaluations of the underlying biological interactions and processes driving ecosystems, and the predation process will continue to be a key focus for wildlife ecologists and managers as this landscape continues to change.

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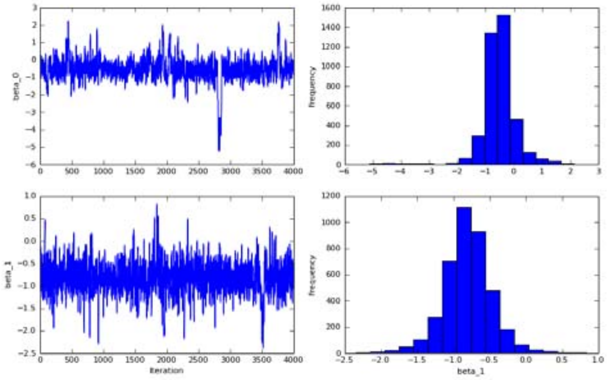
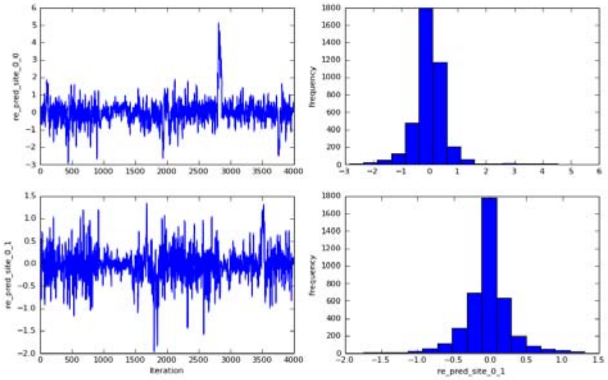
APPENDIX A

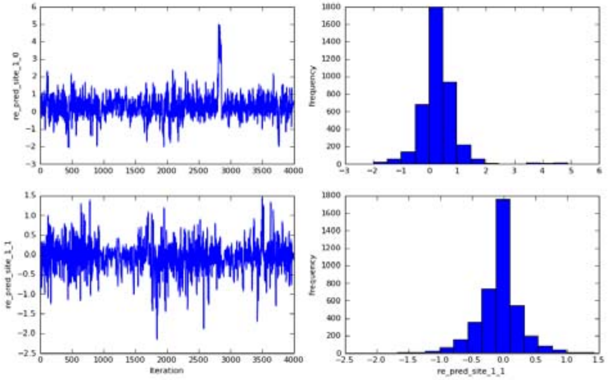
TRACE AND POSTERIOR DISTRIBUTIONS FOR CHAPTER 2 MODELS



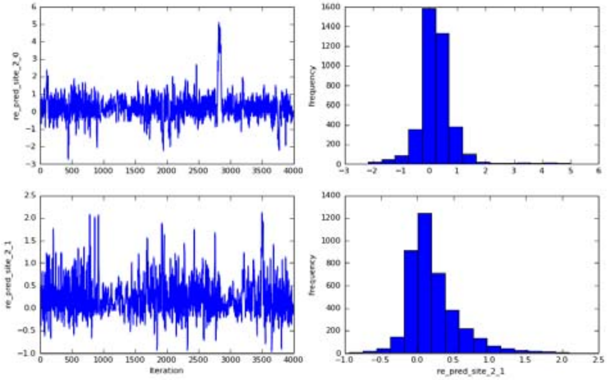
(a) Intercept



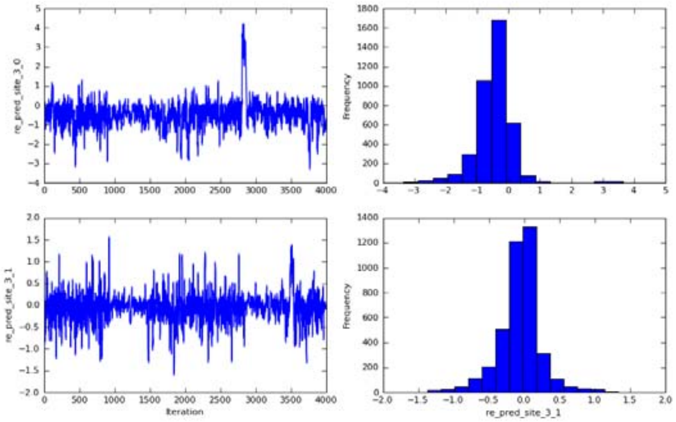
(b) Random effect of site – Pinebloom West



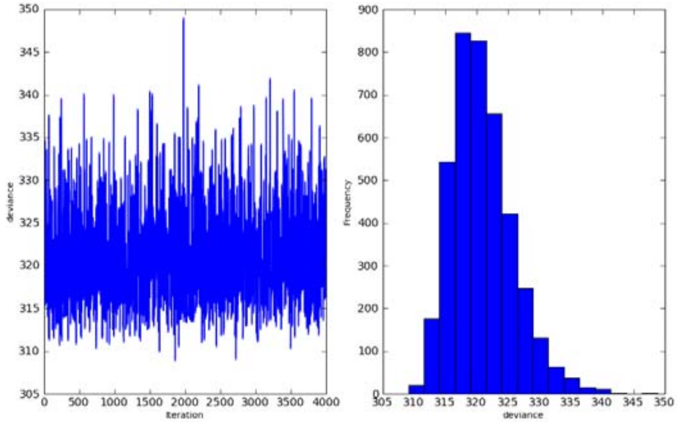
(c) Random effect of site – Pebble Hill



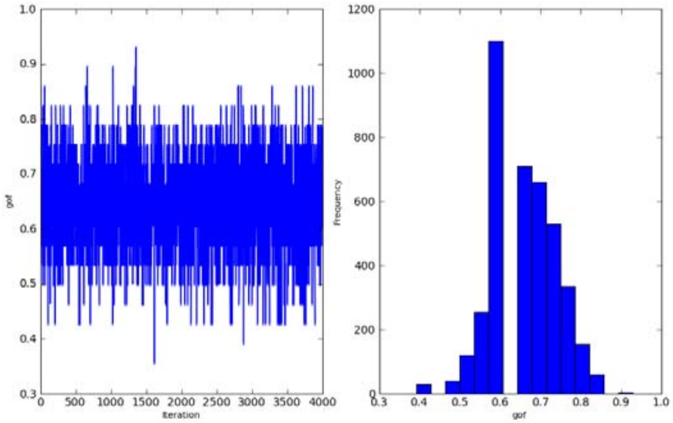
(d) Random effect of site – Pebble Hill



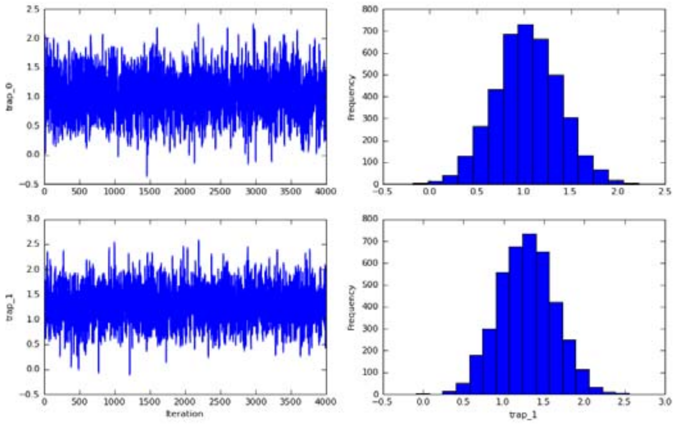
(e) Random effect of site for – Tall Timbers



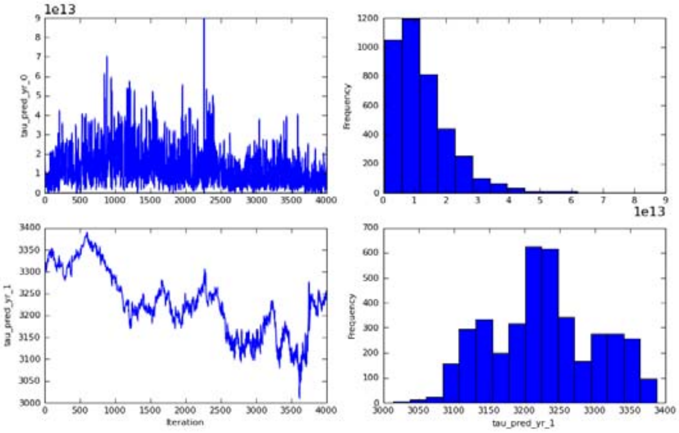
(f) Deviance



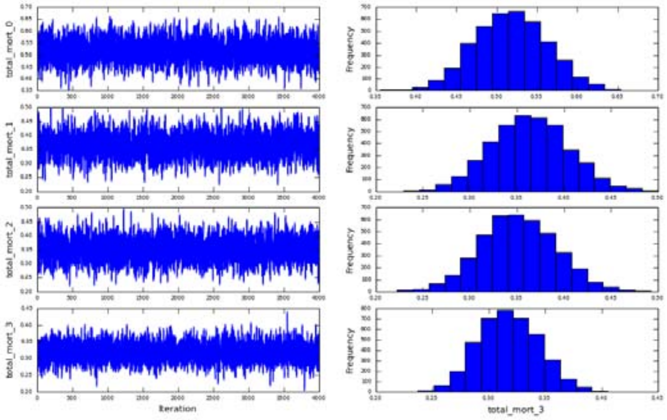
(g) Goodness-of-fit



(h) Trap effect

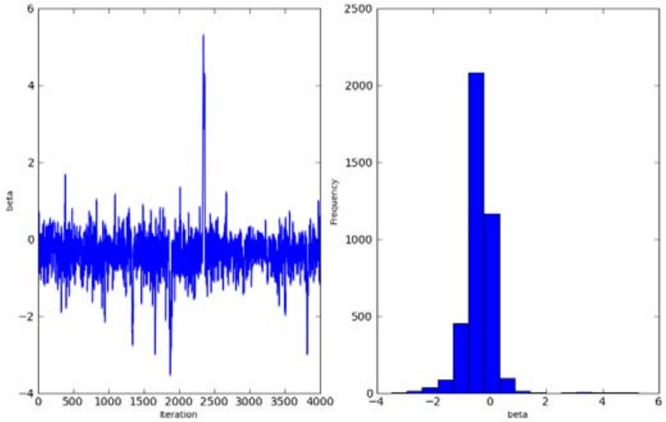


(i) Precision for the year random effect

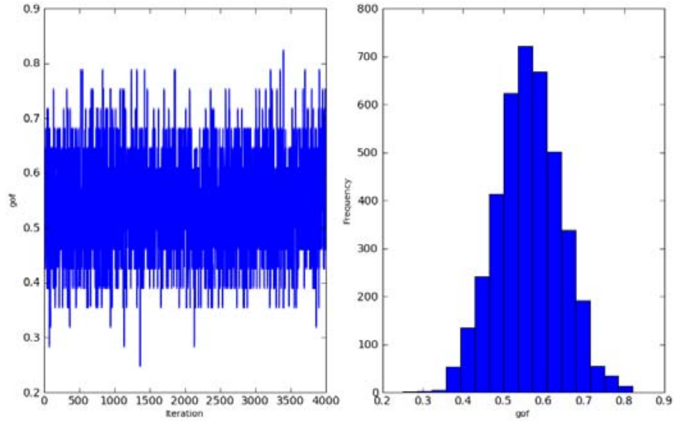


(j) Total mortality for the 4 sites (From top to bottom: Pinebloom West, Pinebloom East, Pebble Hill, and Tall Timbers).

