The Effects of Urbanization on Reptiles and Amphibians in the Sandhills Region of North Carolina

by

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Dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Environment in the Graduate School of Duke University

2009
ABSTRACT

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Abstract

Rapid urbanization threatens the survival of native wildlife species worldwide. In order to fully grasp the implications of the ongoing growth of urban areas on biodiversity, conservationists need to be able to quantify the response patterns of a wide range of different species to the expansion of urban and suburban land use. In this study, we set up two road-based transects across gradients of urbanization and habitat loss in the diverse longleaf pine forests of the Sandhills region of North Carolina, USA. With funding provided by the NC Wildlife Resources Commission, we drove the transects repeatedly at night in the field seasons of 2006-2008, tallying all vertebrate animals encountered (live or dead). The first transect (driven in all three years; 75 km long) ran from the urban areas of Southern Pines and Pinehurst down to the remote and relatively pristine habitats associated with the state-owned Sandhills Gamelands. The second transect (driven in 2007 and partially in 2008; 69 km long) began at the terminus of the first transect in the Gamelands, and then stretched down to the urban zones of Hamlet and Rockingham.

A total of 4900 vertebrate animals representing 69 species were observed on or near the road routes after driving a total of 16,625 km. This total includes 592 nightjars (ground-nesting nocturnal birds; e.g. whip-poor-wills) that we heard while driving the transects. In addition, in 2007 we surveyed for the nightjars and for quail (a high-priority...
game species that also nests on the ground) using 75 point count locations evenly
distributed along the northern road route.

Regression tree analysis (a robust, nonparametric technique with minimal
assumptions) was used to model the animal observation rates for a given 1 km road
segment or point count as a function of various habitat variables measured within
corresponding buffer zones for each segment. We also modeled snake and bird
encounter rates as a function of mesopredator mammal observations.

Our results reveal that amphibian, snake, and ground-nesting bird observation
rates are negatively associated with increasing levels of traffic and impervious surface.
Conversely, mesopredator mammals (and domestic cats in particular) responded
slightly positively to increasing urbanization, and negatively to protected area coverage.
Both ground-nesting birds and snakes showed signs of negative correlations with
mesopredator encounter rates, although these trends were not always significant due to
high variability in the mesopredator data.

In order to try and confirm the results of the regression tree analyses, we also
used a multivariate ordination approach (non-metric multidimensional scaling) to
visualize the integrated community structure of all of the major vertebrate groups we
observed in the Sandhills. The ordinations revealed that while the snake, ground-nesting
bird, and amphibian groups were similar to each other in terms of their avoidance of
urban conditions, the cats and native mesopredator species actually seemed to define
widely divergent axes of community variation. Cats in particular were separated from
the other groups on 2 out of 3 axes of the species-space ordination. Still, as we noted
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set whether cats and other mesopredators truly played an independent role in
structuring and/or depleting the other wildlife guilds along our route. More
experimental approaches are recommended for trying to resolve whether overabundant
predators or road mortality and inappropriate habitat are more to blame for the much
reduced encounter rates we observed for the snakes, birds, and amphibians in urban
areas. Future studies will also be needed to confirm the logical assumption that road
encounter rates provide a reasonably accurate index of the relative abundance of the
different animal groups along the survey routes.
Dedication

This dissertation is dedicated to the memory of my grandfather, David B. Sutherland, who passed away on April 15th, 2008.
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Chapter 1. Introduction

1.1 Wildlife abundance and interspecies interactions across urbanizing natural landscapes

The earth remains in the grips of a human-driven biodiversity crisis, with species extinction rates rising to levels unprecedented since hyper-catastrophic events in deep geologic time. This crisis is both immense and rather poorly abated. Indeed, in the 20 years since the publication of the book "Biodiversity" (Wilson and Peter 1988); one of the seminal works that raised global awareness of the looming threats to the diversity of life), more than 1.6 billion people have been added to the world’s population (US Census Bureau 2008), an astounding level of growth equivalent to adding the current populations of both China and the USA to an already-stressed planetary biosphere. While human population growth is generally recognized as the ultimate causation for the continued loss of biological diversity, a number of major proximate causes have been identified. These include climate change, pollution, invasive species, emerging diseases, and habitat loss. Despite the enormous amount of public attention now being paid to mitigating climate change, fighting invasive species, and controlling disease, most conservation biologists still agree that habitat destruction remains the primary driver of species extinction (Wilcove et al. 1998).

Historically speaking, most of the habitat loss that has occurred around the world over the last several centuries has resulted from the expansion and intensification of agricultural land uses. Now, however, half of the earth's human population lives in
urban areas (UNFPA 2007), and the rapid expansion of cities is driving a new wave of modern habitat loss (McKinney 2002, 2006). Urbanization plays both direct and indirect roles in driving many species closer to extinction (McKinney 2002). Clearly, as cities grow larger they directly replace natural habitats with artificial structures, impervious concrete and asphalt surfaces, and manicured lawns and gardens full of exotic plant species. These urban landscapes often fail to support native species of plants and animals, particularly the more specialized taxa whose food and shelter requirements do not match the homogenized habitats available in cities and suburbs. Also, the spread of urbanization increases levels of air and water pollution, jeopardizing the survival of many forms of sensitive wildlife. And it is well known that native animal species attempting to persist in urbanized environments also suffer significant mortality from being struck by automobiles.

Indirect effects of urbanization on native wildlife are equally severe but perhaps less-well understood. Often top carnivore species (such as wolves or large cats) are among the first animals to disappear from urban settings, and the loss of these predators has been documented to dramatically increase the abundance of smaller mesopredators such as raccoons or opossums. The mesopredators then drive smaller animals to extinction, with cascading ecological effects on the other trophic levels in these systems (Crooks and Soule 1999, Henke and Bryant 1999). Invasive species (some of whom are also mesopredators, such as feral cats in the USA) tend to become more common in
urban environments, out-competing and over-consuming native plants and animals (Riley et al. 2005, Seabloom et al. 2006, Jodoin et al. 2008). Another major impact of urbanization is that increased human density often precludes many beneficial forms of habitat restoration and management. Prescribed burning is the perfect example, since many terrestrial ecosystems need fire to maintain healthy plant communities, and burning may be impossible in small remnant tracts of habitat surrounded by human land use (NC WRC 2005).

Given that the expansion of urban areas is predicted to continue at a rapid pace in the decades to come (UNFPA 2007), it is imperative that we reach a scientific understanding of the ways in which the negative impacts listed above will combine to threaten the survival of native wildlife species around the world. Research studies that investigate the effects of urbanization will assist conservation efforts in three major ways. First, we can determine which species or groups of species are the most sensitive to the direct and indirect impacts of intensifying human land use. These species can then be targeted for more focused conservation activities. Second, we can estimate threshold levels of urbanization that mark the tolerance limits for these sensitive species. Such thresholds can then be used to map the predicted range of a given species under current and future patterns of urbanization, allowing for more refined assessment of the conservation status of imperiled plants and animals. Finally, we can use scientific information on how different species respond to urbanization to develop better
guidelines for land-use planning. Such guidelines could help constrain otherwise uncontrolled urban expansion into remaining natural habitat areas, and steer new development towards lower priority, less pristine environments.

Well-controlled, well-replicated experimental manipulation of urban land use patterns would provide the ideal mechanism for studying the response of wildlife populations to urbanization. Planned urbanization experiments are extremely rare, however, due to the numerous difficulties involved. The second best approach, and one that is relatively inexpensive and widely applicable across most terrestrial habitat types, is to use existing patterns of urban development as a "natural experiment" (Shaffer 1981, Gibbs 1998). By measuring plant or animal abundance in habitat fragments (and even in non-habitat matrix environments) along gradients of pre-existing urbanization, we can estimate response patterns for different species. Natural-experiment type studies will be especially useful if they incorporate the full gradient of urban land use intensities (e.g. ranging from remote and uninhabited wilderness areas to busy urban centers). Only with full-gradient studies can we be assured of finding any particular threshold levels of urbanization that may exist for certain species. Also, full-gradient studies allow for more accurate projection of species abundance patterns across broader landscapes. Given the potential for indirect species interaction effects (such as mesopredator release) that may occur with increasing urbanization, it is also essential to simultaneously investigate the
urban-response patterns of multiple taxonomic groups along the same land use
gradients.

1.2 Road-cruising along urban gradients

One technique that seems well-suited to studying the abundance patterns of a
wide range of animal species along urban gradients is road-cruising (driving roads
looking for wildlife; (Shaffer and Juterbock 1994)). Road-cruising exploits the readily
available transects provided by the road system of any given urban environment. Most
if not all non-flying vertebrates can be observed either as they cross roads alive, or as
they lie dead on the road after being killed by vehicle collisions. Previous multi-taxa
surveys of wildlife populations along roads have tended to take place in the mornings,
when animals that were killed the previous night can be quickly tallied (Ashley and

While visibility is certainly higher in daylight conditions, the morning road
survey method suffers from two major drawbacks. First, a significant number of road-
killed animals are promptly removed each morning (and possibly during the same night
in which they were killed) by scavengers such as raccoons and vultures (Antworth et al.
2005). Second, measuring road-kill patterns gives a very incomplete picture of animal
abundance along the survey route, as roads with the least traffic (and therefore
potentially the healthiest wildlife populations) would be expected to have less road-kill
simply due to a paucity of vehicles.
Nighttime surveys along roads, although less often employed than morning road-kill surveys, provide a powerful technique for counting both live and dead vertebrate animals of a variety of amphibian, reptile, and mammal species. Snakes in particular are easily observed along roads at night (Rosen and Lowe 1994, Sullivan 2000), and other available snake survey techniques (such as drift fences with funnel traps) are logistically difficult to employ across broad enough scales to capture full urban impacts.

1.3 Overview of the remainder of the dissertation

In the three chapters that follow, I detail my results from an innovative nighttime road-cruising project that I conducted over the course of three summers in the Sandhills region of North Carolina. With the help of several field assistants and volunteers, I repeatedly drove along a transect of roads that spanned across much of the available gradient in urban conditions in the immediate study area.

Chapter Two presents the amphibian encounter data from the road surveys. The large sample sizes I recorded for frogs and toads, combined with the mark-recapture study I attempted for toads in 2008, and the additional calling frog surveys I added in 2007-8, justify splitting off the amphibian data into a separate article for publication. In Chapter Two I use nonparametric regression tree analyses to try and relate amphibian detection rates to measures of urbanization, traffic, and habitat loss along the road routes. Focusing in on one particular variable, I ask whether the ratio of live to dead
amphibians encountered on a given stretch of road can be predicted as a function of average vehicle traffic. I also attempt to determine whether the different frog and toad groups respond to environmental conditions more strongly at particular ranges of buffer scales.

Next, in Chapter Three, I again use the regression tree approach to relate encounter rates for various groups of snakes, ground-nesting birds, and mesopredator mammals to a similar set of metrics of urbanization and habitat loss. I also attempt to quantify the potential predator-prey relationships that potentially exist between these three different groups. Snakes and mammalian mesopredators are both known to prey upon ground-nesting birds, and the mammals also prey upon the snakes. Since all three groups are expected to change in abundance as a function of the direct impacts of urbanization (such as traffic mortality), empirically sorting out the indirect trophic relationships between the different wildlife groups becomes an interesting and challenging endeavor.

Chapter 4 takes a very broad look at the overall wildlife community structure along the urban gradients I sampled in the Sandhills, using data from all of the vertebrate groups discussed above simultaneously. I use multivariate ordination techniques (NMS) to reduce the inherent complexity of vertebrate co-occurrence patterns and environmental gradients down to a level that can be easily visualized and
explored. I also closely examine the design of my road transect network from the standpoint of whether or not it adequately surveyed the urban gradient as intended.

All three data chapters (#s 2-4) are built off the same large data set (nearly 5000 vertebrate observations) from my Sandhills road-cruising research. As such, the reader should be forewarned that there is a considerable amount of repetitive description within certain sections of my introduction and methods components of all three papers. In the event that one of these chapters is published before the others, it will then be an easy matter to sharply reduce the amount of repetitive methodological details in the remaining manuscripts.

I should also note that the data chapters were written from a plural authorship point of view (i.e. using "we" and "our"), which reflects my intention of rewarding my field assistants with co-authorship of any papers that result from the road-cruising research. However, I would like to reassure the Graduate School and the members of my committee that I performed all of the fund-raising, statistical analysis, interpretation, and writing that went into the research, not to mention at least half of the actual field work. I was fortunate enough to have some funding to hire field assistants to help with some of the driving, and their hard work in the summers of 2006 and 2007 seems to provide ample justification for including them as co-authors of my soon to be submitted journal articles.
For the purposes of this dissertation I have not attempted to track down the latest scientific names for all of the species we observed on the road routes in the Sandhills. Given the extremely fast rate of taxonomic nomenclature change that is now underway as we surge past the cusp of the "genomic era", I have saved time by simply relying on traditional names such as those employed by standard texts such as Palmer and Braswell (1995). For example, instead of *Anaxyrus terrestris* (southern toad) I use *Bufo terrestris*, and instead of *Scotophis alleghaniensis* (black rat snake) I use the old standby *Elaphe obsoleta*. Bibliographic references for the entire dissertation are listed at the end of the document, and Figures and Tables are numbered consecutively without regard for the Chapter they reside in.

The last two chapters (5 and 6) represent generalized discussion and conclusion sections that are intended to provide some measure of synthesis of the various findings of this dissertation. The discussion section deals mainly with general methodological issues, caveats, and assumptions related to the road-cruising methodology. It also includes my suggestions for extending this research (using improved techniques) into additional field seasons and other geographic areas. The conclusion section presents my seven major findings from the dissertation, and also a summary of the conservation implications of the research. This final section ends with a small set of specific conservation policy recommendations that logically flow from my results.
Chapter 2. Amphibian encounter rates plummet on roads with increasing levels of traffic and urbanization

2.1 Introduction

Among vertebrate groups, amphibians seem to be particularly vulnerable to suffering negative impacts from urbanization, due to their general reliance on both terrestrial and aquatic ecosystems during their lifecycles (Semlitsch 2000, Cushman 2006, Hamer and McDonnell 2008). This dual dependency makes amphibian species sensitive to degradation of either type of habitat, and also results in high levels of mortality when roads interfere with breeding migrations or natal dispersal (Puky 2006). Many studies have determined that ponds and wetlands situated in more urbanized landscapes contain fewer species or lower abundances of frogs, toads, and salamanders (Vos and Chardon 1998, Knutson et al. 1999, Lehtinen et al. 1999, Carr and Fahrig 2001, Pellet et al. 2004, Rubbo and Kiesecker 2005, Pillsbury and Miller 2008). Similarly, Willson and Dorcas (2003) and Riley et al. (2005) found that streams flowing through more urbanized watersheds also had reduced amphibian faunas.

An alternative approach to studying the impacts of urban development on amphibian populations has been to measure the relative abundance of the animals as they attempt to cross roads under various traffic and land-use conditions (Shaffer and Juterbock 1994, Lode 2000, Langen et al. 2007, Orlowski 2007, Glista et al. 2008). By using urban infrastructure as a sampling tool, road surveys provide a picture of amphibian abundance and mortality rates that complements the information available from surveys
of aquatic breeding habitats. In one widely cited but not necessarily extreme example, Ashley and Robinson (1996) recorded over 30,000 dead amphibians along a 3.6 km road running through a large wetland over four years.

However, it is not clear when we should expect road mortality to actually cause the decline of local amphibian populations, given the high reproductive rates of certain species, and the possibility that density-dependent survivorship may compensate for road-killed individuals (Ashley and Robinson 1996, Hels and Buchwald 2001). Also, since road mortality rates logically depend on both the volume of traffic (Hels and Buchwald 2001, Mazerolle 2004) and the local abundance of the animals in question, road-kill counts for urban-sensitive species might be ambiguously low on roads with traffic levels at both the lower and upper extremes. In a brief yet elegant test of this important relationship, Fahrig et al. (1995) counted the numbers of live and dead frogs and toads along roads with different levels of traffic. They found that roads with the lowest levels of traffic had the highest absolute numbers of both live or dead amphibians, even though the proportion of dead animals was at a minimum. This conclusion, which Fahrig et al. (1995) documented with only six nights of road survey data across a coarse gradient of three levels of vehicle traffic, has yet to be confirmed or refined by similar investigations in other regions. As a result, it remains surprisingly unclear whether hotspots of mortality on certain stretches of road (Clevenger et al. 2003,
Langen et al. 2009) signal the most vulnerable or the most robust amphibian populations in a given area.