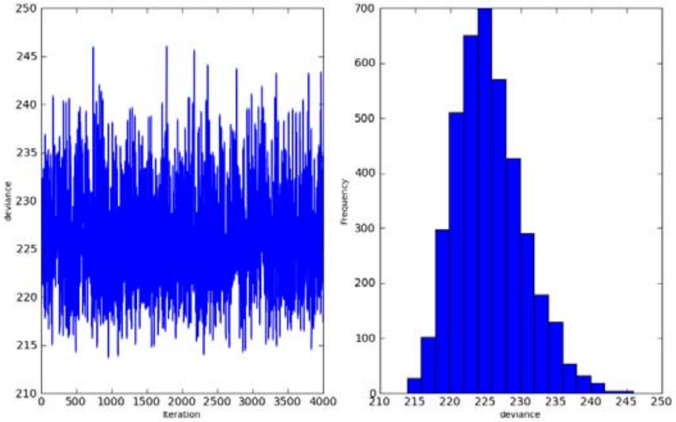
Figure A.2.1: Traces and posterior distributions for the top 3-failure cause (meso-mammal, snake, and other) model with site-specific compensation and a trap effect after 1 million MCMC iterations (burn-in = 800,000, thin = 50).



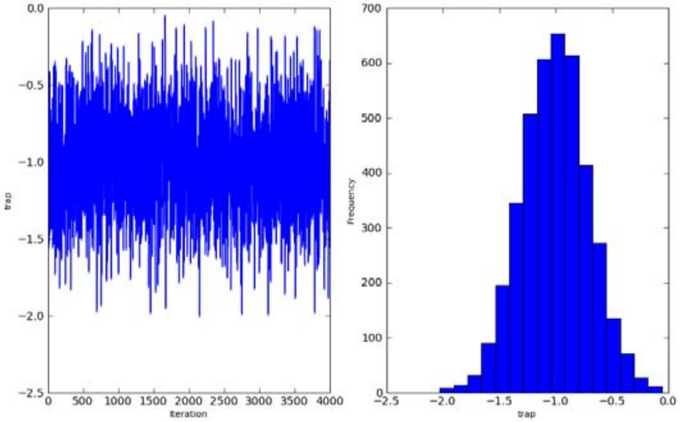
(a) Intercept



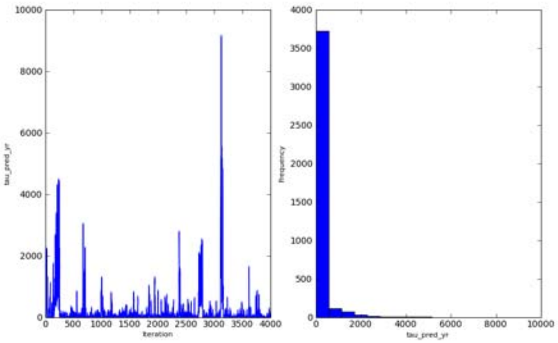
(b) Goodness-of-fit



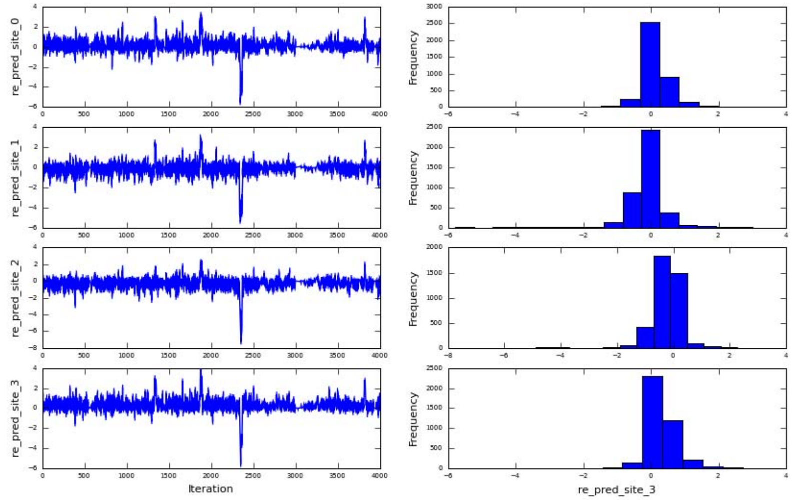
(c) Deviance



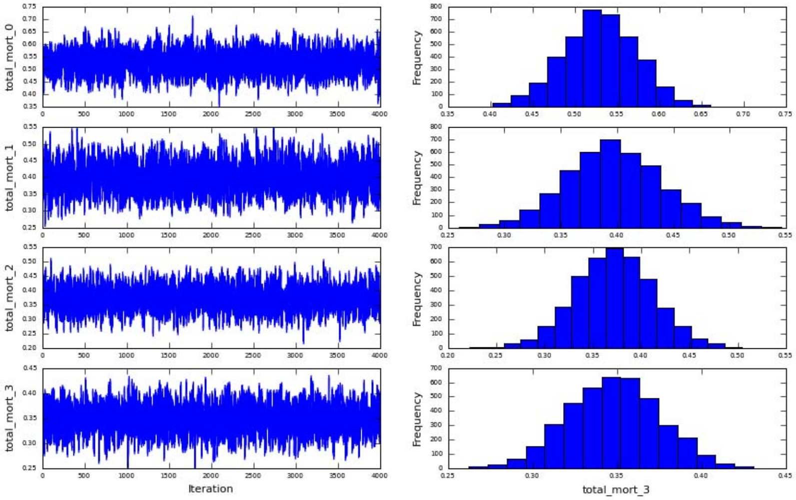
(d) Trap Effect



(e) Precision for random effect of year



(f) Random effect for the 4 sites (From top to bottom: Pinebloom West, Pinebloom East, Pebble Hill, and Tall Timbers).



(g) Total mortality by site (From top to bottom: Pinebloom West, Pinebloom East, Pebble Hill, and Tall Timbers)

Figure A.2.2: Trace and posterior distributions for the top 2-failure cause model (meso-mammal and other) with site-specific compensation and a trap effect after 1 million MCMC iterations (burn-in = 800,000, thin = 50).

APPENDIX B

CHAPTER 3 ADDITIONAL TABLES AND FIGURES FROM LANDSCAPE FEATURES ANALYSIS

Appendix B.3.1: Model selection using AICc to examine landscape features influencing the probability of Northern Bobwhite nest failure at the 3.1-ha scale at study areas located in northern Florida and southern Georgia, 2000-2006.

Model	**K**	**AIC_c**	**ΔAIC_c**	**Weight**
Int + Hardwood_Dist	2	915.05	0.00	0.557
Int + Hardwood_Dist + Field_Dist	3	916.96	1.91	0.215
Int + Wetland_Dist + Hardwood_Dist + Feed_Dist + Road_Dist	5	919.52	4.47	0.060
Int + Wetland_Comp	2	920.20	5.15	0.042
Int + Wetland_Dist	2	921.29	6.24	0.025
Int + Hardwood_Comp + Wetland_Comp	3	922.18	7.13	0.016
Int + Road_Dist	2	922.31	7.26	0.015
Int + EdgeDensity	2	922.59	7.54	0.013
Int + Field_Comp	2	922.76	7.71	0.012
Int + Hardwood_Comp	2	922.77	7.72	0.012
Int + Feed_Dist	2	922.78	7.73	0.012
Global Model	9	923.55	8.50	0.008
Int + Hardwood_Comp + Wetland_Comp + Field_Comp	4	924.10	9.05	0.006
Int + Feed_Dist + Road_Dist	3	924.33	9.27	0.005
Int + Field_Comp + Feed_Dist	3	924.79	9.73	0.004

Appendix B.3.2: Model-averaged parameter estimates of coefficients of landscape features influencing the probability of Northern Bobwhite nest failure at the 3.1-ha scale on study areas located in northern Florida and southern Georgia, 2000-2006. Odds ratios were scaled to biologically meaningful values for management.

Parameter	**Estimate**	**SE**	**95% LCI**	**95% UCI**	**Unit Scalar**	**Scaled Odds Ratio**	**Scaled LCI**	**95% UCI**
Intercept	-0.4564	0.1415	-0.7338	-0.1791				
Hardwood Composition	0.0002	0.0073	-0.0141	0.0146	10%	1.002	0.8685	1.1571
Wetland Composition	0.0128	0.0085	-0.0038	0.0295	10%	1.137	0.9627	1.3425
Field Composition	0.0029	0.0081	-0.0130	0.0187	10%	1.029	0.8783	1.2053
Wetland Distance	-0.0001	0.0003	-0.0007	0.0005	50 m	0.995	0.9671	1.0228
Hardwood Distance	0.0004	0.0002	0.0001	0.0007	50 m	1.022	1.0055	1.0377
Feedline Distance	0.0001	0.0002	-0.0003	0.0004	50 m	1.004	0.9866	1.0207
Road Distance	-0.0013	0.0015	-0.0043	0.0016	50 m	0.936	0.8073	1.0838
Edge Density	-0.0007	0.0008	-0.0023	0.0010	1	0.999	0.9978	1.0010

Appendix B.3.3: Model selection using AICc to examine landscape features influencing the probability of Northern Bobwhite nest failure at the 19.6-ha scale on study areas located in northern Florida and southern Georgia, 2000-2006.

Model	K	AIC_c	ΔAIC_c	Weight
Int + Hardwood_Dist	2	915.05	0.00	0.549
Int + Hardwood_Dist + Field_Dist	3	916.96	1.91	0.212
Int + Wetland_Dist + Hardwood_Dist + Feed_Dist + Road_Dist	5	919.52	4.47	0.059
Int + Wetland_Comp	2	920.65	5.59	0.033
Int + Field_Comp	2	920.71	5.65	0.032
Int + Wetland_Dist	2	921.29	6.24	0.024
Int + Road_Dist	2	922.31	7.26	0.015
Int + Hardwood_Comp + Wetland_Comp	3	922.67	7.62	0.012
Int + Field_Comp + Feed_Dist	3	922.70	7.65	0.012
Int + Feed_Dist	2	922.78	7.73	0.012
Int + EdgeDensity	2	922.78	7.73	0.012
Int + Hardwood_Comp	2	922.78	7.73	0.012
Int + Hardwood_Comp + Wetland_Comp + Field_Comp	4	923.19	8.14	0.009
Int + Feed_Dist + Road_Dist	3	924.33	9.27	0.005
Global Model	9	925.30	10.25	0.003

Appendix B.3.4: Model-averaged parameter estimates for the coefficients of landscape feature influencing the probability of Northern Bobwhite nest failure at the 19.6-ha scale on study areas located in northern Florida and southern Georgia, 2000-2006. Odds ratios were scaled to biologically meaningful values for management.

Parameter	Estimate	SE	95% LCI	95% UCI	Unit Scalar	Scaled Odds Ratio	Scaled LCI	95% UCI
Intercept	-0.4537	0.1455	-0.7388	-0.1685				
Hardwood Composition	0.0006	0.0076	-0.0144	0.0156	10%	1.0061	0.8662	1.1685
Wetland Composition	0.0087	0.0067	-0.0046	0.0219	10%	1.0904	0.9555	1.2443
Field Composition	-0.0160	0.0118	-0.0392	0.0072	10%	0.8518	0.6755	1.0741
Wetland Distance	-0.0001	0.0003	-0.0007	0.0005	50 m	0.9945	0.9671	1.0228
Hardwood Distance	0.0004	0.0002	0.0001	0.0007	50 m	1.0217	1.0055	1.0377
Feedline Distance	0.0001	0.0002	-0.0003	0.0004	50 m	1.0040	0.9876	1.0207
Road Distance	-0.0012	0.0014	-0.0039	0.0016	50 m	0.9436	0.8228	1.0827
Edge Density	0.0000	0.0011	-0.0022	0.0021	1	1.0000	0.9979	1.0021

Appendix B.3.5: Model selection using AICc to examine landscape features influencing the probability of Northern Bobwhite nest failure at the 50.3-ha scale on study areas located in northern Florida and southern Georgia, 2000-2006.

Model	**K**	**AIC_c**	**ΔAIC_c**	**Weight**
Int + Field_Comp + Field_Dist	3	914.52	0.00	0.455
Int + Hardwood_Dist	2	915.05	0.53	0.349
Int + Field_Dist + Hardwood_Dist + Feed_Dist + Road_Dist	5	919.05	4.53	0.047
Int + Field_Comp	2	919.37	4.85	0.040
Int + Field_Dist	2	921.25	6.73	0.016
Int + Field_Comp + Feed_Dist	3	921.29	6.77	0.015
Int + Wetland_Comp	2	921.47	6.95	0.014
Global Model	9	921.60	7.08	0.013
Int + Road_Dist	2	922.31	7.79	0.009
Int + Hardwood_Comp	2	922.41	7.88	0.009
Int + Hardwood_Comp + Wetland_Comp + Field_Comp	4	922.47	7.95	0.009
Int + EdgeDensity	2	922.77	8.24	0.007
Int + Feed_Dist	2	922.78	8.26	0.007
Int + Hardwood_Comp + Wetland_Comp	3	923.22	8.70	0.006
Int + Feed_Dist + Road_Dist	3	924.33	9.80	0.003

Appendix B.3.6: Model-averaged parameter estimates for the coefficients of landscape feature influencing the probability of Northern Bobwhite nest failure at the 50.3-ha scale on study sites located in northern Florida and southern Georgia, 2000-2006. Odds ratios were scaled to biologically meaningful values for management.

Parameter	**Estimate**	**SE**	**95% LCI**	**95% UCI**	**Unit Scalar**	**Scaled Odds Ratio**	**Scaled LCI**	**95% UCI**
Intercept	-0.1000	0.3982	-0.8804	0.6805				
Hardwood Composition	-0.0005	0.0095	-0.0190	0.0181	10%	0.9954	0.8269	1.1982
Wetland Composition	0.0039	0.0074	-0.0106	0.0184	10%	1.0396	0.8996	1.2014
Field Composition	-0.0497	0.0196	-0.0881	-0.0114	10%	0.6083	0.4145	0.8926
Hardwood Distance	0.0004	0.0002	0.0001	0.0008	50 m	1.0219	1.0060	1.0382
Field Distance	-0.0021	0.0010	-0.0041	-0.0001	50 m	0.8999	0.8155	0.9930
Feedline Distance	0.0001	0.0002	-0.0002	0.0004	50 m	1.0049	0.9886	1.0217
Road Distance	-0.0010	0.0014	-0.0038	0.0018	50 m	0.9509	0.8274	1.0931
Edge Density	0.0003	0.0017	-0.0030	0.0035	1	1.0003	0.9970	1.0035

Appendix B.3.7: Model selection using AICc to examine landscape features influencing the probability of Northern Bobwhite nest failure at the 176.7-ha scale on study sites located in northern Florida and southern Georgia, 2000-2006.

Model	**K**	**AIC$_c$**	**ΔAIC$_c$**	**Weight**
Int + Field_Dist + Field_Comp	3	916.97	0.00	0.367
Int + Field_Comp	2	918.88	1.91	0.141
Int + Wetland_Comp	2	919.18	2.21	0.122
Int + Hardwood_Comp + Wetland_Comp + Field_Comp	4	920.58	3.61	0.060
Int + Field_Comp + Feed_Dist	3	920.65	3.68	0.058
Int + EdgeDensity	2	920.89	3.92	0.052
Int + Hardwood_Comp + Wetland_Comp	3	920.95	3.97	0.050
Int + Field_DIST	2	921.25	4.28	0.043
Int + Hardwood_Comp	2	921.68	4.71	0.035
Int + Road_Dist	2	922.31	5.34	0.025
Int + Feed_Dist	2	922.78	5.81	0.020
Global Model	8	924.17	7.19	0.010
Int + Feed_Dist + Road_Dist	3	924.33	7.35	0.009
Int + Field_Dist + Feed_Dist + Road_Dist	4	924.91	7.94	0.007

Appendix B.3.8: Model-averaged parameter estimates for coefficients of landscape features influencing the probability of Northern Bobwhite nest failure at the 176.7-ha scale on study sites located in northern Florida and southern Georgia, 2000-2006. Odds ratios were scaled to biologically meaningful values for management.

Parameter	**Estimate**	**SE**	**95% LCI**	**95% UCI**	**Unit Scalar**	**Scaled Odds Ratio**	**Scaled LCI**	**95% UCI**
Intercept	-0.0349	0.3171	-0.6564	0.5866				
Hardwood Composition	-0.0046	0.0097	-0.0236	0.0143	10%	0.9546	0.7896	1.1541
Wetland Composition	0.0097	0.0060	-0.0020	0.0215	10%	1.1020	0.9798	1.2395
Field Composition	-0.0548	0.0260	-0.1058	-0.0038	10%	0.5780	0.3470	0.9626
Field Distance	-0.0015	0.0008	-0.0031	0.0001	50 m	0.9280	0.8560	1.0055
Feedline Distance	0.0001	0.0002	-0.0003	0.0004	50 m	1.0025	0.9866	1.0187
Road Distance	-0.0010	0.0014	-0.0037	0.0018	50 m	0.9528	0.8319	1.0914
Edge Density	-0.0023	0.0019	-0.0059	0.0013	1	0.9977	0.9941	1.0013

Appendix B.3.9: Model selection using AICc to examine landscape features influencing the probability of failure by specific predators (meso-mammals, snakes, ants, other) at Northern Bobwhite nests at the 3.1-ha scale on study sites located in northern Florida and southern Georgia, 2000-2006.

Model	AIC	ΔAIC	Weight
Int + Field_Comp	549.75	0.00	0.659
Int + Field_Comp + Feed_Dist	551.97	2.22	0.217
Int + Hardwood_Comp	556.10	6.35	0.027
Int + Feed_Dist	556.29	6.54	0.025
Int + Hardwood_Comp + Wetland_Comp + Field_Comp	556.30	6.55	0.025
Int + EdgeDensity	556.78	7.04	0.020
Int + Wetland_Dist	558.71	8.97	0.007
Int + Hardwood_Dist	559.13	9.38	0.006
Int + Wetland_Comp	559.73	9.98	0.004
Int + Road_Dist	559.93	10.19	0.004
Int + Hardwood_Comp + Wetland_Comp	560.58	10.83	0.003
Int + Feed_Dist + Road_Dist	561.65	11.90	0.002
Int + Hardwood_Dist + Wetland_Dist	563.78	14.03	0.001
Int + Wetland_Dist + Hardwood_Dist + Feed_Dist + Road_Dist	570.01	20.27	0.000
Global	573.07	23.32	0.000

Appendix B.3.10: Model-averaged parameter estimates for the coefficients of landscape features influencing the probability of Northern Bobwhite nest failures by specific predators (meso-mammals, snakes, ants, and other) at the 3.1-ha scale on sites located in northern Florida and southern Georgia, 2000-2006. Odds ratios were scaled to biologically meaningful values for management.