To address this crucial gap in our knowledge of amphibian road ecology, in this study we used night-time driving to sample live and dead frogs and toads across a 165-km road route representing two gradients of urbanization in the Sandhills region of North Carolina (Figure 1). We use our results to test three important hypotheses. First, we predicted that total amphibian encounter rates would decline sharply and nonlinearly as a function of either increasing levels of traffic and urbanization, or decreasing availability of terrestrial and aquatic habitats. Second, we predicted that relative mortality rates would increase sharply with higher levels of vehicle traffic, even as total encounter rates fall. Our third hypothesis was that amphibian groups will each exhibit their strongest relationships with the traffic, urbanization, and habitat variables at a particular range of scales and intensities that correspond with the relative mobility of the species in question (Carr and Fahrig 2001, Homan et al. 2004). We also use our data to project amphibian road encounter rates across the broader Sandhills region of North Carolina, following the example set by Vos and Chardon (1998). Our results indicate that conservation organizations will need to accelerate their efforts to protect habitat for the rich amphibian fauna associated with critically endangered longleaf pine ecosystems.
2.2 Methods

2.2.1 Study area

The original vegetation of the Sandhills consisted of savannahs of longleaf pine (*Pinus palustris*), turkey oak (*Quercus laevis*) and wiregrass (*Aristida stricta*) in the xeric uplands, and dense "pocosin" type vegetation and mixed pine/hardwood tree overstory in the bottomlands and blackwater creeks dissecting the sand ridges (Wells and Shunk 1931, Sorrie et al. 2006). The longleaf pine ecosystem is renowned for containing a very high diversity of herbaceous plants (Peet 2006) and also reptiles and amphibians (Means 2006). Unfortunately, longleaf pine forests are also recognized as one of the most endangered major habitat types in North America, with over 97% of the original extent destroyed (Earley 2004, Varner and Kush 2004, Van Lear et al. 2005, Frost 2006). The Sandhills region retains by far the largest concentration of longleaf pine forests within North Carolina. Much of this forest is now protected within either the Ft. Bragg/Camp Mackall military bases (~73,000 ha) or the Sandhills Gamelands, a state-owned wildlife management area (~24,000 ha). The large amount of protected longleaf forest in the Sandhills now serves as a background matrix for rapidly increasing levels of urbanization and human impact in recent decades.

2.2.2 Road-cruising Techniques

For our study we drove at night along road-based transects that were established across two clear gradients of urbanization in the Sandhills (Figure 2). The routes were
designed to capture a wide range of traffic, urbanization, and habitat loss conditions, with average daily traffic counts (ADT) ranging from a low of 20 to a high of 14,000 cars per day, according to NC Dept. of Transportation data. The approximate length of each transect (northern route: 75 km, southern route: 69 km, plus 21 km of access roads) was chosen specifically to allow for a round-trip (out and back) of a single route (or a one-way traverse of both routes) in the roughly four hour period from dusk to midnight. We avoided including busy highways with posted speed limits of 55 mph or higher, as these roads were deemed unsafe for road-cruising, and the vast majority of the lengths of the two transects consisted of 2-lane paved roads.

We only drove on the northern route in 2006 and 2008, whereas in 2007 we surveyed both the northern and southern routes in roughly equal proportions. During the period of May-August of each year, we drove 39 nights in 2006, 46 nights in 2007, and 4 nights in 2008, for a total of 16,625 km surveyed in the three field seasons of the study. Further details about the survey effort are summarized in Table 1. In order to prevent any biases associated with the time of traverse across various sections of the transects, we randomly alternated amongst a series of standardized routes with different starting and stopping locations.

We drove the routes at a consistent low speed of 48-56 km/h, tallying all live or dead amphibians we encountered. Often it was not possible to identify frogs and toads to the species level, as live animals tended to escape off the road (though the hopping
behavior of each genus was characteristic). Also, dead animals were frequently quite badly mangled by ongoing traffic. We were able to classify most amphibians to the genus level without stopping the car, a convenience which provided significant time savings. In 2008, however, we did stop to capture and identify every toad above 2 cm SVL. These more intensive surveys (which often took > 6 hours) revealed that the similar morphology of the spadefoot (*Scaphiopus holbrooki*) and *Bufo* toads prevented accurate separation of the two genera while in transit. For this reason we combined all of the toad encounter data into a single index for statistical analysis. To further expedite the transect driving, most dead amphibians were left on the road, where they quickly decomposed overnight (Langen et al. 2007) due to the combined effects of additional traffic, rain, and scavenging ants.

### 2.2.3 Geospatial Analyses

Amphibian locations were originally recorded as vehicle mileages from adjacent intersections. These were converted into digital coordinates using ARCGIS software (versions 8.2-9.3, ESRI 2005), and we then performed a thorough search to remove possible repeat observations of the same dead animals on the same night. To enable calculation of encounter rates, we divided the route into a series of 165 segments, each roughly 1 km in length (range 800-1200 m). Encounter rates for the amphibians were calculated by dividing the total number of animals of a given group observed on a
segment, by the total distance driven on that segment (# one way trips * length of segment).

A standard set of seven types of habitat variables corresponding to each of the 1-km road segments were then calculated using ARCGIS. The simplest predictor variable was average daily traffic volume ("ADT05", derived for each road segment using the most recent traffic data available from the NC Dept. of Transportation. The remaining variables were calculated as average values for buffer polygons established around each road segment at a range of 11 different scales (30, 250, and 500m, plus 1, 2, 3, 4, 5, 6, 8, and 10 km). The multi-scale variables included traffic density ("trafden", an improved version of road density in which the traffic of the roads is taken into account; Pellet et al. 2004), percent impervious surface ("impsf", an index of urban development; (Morse et al. 2003), proportion forest cover ("for", all forest types within the buffers), and the fraction of the buffers that was occupied by protected or managed areas ("marea"). With the protected/managed area variable we hoped to capture an index of the amount of regularly burned habitat around each of the road segments, with the expectation that this index might be more crucial to explaining the abundance of certain longleaf-dependent species than mere forest cover alone. The last two variables, open water ("pdswtr", ponds and lakes) and wetlands ("wet"), were included to provide measurements of the relative amount of aquatic habitat available along the road route.
Additional information about the variables used in all three data chapters of this dissertation is provided in Table 11.

Obviously there was a high potential for the 67 total variables to be highly correlated amongst themselves, both across scales and across categories. However, for this analysis we resisted the temptation to reduce the dimensionality of the habitat measures using PCA or some other ordination technique. We also decided to include all 11 concentric scales in our analyses, following the lead of Pellet et al. (2004), who actually utilized 300 total variables in their research into the habitat relationships of the European tree frog (*Hyla arborea*). Other similar investigations have limited their scope to "standard" 1 km buffers for habitat analyses, thereby potentially missing the impacts of environmental conditions at broader scales (Gibbs et al. 2005, Smith and Green 2005).

**2.2.4 Statistical Analysis**

Since it was inevitable that both our response and predictor variables would exhibit spatial autocorrelation, we used an improved version of the regression tree methodology described by De’Ath and Fabricius (2000). Regression trees work by recursively splitting the response data into increasingly pure groups, with each split based on a single division amongst one of the predictor variables (e.g. ADT > 535 cars per day). The method does not make strict assumptions of independence among the data points, and is able to filter through large numbers of variables to choose the best sets of predictors in the final tree, a capacity well-suited to our analysis of habitat
variables measured at a wide range of spatial scales. The optimal splitting procedure
also forces the model to identify the thresholds or break-points in the predictor variables
that are associated with the sharpest distinctions within the response data.

Recent advances in computing power have enabled the creation of more
complicated versions of regression tree analysis with lower tendencies to over-fit the
data, including boosted regression trees (De’ath 2007, Elith et al. 2008) and Random
Forests (Breiman 2001, Prasad et al. 2006). However, these newer techniques do not as a
rule yield the single, easily interpretable decision tree that makes single regression trees
so intuitive to understand. Rather than sacrifice interpretability for the sake of small
gains in predictive power, we chose to modify the single regression tree approach to
make it more robust. Following the advice of De’Ath and Fabricius (2000) and Therneau
and Atkinson (1997), we changed the RPART routine in the R statistical language (R
Development Core Team 2007) such that the cross validation tree pruning process was
repeated 200 times (each time with k=20), yielding a much more stable estimate of the
most robust number of splits for the final models. To test whether the optimally pruned
models were different than what would be returned in the absence of actual
relationships between the response and predictor variables, we also implemented a
Monte Carlo significance test (with 500 random permutations) for each final tree (Manly
1997).
To test our first two hypotheses, we fit regression trees for each of four groupings of amphibian species, relating each group to the full range of 67 variables representing traffic, urbanization, and habitat loss at various spatial scales. We also fit trees for each single predictor variable independently, to enable comparison across the different scales and variable categories. In order to investigate our third hypothesis concerning the impact of traffic volume on relative mortality rates, we calculated the fraction of the total encounter rates for each road amphibian group that was made up of dead animals. To avoid dividing by zero, for each group the regression tree analysis (percent dead vs. ADT) was truncated to only those road segments that had non-zero total encounter rates. For all of three hypothesis tests described above, we considered the overall best model for a given species group to be the regression tree model with the highest cross-validated $R^2$.

Finally, in order to better examine the conservation implications of our results, we took the overall best habitat-traffic-urbanization regression tree model for total amphibians, and projected amphibian encounter rates across the broader Sandhills landscape. Since our model predictions were in terms of animals encounter rates on 1 km segments, we divided the entire state-maintained road network in the 9-county region into a series of 16,099 segments, most of which were 800-1200 m long. Buffers and habitat variables were calculated as described above for the study transects.
2.3 Results

2.3.1 Overview

Amphibians were by far the most numerous vertebrate group we observed along the survey route. Over the course of the three field seasons we recorded a total of 2665 live and dead amphibians on the road, all but two of which were frogs and toads. The lack of salamander observations (only two individuals of *Pseudotriton ruber* were noted) was expected given the fall and winter breeding seasons of many of the salamander species found in the Sandhills. We recorded a total of 14 species of Anurans on the road during the study, including 2184 toads (Genera *Bufo* and *Scaphiopus*, "bufoscaph"), 234 tree frogs (*Hyla*, "hylids"), and 230 true frogs of the genus *Rana* ("Ranids"; Table 2). Most of the animals encountered or observed were from common, widespread species such as the southern toad (*Bufo terrestris*) and bullfrog (*Rana catesbeiana*).

Road encounter rates varied dramatically not only by species but also by year. Severe drought conditions were present across much of the Southeastern USA during 2007, and the lack of rainfall is the obvious explanation for why total amphibian encounter rates plunged from 28 animals/100 km in 2006 to only 7 in 2007. The highest total encounter rates were observed in 2008 (64 animals/100 km), but in that year we only drove on particularly rainy nights, in contrast to the more even sampling of the previous two years. When we merged the data into combined 2006-8 encounter rates, and focused only on the 75 road segments of the northern route which were driven in all
three years (and in fairly even proportions) the models enjoyed much higher performance. Therefore, in the results that follow we focus our attention on the combined model results for the northern route. However, even though the magnitude of encounter rates were different across years, the basic response patterns to our traffic and urbanization variables appeared quite similar. For example, the total amphibian encounter rates across years all show clear negative relationships with Average Daily Traffic (Figure 3). Looking within years, in 2007 the response of total amphibians to traffic volume and other variables appears consistent for both the northern and southern routes.

2.3.2 Hypothesis One Results

Significant, nonlinear relationships were found in the best single variable regression tree models explaining amphibian encounter rates as a function of traffic, urbanization, and habitat availability (Table 3). Most strikingly, we observed very steep declines in predicted bufoscaph toad encounter rates as a function of both traffic variables (ADT05, traffic density) and impervious surface. These steep negative relationships are repeated for the total amphibian group, driven by the preponderance of toads in the overall data. For example, the single variable model relating total amphibians to traffic density (within a 250 m radius of the road) yielded an optimally pruned regression tree with two splits (Figure 4). When trafden250 is less than 45, the total amphibian encounter rate is expected to be 38 animals/100 km driven, whereas
when trafden250 rises above 303, encounter rates plummet to only 2 (Figure 5). Hylid and ranid encounter rates also generally declined with traffic and urbanization, although for these groups the relationship was complicated by the presence of secondary peaks in observations at low-intermediate levels of human impact.

The single variable regression tree models describing terrestrial habitat conditions were also nonlinear, but instead of sharp exponential declines, most of the amphibian groups exhibited unimodal-type responses to forest cover and protected area. Ranid frogs typified this pattern, with highest encounter rates predicted when forest cover at a 2 km radius ranges from 57-68 percent (Figure 6), or when protected area at a 1 km radius falls within the range of 26 to 52 percent. The observed relationships between the encounter rates and the two variables measuring aquatic habitat (ponds and water, wetlands) varied considerably between groups and across the two variables. For bufoscaph, hylids, and totamphibs, the best ponds and water models showed a strong negative response to the amount of water at fairly broad scales (4-5 km). This relationship appeared to be related to the strong positive correlation that exists between impervious surface/traffic density and the prevalence of ponds and lakes at these broader scales. In contrast, the best water model for ranids showed a positive relationship at the 500 m scale. All of the best wetlands models indicated positive relationships between encounter rates and wetland coverage, and the 30 m wetland variable provided the best overall model for ranids.
When we plotted total amphibian encounter rates as a function of local-scale (250 m) urbanization and aquatic habitat variables simultaneously, quite interesting patterns were revealed. High pond or high wetland conditions were only found along the low traffic density/low urbanization segments of the routes. However, within the rural, low-traffic regions, amphibian encounter rates appear to be only weakly correlated with the availability of ponds or wetlands (Figure 7). The steep declines in encounter rates that occur with small increases in traffic or impervious surface are clearly the dominant effect. These steep negative relationships retain their characteristic shape even when plotted separately for road segments with high and low amounts of aquatic habitat nearby, respectively (Figure 8). In these graphs, the main effect of increased ponds/water and wetlands values seems to be an upward shift (by a factor of 2) of the highest amphibian encounter rates at the low urbanization/low traffic extremes.

2.3.3 Hypothesis Two Results

When we modeled mortality rates (instead of total encounter rates) as a function of average daily traffic (ADT05), the resulting scatterplots and regression trees confirmed the expected positive relationship for bufo species, toads, ranids, and total amphibians (Table 4). For example, the predicted fraction of dead total amphibians rises from only 15 % when traffic is less than 885 vehicles/day, to a high of 47 % when ADT05 exceeds 5200. This increasing relative mortality rate occurs at roughly the same traffic range as when the total (live plus dead) amphibian encounter rate plunges from 35
animals/100 km (ADT05 < 535) to only 2 animals/100 km when traffic is above 2048 vehicles/day (Figure 9). The decline in total amphibian encounter rates did appear to be a much steeper function of traffic levels than the increase in the percentage of animals that were dead when encountered. In contrast to the total amphibian results, the hylids model suggested a peak of just over 50 percent dead tree frogs when traffic ranged between 758 and 1365 vehicles/day, with lower mortality rates above and below this narrow range. Model performance was low for all of the percent-dead tests (e.g. for total amphibians x-val R² = 0.07, compared to 0.387 for the total encounter rate ADT05 model for that group), due to the high variance observed in the fraction of dead animals across the different segments.

2.3.4 Hypothesis Three results

Our results did not confirm our expectations that the amphibian groups with higher relative mobility (hylids and ranids) would respond best to the habitat, urbanization, and traffic variables at larger scales than the lower-mobility bufoscaph toads. Quite the contrary, the toads had the second highest average scale (3708 m) when looking at the best scale of each of the six variables that we measured at varying distances from the road segments (Table 3). The toads were only exceeded by the total amphibian group, whose average best scale was 4708 m, nearly three times the value of ranid frogs, which had the lowest average scale of only 1463 m. Even though the average best scale for the different groups thus ranged from 1.4 to 4.7 km when looking across
variables, if we examine only the single best overall model for each of the four main groupings, the scale involved drops precipitously to an average of only 195 m (Table 5).

For a given variable and amphibian group, the regression tree model performance was fairly stable across the 11 different scales. The differences between amphibian groups were in fact much more pronounced than the differences between scales, with the bufoscaphe and total amphibian models consistently achieving higher x-val R²'s than the other groups except at the 30-500 m scales. Figure 10 provides an example of this trend for the impervious surface variable, where bufoscaphe and total amphibian x-val R²'s quickly rise to a plateau of roughly 0.4 at 500 m, and only decline noticeably at the 10 km scale. The hylids and ranids models tended to peak at the sub-1 km scales, and beyond that range rarely achieved even half of the x-val R² of the bufoscaphe group.

2.3.5 Predicted Encounter Rates Across the Study Region

We chose to project the environment-only model with the highest x-val R²: total amphibians vs. traffic density at a 250 m radius. When we applied the model to all of the 16,000 road segments across our study region, a clear pattern of greatly reduced amphibian encounter rates in urban areas emerged. According to the projections, a majority (64 %) of the total state-maintained road network in the Sandhills will have an amphibian encounter rate that is less than half of what would be predicted in the absence of vehicle traffic (Figure 11). This provides some sense of the scale of the road-
suppression effect that seems to be occurring in our study area. If the depleted amphibian encounter rates on the roads also correspond to equivalent declines in amphibian abundance in the areas along the roads, then the area of the Sandhills affected will also be large. For example, if the full road effect extends 250 m, which might seem reasonable given the scale of the predictor variable involved, then 24% of the area of the nine-county study region will have amphibian populations with greatly reduced abundance.

2.4 Discussion

We have documented a very steep decline in total amphibian encounter rates as a function of increasing traffic and urbanization in the Sandhills. This negative relationship was especially evident for toads (*Bufo* and *Scaphiopus*), which constituted the great majority of our road amphibian data. The vulnerability of toads to vehicle traffic has been well-documented by previous road-kill surveys, such as Orlowski (2007) and Vangelder (1973). Pond-based surveys have also revealed lower abundances of breeding *Bufo* (Tupper and Cook 2008) and spadefoot (Nystrom et al. 2002) toads in urban, high traffic areas. Our data, however, provide the first quantification of total (live + dead) road encounter rates for any amphibian group across a nearly complete gradient of traffic and urban impacts. The traffic threshold we derived for total amphibians (>2000 vehicles/day) corresponds well with the empirical observations of Vangelder (1973), who calculated that 90% of adult toads in his study population would be killed
each year by a road with only 3600 cars/day. The impervious surface thresholds are actually much lower than the threshold levels of watershed urbanization that typically lead to severe impairment of water quality (Morse et al. 2003, Ourso and Frenzel 2003). This indicates that toads may largely disappear (from roads at least) in urbanizing landscapes long before water quality becomes a limiting factor on their breeding success.

The frog groups we recorded (hylids and ranids) displayed similar negative relationships with traffic and urbanization to those of the toads, but the rates of decline for the frogs did not appear to be as severe. For the most common ranid frogs in the Sandhills (bullfrogs, green frogs) this trend can almost certainly be explained by the year-round association of these species with aquatic habitats (Rubbo and Kiesecker 2005). With little need to cross roads on a regular basis, adult bullfrogs and green frogs should be able to persist and breed in urban ponds and lakes long after more terrestrial species of frogs, toads, and salamanders are driven locally extinct by traffic mortality. Hylid tree frogs typically do use some form of upland habitats in their life cycles (with the possible exception of green tree frogs, *H. cinerea*, which are closely tied to wetlands), but the tree frogs are able to cross roads more rapidly than the ranids and much more quickly than the toads. In contrast, our observations lead us to believe that many of the toads we encountered on the road on summer nights were actively searching (or at least
waiting) for insects on the road surface, in agreement with the behavioral observations of Clarke (1974).

Surprisingly, the aquatic habitat variables (wetlands, ponds-water) did not appear to be as important in structuring total amphibian encounter rates in our study region as the metrics of traffic or urbanization. In many previous amphibian road-kill studies (Ashley and Robinson 1996, Glista et al. 2008, Langen et al. 2009), the highest levels of mortality are found in places where roads intersect major wetlands or other aquatic breeding habitats. The consistent nightly presence of foraging *Bufo* toads on low traffic roads during the summer seems to have played a dominant role in structuring our Sandhills results. For the toads at least, higher traffic and urbanization conditions appear to lead to a 20-fold decline in total encounter rates, whereas low availability of ponds or wetlands only cut encounter rates by half. The heavy influence of urbanization on amphibian road encounter rates in the Sandhills is consistent with the findings of many pond-based surveys that have also documented the importance of road density, traffic density, and urbanization variables in limiting amphibian breeding populations (Knutson et al. 1999, Pellet et al. 2004, Rubbo and Kiesecker 2005, Pillsbury and Miller 2008).

Unfortunately, we lack the data to reliably plot out the locations of ephemeral ponds and wetlands along our road transect. Such temporary aquatic habitats would certainly be expected to heavily influence the distribution and abundance patterns of
many of the less common amphibians in the Sandhills, such as barking tree frogs (*Hyla gratiosa*) and Ornate Chorus Frogs (*Pseudacris ornata*). Numerous studies have illustrated the importance of hydroperiod in determining amphibian species richness at breeding ponds, with higher richness usually occurring at ponds that do not permanently contain water or fish (Rubbo and Kiesecker 2005, Pillsbury and Miller 2008).

Another highly significant result of this study is that our models for road mortality rates as a function of traffic volume provide much-needed confirmation of the mechanisms that determine the frequency with which road-killed amphibians are encountered in different areas. As also shown by Fahrig et al. (1995) and Orlowski (2007), it appears to be a general trend that more dead amphibians are found on roads with less traffic. According to our results and those of Fahrig et al. (1995), this is because the total number of amphibians on the road is much higher on roads with low traffic conditions. Therefore, even though the relative mortality rate (percentage of total amphibians that are dead when encountered) rises when traffic volume goes up, this tendency is swamped by the strong trend in total encounter rates. In the Sandhills at least, total amphibian encounter rates will have been severely depleted long before the proportion of dead animals observed reaches 50%. Clearly this finding has important implications for interpreting the results of morning road-kill surveys for amphibians and other groups. Rather than signaling remnant populations doomed to imminent local extinction, hotspots for road mortality may represent some of the most abundant animal
populations remaining on a given stretch of survey route. Therefore, we suggest that limited road mortality mitigation dollars should often be targeted towards situations where populations of rare species are clearly threatened by the existence (or expansion) of higher-traffic roads.

From a movement ecology perspective we were quite surprised by the fact that *Bufo/Scaphiopus* toads seem to be best explained on average by habitat variables at much broader scales than the other anuran groups. The absolute scale of the response patterns for the different frogs and toads in the Sandhills is not unprecedented, as Gibbs et al. (2005) similarly found frog and toad distributions to be associated most closely with variables ranging from 5 to 10 km. Also, as reviewed by Smith and Green (2005), many species of frogs and toads have demonstrated surprisingly large maximum dispersal distances, ranging up to 24 km (*Rana*), 13 km (*Hyla*), and 34 km for *Bufo* (which may also indicate that our a priori assessment of toads as less-mobile than the frog species may be in error). Ponds and wetlands located within 11-13 km of each other may exchange dispersing juvenile and adult anurans often enough to prevent local extinctions, according to the inverse power law functions presented by Smith and Green (2005). Such long-distance dispersal events would be much less successful in urbanized, high traffic landscapes, especially for the terrestrial toad species. Ranids and hylids may utilize riparian corridors much more effectively for dispersing to new ponds and wetlands, and such corridors are often relatively intact in urban areas due to flood damage mitigation.
efforts. Even though the average best scale across habitat variables was much higher for toads than the frogs, the overall best models for all of the amphibian groups used single variables at much smaller scales. The driver for this interesting trend seems to be that the traffic, impervious surface, and wetland variables all seemed to achieve their highest degree of influence at very small scales (30-250 m), whereas the less influential forest and protected area variables performed better at much larger scales.

One obvious limitation of using road transects to survey amphibian populations is that the relationships we observed are expressed in terms of road encounter rates, and thus cannot be directly extended to actual patterns of local or regional amphibian population density along the roads. It is conceivable that amphibians living alongside of busy roads have either learned to avoid crossing roads on an individual basis, or have experienced selection pressure for behaviors that reduce the tendency to cross roads (Dodd et al. 1989). Such differential behaviors would result in a negative correlation between amphibian detection probabilities (Bailey et al. 2004a, Mazerolle et al. 2007) and the urbanization and traffic variables we measured along the route, possibly even in the absence of reduced local population size.

We conducted two smaller projects (both of which will be reported on more fully in future papers) during our road-cruising effort in order to try and connect road encounter rates to local abundance. First, in 2007 and 2008 we recorded the location of every "chorus" of one or more calling frogs or toads that we detected while driving the
routes at night with our vehicle windows down. Similar to Fahrig et al. (1995), our preliminary results indicate that total amphibian road encounter rates are significantly positively related to the frequency with which we detected frog and toad choruses along the routes. In addition to the chorus counts, we also attempted a mark-recapture study for the Bufo toads during the brief 2008 field season. Our plan was to test whether higher toad encounter rates were merely a function of more frequent repeat observations of the same animals on low-traffic, low-urbanization parts of the route. However, when we systematically examined digital photos of all of the live and dead Bufo toads found in 2008, no recaptures were apparent. This does provide limited evidence against the notion that detection probability alone is driving the striking trends in toad encounter rates we observed along the urban gradients in the Sandhills. We will be exploring in much greater detail the determinants of nightly detection probabilities (e.g. rainfall, temperature, humidity, driver identity, etc.) for amphibians and other animals along our route in a subsequent paper.

Very low toad recapture rates and positive correlations with chorus detection rates lend additional credence to the idea that the encounter rate depletion effect we have documented is a real phenomenon, one that may extend for an unknown distance from busy roads (Forman and Deblinger 2000). We plan to conduct future studies to elucidate the road effect zone for amphibians in the Sandhills. We anticipate that the negative effects of roads on local amphibian populations will be additive, such that
habitats that are within a certain distance of two busy roads will suffer twice (or more) the population depletion due to traffic mortality. Mitigating the distance effects of roads would be factors influencing the productivity of the local amphibian populations, such as the size and connectivity of wetland complexes. Determining these relationships for amphibians and other traffic-sensitive vertebrate groups will provide the perfect means for extending the results of convenient road-based studies across broader landscapes.

2.5 Conclusions and Conservation implications

The fact that the bulk of our amphibian encounter data consists of generalist species capable of breeding in permanent ponds in suburban areas, such as southern toads (*B. terrestris*), bull and green frogs (*R. catesbeiana* and *R. clamitans*), and green tree frogs (*H. cinerea*) is a very troubling result from the standpoint of conserving the amphibians that are more closely tied to ephemeral wetlands in longleaf pine forests. Sadly, we lack data on pre-settlement (or even pre-automobile) amphibian populations associated with upland longleaf forests and associated wetlands in the southeastern USA. Even for the common amphibians that largely characterize our data set, it appears that moderate levels of traffic (>2000 vehicles/day) and urbanization (>1-2% impervious surface) can lead to severe reductions in local populations along roads in the Sandhills. In fact, 7 out of the 75 segments on our northern route ended up with zero total amphibian encounters, even after we had made well over 100 trips on warm summer nights down these urban roads.
According to our projections, and assuming our road route is fairly representative of the broader study region, well over half of the road network in the Sandhills is likely to have already suffered population reductions of 50% or more. Regardless of how far the road depletion effect extends into the surrounding habitats, this is a very sobering statistic that has relevance towards the overall impact of roads, traffic, and urbanization on amphibian populations throughout the former range of longleaf pine forests in the southeastern USA. It seems plausible to us that urbanization-induced habitat loss and traffic growth alone can account for a good deal of the recent declines in global amphibian abundance, at least in areas experiencing rapid expansion of cities and suburban developments. Mitigating current hotspots of wildlife mortality via underpasses and barrier walls is certainly a worthwhile endeavor. Even more important in our view is the difficult task of employing land-use planning and habitat conservation efforts to deliberately forestall future traffic growth on quiet roads near robust populations of high-priority native species. Of course, since even low traffic roads can apparently inflict severe rates of road-mortality, the most reliable way to protect urban-sensitive wildlife will always be to prevent new road construction within our remaining wilderness-quality natural areas.
Chapter 3. Native snakes and ground-nesting birds decline in parallel along gradients of increasing urbanization and mesopredators

3.1 Introduction

Urbanization plays both direct and indirect roles in driving many species closer to extinction (McKinney 2002). As cities grow larger they directly replace natural habitats with artificial structures, impervious concrete and asphalt surfaces, and manicured lawns and gardens full of exotic plant species. Also, the spread of urbanization increases levels of air, water, noise, and light pollution, jeopardizing the survival of many forms of sensitive wildlife. And it is well known that native animal species attempting to persist in urbanized environments also suffer significant mortality from being struck by automobiles (Forman and Alexander 1998).

Indirect effects of urbanization on native wildlife are also potentially severe but perhaps less well understood (Faeth et al. 2005, Shochat et al. 2006). Often top carnivore species (such as wolves or large cats) are among the first animals to disappear from urban settings, and the loss of these predators has been documented to dramatically increase the abundance of smaller mesopredators such as raccoons or opossums. Mesopredators then drive smaller animals to extinction, with cascading ecological effects on the other trophic levels in these systems (Crooks and Soule 1999, Henke and Bryant 1999).
Likewise, snakes are an important predator group in many parts of the world, but due to the cryptic nature of these animals, very few empirical studies have managed to quantify trends in snake abundance as a function of urbanization. Snakes also suffer high rates of road mortality (Rosen and Lowe 1994, Roe et al. 2006) due to their slow locomotion and tendency to linger on sun-warmed surfaces (Andrews and Gibbons 2005). The negative impacts of vehicle traffic may be compounded by the enhanced abundance of mammalian predators, particularly cats, which are known to consume large numbers of native snakes (Whitaker and Shine 2000). At the same time, certain birds and small rodents are known to reach higher densities in urban/high traffic environments (Rytwinski and Fahrig 2007), possibly leading to enhanced snake populations in proximity to human settlements (Minton Jr. 1968) and along increasingly busy roads (Sullivan 2000).

In light of the conflicting forces that may determine snake and mesopredator abundance in urban environments, the response of native bird species to the combined effects of habitat alteration and variable predator densities becomes surprisingly uncertain. Ground-nesting birds in particular are known to be especially vulnerable to nest predation by both mesopredators and snakes (Rollins and Carroll 2001, Morrison and Bolger 2002, Weatherhead and Bloun-Demers 2004, Staller et al. 2005, Rader et al. 2007). But if snakes and mammalian predators sharply diverge in their response to urban growth, it is conceivable that ground-nesting bird populations experience nearly
stable predation pressures across urban gradients. Evidence does exist that snakes can overtake mammals as the most important nest predators in old field (Thompson and Burhans 2003) and edge habitats (Chalfoun et al. 2002). Even more intriguingly, Patten and Bolger (2003) found that although snake abundance and overall predation rates upon the nests of ground-nesting birds were both highest in rural regions, the birds themselves declined in more urbanized, low-snake environments.

In this study, we used nocturnal road-cruising to sample snake, mammal, and ground-nesting bird populations across multiple gradients of urbanization in the Sandhills region of North Carolina (Figure 1). The Sandhills retain some of the most extensive tracts of the critically endangered longleaf pine ecosystem remaining in the southeastern USA, yet these protected areas are interspersed within a rapidly expanding matrix of urban and exurban developments (NC WRC 2005). The goals of our study were to better understand how different wildlife taxa respond to urban development and associated habitat loss, and to provide new empirical insights into the complex species interactions that may occur with changes in the intensity of human land use. We use our results to test three associated hypotheses:

**Research Hypotheses:**

1. Snake and ground-nesting bird detection rates will decline sharply as a function of increasing levels of traffic and urbanization.
2. Mesopredator mammal encounter rates will increase with increasing levels of traffic and urbanization, but will decline again within the most extreme urban environments.

2. Snake and ground-nesting bird detection rates will show significant negative relationships with mesopredator encounter rates, even after accounting for the effects of traffic and urbanization on the prey groups.

3.2 Methods

3.2.1 Study Area and road transect design

Our research took place in the Sandhills region located in the south-central portion of North Carolina, USA (Figure 1). The original vegetation of the Sandhills consisted of savannas of longleaf pine (*Pinus palustris*), turkey oak (*Quercus laevis*) and wiregrass (*Aristida stricta*) in the xeric uplands, and dense "pocosin" type vegetation and mixed pine/hardwood tree overstory in the bottomlands and creek drains dissecting the sand ridges (Wells and Shunk 1931, Sorrie et al. 2006). The longleaf pine ecosystem is currently recognized as one of the most endangered major habitat types in North America, with over 97% of the original extent destroyed (Van Lear et al. 2005, Frost 2006). The relatively large amount of protected longleaf forest in the Sandhills now serves as a background matrix for the rapid urban development that has occurred in recent decades across the region. Given that urbanization is a rampant phenomenon across the coastal plain of the southeastern USA, results from the Sandhills should be
very informative about the status of native longleaf pine animal communities across the original range of this ecosystem.