Parameter	Estimate	SE	LCI	UCI	Unit Scalar	Scaled Odds Ratio	Scaled LCI	95% UCI
Intercept[1]	-0.816	8.624	-17.720	16.088				
Intercept[2]	-1.510	9.872	-20.860	17.839				
Intercept[3]	-0.395	4.833	-9.867	9.077				
Hardwood Composition[1]	0.003	0.081	-0.156	0.163	10%	1.034	0.210	5.097
Hardwood Composition[2]	0.032	0.075	-0.115	0.178	10%	1.372	0.316	5.958
Hardwood Composition[3]	-0.006	0.070	-0.144	0.132	10%	0.944	0.238	3.754
Wetland Composition[1]	0.003	0.065	-0.125	0.131	10%	1.030	0.286	3.702
Wetland Composition[2]	-0.019	0.109	-0.234	0.195	10%	0.823	0.096	7.033
Wetland Composition[3]	0.002	0.056	-0.108	0.113	10%	1.022	0.339	3.083
Field Composition[1]	-0.077	0.206	-0.480	0.326	10%	0.462	0.008	26.050

Field Composition[2]	0.026	0.099	-0.168	0.221	10%	1.301	0.186	9.105
Field Composition[3]	0.010	0.065	-0.118	0.138	10%	1.105	0.307	3.984
Edge Density[1]	0.001	0.005	-0.008	0.011	1	1.001	0.992	1.011
Edge Density[2]	0.003	0.005	-0.007	0.013	1	1.003	0.993	1.013
Edge Density[3]	0.000	0.003	-0.006	0.006	1	1.000	0.994	1.006
Wetland Distance[1]	0.000	0.003	-0.007	0.007	50 m	0.999	0.721	1.385
Wetland Distance[2]	0.000	0.004	-0.007	0.007	50 m	1.008	0.701	1.450
Wetland Distance[3]	-0.001	0.003	-0.006	0.004	50 m	0.966	0.753	1.239
Feedline Distance[1]	0.000	0.003	-0.005	0.005	50 m	1.002	0.780	1.288
Feedline Distance[2]	0.001	0.002	-0.004	0.005	50 m	1.036	0.823	1.303
Feedline Distance[3]	0.000	0.002	-0.003	0.004	50 m	1.005	0.848	1.192
Road Distance[1]	-0.003	0.022	-0.046	0.039	50 m	0.843	0.100	7.068
Road Distance[2]	-0.002	0.024	-0.049	0.045	50 m	0.901	0.087	9.292
Road Distance[3]	0.000	0.014	-0.027	0.027	50 m	0.995	0.256	3.869
Hardwood Distance[1]	0.000	0.002	-0.003	0.003	50 m	1.012	0.861	1.189
Hardwood Distance[2]	0.000	0.002	-0.005	0.004	50 m	0.992	0.791	1.245

Hardwood Distance[3]	0.000	0.001	-0.002	0.003	50 m	1.012	0.895	1.144

[1] Other nest failure causes relative to meso-mammals depredations.

[2] Nest failures due to ants relative to meso-mammals depredations.

[3] Nest failures due to snakes relative to meso-mammal depredations.

Appendix B.3.11: Model selection using AICc to examine landscape features influencing the probability of Northern Bobwhite nest failures by specific predators (meso-mammals, snakes, ants, other) at the 19.6-ha scale on study sites in northern Florida and southern Georgia, 2000-2006.

Model	**AIC**	**ΔAIC**	**Weight**
Int + Feed_Dist	556.30	0.00	0.239
Int + Field_Comp	556.57	0.27	0.209
Int + Hardwood_Comp	556.90	1.00	0.145
Int + Wetland_Dist	558.71	2.41	0.071
Int + EdgeDensity	558.95	2.00	0.088
Int + Field_Comp + Feed_Dist	558.99	2.69	0.062
Int + Hardwood_Dist	559.13	3.00	0.053
Int + Road_Dist	559.93	3.63	0.039
Int + Wetland_Comp	560.14	4.00	0.032
Int + Feed_Dist + Road_Dist	561.65	5.35	0.016
Int + Hardwood_Comp + Wetland_Comp	562.29	5.00	0.020
Int + Hardwood_Dist + Wetland_Dist	563.78	7.48	0.006
Int + Hardwood_Comp + Wetland_Comp + Field_Comp	564.27	6.00	0.012
Int + Wetland_Dist + Hardwood_Dist + Feed_Dist + Road_Dist	570.01	13.71	0.000
Global	582.58	7.00	0.007

Appendix B.3.12: Model-averaged parameter estimates for the coefficients of landscape features influencing the probability of Northern Bobwhite nest failures by specific predators (meso-mammals, snakes, ants, and other) at the 19.6-ha scale on sites located in northern Florida and southern Georgia, 2000-2006.

Parameter	Estimate	SE	LCI	UCI	Unit Scalar	Scaled Odds Ratio	Scaled LCI	95 % UCI
Intercept[1]	-1.079	8.419	-17.580	15.422				
Intercept[2]	-1.327	8.651	-18.282	15.628				
Intercept[3]	-0.228	6.077	-12.139	11.683				
Hardwood Composition[1]	0.003	0.081	-0.155	0.160	10%	1.027	0.212	4.977
Hardwood Composition[2]	0.028	0.072	-0.112	0.169	10%	1.329	0.326	5.414
Hardwood Composition[3]	-0.006	0.064	-0.130	0.119	10%	0.946	0.271	3.301
Wetland Composition[1]	0.010	0.063	-0.113	0.134	10%	1.106	0.322	3.801
Wetland Composition[2]	0.006	0.068	-0.127	0.138	10%	1.060	0.282	3.987
Wetland Composition[3]	-0.002	0.060	-0.120	0.116	10%	0.983	0.301	3.206
Field Composition[1]	-0.059	0.173	-0.397	0.280	10%	0.555	0.019	16.380

Field Composition^2	0.025	0.143	-0.254	0.305	10%	1.290	0.079	21.126
Field Composition^3	-0.018	0.114	-0.241	0.206	10%	0.839	0.090	7.831
Wetland Distance^1	0.000	0.003	-0.007	0.007	50 m	1.003	0.712	1.412
Wetland Distance^2	0.000	0.003	-0.007	0.007	50 m	1.011	0.718	1.422
Wetland Distance^3	0.000	0.004	-0.007	0.007	50 m	1.000	0.696	1.439
Hardwood Distance^1	0.000	0.002	-0.003	0.003	50 m	1.012	0.861	1.189
Hardwood Distance^3	0.000	0.002	-0.005	0.005	50 m	0.997	0.784	1.268
Hardwood Distance^3	0.000	0.001	-0.002	0.003	50 m	1.013	0.894	1.147
Feedline Distance^1	0.000	0.003	-0.005	0.005	50 m	1.004	0.784	1.285
Feedline Distance^2	0.001	0.002	-0.004	0.005	50 m	1.038	0.837	1.288
Feedline Distance^3	0.000	0.002	-0.004	0.005	50 m	1.006	0.799	1.267
Road Distance^1	-0.003	0.019	-0.041	0.034	50 m	0.848	0.129	5.561
Road Distance^2	-0.002	0.019	-0.040	0.036	50 m	0.899	0.136	5.917
Road Distance^3	0.000	0.013	-0.026	0.025	50 m	0.992	0.276	3.565
Edge Density^1	0.001	0.009	-0.016	0.018	1	1.001	0.984	1.019
Edge Density^2	-0.003	0.007	-0.017	0.011	1	0.997	0.983	1.011

Edge Density[3]	-0.002	0.006	-0.013	0.009	1	0.998	0.987	1.009

[1] Other nest failure causes relative to meso-mammals depredations.

[2] Nest failures due to ants relative to meso-mammals depredations.

[3] Nest failures due to snakes relative to meso-mammal depredations.

Appendix B.3.13: Model selection using AICc to examine landscape features influencing the probability of Northern Bobwhite nest failure by specific predators (meso-mammals, snakes, ants, other) at the 50.3-ha scale on study sites located in northern Florida and southern Georgia, 2000-2006.

Model	**AIC**	**ΔAIC**	**Weight**
Int + Feed_Dist	556.30	0.00	0.265
Int + Hardwood_Comp	556.91	0.61	0.195
Int + Field_Comp	557.51	1.21	0.145
Int + Field_Dist	558.69	2.39	0.080
Int + Hardwood_Dist	559.13	2.83	0.064
Int + Field_Comp + Feed_Dist	559.19	2.89	0.063
Int + EdgeDensity	559.61	3.31	0.051
Int + Wetland_Comp	559.86	3.56	0.045
Int + Road_Dist	559.93	3.63	0.043
Int + Feed_Dist + Road_Dist	561.65	5.35	0.018
Int + Hardwood_Comp + Wetland_Comp	561.85	5.55	0.017
Int + Field_Comp + Field_Dist	562.67	6.38	0.011
Int + Hardwood_Comp + Wetland_Comp + Field_Comp	564.98	8.68	0.003
Int + Field_Dist + Hardwood_Dist + Feed_Dist + Road_Dist	569.26	12.96	0.000
Global	590.52	34.23	0.000

Appendix B.3.14: Model-averaged parameter estimates for the coefficients of landscape features influencing the probability of Northern Bobwhite nest failures by specific predators (meso-mammals, snakes, ants, and other) at the 50.3-ha scale on sites located in northern Florida and southern Georgia, 2000-2006. Coefficients were backtransformed to odds ratios scaled to biologically meaningful values for management.