3.2.2 Road-cruising techniques

We established road-based transects across two gradients of urbanization in the Sandhills (Figure 2). We drove the road transects at night, beginning at dusk (19:30-21:00 hrs) and finishing shortly after midnight. To avoid biasing the results, we employed a number of different starting locations on the northern and southern routes, and alternated between starting points and route directions using a stratified random design. The vehicles were driven at a consistent low speed (between 48-56 km/h), and we recorded the locations of all vertebrate animals, live or dead, encountered on the roads. We also recorded free-ranging animals that were within 20 m of the road. We drove the transects on 39 nights in 2006 (northern route only), and 46 nights in 2007 (northern and southern routes). Our survey effort was much lower in 2008, as the focus was on a mark-recapture project for amphibians (discussed in Chapter 2), and we only drove the northern route on 4 nights. These statistics, along with further details about our survey effort across the three years, are summarized in Table 1. On certain nights in 2006, and on the great majority of nights in 2007-2008, we drove the transects with the vehicle windows down, to enable detection of the loud and distinctive calls of the three species of nightjars (Aves:Caprimulgidae) that breed in the Sandhills region.
3.2.3 Ground-nesting bird point counts

In order to provide an independent estimate of the numbers of nightjars calling along the route, we performed replicate pairs of 3-minute point counts at 75 stations placed at the midpoints of the 1-km segments used to calculate road animal encounter rates along the northern route (see below). The surveys were conducted on clear nights over a nine day period (30 May - 7 June, 2007) corresponding to the dates of the full or nearly full moon, conditions under which nightjars are thought to call more reliably. The same 75-point count locations were later resurveyed during the morning hours for bobwhite quail (*Colinus virginianus*). Again, two three-minute point counts were conducted at each site over a period of three consecutive mornings, June 19-21, 2007. For both the quail and nightjar point counts, if passing vehicle traffic made it impossible to hear the birds, we temporarily stopped the count timer until the road was quiet again.

3.2.4 Animal Encounter Rates and Habitat Variable Calculations

We used ARCGIS software (ESRI 2005) to plot animal locations at the appropriate points along the roads. The road routes themselves were then broken into a series of segments, each roughly 1 km in length (range 800-1200 m). We then simply divided the total number of animals for each species or analysis group that were observed on each segment by the total distance driven on that segment (actual length * number of trips), and then adjusted the units so that the final encounter rates would be more intelligibly expressed as "number of animals/100 km driven."
Four types of habitat variables were calculated for each road segment for statistical comparison with the animal data. These included measures of traffic flow, impervious surface, forest cover, and protected area coverage along the routes. The simplest predictor variable was average daily traffic volume ("ADT05"; range 20 to 14,000 vehicles/day), derived for each road segment using the most recent traffic data available from the NC Dept. of Transportation (NC DOT, 2005). The remaining variables were calculated as average values for overlapping polygons established as buffers around each road segment at a range of 11 different buffer distances (30, 250, and 500 m, plus 1, 2, 3, 4, 5, 6, 8, and 10 km). The multi-scale variables included traffic density ("trafden", an improved version of road density in which the traffic of the roads is taken into account; Pellet et al. 2004), percent impervious surface ("impsf", an index of urban development; Morse et al. 2003), proportion forest cover ("for", all forest types within the buffers), and the fraction of the buffers that was occupied by protected or managed areas ("marea"). Protected areas in the Sandhills are generally managed with prescribed fire, especially the upland longleaf forests, and we hypothesized that this index might be more useful for explaining the abundance of certain longleaf-dependent species.

Gibbs et al. (2005) recently demonstrated that environmental characteristics measured within 5 - 10 km scale pond buffers were unexpectedly the most powerful determinants of frog and toad population persistence. Since the birds, mesopredator mammals, and many of the snakes we targeted in the present study occupy much larger
home ranges than frogs and toads, we favored the use of a broad range of buffer scales. Although we could have attempted to restrict the variable calculations to non-overlapping buffers extending perpendicularly from the segment edges, such a design would have represented a highly contrived and unrealistic model of the influence of traffic and land use characteristics on animal abundance along the transect.

3.2.5 Statistical Analyses

In place of traditional linear models that have often been used for similar data sets, we instead employed an improved version of single regression tree analysis, a powerful nonparametric statistical approach based on recursive partitioning (splitting) of the data set into more homogenous subgroups (De’ath and Fabricius 2000).

Regression tree models offer two key advantages relevant to our data set: they do not make strict assumptions about the independence of sample points, and they easily capture complex nonlinear relationships between the response and predictor variables without requiring transformations or other impediments to clear interpretation (De’ath and Fabricius 2000). The only major disadvantage of the regression tree approach is the tendency of the resulting models to over-fit the data unless pruned with some cross-validation technique. For our tree analyses, we used the RPART library (Therneau and Atkinson 1997) for the free statistical software package R (R Development Core Team 2007). We modified the standard RPART protocol by increasing the number of cross
validation trials (from 1 to 200), and by adding a Monte Carlo test of significance with 500 random permutations of the animal data (see Chapter 2).

To test our first two hypotheses, we ran the different snake, bird, and mammal groups against the full set of 45 habitat variables (11 scales each of forest, impervious surface, protected area, and traffic density, plus ADT05). We also evaluated the response of each animal species or group of species to each of the 45 habitat variables individually, to see how the resulting models might compare to those derived from the full set of predictors, and to allow for comparison across species of their relationships to particular environmental factors. In order to test the third hypothesis concerning potential predator-prey relationships, we first ran the prey groups against a combination of the full set of habitat variables and the relevant predator encounter rates. Single variable regression trees were also developed predicting prey encounter rates as a function of each individual predator group. We then used the predictions of the best single-scale traffic or urbanization tree model for each prey group to create new sets of residuals, representing the unexplained variance leftover after accounting for traffic or urbanization. These residuals were run against the predator encounter rates (which had not been similarly adjusted for urbanization/traffic) to search for “pure” predator effects on the prey encounter rates.

We ran the regression tree models described above for the combined data set representing the total wildlife encounter rates for the 75 segments of the northern route.
across the three years of surveying (2006-8), with the segment encounter rates serving as the unit of analysis. Weather conditions differed substantially between the two main field seasons, in that 2007 brought near-record drought conditions statewide in North Carolina, whereas 2006 had essentially normal rainfall. Including the data from the segments of the southern route, which were only driven during the drought conditions of 2007, tended to reduce the cross-validation performance of the models significantly.

### 3.3 Results

#### 3.3.1 General animal results

We observed a total of 4900 vertebrate animals on or near the road transects during the three field seasons, representing a minimum of 69 species. Broken into groups, our combined 2006-2008 data includes 2665 amphibians (14 species), 250 snakes (27 species), 6 lizards (2 species), 18 turtles (3 species), 1356 mammals (17 species), and 9 live or dead birds seen directly on the road (3 species). Also included in the overall total were 592 birds we heard at night while driving the route, representing all 3 local species of nightjars. Chuck-will’s-widows (*Caprimulgus carolinensis*) were detected twice as often as whip-poor-wills (*C. vociferus*) and three times more frequently than common nighthawks (*Chordeiles minor*). Black rat snakes (*Elaphe obsoleta*, n=46), copperheads (*Agkistrodon contortrix*, n=37), black racers (*Coluber constrictor*, n=24), corn snakes (*Elaphe guttata*, n=20), and scarlet snakes (*Cemophora coccinea*, n=19) were the 5 snakes most frequently encountered along the transects. The fact that even these common snakes
ended up with fewer than 50 individuals in our data set precluded species-specific regression tree analyses. Domestic dogs (Canis familiaris) were the dominant component of the mammal fauna we observed on the road transects in all three years (633 dogs out of 880 total mesopredators). This appeared to be chiefly the result of a single remote household where large numbers of dogs (5-15) were allowed to roam freely each night. Domestic cats represented over half of the remaining mesopredators (134 out of 247), followed by possums, raccoons, and two species of foxes. Only one coyote and one bobcat were seen on the road routes during the study, both in rural areas with mixed agricultural and forest land use. Tables 6 and 7 collate the road-based observation data for snakes, birds, and mammals from all three years of the study. Not shown in the mammal and bird tables are certain miscellaneous species that were not included in the analyses due to very low sample sizes, but which are included in the species and total individual counts listed above. These include birds which were seen on the road but not heard (e.g. quail, wild turkey), and also various mammals such as beaver, mice, bats, and rats.

### 3.3.2 General results from the bird point count data

Summing across the three-day sampling period of the morning quail counts, we detected 68 total calling quail at the 75 sites (range 0-4 birds/point count). During the four evenings when we conducted the nightjar point count surveys, 218 chuck-will’s-widows (C. carolinensis), 125 whip-poor-wills (C. vociferus), and 6 nighthawks (Chordeiles
minor) were detected. Comparison with the driving-based detection data indicates that
the nighthawks were severely under-sampled by the nocturnal point counts. Our
impression (which will be tested explicitly in future analyses) is that peak nighthawk
detection rates occurred later in the summer, earlier in the evening, and with much less
correlation to the brighter moon phases, than did the rates for chucks and whips. Also,
nighthawks vocalize only while flying, and their relatively modest calls are thus further
attenuated by the altitude at which the birds are feeding.

3.3.3 Snakes vs. traffic and urbanization

Results for the snake regression tree models confirm our first hypothesis that
encounter rates would steeply decline as a function of traffic and urbanization.
Nocturnal snakes (abbreviated as "noctsnakes") were accounted for separately from total
snakes ("totsnakes"), because the small number of strictly diurnal snakes we found on
the road were all dead. We also pooled together the encounter data for all of the snake
species that had the potential to include rodents and ground-nesting bird eggs or
nestlings in their diet ("ratbirdsnakes"). For all three snake groups, the best single
variable models (those with the highest cross-validation $R^2$; Table 8) predict that
encounter rates fall by a factor of 3 to 5 as traffic and impervious surface increase to their
highest levels along the road transects (Figure 12). For example, nocturnal snake
encounter rates drop from 1.8 animals/100 km on roads with less than 2048 vehicles/day,
to only 0.3 animals/100 km on roads above that threshold.
The traffic and impervious surface models performed consistently across a broad range of buffer scales, generally from 250 m to 5 km for the nocturnal and total snake groups (and also the bird indices described below). Alternative single variable models based on forest cover or protected area did not explain as much of the variation in snake encounter rates as did traffic density or urbanization. The simple Average Daily Traffic volume metric (ADT05) was generally outperformed by all four of the other variables, at least when the other variables were measured at their best scales. Nocturnal snake encounter rates from the southern route (driven in 2007 only) matched those of the northern route fairly consistently across the different habitat variables (Figure 13), and this pattern was repeated for the bird and mesopredator mammal data described below.

### 3.3.4 Ground-nesting birds vs. traffic and urbanization

Similar to what we observed for the snakes, all four species of ground-nesting birds displayed sharp declines in detection rates as a function of traffic and urbanization. For example, our models indicate that the single species road nightjar encounter rates fell by a factor of 4-10x or more between the low and high traffic density portions of the combined route, and the total road nightjar detection rate ("totcaprim") plunged by 20x in response to increases in traffic density at a 2 km radius (Figure 14). Likewise, the average point counts for the nightjars (e.g. "avgchucks") also declined precipitously, up to 32x for the whip-poor-wills, and 4-5x for the chuck-will’s-widows. The most striking patterns in the ground-nesting bird data sets, however, were
displayed by the point counts for bobwhite quail. The raw data from the point counts confirm the regression tree prediction that zero quail will be detected when impervious surface at a 4 km radius rises above a threshold of only 0.58% (Figure 15). The same striking trend holds for impervious surface and traffic density when measured at scales from 1 to 5km – we simply did not record any calling quail at points along the more urban stretches of the northern road transect. The index bird groups (equally-weighted combinations of relativized road and point count detection rates) generally outperformed either of the single methods alone. In fact, the indices for total nightjars ("indexcaprim") and for total ground-nesting birds ("indexgroundbirds") achieved the highest cross-validation and apparent $R^2$ values of any models in the current analysis.

3.3.5 Mesopredator mammals vs. traffic and urbanization

Quite different results were obtained when we applied the regression tree models to the mesopredator mammal encounter rates. Instead of declining as a function of traffic and urbanization, all of the mesopredator groups except domestic dogs reached their highest detection frequencies along the urban components of our road transects. For example, total mesopredators ("mesopreds" - excluding dogs) were predicted to be detected twice as often in areas with higher traffic density (best scale = 3 km, Figure 16) and impervious surface (best scale = 10 km). Similarly, the regression tree models predict that 4-5 times as many cats will be detected at higher levels of trafden5km and impsf4km.
The native mesopredators ("mesnocats", not including dogs or cats) were also predicted to reach peak encounter rates on roads in urban areas (e.g., with impervious surface at a 250m radius between 4.7 and 13%). However, both the impervious surface and traffic density best-scale models for mesnocats indicated that encounter rates for these animals would decline on roads with the highest levels of urbanization (Figure 17). None of the dog regression tree models returned significant results until we adjusted one segment (which was a clear outlier, with > 200 dogs/100 km driven encountered) to be equal in magnitude to the second highest rate observed for the canines (10.8/100 km driven). Then, and in contrast to our results for the other mesopredators, 4 times higher dog encounter rates were predicted for road segments with the lowest levels of traffic density (250 m radius).

While the models for forest cover were not generally informative, both the cats and the total mesopredators displayed strong negative relationships with the amount of protected area surrounding the road segments (Figure 18). Protected area coverage was inversely related to traffic density, but a 3-way plot of mesopredator encounter rates as a function of both protected areas and traffic shows that the variables potentially have independent effects. Consistently low mesopredator rates were observed on segments with low traffic and high protected area, whereas low traffic, low protected area segments often had moderate levels of mesopredators (Figure 19).
3.3.6 Snakes and ground nesting birds vs. mesopredators

When we tested for direct relationships between the prey species and their potential predators, significant regression trees were returned for only 8/11 bird groups and the nocturnal snakes (Table 9). The models for three of the bird indices (indexcaprim, indexchucks, and indexgroundbirds) showed the hypothesized negative relationship with mesopredator mammals. When mesopredator encounter rates were above 2.1 animals/100 km, bird detections fell to only 1/3 or 1/2 of their maximal values on low mesopredator portions of the road route. In contrast, most of the bird groups were associated positively in the regression tree models with ratbirdsnakes. These models predicted twice as many bird detections on road segments with more than 0.5-2 ratbirdsnakes encountered per 100 km driven.

Neither the snakes nor the mammal predators appear to be as influential at limiting bird encounter rates as the traffic or urbanization variables. The trend can be visualized by plotting bird encounter rates against the predator and urbanization variables simultaneously (Figure 20). Such graphs make it evident that medium to high bird detection rates occur across the entire range of ratbirdsnake values, and across all but the highest levels of mesopredators. In contrast, the bird detection rates decline much more dramatically across the axes of traffic or impervious surface.

From the snakes' perspective, the only non-empty predator tree that was returned was for the relationship between nocturnal snakes and cats, with 60% more
snakes expected when cat encounter rates fell below 0.58 animals/100 km driven. This model actually had a negative cross-validation $R^2$, and undoubtedly was not statistically significant (no permutation test was run due to the low $R^2$). But the prediction does match the obvious trend in the data that is evident in the scatterplots of the nocturnal snakes vs. cats and total mesopredators (Figure 21).

None of the full models we ran considering both the habitat and urbanization variables and the predator encounter rates ended up using a snake or mammal predator group in the final level of cross-validation pruning. Likewise, the residual models for the birds and the snakes did not yield any results that appeared ecologically meaningful or even visually interpretable.

### 3.4 Discussion

To our knowledge this is the first study to associate snake road encounter rates (live plus dead) with a wide range of traffic conditions and across gradients of urbanization. Other projects with similar methodologies have typically focused on rural areas (e.g. Bernardino and Dalrymple 1992, Mendelson and Jennings 1992, Rosen and Lowe 1994, Sullivan 2000, Coleman et al. 2008, Shepard et al. 2008) or very short stretches of suburban roads (Enge and Wood 2002, Ciesiolkiewicz et al. 2006). Only a few trapping (Cagle 2008) or visual-encounter based investigations (Patten and Bolger 2003) have been conducted on snake populations at differing levels of urban development, and these also have yielded more frequent snake detections in rural areas.
The steep decline in snake encounter rates we observed in the Sandhills as a function of traffic and urbanization implies that snake populations along the urban roads of the transects have already been depleted by years of ongoing traffic mortality. A similar trend was documented for a road through Organ Pipe National Monument in Arizona, where nearly 10 times more snakes per km driven were found in 1949 (3 years after the road had been first paved) than between 1988-1991 (Rosen and Lowe 1994). However, our results seem to contradict the findings of another road survey of snake populations in California, where snake encounter rates appeared to increase over time despite a doubling of traffic volume (Sullivan 2000). We note, though, that even after doubling in traffic volume, Sullivan's route only supported 660 vehicles/day, well under the threshold we observed for nocturnal snakes in the Sandhills (2048 vehicles/day). Also, under very low traffic conditions, increasing numbers of vehicles may yield an increase in the number of dead snakes observed on the road, at least until the level of mortality begins to deplete the local abundance of snake populations. Snakes, like turtles (Gibbs and Shriver 2002, Aresco 2005), seem to be quite sensitive to urbanization (Andrews and Gibbons 2005, Roe et al. 2006, Row et al. 2007), and this intolerance undoubtedly has played a key role in the general declines reported for reptile species around the world (Gibbons et al. 2000).