Parameter	Estimate	SE	LCI	UCI	Unit Scalar	Scaled Odds Ratio	Scaled LCI	95% UCI
Intercept[1]	-1.009	8.682	-18.026	16.008				
Intercept[2]	-1.324	8.792	-18.556	15.908				
Intercept[3]	-0.287	5.905	-11.861	11.287				
Hardwood Composition[1]	-0.003	0.086	-0.172	0.166	10%	0.971	0.179	5.277
Hardwood Composition[2]	0.030	0.076	-0.119	0.178	10%	1.345	0.304	5.943
Hardwood Composition[3]	-0.005	0.066	-0.134	0.125	10%	0.956	0.263	3.477
Wetland Composition[1]	0.011	0.068	-0.122	0.144	10%	1.117	0.294	4.239
Wetland Composition[2]	0.013	0.069	-0.123	0.149	10%	1.139	0.292	4.440
Wetland Composition[3]	0.006	0.055	-0.101	0.113	10%	1.061	0.362	3.105

Field Composition[1]	-0.084	0.294	-0.659	0.492	10%	0.433	0.001	137.238
Field Composition[2]	-0.002	0.254	-0.501	0.497	10%	0.979	0.007	143.513
Field Composition[3]	-0.026	0.189	-0.397	0.346	10%	0.774	0.019	31.680
Hardwood Distance[1]	0.000	0.001	-0.003	0.003	50 m	1.012	0.881	1.161
Hardwood Distance[2]	0.000	0.002	-0.003	0.003	50 m	0.992	0.843	1.168
Hardwood Distance[3]	0.000	0.001	-0.002	0.002	50 m	1.013	0.918	1.118
Field Distance[1]	0.002	0.010	-0.017	0.022	50 m	1.120	0.425	2.948
Field Distance[2]	-0.001	0.011	-0.022	0.020	50 m	0.955	0.339	2.689
Field Distance[3]	0.000	0.008	-0.016	0.015	50 m	0.982	0.459	2.102
Feedline Distance[1]	0.000	0.002	-0.005	0.005	50 m	1.004	0.792	1.273
Feedline Distance[2]	0.001	0.002	-0.003	0.005	50 m	1.039	0.846	1.277
Feedline Distance[3]	0.000	0.002	-0.003	0.004	50 m	1.006	0.843	1.201
Road Distance[1]	-0.003	0.019	-0.041	0.034	50 m	0.842	0.131	5.424
Road Distance[2]	-0.002	0.019	-0.040	0.035	50 m	0.900	0.138	5.888
Road Distance[3]	0.000	0.013	-0.025	0.025	50 m	0.995	0.279	3.545
Edge Density[1]	-0.003	0.009	-0.021	0.016	1	0.997	0.979	1.016

Edge Density[2]	-0.003	0.011	-0.025	0.018	1	0.997	0.976	1.018
Edge Density[3]	-0.001	0.007	-0.014	0.013	1	0.999	0.986	1.013

[1] Other nest failure causes relative to meso-mammals depredations.

[2] Nest failures due to ants relative to meso-mammals depredations.

[3] Nest failures due to snakes relative to meso-mammal depredations.

Appendix B.3.15: Model selection using AICc to examine landscape features influencing the probability of Northern Bobwhite nest failures by specific predators (meso-mammals, snakes, ants, other) at the 176.7-ha scale on study sites located in northern Florida and southern Georgia, 2000-2006.

Model	AIC	ΔAIC	Weight
Int + Feed_Dist	556.30	0.00	0.341
Int + EdgeDensity	558.52	2.22	0.112
Int + Field_Comp	558.60	2.30	0.108
Int + Field_Dist	558.69	2.39	0.103
Int + Field_Comp + Feed_Dist	558.80	2.50	0.097
Int + Wetland_Comp	559.55	3.25	0.067
Int + Hardwood_Comp	559.65	3.35	0.064
Int + Road_Dist	559.93	3.63	0.055
Int + Feed_Dist + Road_Dist	561.65	5.35	0.023
Int + Field_Dist + Field_Comp	562.48	6.18	0.015
Int + Hardwood_Comp + Wetland_Comp	563.60	7.30	0.009
Int + Feed_Dist + Road_Dist + Field_Dist	565.61	9.31	0.003
Int + Hardwood_Comp + Wetland_Comp + Field_Comp	567.37	11.07	0.001
Global	583.96	27.66	0.000

Appendix B.3.16: Model-averaged parameter estimates for the coefficients of landscape features influencing the probability of Northern Bobwhite nest failures by specific predators (meso-mammals, snakes, ants, and other) at the 176.7-ha scale on sites located in northern Florida and southern Georgia, 2000-2006. Coefficients were backtransformed to odds ratios scaled to biologically important values for management.

Parameter	Estimate	SE	LCI	UCI	Unit Scalar	Scaled Odds Ratio	Scaled LCI	95% UCI
Intercept[1]	-0.960	9.137	-18.869	16.950				
Intercept[2]	-1.101	10.270	-21.230	19.029				
Intercept[3]	-0.198	7.011	-13.939	13.543				
Hardwood Composition[1]	-0.003	0.109	-0.216	0.210	10%	0.974	0.116	8.203
Hardwood Composition[2]	0.022	0.115	-0.203	0.246	10%	1.243	0.132	11.742
Hardwood Composition[3]	0.004	0.083	-0.159	0.167	10%	1.038	0.204	5.293
Wetland Composition[1]	-0.002	0.070	-0.139	0.136	10%	0.984	0.248	3.899
Wetland Composition[2]	0.012	0.070	-0.126	0.150	10%	1.126	0.284	4.467
Wetland Composition[3]	0.010	0.051	-0.090	0.109	10%	1.103	0.407	2.989
Field Composition[1]	-0.064	0.364	-0.777	0.648	10%	0.526	0.000	654.614

Field Composition[2]	-0.070	0.391	-0.836	0.696	10%	0.497	0.000	1053.153
Field Composition[3]	-0.074	0.273	-0.609	0.461	10%	0.477	0.002	100.451
Field Distance[1]	0.002	0.008	-0.014	0.019	50 m	1.127	0.491	2.587
Field Distance[2]	-0.001	0.010	-0.021	0.019	50 m	0.953	0.359	2.534
Field Distance[3]	0.000	0.007	-0.014	0.014	50 m	0.982	0.489	1.974
Feedline Distance[1]	0.000	0.002	-0.004	0.005	50 m	1.004	0.799	1.262
Feedline Distance[2]	0.001	0.002	-0.004	0.005	50 m	1.041	0.835	1.298
Feedline Distance[3]	0.000	0.002	-0.003	0.004	50 m	1.007	0.847	1.197
Road Distance[1]	-0.003	0.019	-0.040	0.033	50 m	0.842	0.135	5.250
Road Distance[2]	-0.002	0.019	-0.040	0.036	50 m	0.902	0.136	5.963
Road Distance[3]	0.000	0.013	-0.025	0.025	50 m	0.996	0.280	3.546
Edge Density[1]	-0.004	0.011	-0.025	0.018	1	0.996	0.975	1.018
Edge Density[2]	-0.007	0.014	-0.034	0.020	1	0.993	0.967	1.020
Edge Density[3]	-0.002	0.010	-0.022	0.017	1	0.998	0.979	1.018

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[1] Other nest failure causes relative to meso-mammals depredations.

[2] Nest failures due to ants relative to meso-mammals depredations.

[3] Nest failures due to snakes relative to meso-mammal depredations.

APPENDIX C

CHAPTER 4 OCCUPANCY MODELING ESTIMATE TABLES

The following tables present the full candidate models set examined and the model-averaged individual parameter estimates for the 6-species community occupancy model presented in Chapter 4.

Appendix C.4.1: Model selection table based upon Akaike's Information Criterion (AICc) for all 41 candidate models evaluating meso-mammal community occupancy (Ψ), local extinction (ε), and detection probability (p; where detection is different by year when denoted as p_t for t = 1 – 7 and constant across years when denoted as p) with respect to trapping efforts during 2000-2006 in southern Georgia and northern Florida. Table includes number of parameters (K), model weight (W_i), model likelihood (L_i), and deviance.

Model	**K**	**AICc**	**Δ AICc**	**W_i**	**L_i**	**Deviance**
Ψ(trap+region), ε(trap+region), p_t(sp + region)	57	7590.62	0.00	0.22	1.00	7475.54
Ψ(trap+region+sp), ε(trap+region), p_t(sp + region)	60	7590.98	0.36	0.19	0.84	7469.78
Ψ(trap), ε(trap), p_t(sp + region)	55	7591.39	0.76	0.15	0.68	7480.37
Ψ(trap+site), ε(trap), p_t(sp + region)	58	7592.08	1.46	0.11	0.48	7474.96
Ψ(trap+year), ε(trap+region), p_t(sp + region)	62	7592.47	1.85	0.09	0.40	7467.19
Ψ(trap+region+year), ε(trap+region), p_t(sp + region)	63	7592.74	2.12	0.08	0.35	7465.41
Ψ(trap), ε(trap+region), p_t(sp + region)	56	7592.82	2.20	0.07	0.33	7479.78
Ψ(trap+region), ε(trap+site), p_t(sp + region)	59	7594.41	3.78	0.03	0.15	7475.24
Ψ(trap+region), ε(trap), p_t(sp)	49	7594.65	4.03	0.03	0.13	7495.85
Ψ(trap), ε(trap+site), p_t(sp + region)	58	7596.59	5.97	0.01	0.05	7479.46

Appendix C.4.1 (continued)

Model	K	AICc	Δ AICc	W_i	L_i	Deviance
Ψ(trap+site), ε(trap), p_t(sp)	51	7597.33	6.71	0.01	0.04	7494.46
Ψ(trap+region), ε(trap+site), p_t(sp)	52	7599.75	9.12	0.00	0.01	7494.84
Ψ(trap+region), ε(region), p_t(sp + region)	54	7601.60	10.98	0.00	0.00	7492.62
Ψ(trap+region), ε(trap+sp), p_t(sp)	54	7602.36	11.74	0.00	0.00	7493.39
Ψ(trap+region), ε(site), p_t(sp + region)	56	7604.89	14.27	0.00	0.00	7491.84
Ψ(trap+sp), ε(trap), p_t(sp)	53	7605.40	14.78	0.00	0.00	7498.46
Ψ(trap+region), ε(.),p_t(sp)	46	7606.28	15.66	0.00	0.00	7513.57
Ψ(trap+region), ε(t), p_t(sp)	51	7609.57	18.95	0.00	0.00	7506.70
Ψ(trap), ε(.), p_t(sp)	45	7614.50	23.88	0.00	0.00	7523.83
Ψ(year), ε(trap+region), p_t(sp + region)	61	7635.21	44.58	0.00	0.00	7511.96
Ψ(region), ε(trap+region), p_t(sp + region)	56	7636.14	45.51	0.00	0.00	7523.09
Ψ(region), ε(trap+site), p_t(sp + region)	58	7639.25	48.63	0.00	0.00	7522.13
Ψ(.), ε(.), p_t(sp + region)	51	7639.61	48.99	0.00	0.00	7536.74

Appendix C.4.1 (continued)