Our results also confirm the emerging consensus in the literature that ground-nesting birds are negatively effected by increasing intensities of human land use. The
sharp declines we observed for the three nightjar species closely parallel the results of Liley and Clark (2003), who found that densities of European Nightjars (Caprimulgus europaeus) were inversely correlated with urban development. Our data also provide the first direct examination of quail detection rates across a single, spatially coherent gradient of urbanization. Previously, Veech (2006) demonstrated that US Breeding Bird Survey (BBS) routes which recently lost their bobwhite quail populations were located in heavily urbanized landscapes (mean 29.4% urban at a 25 km radius). The severe decline in quail detection rates that we have documented in the urban areas of the Sandhills (a region which is otherwise known for its abundant quail populations), combined with the broader scale analysis of Veech (2006), should cause quail biologists and southeastern land managers to reconsider the importance of urban development as a primary factor in the decline of this game species. Other than the presence of more abundant mesopredators (discussed below), there are several potential reasons why either the quail or the nightjars would be intolerant to urban growth. These include direct road mortality (we found chuck-will’s-widows and quail dead on the road during the surveys), noise pollution (Reijnen et al. 1997), and lack of appropriate food resources or sheltering habitats.

In contrast to the snakes and ground-nesting birds, mesopredator mammals generally reached their highest encounter rates in the more urbanized regions along our route. Higher urban cat populations were expected based on results from other studies
in the western USA (Crooks and Soule 1999, Crooks 2002, Maestas et al. 2003), although Caro et al. (2000) found no differences in cat road-kill rates between areas characterized as urban or rural in an agricultural region of California. The native mesopredators in the Sandhills (raccoons, possums, and red and gray foxes) were less strongly associated with urbanization than the cats, a result that is consistent with the ambiguous findings of previous studies. For example, Prange and Gehrt (2004) found raccoon road-kills near Chicago, Illinois to be more positively associated with urban developments than possums, whereas Caro et al. (2000) documented the exact opposite trend in California. Explanations for the avoidance of well-protected landscapes by cats and other mesopredators in the Sandhills include decreased trash and pet food subsidies, lack of households to shelter indoor/outdoor cats at night, greater abundance of coyotes (Crooks and Soule 1999), intolerance of the various effects of prescribed burning, or exposure to larger numbers of human hunters on public lands.

Our road survey represents the first simultaneous measurement of snake, ground-nesting bird, and mesopredator mammal encounter rates across a gradient of urbanization. In agreement with Patten and Bolger (2003), we found that snake and ground-nesting bird encounter rates declined in parallel as the amount of urbanization increased. At the same time, our results also confirm the negative relationship between detection rates of mesopredator mammals and native birds presented by Crooks and Soule (1999). This leaves us with the same intriguing paradox mentioned by Patten and
Bolger: why do higher snake populations in rural areas fail to limit ground-nesting bird populations to the same extent apparently achieved by urban mesopredators? One possibility is that even though snakes are effective nest predators, the demographic consequences of predation on fledgling and adult birds by mesopredator mammals are much more severe (Patten and Bolger 2003). Our results do suggest that land managers and wildlife biologists should abandon the antiquated idea (Stoddard 1931, Imler 1945) that snake-control efforts on rural protected areas are an effective way of promoting greater abundance of quail and other ground-nesting birds. Instead, wildlife conservationists should focus more of their attention on disentangling the complex trophic mechanisms and habitat relationships that drive local extinctions of both ground-nesting birds and snakes in urbanizing areas.

Fairly robust empirical arguments can be made in support or denial of our central assumption, which is that road encounter rates provide a reasonable index of relative population density for the different animals along the transects. For example, Gehrt (2002), Baker et al. (2004), and Fahrig et al. (1995) all found that road surveys (for raccoons, foxes, and amphibians, respectively) provided similar results to abundance estimates derived using other techniques. Alternatively, many species of mammalian carnivores seem to display patterns of behavior that limit exposure to high-traffic roads in urban areas (Harrison 1997, Riley et al. 2003, Baker et al. 2007). Snakes might also be more difficult to detect in urbanized areas due to activity level adjustments. Bonnet and
Naulleau (1996) describe a high-density yet extremely sedentary population of asps (*Vipera aspis*) in France, in which none of 64 radiotelemetered snakes were ever observed crossing the roads that bordered the 33 ha study site.

Finally, even though our limited sample sizes forced the aggregation of the snakes and mammals into analysis groups, we are not implying that all species within these groups responded with equal sensitivity to urbanization. For the Sandhills native mesopredators, which were all large enough to easily observe on the roads, conflicting levels of urban tolerance would likely have the effect of canceling each other out, yielding combined models showing weak or neutral effects of traffic and impervious surface. For the snakes, it is conceivable that biased detection in favor of the larger species may have obscured higher levels of urban tolerance among the smaller snakes. Several of the smallest snake species we captured (e.g. *Carphophis, Storeria, Virginia*) are known to reach high densities in urban areas in North Carolina (Palmer and Braswell 1995), quite possibly due to escape from predation by larger snakes such as *Coluber* and *Lampropeltis*. Along our route, however, these same small snakes were observed just as often (if not more frequently) in lowland swamp areas as they were on roads passing through cities and suburbs.

There may also be important inter-specific differences among the ground-nesting birds in terms of their sensitivities to urbanization. Although Common Nighthawks were most frequently observed along our study route near the large, well-burned tracts
of the Sandhills Gamelands, this species is occasionally abundant in urban areas in other regions, particularly as the birds forage at night around bright stadium lights. Nighthawks fly much higher off the ground while feeding than the two species of *Caprimulgus*, which often perch on roads to watch for passing moths (Jackson 2003). Also, nighthawks have demonstrated a capacity for breeding on flat rooftops in urban areas, which would largely shield them from cats and other nest predators.

We plan additional studies based on the current data set to address some of the uncertainties described above. The best way to address the question of how road encounter rates compare to absolute local densities will be to conduct other census techniques for the snakes (drift fences with funnel traps) and mammals (track stations and camera traps) at various intervals along the same road routes, concurrent to additional driving surveys. These sampling efforts, in combination with more point counts for the birds, would be even more useful if also conducted at varying distances from the surveyed roads, in order to estimate how far the road depletion/enhancement effects extend (Reijnen et al. 1996, Rudolph et al. 1999, Forman and Deblinger 2000). We predict that such studies will show not only that the width of the road effect zone depends on the traffic volume of the road (Reijnen et al. 1996, Forman et al. 2002), but also that overlapping road effect zones will inflict additive demographic impacts on the wildlife populations involved. This type of data will also prove instrumental in better addressing the key landscape-scale question of road ecology: "under what circumstances
do roads affect population persistence?” (Roedenbeck et al. 2007). At present, our results from the Sandhills seem to indicate that quail, nightjars, and many species of larger snakes will fail to maintain viable populations in urbanizing regions within the former range of longleaf pine.

3.5 Conclusions

Our results have clear and urgent implications for conservation policy improvements in the Sandhills and other longleaf pine ecosystems in North Carolina and neighboring states. The two groups of urbanization-sensitive wildlife species we have identified in this study (snakes and ground-nesting birds) will apparently suffer dramatic declines in local abundance if urban development is allowed to penetrate into the dwindling supply of low-traffic, low-impervious surface environments. The expansion of urbanization into formerly remote regions of the Southeast will also eventually lead to the general collapse of robust and healthy native wildlife populations outside of the largest currently protected habitats, which by themselves reflect only a very small percentage of the historical range of the diverse longleaf ecosystem. Ironically, such declines may not be apparent to nature-loving citizens already living in cities and suburbs, since according to our results from the Sandhills, wildlife populations in existing urban areas will have already been diminished to levels far below their historical potential (i.e. the "shifting baselines" phenomena, (Turner et al. 2004). On a more encouraging note, our results do suggest that large protected areas (on
the order of 10,000+ ha in the Sandhills) have reduced feral cat and native mesopredator densities, and relatively robust populations of native snakes and ground-nesting birds. Establishment of additional protected landscapes at this scale should therefore continue to be a high priority for land conservationists.

Chapter 4. Wildlife Community Structure across a Gradient of Urbanization in the North Carolina Sandhills

4.1 Introduction

Conservation biologists around the world are increasingly concerned with quantifying the effects of urbanization on native biodiversity (McKinney 2002, 2006). In the absence of experimental manipulations of land use intensity (which are very rarely attempted due to their cost), most of the comparative studies of urban impacts on native species have relied on sampling the abundance of target organisms along existing gradients of urban expansion (McDonnell and Pickett 1990, Crooks et al. 2004, McDonnell and Hahs 2008). This correlative approach is challenging from a research design perspective due to the fact that urban development imposes spatially-complex and temporally-dynamic changes to the natural environment (Zhang et al. 2004, Yu and Ng 2007, McDonnell and Hahs 2008). There are many important components within the overall process of urbanization that each can be measured independently, including human population density, road density, traffic flow, and the overall amount of impervious surfaces such as concrete or asphalt. Also, single species may respond to the influence of these land use characteristics at multiple different scales, and empirical
measurements have often shown the range of influential scales to be larger than would be assumed based on theory alone (Pellet et al. 2004, Gibbs et al. 2005).

In idealized terms, then, a comprehensive study of the abundance of a target species along an urban gradient would include a very large number of sites, well-stratified across conditions representing all possible combinations of landscape metric types and scales. Unfortunately, even if such a study could be afforded, in the real world many potential measures of urbanization intensity are correlated with each other (and across scales) to such an extent that certain combinations are impossible to identify. Fortunately, the intercorrelated variables are susceptible to being reduced to much simpler axes of urban impact, using multivariate ordination procedures which have been developed for this purpose (Hahs and McDonnell 2006). Such reduced axes can then be compared to wildlife abundance trends to determine how different species respond to more integrated, comprehensive indices of urban impact. Even though species interactions are believed to be highly important mechanisms for determining the persistence of particular animals within urban environments, only a few studies have simultaneously compared the multivariate structure of wildlife communities to the multi-dimensional aspects of urban development (Melles et al. 2003, Cagle 2008, Pillsbury and Miller 2008).

Also, given the constraints imposed by different trends in landscape pattern upon each other (Wu 2004, Turner 2006), it is challenging to identify an optimal group of
study sites that will allow for effective disentanglement of the various forces that may constrain or enhance target species across the urbanization gradient in question. It is therefore understandable that few studies of the response of wildlife populations to urban development have assessed the adequacy of their sampling design with respect to the multivariate structure of human influence on their study region, either before or after the animal census work took place.

In this investigation, we use a powerful nonparametric ordination technique to investigate the integrated response patterns of four vertebrate guilds (amphibians, snakes, ground-nesting birds, and mesopredator mammals) to urbanization. By repeatedly driving a set of road transects crossing urban gradients in the Sandhills region of NC, and by conducting bird point counts along the same routes, we were able to derive relative encounter rates for a wide range of species. We then employ non-metric multidimensional scaling (Kruskal 1964, McCune and Grace 2002) to examine the holistic arrangement of wildlife communities along the urban transects. Our research was aimed at discovering how the different wildlife species and taxonomic groups separate out along reduced axes representing the multivariate composition of animal communities along road transects in the NC Sandhills. Our results prove quite informative regarding the relative sensitivities of different wildlife groups to urbanization, the potential for interactions between the animal groups, and the adequacy of the road route we used to sample the urban gradient.
4.2 Methods

4.2.1 Study area

Our research took place in the Sandhills region located in the south-central portion of North Carolina, USA (Figure 1). The original vegetation of the Sandhills consisted of savannas of longleaf pine (*Pinus palustris*), turkey oak (*Quercus laevis*) and wiregrass (*Aristida stricta*) in the xeric uplands, and dense "pocosin" type vegetation and mixed pine/hardwood tree overstory in the bottomlands and creek drains dissecting the sand ridges (Wells and Shunk 1931, Sorrie et al. 2006). The longleaf pine ecosystem is currently recognized as one of the most endangered major habitat types in North America, with over 97% of the original extent destroyed (Varner and Kush 2004, Van Lear et al. 2005, Frost 2006). The relatively large amount of protected longleaf forest in the Sandhills now serves as a background matrix for rapid urban development, mirroring the land use patterns of much of the rest of the coastal plain of the southeastern USA. In fact, according to the estimates provided by Frost (2006), the amount of urban development within the former range of longleaf pine increased by ~1500% from 1900 to 2000 (rising from 460,000 ha to more than 7.5 million ha). Urban growth can therefore be considered one of the top potential threats to the persistence of wildlife communities in what remains of the once vast acreage of longleaf ecosystems.
4.2.2 Route Description

We established two non-overlapping road-based transects across gradients of urbanization in the Sandhills (Figure 2). The first route (~75 km long, hereafter the "northern route") started in the urban centers of Southern Pines, Pinehurst, and Aberdeen, ran briefly between Weymouth Woods State park (363 ha) and the western edge of Fort Bragg (~73,000 ha), crossed back into some moderately urbanized areas south of Pinehurst, and then headed southwest through a mixture of rural land uses until it wrapped around the large northern block of the state-owned Sandhills Gamelands (which total ~24,000 ha in various tracts). The second route (~69 km long, the "southern route") started from the end of the northern route, then trended south to wrap between two additional large blocks of the Gamelands, finally heading south and west through rural areas before hitting the urban cores of former mill towns Rockingham and Hamlet. The approximate length of each transect was chosen specifically to allow for a round-trip (out and back) of a single route (or a one-way traverse of both routes) in the roughly four hour period from dusk to midnight.

Average daily traffic volume on the roads ranged from 20 to over 14,000 vehicles per day, according to the most recent survey data available from the NC Dept. of Transportation. As is evident in Figure 2, both transects ended up being weighted in favor of the rural side of the urban gradients. This design, which will be discussed in greater detail in the Results and Discussion sections below, was necessary to allow us to
sample both the extensive longleaf forests associated with the larger Gamelands tracts, and the urban centers of the cities along the route, with the distance between the two extremes preventing us from adding more urban roads to compensate for the traverse.

4.2.3 Road-cruising techniques and bird point counts

We drove the road transects at night, beginning at dusk (19:30-21:00 hrs) and finishing shortly after midnight. To avoid biasing the results, we established a number of different starting locations on the northern and southern routes, and alternated between starting points and route directions using a stratified random design. The vehicles were driven at a consistent low speed (between 48-56 km/h), and we recorded (by dictating odometer readings (0.1 mile accuracy) into a tape recorder) the locations of all vertebrate animals, live or dead, encountered on the roads. We also recorded free-ranging animals (i.e. not constrained by chains or fences) that were within 20 m of the road.

We drove the northern road transect on 39 nights in 2006, for a total distance of 5752 km. In 2007 we drove both the northern and southern routes on 46 nights (total distance of 10,341 km), including 21 km added as frequently-driven access routes to our field housing and various starting points along the northern transect. Our survey effort was much lower in 2008, as the focus was on a mark-recapture project for amphibians, and we only drove the northern route (plus access roads) on 4 nights, for a total of 533 km.
On certain nights in 2006, and on the great majority of nights in 2007-2008, we drove the transects with the vehicle windows down, to enable detection of the loud and distinctive calls of the three species of nightjars (Aves: Caprimulgidae) that breed in the Sandhills region. In 2007, we added a series of 75 point count stations corresponding to the midpoints of each 1-km segment of the northern route. These were surveyed twice for nightjars, on nights with full or nearly full moons when the birds are known to call more intensely, and twice in the morning hours for bobwhite quail, another ground-nesting bird that is highly valued as a game species in the region.

Additional details about the road survey efforts and bird point count methodologies are presented in Table 1 and in the text of Chapters 2 and 3 of this dissertation. In this Chapter, as in the previous chapters, we focus our attention on the 2006-2008 combined results from the northern route. Wildlife encounter rates showed similar trends along the southern route in 2007, but the drought conditions that year had the effect of reducing the frequency of animal observations to the point where it was difficult to merge the data from the two transects together for statistical analysis.