Model	K	AICc	Δ AICc	W_i	L_i	Deviance
Ψ(sp), ε(trap), p_t(sp)	44	7641.25	50.63	0.00	0.00	7552.60
Ψ(sp), ε(trap+region), p_t(sp)	60	7641.97	51.35	0.00	0.00	7520.77
Ψ(site), ε(trap), p_t(sp)	50	7645.96	55.34	0.00	0.00	7545.12
Ψ(site+sp), ε(trap), p_t(sp)	55	7648.59	57.96	0.00	0.00	7537.57
Ψ(year), ε(trap), p_t(sp)	53	7648.69	58.07	0.00	0.00	7541.75
Ψ(.), ε(.), p_t(sp)	44	7651.19	60.57	0.00	0.00	7562.54
Ψ(.), ε(trap), p_t(sp)	47	7652.21	61.59	0.00	0.00	7557.47
Ψ(.), ε(site), p_t(sp)	47	7656.89	66.27	0.00	0.00	7562.15
Ψ(.), ε(site+trap), p_t(sp)	50	7657.29	66.66	0.00	0.00	7556.45
Ψ(.), ε(site+sp), p_t(sp)	52	7659.27	68.65	0.00	0.00	7554.36
Ψ(.), ε(site+trap+sp), p_t(sp)	55	7663.96	73.33	0.00	0.00	7552.94
Ψ(.), ε(.), p(sp+region)	9	7715.04	124.41	0.00	0.00	7697.01
Ψ(.), ε(.), p(sp)	8	7716.82	126.20	0.00	0.00	7700.80

Appendix C.4.1 (continued)

Model	K	AICc	Δ AICc	W_i	L_i	Deviance
Ψ(.), ε(.), p(sp+site)	11	7717.86	127.24	0.00	0.00	7695.82
Ψ(.), ε(.), p(site)	30	7913.83	323.20	0.00	0.00	7853.52
Ψ(.), ε(.), p_t(.)	9	8000.86	410.24	0.00	0.00	7982.83
Ψ(.), ε(.), p_t(t)	37	8015.61	424.99	0.00	0.00	7941.15
Ψ(.), ε(.), p (.)	3	8018.70	428.08	0.00	0.00	8012.70

Appendix C.4.2: Derived estimates of the recolonization with standard error (SE) and 95% confidence intervals (LCI, UCI) for 6 meso-mammal species at 4 study sites in southern Georgia and northern Florida during 2000-2006.

Site	Species	Year	Estimate	SE	LCI	UCI
PB West	Armadillo	2000-2001	0.283	0.112	0.118	0.539
		2001-2002	0.336	0.081	0.199	0.508
		2002-2003	0.341	0.092	0.188	0.536
		2003-2004	0.307	0.134	0.114	0.604
		2004-2005	0.223	0.092	0.092	0.450
		2005-2006	0.250	0.059	0.153	0.381
PB West	Raccoon	2000-2001	0.284	0.114	0.117	0.543
		2001-2002	0.336	0.083	0.196	0.513
		2002-2003	0.341	0.094	0.186	0.540
		2003-2004	0.307	0.137	0.112	0.609
		2004-2005	0.223	0.093	0.091	0.451
		2005-2006	0.250	0.059	0.152	0.382
PB West	Opossum	2000-2001	0.290	0.124	0.111	0.571
		2001-2002	0.343	0.094	0.188	0.540
		2002-2003	0.347	0.103	0.180	0.564
		2003-2004	0.316	0.151	0.106	0.644
		2004-2005	0.228	0.100	0.088	0.475
		2005-2006	0.255	0.069	0.144	0.410

Appendix C.4.2 (continued)

Site	Species	Year	Estimate	SE	LCI	UCI
PB West	Fox	2000-2001	0.236	0.128	0.071	0.554
		2001-2002	0.289	0.124	0.111	0.570
		2002-2003	0.294	0.133	0.106	0.594
		2003-2004	0.255	0.173	0.054	0.670
		2004-2005	0.187	0.103	0.057	0.466
		2005-2006	0.214	0.087	0.090	0.428
PB West	Bobcat	2000-2001	0.357	0.213	0.082	0.774
		2001-2002	0.410	0.178	0.141	0.746
		2002-2003	0.414	0.181	0.140	0.754
		2003-2004	0.437	0.302	0.065	0.896
		2004-2005	0.279	0.170	0.069	0.671
		2005-2006	0.306	0.145	0.104	0.626
PB West	Coyote	2000-2001	0.262	0.112	0.103	0.524
		2001-2002	0.315	0.093	0.164	0.518
		2002-2003	0.320	0.104	0.156	0.545
		2003-2004	0.278	0.150	0.082	0.624
		2004-2005	0.207	0.091	0.080	0.437
		2005-2006	0.234	0.064	0.131	0.380

Appendix C.4.2 (continued)

Site	Species	Year	Estimate	SE	LCI	UCI
PB East	Armadillo	2000-2001	0.234	0.107	0.087	0.495
		2001-2002	0.252	0.058	0.156	0.380
		2002-2003	0.258	0.067	0.149	0.409
		2003-2004	0.470	0.089	0.306	0.641
		2004-2005	0.253	0.156	0.063	0.631
		2005-2006	0.313	0.072	0.192	0.467
PB East	Raccoon	2000-2001	0.234	0.110	0.084	0.504
		2001-2002	0.252	0.058	0.155	0.381
		2002-2003	0.258	0.068	0.148	0.410
		2003-2004	0.470	0.089	0.306	0.641
		2004-2005	0.253	0.157	0.062	0.634
		2005-2006	0.313	0.074	0.189	0.473
PB East	Opossum	2000-2001	0.243	0.132	0.073	0.568
		2001-2002	0.257	0.068	0.147	0.409
		2002-2003	0.263	0.076	0.143	0.434
		2003-2004	0.473	0.087	0.312	0.640
		2004-2005	0.259	0.166	0.060	0.656
		2005-2006	0.320	0.087	0.177	0.507

Appendix C.4.2 (continued)

Site	Species	Year	Estimate	SE	LCI	UCI
PB East	Fox	2000-2001	0.181	0.125	0.041	0.535
		2001-2002	0.215	0.087	0.091	0.429
		2002-2003	0.222	0.096	0.087	0.459
		2003-2004	0.428	0.143	0.193	0.701
		2004-2005	0.206	0.159	0.037	0.636
		2005-2006	0.266	0.108	0.109	0.518
PB East	Bobcat	2000-2001	0.364	0.322	0.036	0.897
		2001-2002	0.308	0.143	0.107	0.625
		2002-2003	0.315	0.145	0.109	0.632
		2003-2004	0.500	0.091	0.328	0.672
		2004-2005	0.326	0.249	0.050	0.816
		2005-2006	0.387	0.184	0.122	0.742
PB East	Coyote	2000-2001	0.205	0.108	0.066	0.485
		2001-2002	0.235	0.063	0.134	0.381
		2002-2003	0.242	0.074	0.126	0.413
		2003-2004	0.456	0.102	0.272	0.652
		2004-2005	0.232	0.152	0.054	0.615
		2005-2006	0.292	0.079	0.163	0.467

Appendix C.4.2 (continued)

Site	Species	Year	Estimate	SE	LCI	UCI
TTRS	Armadillo	2000-2001	0.230	0.090	0.100	0.446
		2001-2002	0.278	0.082	0.147	0.462
		2002-2003	0.283	0.099	0.132	0.506
		2003-2004	0.224	0.132	0.061	0.561
		2004-2005	0.173	0.068	0.076	0.347
		2005-2006	0.196	0.045	0.122	0.300
TTRS	Raccoon	2000-2001	0.230	0.089	0.100	0.445
		2001-2002	0.278	0.082	0.148	0.461
		2002-2003	0.283	0.098	0.133	0.505
		2003-2004	0.224	0.132	0.061	0.560
		2004-2005	0.173	0.068	0.076	0.346
		2005-2006	0.196	0.044	0.123	0.297
TTRS	Opossum	2000-2001	0.235	0.096	0.097	0.468
		2001-2002	0.283	0.087	0.146	0.477
		2002-2003	0.288	0.102	0.132	0.519
		2003-2004	0.229	0.135	0.062	0.570
		2004-2005	0.176	0.071	0.076	0.359
		2005-2006	0.199	0.048	0.121	0.310

Appendix C.4.2 (continued)

Site	Species	Year	Estimate	SE	LCI	UCI
TTRS	Fox	2000-2001	0.194	0.103	0.062	0.467
		2001-2002	0.242	0.113	0.087	0.517
		2002-2003	0.247	0.127	0.079	0.556
		2003-2004	0.194	0.151	0.035	0.615
		2004-2005	0.148	0.081	0.047	0.381
		2005-2006	0.171	0.072	0.071	0.358
TTRS	Bobcat	2000-2001	0.286	0.167	0.075	0.667
		2001-2002	0.335	0.146	0.122	0.645
		2002-2003	0.340	0.154	0.118	0.664
		2003-2004	0.295	0.194	0.063	0.722
		2004-2005	0.211	0.113	0.066	0.503
		2005-2006	0.235	0.091	0.102	0.454
TTRS	Coyote	2000-2001	0.214	0.089	0.087	0.435
		2001-2002	0.262	0.091	0.124	0.471
		2002-2003	0.267	0.107	0.111	0.515
		2003-2004	0.208	0.139	0.048	0.579
		2004-2005	0.162	0.070	0.065	0.348
		2005-2006	0.185	0.053	0.102	0.313

Appendix C.4.2 (continued)

Site	Species	Year	Estimate	SE	LCI	UCI
PH	Armadillo	2000-2001	0.168	0.083	0.060	0.392
		2001-2002	0.202	0.052	0.118	0.323
		2002-2003	0.208	0.067	0.106	0.367
		2003-2004	0.404	0.094	0.241	0.593
		2004-2005	0.208	0.136	0.049	0.571
		2005-2006	0.262	0.073	0.146	0.426
PH	Raccoon	2000-2001	0.168	0.082	0.060	0.390
		2001-2002	0.202	0.051	0.119	0.321
		2002-2003	0.208	0.066	0.107	0.366
		2003-2004	0.405	0.093	0.241	0.592
		2004-2005	0.208	0.136	0.049	0.570
		2005-2006	0.263	0.072	0.146	0.425
PH	Opossum	2000-2001	0.173	0.090	0.058	0.419
		2001-2002	0.205	0.054	0.119	0.331
		2002-2003	0.211	0.068	0.108	0.374
		2003-2004	0.408	0.090	0.249	0.589
		2004-2005	0.213	0.142	0.049	0.587
		2005-2006	0.267	0.079	0.142	0.446

Appendix C.4.2 (continued)

Site	Species	Year	Estimate	SE	LCI	UCI
PH	Fox	2000-2001	0.138	0.094	0.033	0.430
		2001-2002	0.177	0.078	0.070	0.382
		2002-2003	0.183	0.090	0.064	0.423
		2003-2004	0.369	0.145	0.147	0.664
		2004-2005	0.172	0.140	0.029	0.588
		2005-2006	0.226	0.101	0.086	0.476
PH	Bobcat	2000-2001	0.239	0.187	0.041	0.701
		2001-2002	0.241	0.093	0.105	0.461
		2002-2003	0.247	0.099	0.103	0.482
		2003-2004	0.435	0.084	0.282	0.601
		2004-2005	0.264	0.203	0.044	0.735
		2005-2006	0.319	0.147	0.111	0.638
PH	Coyote	2000-2001	0.152	0.084	0.048	0.391
		2001-2002	0.191	0.061	0.098	0.337
		2002-2003	0.197	0.074	0.089	0.381
		2003-2004	0.391	0.110	0.207	0.613
		2004-2005	0.191	0.133	0.042	0.562
		2005-2006	0.246	0.079	0.124	0.430

Appendix C.4.3: Model-averaged beta estimates for detection probability in 2000 (*p*1) including the predictor, estimate, standard error, 95% confidence intervals of the estimate (LCI, UCI), the odds ratio, and the 95% confidence intervals of the odds ratio.

Parameter	Estimate	SE	LCI	UCI	Odds Ratio	95% LCI Odds Ratio	95% UCI Odds Ratio
Intercept	-2.963	2.992	-8.826	2.900			
Raccoon[1]	2.124	3.133	-4.016	8.265	8.367	0.018	3885.013
Opossum[1]	-0.055	3.858	-7.618	7.508	0.947	0.000	1821.885
Fox[1]	-1.064	6.112	-13.044	10.916	0.345	0.000	55051.739
Bobcat[1]	-0.886	4.729	-10.154	8.382	0.412	0.000	4368.550
Coyote[1]	-0.319	4.244	-8.637	7.999	0.727	0.000	2976.943
Region[2]	0.125	2.273	-4.330	4.580	1.133	0.013	97.480

[1] Species relative to armadillos

[2] Thomasville region is relative to Albany

Appendix C.4.4: Model-averaged beta estimates for detection probability in 2001 (*p*2) including the predictor, estimate, standard error, 95% confidence intervals of the estimate (LCI, UCI), the odds ratio, and the 95% confidence intervals of the odds ratio.

Parameter	Estimate	SE	LCI	UCI	Odds Ratio	95% LCI Odds Ratio	95% UCI Odds Ratio
Intercept	-3.382	4.095	-11.408	4.643			
Raccoon[1]	1.308	4.032	-6.594	9.210	3.699	0.001	9999.020
Opossum[1]	0.777	4.255	-7.563	9.118	2.175	0.001	9115.552
Fox[1]	-0.183	6.218	-12.370	12.004	0.833	0.000	163396.223
Bobcat[1]	0.277	4.399	-8.345	8.899	1.319	0.000	7324.185
Coyote[1]	-0.548	5.757	-11.832	10.737	0.578	0.000	46030.238
Region[2]	0.583	2.484	-4.286	5.453	1.792	0.014	233.370

[1] Species relative to armadillos

[2] Thomasville region is relative to Albany

Appendix C.4.5: Model-averaged beta estimates for detection probability in 2002 (*p*3) including the predictor, estimate, standard error, 95% confidence intervals of the estimate (LCI, UCI), the odds ratio, and the 95% confidence intervals of the odds ratio.

Parameter	**Estimate**	**SE**	**LCI**	**UCI**	**Odds Ratio**	**95% LCI Odds Ratio**	**95% UCI Odds Ratio**
Intercept	-2.697	3.098	-8.769	3.375			
Raccoon[1]	1.503	3.376	-5.115	8.120	4.494	0.006	3360.869
Opossum[1]	0.229	3.827	-7.271	7.729	1.258	0.001	2274.372
Fox[1]	-1.806	7.410	-16.330	12.718	0.164	0.000	333771.951
Bobcat[1]	-0.812	4.778	-10.177	8.552	0.444	0.000	5178.924
Coyote[1]	-0.662	4.695	-9.866	8.541	0.516	0.000	5118.066
Region[2]	0.085	2.574	-4.960	5.130	1.089	0.007	168.988

[1] Species relative to armadillos

[2] Thomasville region is relative to Albany

Appendix C.4.6: Model-averaged beta estimates for detection probability in 2003 (*p*4) including the predictor, estimate, standard error, 95% confidence intervals of the estimate (LCI, UCI), the odds ratio, and the 95% confidence intervals of the odds ratio.

Parameter	Estimate	SE	LCI	UCI	Odds Ratio	95% LCI Odds Ratio	95% UCI Odds Ratio
Intercept	-2.624	3.381	-9.249	4.002			
Raccoon[1]	1.047	3.717	-6.238	8.332	2.849	0.002	4152.781
Opossum[1]	0.748	3.767	-6.636	8.131	2.112	0.001	3399.133
Fox[1]	-0.413	5.299	-10.800	9.974	0.662	0.000	21455.756
Bobcat[1]	-0.929	5.399	-11.511	9.654	0.395	0.000	15580.819
Coyote[1]	0.196	4.053	-7.749	8.140	1.216	0.000	3429.861
Region[2]	-0.541	2.561	-5.561	4.480	0.582	0.004	88.206

[1] Species relative to armadillos

[2] Thomasville region is relative to Albany

Appendix C.4.7: Model-averaged beta estimates for detection probability in 2004 (*p*5) including the predictor, estimate, standard error, 95% confidence intervals of the estimate (LCI, UCI), the odds ratio, and the 95% confidence intervals of the odds ratio.

Parameter	Estimate	SE	LCI	UCI	Odds Ratio	95% LCI Odds Ratio	95% UCI Odds Ratio
Intercept	-2.440	3.216	-8.743	3.864			
Raccoon[1]	1.153	3.472	-5.652	7.959	3.168	0.004	2860.036
Opossum[1]	-0.529	4.378	-9.109	8.051	0.589	0.000	3135.639
Fox[1]	-1.342	6.319	-13.726	11.043	0.261	0.000	62484.443
Bobcat[1]	-0.280	4.420	-8.943	8.382	0.755	0.000	4366.960
Coyote[1]	-0.090	4.004	-7.938	7.758	0.914	0.000	2340.563
Region[2]	-0.566	2.693	-5.844	4.712	0.568	0.003	111.299

[1] Species relative to armadillos

[2] Thomasville region is relative to Albany

Appendix C.4.8: Model-averaged beta estimates for detection probability in 2005 (*p*6) including the predictor, estimate, standard error, 95% confidence intervals of the estimate (LCI, UCI), the odds ratio, and the 95% confidence intervals of the odds ratio.

Parameter	Estimate	SE	LCI	UCI	Odds Ratio	95% LCI Odds Ratio	95% UCI Odds Ratio
Intercept	-2.393	3.340	-8.939	4.153			
Raccoon[1]	0.139	3.817	-7.342	7.620	1.149	0.001	2039.451
Opossum[1]	-1.106	4.925	-10.759	8.548	0.331	0.000	5156.689
Fox[1]	-1.208	6.337	-13.628	11.212	0.299	0.000	73987.533
Bobcat[1]	-0.155	3.944	-7.885	7.576	0.857	0.000	1951.018
Coyote[1]	0.035	4.040	-7.883	7.953	1.036	0.000	2844.197
Region[2]	0.128	2.721	-5.206	5.462	1.137	0.005	235.591

[1] Species relative to armadillos

[2] Thomasville region is relative to Albany

Appendix C.4.9: Model-averaged beta estimates for detection probability in 2006 (*p*7) including the predictor, estimate, standard error, 95% confidence intervals of the estimate (LCI, UCI), the odds ratio, and the 95% confidence intervals of the odds ratio.

Parameter	**Estimate**	**SE**	**LCI**	**UCI**	**Odds Ratio**	**95% LCI Odds Ratio**	**95% UCI Odds Ratio**
Intercept	-2.139	2.891	-7.806	3.528			
Raccoon[1]	0.723	3.196	-5.542	6.988	2.060	0.004	1083.258
Opossum[1]	-1.087	4.166	-9.251	7.078	0.337	0.000	1185.545
Fox[1]	-1.806	6.459	-14.465	10.853	0.164	0.000	51711.093
Bobcat[1]	-1.364	4.506	-10.196	7.467	0.256	0.000	1750.100
Coyote[1]	-2.892	8.289	-19.139	13.354	0.055	0.000	630594.010
Region[2]	0.100	2.736	-5.262	5.462	1.105	0.005	235.590

[1] Species relative to armadillos

[2] Thomasville region is relative to Albany

Appendix C.4.10: Derived estimates for the rate-of-change in predator use with standard error (SE) and 95% confidence intervals (LCI, UCI) for 6 meso-mammal species at 4 study sites in southern Georgia and northern Florida during 2000-2006.