4.2.4 Wildlife Encounter Rates by Group

Road encounter rates (total animals observed (live plus dead)/100 km traveled) and average point count detection rates (birds per 3-minute point count) were combined into a set of 13 wildlife groups for this analysis (Table 10). These included three groups each of frogs and toads, snakes, and mammalian mesopredators, plus four species-
specific encounter rate indices for ground-nesting birds. Prior to their inclusion in the
ordinations, each of the 13 groups were relativized by the maximum value for each
group, to avoid having the most abundant taxa (e.g. toads) swamp the community
structure results.

4.2.5 Environmental Variables

We also used ARCGIS software to generate 110 different environmental
variables, including Average Daily Traffic volume for the roads themselves (ADT05)
and 11 scales each for traffic density, impervious surface, and coverage values for forest,
longleaf pine forest, protected areas, crops, grasslands/pastures, wetlands, and water.
The scales, which corresponded to the radii of the buffers around each 1-km segment of
the northern route, included 30, 250, and 500 m, plus 1, 2, 3, 4, 5, 6, 8, and 10 km (Table
11). The final variable used was relative elevation (250 m - 10 km), which was not
calculated at the 30 m scale, as it was based on comparing the elevation of the 30 m
pixels along each segment of road to the average elevation in the road buffers. Each of
the 110 variables was further relativized by its maximum value prior to inclusion in the
ordinations.

4.2.6 Multivariate ordination techniques

Non-metric multidimensional scaling (NMS) attempts to find the arrangement of
samples in a new n-dimensional ordination space that best maintains the rank-order of
the original Euclidean ecological distances between samples (Kruskal 1964, McCune and
Grace 2002). Beginning with an essentially random assortment of points, NMS shifts the location of each point in a given dimensionality ordination until the relationship between ecological distance and ordination distance is most-clearly monotonic (=lower "stress" level). NMS is increasingly favored among community ecologists, who appreciate the lack of assumptions about the structure and dimensionality of the original data sets used in the analysis (McCune and Grace, 2002).

We used the program PCORD (McCune and Mefford 2007) to run NMS ordinations, employing McCune and Grace (2002)’s step-down technique to identify the optimal number of axes by running ordinations from 6 axes down to one. For each level of dimensionality, 100 runs with the real data were performed, with a stability criterion of 0.00001 and using up to 100 iterations to find stable results. A random number was used to generate the starting coordinates for the ordination, and Bray-Curtis distances were employed to create the distance matrix used for evaluating the segment arrangements in ordination space. Monte Carlo randomization (with 250 permutations) was performed to evaluate the significance of the final lowest stress level achieved by each of the tested number of axes. The axes themselves were also varimax rotated to ensure better correspondence with the environmental variables. After we identified the best number of axes to use (based on looking for natural breaks in the stress vs. number of axes curve) we re-ran the NMS ordination using only this number of axes, and the same parameter values and procedures listed above, to generate a final solution for each
analysis. We then employed McCune and Grace (2002)'s method of using partial Mantel Regressions of high-dimensional ecological distance on the low-dimensioned ordination distance to calculate the fraction of the total compositional variation that was explained by each ordination axis (= R²).

The species-space ordination we created was based only on the matrix of relativized encounter rates for the 13 wildlife groups. The ordination procedure calculated optimal axis scores for each road segment along each of the final number of dimensions. We then calculated the position of each wildlife group across the same axes, using the encounter rates for that group from each segment to derive the weighted average axis scores. Next, the correlation coefficients between the relativized group encounter rates and each of the sets of axis scores was determined (Pearson’s r). The same correlation strengths were also calculated for each of the 110 environmental variables, to indicate the degree to which they were associated with the different primary axes. Finally, we graphed these results in "joint-plots" (McCune and Grace 2002) showing, for each possible pairing of different NMS axes, the weighted average scores of the wildlife groups overlain with the "trajectory" of each environmental variable. We also graphed the relative encounter rates for each group as a function of the various pairings of axis scores.
All of the ordination plots were visually inspected to determine the degree of correspondence between the wildlife groups, the environmental variables, and the NMS axes.

4.2.7 Evaluation of the road transect

The final step in our analysis was to examine the degree to which the road route captured the available range of urbanization conditions in the Sandhills region. Here we used the same 16,099 road segments that were employed in Chapter 2 to map out the projected road encounter rates for amphibians across the 9-county region (see Figure 11, Ch. 2). For each segment we calculated the average impervious surface value within buffer polygons with a 1 km radius from the route. The resulting distribution of available conditions was then compared to a histogram of the impervious surface values that were sampled by the northern route.

4.3 Results

4.3.1 NMS ordinations in species-space

The dimensionality step-down procedure indicated that a three-axis solution was optimal for efficiently capturing the variation in the species-space distance matrix, with a cumulative $R^2$ of 0.859. The total amount of variation explained by each axis in the final 3-dimensional NMS ordination was relatively even, with incremental $R^2$ values (adjusted for lack of orthogonality between axes) of 0.240, 0.378, and 0.241 for axes 1, 2,
and 3, respectively. Table 12 provides a complete listing of the stress-level and other parameters for the species-space ordination.

Weighted average axis scores for the snake, ground-nesting bird, and amphibian groups clustered together on all three axes, indicating close associations between these species in terms of their mutual distributions along the route. Cats and native mesopredators, however, differed sharply from the other wildlife groups, which can be clearly seen on axis pairings 2 vs. 1 and 3 vs. 1 (Figures 22 and 23). The native mesopredators seemed to define much of the variation in axis 1, whereas the cats were separated from all of the other groups on axes 2 and 3 (Figure 24). Apart from the wide gaps between the two groups of mammal predators and their potential prey items, other distinctions in the plots were relatively minor. The ground-nesting birds tended to cluster together at low levels of axis 3, in a position that put them the furthest away from the cats and native mesopredators on plots involving this dimension. Axis 3 also sorted the wetland associated species together closely, including the hylid tree frogs, ranid true frogs, and the aquatic snakes.

The 110 road variables sorted out in fairly consistent patterns across the three axes of the species-space ordination. Traffic and impervious surface at all scales were strongly negatively associated with axis 1 and axis 2, and slightly positively associated with axis 3. The water variables from 2-5 km showed the same pattern as the urbanization metrics on axes 1 and 2, as did the various scales of relative elevation. In
the opposite direction, the longleaf pine, protected areas, forest, crops, grasslands, and wetlands all showed positive correlations with the first two axes. Axis 2 seemed to correspond more with the wetland, crops, and grassland variables, whereas longleaf pine, forest, and protected areas were more correlated with axis 1. None of the habitat or urbanization variables had tight correlations with axis 3, with traffic density at 2 km ($r = 0.421$) and longleaf pine at 1 km ($r = -0.345$) defining the limited extremes.

Comparison of the correlation strengths between the species encounter rates and the axis scores and the between the environmental variables and the axis scores indicates that urbanization (or the lack thereof) clearly is the defining trend across the first two dimensions of the species-space ordination (Table 13). The urban-sensitive species are aligned away from the urbanization metrics and from the cats and native mesopredators on these two axes. Neither group of predators, however, closely matches the trajectories of urbanization and traffic. Actually, since the axes in the species-space ordination are defined only by the animal encounter rates, it is more accurate to state that the traffic and urbanization variables did not precisely match the variation in wildlife community structure that seemed to be correlated with the presence of cats and native mesopredators. This discrepancy is easiest to visualize in a 3-dimensional plot showing all three axes at once (Figure 25), where it is much more clear how the urban-sensitive groups are oriented directly away from the urbanization variables in all three
dimensions, whereas the predators are angled off from this angle in nearly orthogonal directions from each other.

The scale at which the environmental variables are measured has a high degree of influence on the relative strength of their correlations with the axes of the species-space ordination. For example, forest cover at a 4 km radius has a much higher correlation coefficient with axis 1 ($r = 0.674$) than forest cover at a 6 km radius ($r = 0.048$). While the magnitude of the variable correlations changed with scale, the direction of these correlations was more stable. Longleaf pine and water were the only variables to make sharp changes in polarity across scales, in each case switching to be more positively associated with urbanization at broader scales.

4.3.2 Observations about the adequacy of the route for sampling the urban gradient

When we looked instead at the distribution of urbanization conditions across the broader 9-county Sandhills region, the road transect matched the heavy skew of the available impervious surface (1 km radius) values towards more rural environments. Out of the 16,099 road segment buffers created in the broader Sandhills, just over 70 percent contained average impervious surface values between 0 and 5 percent, whereas 80 percent of the 75 segments on our northern route fell into this least-urbanized category (Figure 26). Otherwise, the major difference between the two distributions seemed to be the much longer "tail" of the Sandhills-wide buffer compilation, which reached a maximum value (56.3% impervious) that was nearly 4 times higher than the
maximum value on the northern transect (16.1 %). The most intense levels of urbanization in the Sandhills largely occur within the city of Fayetteville, NC, which unfortunately was too far from our base of operations to allow for inclusion in the transects.

### 4.4 Discussion

#### 4.4.1 Community response of wildlife groups to urbanization

The multivariate ordination of wildlife encounter rates yielded a number of significant insights into the structure of animal communities along the urban gradient we sampled. First, the snakes, ground-nesting birds, and amphibians were all associated with each other, with only minor distinctions evident between the upland species (particularly the birds) and the wetland species (the frogs, aquatic snakes, and small snakes). The center of the cluster of wildlife group weighted averages was not surprisingly occupied by toads, which numerically were the dominant group across all of the species we recorded.

The two groups which differed most dramatically from the toads and other species were the cats and native mesopredators. Our results suggest that while the cats are more commonly encountered in urban areas, the road segments within the urban areas where cats were particularly abundant had different wildlife community structure than would have been expected based on the urban conditions alone. The native mesopredators, on the other hand, were widely distributed across the urban gradient,
but in portions of the route where they were abundant, they too seemed to play a role in defining the major axes of community structure. These tendencies provide much stronger support for an independent negative effect of mesopredator mammals on the abundance of their potential prey species (especially the ground-nesting birds and snakes, but possibly including the amphibians as well) than was achieved via the regression tree approach reported in Chapter 3 of this dissertation.

Regardless of the existence of an independent mesopredator effect, it is clear that traffic and impervious surface were the dominant environmental variables associated with the primary axes of the species-space ordination. This result is consistent with the regression tree results for amphibians (Chapter 2) and the snakes, birds, and mesopredator mammals (Chapter 3). Other studies using the ordination approach to examine vertebrate relationships with urban gradients have found similar results. For example, Pillsbury and Miller (2008) determined that urbanization constituted the primary axis of their Canonical Correspondence Analysis (CCA) ordination of frog and toad community structure among wetlands in Iowa. Interestingly, two species in that study, the bullfrog (*Rana catesbeiana*) and cricket frog (*Acris crepitans*) were both positively associated with urban conditions, with the bullfrog showing the greatest tolerance for increased levels of road density. While none of the amphibian groups we studied in the Sandhills showed a positive trend in with urbanization or traffic in the ordinations we conducted across all wildlife groups, the ranid frogs (which included a
number of bullfrogs) were consistently the amphibians which were the least negatively correlated with urbanization.

Both Melles et al. (2003) and Chapman et al. (2007) also found that urbanization served as the major CCA axis sorting out a diverse array of bird species in Canada and Minnesota, respectively. Only one of the ground-nesting species studied by Melles et al. (2003) showed a statistical predilection for urban environments, and that was the Canada Goose, which is large and aggressive enough to defend its nest against many potential predators. Chapman et al. (2007) indicate that a group of sensitive native bird species dropped in abundance by roughly 80% across the transition from rural to suburban land use. This steep decline is consistent with the reduction in ground-nesting bird encounter rates we documented in Chapter 3.

Cagle (2008) used NMS to examine snake community structure as a function of grassland conditions and urbanization in Illinois. In her study, Cagle found that urban cover (at both the 1 km and 10 km scales) and road density (1 km scale) were significantly associated with snake occurrence and community composition patterns. In the only other ordination-based survey of reptile response patterns to urbanization that we are aware of, Germaine and Wakeling (2001) report that lizard communities in and around Tucson, Arizona were significantly related to a primary CCA axis representing the degree of urban development. One of the lizard species was strongly associated with higher levels of housing development, whereas several others reached higher densities
in more natural desert conditions. Few studies have apparently used multivariate ordination techniques to explore the community structure of mammals along urban gradients. Prange and Gerht (2004) used logit models to show that rates of raccoon road-kill and trapping observations were more positively associated with urban and suburban development in the Chicago, Illinois metropolitan area, than two other mesopredators (opossums and skunks). Interestingly, total mesopredator detection rates (for all three species combined) were roughly an order of magnitude higher (~10 mesopredators/100 km driven) than what we recorded in the Sandhills, a difference that can perhaps be attributed to the lower productivity of the sandy soils in our study region, and the lower intensity of urban development.

4.4.2 Environmental Structure across scales along the urban gradient

Several of the environmental variables also displayed interesting changes in their degree of association with the primary axis of urbanization. In our regression tree analyses of amphibian encounter rates (Chapter 2), we noted how the amount of water in the road buffers shifts from being an important indicator of aquatic habitat availability at the lower scales, to serving as a powerful index of the degree of urbanization at the 1 km and larger scales, due to the greater abundance of lakes and ponds in urban and suburban residential developments. We are not sure how to explain the fact that longleaf pine coverage also shifted from rural to urban association as the scale increased. At the broader scales, the urban areas were more uniformly situated in
upland environments, and so may have contained more residual longleaf pines than some of the rural areas that were composed of mixtures of agriculture and wetlands. In contrast, it is also quite interesting how many of the other variables shifted in trajectory as the scale increased, such that they were increasingly negatively correlated with urbanization. This result undoubtedly stems from the simple lack of space for patches of other land use types as the amount of urbanization peaks at very broad scales.

4.4.3 Evaluation of the study route

Our final goal in this research was to evaluate, with the benefit of hindsight and multivariate ordinations, the degree to which the road transects we employed in the Sandhills from 2006-8 provided a reasonable sampling frame for measuring the impact of urbanization on local wildlife. Given the spatial autocorrelation that exists between the segments, it could be argued that much of our replication was in fact pseudoreplication (Hurlbert 1984). The long strings of road segments with overlapping buffers certainly do not provide the sort of independent landscape-scale assessment envisioned by Brennan et al. (2002). However, short of wasting large amounts of gasoline to reach isolated stretches of road scattered 10+ km apart across the study region (and ignoring animals observed while in transit), it seems that spatial autocorrelation is an inevitable feature of transect-based wildlife research. In our view, the spatial autocorrelation that exists amongst adjacent segments of an urbanization transect should be treated as an essential structural component of the holistic impacts.
imposed by real urban gradients on native wildlife. If we were to remove the
autocorrelation from the environmental variables and animal encounter rates in a
misguided attempt to justify the use of standard parametric statistics, it is not clear that
the residual "pure" effects would be meaningful from the standpoint of wildlife ecology
or conservation. Urbanization and species persistence are both inherently spatial
phenomena, and we are thus skeptical of the variety of autocorrelation correction
procedures that have emerged in recent years, most of which are based on stripping
away the spatial structure of the variables of interest.

In retrospect, of course, it would have been more powerful from a statistical
perspective to reduce the overabundance of road segments at the rural/wild end of the
transect by replacing them with even more replicates of the gradient-spanning nature
just described. Our southern route was designed more with these goals in mind, but the
severe drought that struck in 2007 reduced the cross-transect comparability of the results
to a surprising extent. We do plan to undertake an ordination-based comparison of the
2007-only animal observations for the northern and southern routes, in the hopes that
despite the lower sample sizes available for just that year, the data will still provide an
indication of whether the wildlife community structure was similar across routes.

Even with the assistance of computer-aided transect design, we anticipate that
efficiently capturing landscape variation that is well-stratified across all of the spatial
scales that may be important for a wide range of wildlife species will remain a
fundamentally challenging endeavor. We suspect this difficulty is the reason why so few
studies similar in scope and purpose to the current investigation have quantified the
multivariate, multi-scale structure of the environmental conditions that were actually
sampled for wildlife abundance. Ideally this quantification would take place prior to the
initiation of fieldwork, but even post-hoc evaluations such as we present in this report
would lead to greater transparency regarding the adequacy of wildlife research design.
NMS, CCA, or PCA ordination plots are useful to a certain extent for this purpose, but it
must be remembered that such graphs indicate trends relevant to the average conditions
amongst the field sites that were actually employed. A better approach, and one that we
have very modestly attempted here for a single variable at a single scale (impervious
surface 1 km), is to examine the environmental conditions that exist across the entire
study region of interest. Such information can then be used to strategically arrange
transects or field sites in order to capture a more balanced and efficient representation of
the environmental gradients of interest (Urban et al. 2002).