Site	**Species**	**Year**	**Trap**	**Estimate**	**SE**	**LCI**	**UCI**
PB West	Armadillo	2000-2001	N-N	0.971	0.078	0.122	1.000
		2001-2002	N-N	1.040	0.110	0.824	1.255
		2002-2003	N-N	1.015	0.064	0.888	1.141
		2003-2004	N-T	0.618	0.072	0.471	0.746
		2004-2005	T-T	0.938	0.148	0.092	1.000
		2005-2006	T-T	1.033	0.120	0.798	1.268
PB West	Raccoon	2000-2001	N-N	0.971	0.078	0.122	1.000
		2001-2002	N-N	1.040	0.110	0.824	1.255
		2002-2003	N-N	1.015	0.064	0.888	1.141
		2003-2004	N-T	0.618	0.072	0.471	0.746
		2004-2005	T-T	0.938	0.148	0.092	1.000
		2005-2006	T-T	1.033	0.120	0.798	1.268
PB West	Opossum	2000-2001	N-N	0.971	0.078	0.122	1.000
		2001-2002	N-N	1.040	0.110	0.824	1.255
		2002-2003	N-N	1.015	0.064	0.888	1.141
		2003-2004	N-T	0.620	0.074	0.469	0.751
		2004-2005	T-T	0.938	0.148	0.092	1.000
		2005-2006	T-T	1.033	0.120	0.798	1.268

Appendix C.4.10 (continued)

Site	Species	Year	Trap	Estimate	SE	LCI	UCI
PB West	Fox	2000-2001	N-N	0.971	0.078	0.122	1.000
		2001-2002	N-N	1.040	0.110	0.824	1.255
		2002-2003	N-N	1.015	0.064	0.888	1.141
		2003-2004	N-T	0.592	0.089	0.413	0.749
		2004-2005	T-T	0.938	0.148	0.092	1.000
		2005-2006	T-T	1.033	0.120	0.798	1.268
PB West	Bobcat	2000-2001	N-N	0.971	0.078	0.122	1.000
		2001-2002	N-N	1.040	0.110	0.824	1.255
		2002-2003	N-N	1.015	0.064	0.888	1.141
		2003-2004	N-T	0.639	0.085	0.462	0.784
		2004-2005	T-T	0.938	0.148	0.092	1.000
		2005-2006	T-T	1.033	0.120	0.798	1.268
PB West	Coyote	2000-2001	N-N	0.971	0.078	0.122	1.000
		2001-2002	N-N	1.040	0.110	0.824	1.255
		2002-2003	N-N	1.015	0.064	0.888	1.141
		2003-2004	N-T	0.608	0.075	0.456	0.742
		2004-2005	T-T	0.938	0.148	0.092	1.000
		2005-2006	T-T	1.033	0.120	0.798	1.268

Appendix C.4.10 (continued)

Site	Species	Year	Trap	Estimate	SE	LCI	UCI
PB East	Armadillo	2000-2001	N-T	0.581	0.074	0.432	0.716
		2001-2002	T-T	1.060	0.168	0.730	1.390
		2002-2003	T-T	1.023	0.104	0.819	1.227
		2003-2004	T-N	1.646	0.168	1.317	1.974
		2004-2005	N-N	0.955	0.109	0.128	1.000
		2005-2006	N-N	1.022	0.081	0.864	1.181
PB East	Raccoon	2000-2001	N-T	0.581	0.075	0.432	0.717
		2001-2002	T-T	1.060	0.168	0.730	1.390
		2002-2003	T-T	1.023	0.104	0.819	1.227
		2003-2004	T-N	1.646	0.169	1.315	1.976
		2004-2005	N-N	0.955	0.109	0.128	1.000
		2005-2006	N-N	1.022	0.081	0.864	1.181
PB East	Opossum	2000-2001	N-T	0.583	0.078	0.428	0.724
		2001-2002	T-T	1.060	0.168	0.730	1.390
		2002-2003	T-T	1.023	0.104	0.819	1.227
		2003-2004	T-N	1.640	0.174	1.298	1.981
		2004-2005	N-N	0.955	0.109	0.128	1.000
		2005-2006	N-N	1.022	0.081	0.864	1.181

Appendix C.4.10 (continued)

Site	Species	Year	Trap	Estimate	SE	LCI	UCI
PB East	Fox	2000-2001	N-T	0.555	0.080	0.398	0.702
		2001-2002	T-T	1.060	0.168	0.730	1.390
		2002-2003	T-T	1.023	0.104	0.819	1.227
		2003-2004	T-N	1.732	0.236	1.269	2.194
		2004-2005	N-N	0.955	0.109	0.128	1.000
		2005-2006	N-N	1.022	0.081	0.864	1.181
PB East	Bobcat	2000-2001	N-T	0.602	0.096	0.409	0.768
		2001-2002	T-T	1.060	0.168	0.730	1.390
		2002-2003	T-T	1.023	0.104	0.819	1.227
		2003-2004	T-N	1.600	0.202	1.205	1.995
		2004-2005	N-N	0.955	0.109	0.128	1.000
		2005-2006	N-N	1.022	0.081	0.864	1.181
PB East	Coyote	2000-2001	N-T	0.571	0.073	0.426	0.705
		2001-2002	T-T	1.060	0.168	0.730	1.390
		2002-2003	T-T	1.023	0.104	0.819	1.227
		2003-2004	T-N	1.673	0.176	1.329	2.018
		2004-2005	N-N	0.955	0.109	0.128	1.000
		2005-2006	N-N	1.022	0.081	0.864	1.181

Appendix C.4.10 (continued)

Site	Species	Year	Trap	Estimate	SE	LCI	UCI
TTRS	Armadillo	2000-2001	N-N	0.969	0.083	0.115	1.000
		2001-2002	N-N	1.043	0.119	0.809	1.277
		2002-2003	N-N	1.016	0.070	0.879	1.153
		2003-2004	N-T	0.575	0.078	0.420	0.716
		2004-2005	T-T	0.936	0.153	0.089	1.000
		2005-2006	T-T	1.034	0.127	0.786	1.283
TTRS	Raccoon	2000-2001	N-N	0.969	0.083	0.115	1.000
		2001-2002	N-N	1.043	0.119	0.809	1.277
		2002-2003	N-N	1.016	0.070	0.879	1.153
		2003-2004	N-T	0.575	0.078	0.420	0.716
		2004-2005	T-T	0.936	0.153	0.089	1.000
		2005-2006	T-T	1.034	0.127	0.786	1.283
TTRS	Opossum	2000-2001	N-N	0.969	0.083	0.115	1.000
		2001-2002	N-N	1.043	0.119	0.809	1.277
		2002-2003	N-N	1.016	0.070	0.879	1.153
		2003-2004	N-T	0.577	0.078	0.422	0.718
		2004-2005	T-T	0.936	0.153	0.089	1.000
		2005-2006	T-T	1.034	0.127	0.786	1.283

Appendix C.4.10 (continued)

Site	Species	Year	Trap	Estimate	SE	LCI	UCI
TTRS	Fox	2000-2001	N-N	0.969	0.083	0.115	1.000
		2001-2002	N-N	1.043	0.119	0.809	1.277
		2002-2003	N-N	1.016	0.070	0.879	1.153
		2003-2004	N-T	0.557	0.092	0.376	0.723
		2004-2005	T-T	0.936	0.153	0.089	1.000
		2005-2006	T-T	1.034	0.127	0.786	1.283
TTRS	Bobcat	2000-2001	N-N	0.969	0.083	0.115	1.000
		2001-2002	N-N	1.043	0.119	0.809	1.277
		2002-2003	N-N	1.016	0.070	0.879	1.153
		2003-2004	N-T	0.593	0.080	0.432	0.736
		2004-2005	T-T	0.936	0.153	0.089	1.000
		2005-2006	T-T	1.034	0.127	0.786	1.283
TTRS	Coyote	2000-2001	N-N	0.969	0.083	0.115	1.000
		2001-2002	N-N	1.043	0.119	0.809	1.277
		2002-2003	N-N	1.016	0.070	0.879	1.153
		2003-2004	N-T	0.568	0.082	0.405	0.717
		2004-2005	T-T	0.936	0.153	0.089	1.000
		2005-2006	T-T	1.034	0.127	0.786	1.283

Appendix C.4.10 (continued)

Site	Species	Year	Trap	Estimate	SE	LCI	UCI
PH	Armadillo	2000-2001	N-T	0.540	0.068	0.406	0.668
		2001-2002	T-T	1.063	0.177	0.716	1.410
		2002-2003	T-T	1.024	0.109	0.810	1.239
		2003-2004	T-N	1.767	0.196	1.383	2.152
		2004-2005	N-N	0.952	0.116	0.121	1.000
		2005-2006	N-N	1.025	0.089	0.850	1.200
PH	Raccoon	2000-2001	N-T	0.540	0.068	0.406	0.668
		2001-2002	T-T	1.063	0.177	0.716	1.410
		2002-2003	T-T	1.024	0.109	0.810	1.239
		2003-2004	T-N	1.767	0.196	1.382	2.152
		2004-2005	N-N	0.952	0.116	0.121	1.000
		2005-2006	N-N	1.025	0.089	0.850	1.200
PH	Opossum	2000-2001	N-T	0.542	0.069	0.406	0.671
		2001-2002	T-T	1.063	0.177	0.716	1.410
		2002-2003	T-T	1.024	0.109	0.810	1.239
		2003-2004	T-N	1.761	0.197	1.374	2.147
		2004-2005	N-N	0.952	0.116	0.121	1.000
		2005-2006	N-N	1.025	0.089	0.850	1.200

Appendix C.4.10(continued)

Site	Species	Year	Trap	Estimate	SE	LCI	UCI
PH	Fox	2000-2001	N-T	0.522	0.077	0.374	0.666
		2001-2002	T-T	1.063	0.177	0.716	1.410
		2002-2003	T-T	1.024	0.109	0.810	1.239
		2003-2004	T-N	1.841	0.270	1.311	2.370
		2004-2005	N-N	0.952	0.116	0.121	1.000
		2005-2006	N-N	1.025	0.089	0.850	1.200
PH	Bobcat	2000-2001	N-T	0.558	0.079	0.402	0.703
		2001-2002	T-T	1.063	0.177	0.716	1.410
		2002-2003	T-T	1.024	0.109	0.810	1.239
		2003-2004	T-N	1.715	0.207	1.309	2.121
		2004-2005	N-N	0.952	0.116	0.121	1.000
		2005-2006	N-N	1.025	0.089	0.850	1.200
PH	Coyote	2000-2001	N-T	0.532	0.070	0.397	0.664
		2001-2002	T-T	1.063	0.177	0.716	1.410
		2002-2003	T-T	1.024	0.109	0.810	1.239
		2003-2004	T-N	1.794	0.215	1.372	2.215
		2004-2005	N-N	0.952	0.116	0.121	1.000
		2005-2006	N-N	1.025	0.089	0.850	1.200

Appendix C.4.11: Correlation coefficient between the species-specific raw scent station index and the occupancy rate for each site.

Site	Species	Correlation Coefficient (r)	Site	Species	Correlation Coefficient (r)
PB West	Armadillo	0.144	TTRS	Armadillo	0.145
	Bobcat	0.266		Bobcat	-0.121
	Coyote	0.290		Coyote	0.430
	Fox	-0.124		Fox	0.420
	Opossum	0.501		Opossum	0.665
	Raccoon	0.802		Raccoon	0.556
PB East	Armadillo	0.834	PH	Armadillo	-0.014
	Bobcat	0.250		Bobcat	0.423
	Coyote	0.455		Coyote	0.424
	Fox	-0.118		Fox	0.099
	Opossum	-0.041		Opossum	-0.164
	Raccoon	0.877		Raccoon	0.150