4.5 Conclusions

Our northern road transect seems to have spanned enough of the modest
gradient of urbanization that exists in the Sandhills region of North Carolina to discover
rather striking patterns of urban sensitivity among multiple species of native wildlife.
Snakes, ground-nesting birds, and amphibians all closely associated with each other
within the rural trajectory-space of the various ordinations. In contrast, domestic cats
displayed a consistent positive relationship with urbanization in the environment-space ordinations. Cats even appear to have defined at least one of the three primary axes of the species-space ordination, indicating a lack of co-occurrence with the prey species, and possibly a strong influence in structuring the overall composition of the small vertebrate communities along the transects. Our route was biased in favor of the rural side of the urbanization transect, mirroring the overall characteristics of the Sandhills, but thereby missing the opportunity to achieve better replication across the crucial intermediate stages of urban development. The fact that we nonetheless were able to document steep declines in native snake, ground-nesting bird, and amphibian encounter rates seems indicative of just how intolerant some of these animals are to the combined effects of traffic, urban development, and enhanced mesopredator populations. Conservationists will need to redouble their efforts to protect, restore, and enlarge the remaining rural wilderness areas that still persist in the rapidly urbanizing states of the southeastern USA.
Chapter 5. General Discussion of Methodology

5.1 Caveats and assumptions

The first obvious caveat that must be emphasized is that my road-cruising methods were designed to measure encounter rates for wildlife species on (or at least very close to) the roads I traveled. I did not attempt to estimate actual animal abundance (e.g. population density) in the areas along the roads, as doing so would have required intensive mark-recapture studies that were not in my judgment a feasible addition to the road-cruising technique, at least given my available budget for the project. Many of the animals I encountered were of course already dead, and therefore not subject to recapture. High levels of ongoing mortality would also violate many of the assumptions of typical methods for estimating abundance and detection probability. Other methods (discussed below) are better suited for trying to assess absolute levels of population density for various animals at certain locations, and these estimates could then be fruitfully compared to simultaneous measurements of road encounter rates. My study was also not intended to provide any kind of precise index of absolute levels of road mortality along the survey routes. As observed by Langen et al. (2007), walking-based surveys are much more effective if accurate counts of small dead vertebrates are desired.

Instead, my focus in this research was on generating estimates of relative local abundance (via encounter rates) for a wide range of species across a large geographic area, and road-cruising seemed to accomplish this task quite admirably. It is a given that
none of the species I encountered were detected with perfect accuracy. It is also certain that the different species varied to a considerable extent in the degree to which they were detectable on roads even when present in local habitats. Much of this variation depends on the size of the organism and the speed at which the animal crosses the road. While we recorded some very small snakes (e.g. < 7 cm total length for one Storeria occipitomaculata) and numerous tiny frogs and toads (~ 1 cm) during the road surveys, the rate at which we failed to observe smaller vertebrates was inevitably much higher than the non-detection rates for the larger species. Other than restricting the species-specific analyses to the larger animals, this sort of variation in detection probability is unlikely to have played a significant role in biasing the final results with respect to the urban gradients, since I did not rely on direct comparison of encounter rates between groups.

Looking within groups, though, (e.g. nocturnal snakes in Chapter 3) it is possible that the negative urban response patterns exhibited by certain easily detected species could have overwhelmed the positive urban affiliations of species that were harder to see on the roads. As I discussed in Chapter 3, certain small snake species are indeed quite common in urban and suburban environments, and even if these small snakes were on the road at night in proportion to their local abundance, we may have missed enough of them to obscure the trend. Small vehicle-flattened Storeria and Virginia (both of which have gray-colored dorsums) would be among the most difficult snakes to
detect on the road under any circumstances. Since more of the snakes would be DOR in urban areas, the potential remains that we missed a sizeable percentage of the urban-tolerant small snakes along our route. Among amphibians, cricket frogs (~2 cm total length) were the only frog species that we heard regularly along the transects but never directly observed live or dead on the road. This could reflect the close year-round association of these frogs to the ponds, or it is possible that we either missed seeing the frogs entirely, or we misidentified them as small hylid tree frogs. Given the lower detection probabilities of these smaller species, my results for snakes and amphibians could perhaps be viewed conservatively as applying only to the larger snakes, toads, and frogs that made up the bulk of the observations for these groups. Even though we observed the large-bodied snakes such as rat snakes, racers, and copperheads more frequently, the smaller snakes almost certainly were an order of magnitude (or more) more abundant in the habitats along the route, highlighting the perils of trying to infer relative densities based on road encounter rates alone.

However, it is also theoretically possible that certain species varied in their detection-rates as a function of urbanization or traffic conditions, in ways that were not directly linked to their absolute local abundance. For example, several studies have indicated that mammalian carnivores living in urban environments can adapt their behavioral patterns so as to reduce their risk of being struck by vehicles (Baker et al. 2007). This sort of behavioral change has yet to be documented for amphibians or
snakes, although this is a worthy subject for future research. If urban animals minimize their road-crossing behaviors to a sufficient degree, the net result would be less road-detections per unit of true local density in urban environments. Such a trend would yield stable or even declining encounter rates for a given species as a function of increasing levels of traffic, even in the absence of reduced local density.

One other behavioral mechanism that could interact with animal learning to disrupt the connection between animal abundance and road-crossing rates is territoriality. When a new road is built through natural habitat, it would cross the established territories of numerous individual animals, who would then be expected to be killed off quickly as they attempted to navigate around their usual environment. Every subsequent year, a smaller number of dispersing animals might attempt to establish home ranges in the newly vacant habitats along the road, and would suffer the same fate. Eventually, however, it is possible that animals successfully living along either side of the road would adjust their territories to line up closely with the road without crossing it, and then only a small number of juvenile dispersers would be run over each year. Some sort of territorial adjustment pattern such as this could explain the frequently observed phenomena of high initial animal mortality along newly built highways followed by long-term decline in road-kill observations, although gradual declines in local population size due to road mortality would cause the same pattern.
Mortality-induced natural selection would also obviously tend to favor heritable behavioral patterns that reduce an animal’s likelihood of being killed on the road.

Surprisingly few studies have been conducted on this crucial issue of how animals either learn or evolve their behavior to avoid being struck by cars in urban areas. I hope that future investigators will more clearly address this obvious possibility in a way that allows for comparison across species (and even across populations or individuals within a species with varying exposure to urbanization) and for correlation with apparent sensitivity to human impacts exhibited by different species over varying lengths of time.

Vehicle avoidance is not the only reason that wildlife species might have been differentially detectable along my study routes in ways that might confound my attempts to relate encounter rates to environmental variables. Based on my own experiences during the study, one certainty is that on higher traffic roads, the additional cars themselves make observing live or dead wildlife more difficult while road-cruising. This can be a function of both direct obstruction (the other cars block the researcher’s view of the animal during the brief window of potential observation) and visual interference from the bright headlights of oncoming vehicles. Traffic noise could also have drowned out the calls of the nightjars and quail we were listening for in the road surveys and point counts. In the point counts at least, we attempted to correct for traffic noise by pausing the count while noisy streams of vehicles drove past. During the road surveys, we could not keep stopping to wait for traffic to diminish. We did however
make a substantial effort to drive each portion of the route during the full range of time periods from 8pm to midnight, and this should have reduced any systematic bias caused by relative traffic levels at different times of night. I did not conduct hourly traffic surveys on the Sandhills routes, but my impression was that traffic in both the urban and rural sections of the route declined significantly after 10 pm.

Animals might have also been easier to detect on the side of the road if the habitats along the road were more open. Herds of deer, for example, were more visible in open fields than they were in dense thickets of pocosin vegetation. Dogs and cats would likewise be easier to detect from the road if they were present in suburban or rural lawns or wide grassy road verges, than if they were hiding in heavier cover.

Other obvious sources of differential detection probabilities include nightly, weekly, or monthly variation in temperature, humidity, and rainfall, and also light levels associated with changing sunset times and moon phases. High amphibian observation rates were closely tied to warm rainy nights, as expected. Nightly weather variation should not have played a strong role in spatially biasing my results, however, since I drove the entire route (for a given field season) on most nights. The huge decline in amphibian abundance between the 2006 and 2007 field seasons should be mostly explained by the shortage of warm rainy nights during the drought in 2007. There could also have been detection biases introduced by the different observers conducting my road surveys. I will eventually incorporate the driver identities, along with the other
factors described above, into a comprehensive analysis of detection probability (MacKenzie et al. 2002, Bailey et al. 2004b, Pellet and Schmidt 2005). The task of coding each of the 100+ "visits" to each of the 165 road segments, for each species and animal group, and according to the detection covariates listed above, will not be insignificant. But the results will be worthwhile, as they should allow us to make some distinctions between variation in detection probability and variation in actual animal abundance.

In the meantime, and absent data to the contrary, the most parsimonious explanation for most of the strong trends I observed in the results is that variance in actual animal abundance along the road transects explains the variance I recorded in animal encounter rates. In my view, the stronger the trend in encounter rates, the less likely said trend is merely the result of detection probability bias, since abundance is widely assumed to be the primary driver of animal detection rates within a species (Royle and Nichols 2003). But I still encourage great caution in extrapolating the significance of my results beyond their strictest interpretation (variation in animal encounter rates along the specific roads I drove in the Sandhills over two and a 1/10th field seasons and between the hours of 8 pm-midnight). New multi-taxon, multi-method studies examining wildlife abundance patterns on and off roads as a function of urbanization and habitat loss will eventually be conducted, perhaps with new funding from the NC Wildlife Resources Commission. Until such studies are complete, my road-cruising results presented in this report, bolstered by similar results from other
investigations around the world, should be considered as strong working hypotheses as to the effects of urbanization on native wildlife species in North Carolina.

5.2 Recommended improvements to my road survey methods

In this section I provide some detailed recommendations for improving and extending my road survey methods:

1. Extend the research for several more seasons on the full set of transects (north and south). The results of my 2.1 year study in the Sandhills, while quite convincing in many respects in their own right, are certainly quite deserving of being confirmed by an additional 2-3 years worth of field work. Many of the regression tree models seemed hampered by variability in the segment by segment encounter rates for the different species of wildlife I studied. Adding a set of additional field seasons to the data already obtained would likely provide more stable estimates of true animal abundance patterns along the full 165-km route from Southern Pines to Rockingham. As noted in Chapter 4, the southern route should provide an essential degree of replication to the results I have documented for the northern transect. Additional years of data would also build up sample sizes for a range of individual species, allowing for better species-specific modeling of urbanization impacts for the snakes and mammals in particular. Of course, even with an additional three years of data, not all of the snake, amphibian, or mammalian carnivore species (especially coyotes and bobcats, and the rare diurnal snakes) would end up with enough unique observations to run individual models. The
amphibian data is much more adequate, at least at the Genus level. For comparison, in the only other road-based census of live and dead amphibians across different levels of traffic, Fahrig et al. (1995) completed their surveys in only six nights, whereas I sampled much of the northern route in the Sandhills on nearly 80 nights and over 100 separate 1-way trips.

2. Undertake measurements of animal abundance along (and at varying distances from) my Sandhills road transects using alternative methods. These estimates could then be compared directly to simultaneously recorded road encounter rates for the same animals. The net result would be much greater confidence as to whether or not road encounter rates provide a useful index of true animal abundance in the areas adjacent to the surveyed roads. It will also be crucial to conduct replicate measurements of animal abundance at a range of distances from the roads used in the survey effort. For example, to estimate reptile and amphibian abundance away from the road route, drift fences with pitfall and funnel traps could be installed in replicate arrays arranged perpendicular to the edge of the road (Rudolph et al. 1999). And for the mammals, camera or live-capture trap stations could be set up in similar arrays. Likewise, bird point counts could be distributed along and at varying distances from the road route, to allow for estimation of the road effect zone (Forman and Deblinger 2000). Playback call surveys might be useful for testing the hypothesis that nightjars or quail are present in urban areas but simply not calling regularly enough to enable detection.
3. Attempt a more exhaustive mark-recapture study of amphibians along selected portions of the route, to try and produce estimates of how many individual animals are represented by a given encounter rate. For example, on the road segments with the highest *Bufo* toad encounter rates (>10 animals/100km driven), do those encounter rates represent the same toad being observed night after night, or different animals?

4. Drive the route during the day as well as at night, to allow for more accurate estimates of encounter rates for diurnal animals. This is especially needed for the rare diurnal snakes, including pine snakes, southern hognoses, and coachwhips. In recent years, Jeff Beane and numerous volunteers have been conducting a substantial amount of daytime road-cruising on the roads in and around the Sandhills Gamelands, under the auspices of "Project Simus". By frequently driving the standardized route I employed in this study during daylight hours (and with guidance from Jeff Beane and others as to the best times of day/seasons of the year to find certain species) it should be feasible to create better indices of rare diurnal snake abundance as a function of urbanization.

5. Make various essential improvements upon the road-cruising technique. These would include: A. Taking a more standardized approach to tallying and removing dead animals observed on the road during the study, such as removing all dead amphibians and snakes, and marking dead mammals with spray-paint (Clevenger et al. 2003); B. Having each field vehicle team record ambient and road temperatures,
humidity, and the start and stop times of rain events at more frequent intervals while
driving the route, to provide more detailed covariate information for estimating
detection probabilities for each wildlife species; and C. Devising a custom system (e.g.
Ramp et al. 2005) that would allow a single driver to quickly and easily plot GPS
locations for each animal encountered, and to match each location with details such as
species, status, notes, etc, without having to stop the car repeatedly.

5.3 Future studies on the effects of urbanization on wildlife populations

In addition to carrying on an additional set of field seasons along my route in the
Sandhills, using the modifications I have proposed above, it would also be interesting to
conduct the same sort of investigation in other regions of North Carolina (and in other
parts of the country/world). Then it would be possible to answer such interesting
questions as: ”Does the same widespread species (e.g. eastern box turtle or black rat
snake) display the same level of sensitivity to urban impacts in widely varying
environmental conditions (e.g. in the mountains, the piedmont, the Sandhills, and the
coastal plain)?”. Carrying out the same research in different regions and thus along
independent gradients of urbanization would also allow for testing the generality of my
Sandhills results.

If it does appear that certain species (e.g. quail, *Bufo* toads, etc.) show drastic
decreases in abundance as a function of increasing urbanization, then conservation
scientists will want to undertake more controlled studies of the underlying mechanisms
that suppress these sensitive species in urban zones. For example, mesopredator control experiments, if properly conducted in urban areas, could quickly reveal whether mesopredators are truly the limiting factor on snake and ground-nesting bird abundance in urban environments. It may of course be difficult to receive public approval for intensive manipulations of cat population densities in urban areas. At the very least it should be relatively simple to measure amphibian and reptile population densities in areas with and without large colonies of feral cats.
Chapter 6. Overall Conclusions and Conservation Implications

6.1 Overview

In this Chapter I compile the major findings from my three data chapters into a series of condensed summary points. Each point is supported by key supportive details from the results, and I also provide a brief synopsis of the significance of the conclusion with respect to the ecological literature. Additional references and discussion are provided in the individual chapters themselves, and the reader is directed there for more extensive review of each topic. Also, keep in mind when reading this section that many of my conclusions are relevant to conservation only if my central assumption in this dissertation is true - that road encounter rates provide a useful index of local wildlife populations along the transects (discussed above). Following the major findings section is a summary of the conservation implications of my dissertation research. Here I present general conclusions that will be widely applicable in other settings where urbanization and traffic threaten the survival of sensitive native species. I conclude the dissertation with a specific list of policy recommendations for achieving greater conservation success in the Sandhills region of North Carolina.
6.2 Summaries of Major Findings from this research

Major Finding 1: Amphibian, snake, and ground-nesting bird encounter rates decline sharply as a function of increasing levels of traffic and urbanization. These declines were starkly obvious in the single variable graphs of encounter rates vs. traffic, traffic density, and percent impervious surface, and were confirmed with significant regression tree results (see Chapters 2 and 3). For example, total amphibian encounter rates plunged by a factor of 16 as the transect progressed from the rural to urban extremes. Projecting total amphibian encounter rates based on traffic density across all of the roads in the broader Sandhills region yields the conclusion that a majority (64%) of the 16,000+ km of roads have enough local vehicle traffic to reduce amphibian encounter rates by 50% or more. Similarly, nocturnal snakes were 3-5 times less common on roads in urban areas, and total nightjars dropped to only five percent of their peak rural abundance in such environments. The most dramatic sensitivities were found for whip-poor-wills (32x decline urban vs. rural) and bobwhite quail, which were not detected at all above the very low threshold of 0.58% impervious surface at a 4 km radius from the road segments. For amphibians, snakes, and ground-nesting birds, my Sandhills study now represents some of the best data available concerning relative detection rates for these animals across a wide-range of traffic and urbanization conditions. My study is the first major cross-taxon survey of live and dead animals along road transects spanning a full gradient of urbanization. Only a few comparable non-
road (e.g. site or trap-based) projects have been completed, such as Maestas et al. (2003), who found significantly higher levels of native biodiversity on rural ranchlands in Colorado, compared to exurban residential developments in the same area.

**Major Finding 2: Peak amphibian road-kill encounter rates are found on road segments with the highest total (live plus dead) amphibian encounter rates.** The percentage of total amphibians that were dead increased with higher levels of traffic, from a low of 15% for roads with less than 885 vehicles/day, to a high of 47% dead when traffic exceeded 5200 vehicles/day. However, the decline in total amphibian encounter rates over the same range of traffic conditions was so severe that the encounter rate for dead amphibians was highest on relatively quiet roads in rural environments. Put another way, on the higher traffic urban roads with at least several thousand cars per day, only around two frogs and toads will be encountered per 100 km driven, and one will be dead. In contrast, on the lowest traffic roads, 35 or more amphibians will be detected per 100 km driven, and five will be dead. Therefore, as also shown by Fahrig et al. (1995) in a short term survey (six nights) across a coarse gradient of traffic conditions (three levels) in Canada, it appears that high levels of road-kill are associated with the most abundant local amphibian populations.

**Major Finding 3: Mesopredator mammal encounter rates are highest on roads passing through urbanized environments.** Domestic cats in particular were 4-5 times more frequently encountered on urban stretches of road, whereas the total mesopredator
encounter rate doubled as the route passed from rural to urban conditions. Native mesopredators (raccoons, possums, foxes) did not show the same clear increase, and in fact the combined encounter rates for these species actually fell at the highest traffic/most urbanized extremes. Free-ranging domestic dogs were the only mammalian carnivore species that were much more abundant in rural, low traffic regions, a trend likely to have been driven by greater human tolerance for loose dogs in rural areas. Other studies, such as Crooks and Soule (1999), have shown higher cat densities in urban areas where larger native predators such as coyotes are absent. My data provides the only road-based comparison of native vs. nonnative mesopredator populations along a comprehensive urban gradient, although unfortunately we did not record enough coyotes or bobcats to enable a full trophic analysis of the mammalian carnivore communities along the route.

**Major Finding 4: Snake and ground-nesting bird encounter rates show weak negative relationships with mesopredator encounter rates.** Nightjar and overall ground-nesting bird detection rates fell to only 1/3 to 1/2 of their maximal predicted values on road segments with total mesopredator encounter rates above 2.1 predators/100 km driven. Similarly, nocturnal snake encounter rates were only half as high on roads with high levels of cats vs. those without. These results were not as strong statistically as the relationships between the snake and bird prey groups and the measures of traffic and urbanization discussed above, probably due to high variance in the cat and
mesopredator data. When I tried to test for an independent effect of the mesopredators on the snake and bird groups, by first accounting for the effects of traffic and urbanization, no significant results were returned. The strong positive relationship between cats and urbanization makes it difficult to determine whether the mesopredators are in fact responsible for the declines observed in the prey species.

**Major Finding 5: Ground-nesting bird detection rates were positively associated with encounter rates for the larger species of snakes.** In fact, twice as many ground-nesting birds were detected along road segments where we also observed the highest levels of potentially bird-eating snake abundance (0.5-2 snakes/100 km). Although rat snakes, kingsnakes, and other similar species have recently been shown to be major nest predators for a variety of birds, my data from the Sandhills indicate that the snakes do not appear to be playing a role in reducing the abundance of nightjar and quail populations. This is the first time that snake abundance has been compared to bird abundance across a wide range of habitat and urbanization conditions, and it appears that low-traffic, low-urbanization areas can harbor robust populations of both groups at the same time. Stoddard (1931)’s assertion that snake control efforts were justified as a means for increasing populations of bobwhite quail appears to have been erroneous.

**Major Finding 6: Cats and native mesopredators appear to play strong roles in structuring the overall wildlife communities along the road route.** NMS ordinations based on all of the different wildlife groups encountered in the Sandhills show that cats
and native mesopredators each define one or more primary axes of species-space variation. Interestingly, neither of the two predator group positions quite matched the angle of the traffic and impervious surface variables in the same species-space ordinations. Instead, the cats and native mesopredators each veered away from the urbanization variables in a different direction. The prey species, on the other hand, were aligned in a tight cluster in essentially the opposite direction from the urban variables. This pattern, which is most apparent in the three-dimensional ordination plot presented in Chapter 4, provides the most direct evidence that the cats and other mesopredators may exert independent effects on vertebrate community composition along my study route. Few (if any?) studies have used the ordination approach to simultaneously examine predator prey relationships along gradients of urbanization or other environmental change.

**Major Finding 7: Cats and total mesopredators showed a strong negative relationship with the amount of protected area along the road route.** The best overall model for the cats suggests that seven times as many of these non-native predators will be encountered on roads with less than 2% protected area within a 6 km radius. Protected area coverage was inversely related to traffic density, but a 3-way plot of mesopredator encounter rates as a function of both protected areas and traffic shows that the variables potentially have independent effects. Consistently low mesopredator rates were observed on segments with low traffic and high protected area, whereas low
traffic, low protected area segments often had moderate levels of mesopredators. These results suggest that some factor associated with large protected landscapes in the Sandhills may be acting to reduce mesopredator populations. Possible mechanisms include increased hunting pressure on public gamelands, lack of food/trash provisioning due to lack of human households, and greater abundance of larger carnivores such as coyotes or bobcats.

**6.3 General Conservation Implications**

Looking across the data chapters, my dissertation results have clear and urgent implications for conservation policy improvements in the Sandhills and other longleaf pine ecosystems in North Carolina and neighboring states. The three groups of urbanization-sensitive wildlife species I have identified in this study (snakes, amphibians, and ground-nesting birds) will suffer dramatic declines in local abundance if urban development continues to penetrate into the dwindling refugia of low-traffic, high-forested environments. Such declines will likely result in the endangerment of scores of additional species with local or even global extinction. The expansion of urbanization into formerly remote regions of the Southeast will eventually lead to the general collapse of robust and healthy native wildlife populations outside of the largest currently protected habitats, which, by themselves, reflect only a very small percentage of the historical range of the diverse longleaf ecosystem. Ironically, such declines may not be apparent to nature-loving citizens already living in cities and suburbs, since
according to my results from the Sandhills, wildlife populations in existing urban areas will have already been diminished to levels far below their historical potential (i.e. the "shifting baselines" phenomena, (Turner et al. 2004)).

If the NC Wildlife Resources Commission and other conservation agencies and organizations in North Carolina want to prevent the collapse of native amphibian, snake, and ground-nesting bird populations outside of the existing set of protected areas in this rapidly developing state, then clearly some combination of the following three policy options must be pursued. First, we can and should substantially increase the amount of publicly-owned natural habitats in the state, in an attempt to coalesce existing smaller protected areas into cohesive reserve networks whose interior environments will be well-removed from the impacts of traffic and urbanization. The Sandhills Gamelands (24,000 ha) provide a useful indicator of the scale that may be necessary to safeguard many urban-sensitive vertebrates over the long-term.

A second option would be to find some financial or regulatory means to encourage private landowners to restore and manage large acreages of natural forests for the benefit of wildlife. Incentives for keeping private land undeveloped will obviously need to be set at a level where the rewards for long-term conservation exceed the short-term benefits of selling properties off to developers. Hopefully, the emergence of robust markets for carbon mitigation will generate substantial amounts of capital for buying agricultural lands in North Carolina and restoring these areas to native forests.
The third policy option is for NC lawmakers to establish a robust land-using planning framework under which local and state agencies would be required (or at least heavily incentivized) to steer new roads and urban developments away from the remaining large blocks of natural habitat. The NC DOT could play an especially useful role in this regard, by working with conservation groups to identify key regions of habitat where new road construction should be avoided. State and local planners could also work together to prevent vehicle traffic from increasing on existing low-traffic roads that pass through such key areas, by blocking new residential or commercial developments at either end of the relevant stretch of highway. According to my data, it only takes between 500 - 2000 cars per day to seriously reduce detection rates for snakes, amphibians, and ground-nesting birds. It would be a relatively simple exercise to identify the set of current low-traffic roads around the state whose location adjacent to high-quality natural habitats makes them ideal candidates for traffic stabilization efforts.

Realistically speaking, it may well take an aggressive combination of these three approaches to maintain some semblance of our historically-rich wildlife heritage in the Sandhills and Coastal Plain of North Carolina.

6.4 Sandhills-Specific Conservation Recommendations

Based on my road-cruising data and other field experiences I have accumulated over the last 7 years of field work in the NC Sandhills, I would like to make a few
specific suggestions for improving the success of conservation efforts in this important region:

1. Using some combination of direct land acquisition, private landowner agreements, and land-use planning, focus on protecting these key areas from urbanization and traffic growth:
   A. the rural buffer along the north side of the northern main block of the Gamelands (block A) - e.g. Millstone Rd, Gibson Mill Rd, Pappy Rabb Rd, Derby Rd, etc.
   B. the remaining rural and natural properties along the north and south sides of Thunder Rd, and the adjacent lands to the north along Rose Ridge and Roseland Rds, and along Hoffman Rd (SR 1004) to the west.
   C. the well-known "gap" that exists in Hoke County between Ft. Bragg and Camp Mackall/the Southern Main block (block B) of the Gamelands.
   D. the private lands that buffer the south side of block B of the Gamelands and connect this block with the smaller outlying Gameland parcels further south.

2. Close some of the existing sand roads through the Gamelands to vehicle traffic during the warm-season months. Roads in other Gameland areas in North Carolina (e.g. Holly Shelter) are typically closed during the intervals between hunting seasons, and the resulting lack of traffic must significantly reduce the amount of road mortality for native snakes and amphibians. In the Sandhills, the ideal road closure period would be mid-
April through mid-October, which would protect the seasonal activity patterns of slow-moving snakes such as southern hognoses, pygmy rattlesnakes, and northern pine snakes. Given the conflicts that such an extended road closure period would pose for existing spring and fall hunting seasons, a more realistic window might be from May 1st through October 1st, a five-month period which captures almost all of the primary active seasons for the resident snakes and for many of the amphibians. Also, closing the road during the summer months (regardless of the cutoff dates) would tend to encourage local residents to adopt alternate commuting patterns that might be continued over the remainder of the year out of habit and convenience.

However, in addition to the impact on hunting seasons, closure of some of the main roads through the southern main block of the gamelands would be politically complicated for two reasons. First, despite being sand-surfaced, the roads are state-maintained, and thus the NC DOT would have to agree to the project. This would undoubtedly require a great deal of negotiations with landowners to the south of the Gamelands, who use routes such as State Rd 1328 (Watson/Hoffman Rd) to access US Highway 1. Such negotiations should not prove intractable, as residents to the south already have two paved routes (SR 1001 to the west, and US 15-501 to the east) to make the same connection. The small inconvenience posed by the summer road closures to the very small number of people who live directly south of the Gamelands is more than justified by the reduction in mortality rates for rare vertebrates that would be achieved.
Furthermore, the private lands to the south of this block of the Gamelands are prime targets for conservation acquisition, and this process would reduce the number of affected citizens as well. Also, by closing the roads during the stormy summer months, the DOT would likely save a considerable amount of maintenance costs. Such savings could be redirected to improved maintenance and repair of the alternative commuting routes mentioned above.

The other complicating factor is that the military uses the Southern block for training exercises during various times of the year, and the state may not even have the authority to close the road to military vehicles. However, the military would undoubtedly prefer that the same roads be closed to public vehicles during their training periods, as this would reduce the risk that soldiers traveling on foot at night would be run over. Therefore the Army might be enlisted as a powerful ally in the closure campaign, at the expense of the continued presence of military vehicles.

Another natural ally in this effort would be the extensive and politically powerful group of people who ride horses (and horse-drawn carriages) through the Gamelands. If more suitable trailer parking/staging areas were provided along the outer edges of the two main Gamelands tracts, the horse community would likely eagerly agree to closing the roads to motorized vehicles, which pose a nuisance and a hazard to people seeking quiet weekend rides. It would also be worth exploring the possibility that any existing hunting seasons in April/May and September/October might be
converted to horseback or foot-travel only expeditions. Hunting for quail by horseback is certainly a popular activity on the larger quail preserves in the Southern USA, and horse-based hunts for larger game species such as deer and elk are highly-esteemed wilderness experiences in the Western USA.

In short, I believe it is much more feasible than commonly assumed to close the interior roads within the two main blocks of the Sandhills Gamelands during the warm season months when native reptiles and amphibians (not to mention quail and ground-nesting birds) are active. Given the NC Wildlife Resource Commission’s passion for increasing populations of quail, my results concerning the relationship between quail detection rates and vehicle traffic should be reason enough to give this idea serious consideration. If more quail are not enough of an incentive, the "stick" may well be the future classification of rare, traffic-sensitive snakes such as the pine snake and southern hognose as Federally Endangered Species.

3. **Create wildlife underpasses at key movement corridors between the larger protected areas in the Sandhills.** Much of the conservation planning that has occurred in the Sandhills has been done for the benefit of Red-cockaded woodpeckers. In light of my results, I suggest that greater attention now needs to be paid to the conservation requirements for road-sensitive species like snakes and amphibians. Currently, the three largest blocks of longleaf forest in the region are separated from each other by at least one major highway each. It is unlikely that many pine snakes or southern hognoses are
able to survive a daytime traverse of busy roads such as US 1 and US 15-501. I have also observed large numbers of nocturnal snakes dead on these same highways, indicating that nighttime traffic is also already a serious threat. Therefore, I would like to recommend that the NC Wildlife Resources Commission work together with the US Army and the NC DOT to establish highway underpasses at the following key locations around the Sandhills:

A. US Highway 1, between blocks A and B of the Gamelands. This highway is actually in the process of being expanded to 4 lanes already, but I am not aware of any plans to mitigate the impacts of the additional lanes and faster traffic on dispersing wildlife.

B. US 15-501, in Hoke County in the area with Sandhills Gamelands tracts on the east and west sides of the highway. An additional underpass could be constructed nearby at the site of the extremely large "dropzone" field at Camp Mackall, specifically for the benefit of pine snakes and coachwhips who use old-field habitats extensively.

C. NC 211, between Ft. Bragg and the state-owned McCain Tract, and possibly also between The Nature Conservancy's Calloway Tract and any new conservation lands that can be purchased on the west side of the highway.
D. Within Ft. Bragg, 2 or more underpasses each could be placed on King Rd (N-S route) and Plank Rd (E-W route). These are both high traffic, high speed roads that pass through large amounts of otherwise high-quality habitat.

E. Ft. Bragg Rd, between the main Weymouth Woods State Park site and the private lands that border Ft. Bragg. This would allow more regular faunal exchange between the small state park and the extensive longleaf forests of the military base.

To have maximum benefits for snakes and amphibians, each underpass should be patterned after the successful design used in Florida to mitigate wildlife mortality on a highway crossing Payne’s Prairie State Park (Dodd et al. 2004). Essential elements include long barrier walls that funnel animals to a set of underpass culverts. The walls should be designed to prevent snakes from simply climbing over the top and onto the roadway, and also should be built out of durable materials (ideally concrete or metal), rather than cheaper products such as silt fencing, which would only last for a few years.

I would be happy to assist with the design or implementation of any of the above recommendations for conservation improvements in the Sandhills.

Thanks for reading my dissertation!
Figures

Figure 1: Study area overview. The blue dashed line shows the northern transect which was driven in all 3 years. The orange dashed line represents additional road segments that were also driven in 2007 (and partially in 2008).
Figure 2: Routing of the road transects we drove in 2006-2008, shown against a background of impervious surface values. The impervious surface values (see inset legend) represent average percentages for 1 km buffers applied to each 30 m pixel of the study area, with red areas being highly urbanized and blue areas lacking significant impervious surface cover.
Figure 3: Total amphibian encounter rates (animals/100km driven) along the Sandhills road transect vs. Average Daily Traffic ("ADT05"= vehicles/day), by year. Blue circles are the 75 1-km road segments driven along the northern route in all three years, red triangles represent the 90 additional 1-km segments driven in 2007, mostly along the southern route.
Figure 4: Optimally pruned regression tree for total amphibians vs. traffic density, with traffic measured at a 250 m radius from each of 75 1-km road segments along the northern route. To read the tree, start at the first split at the top (trafden250 >= 44.91) and proceed downwards. The values at the three endpoints represent the predicted total amphibian encounter rates for each range in traffic density, with the number of road segments that fell into each node listed beneath.
Figure 5: Predicted total amphibian encounter rates (green bars), from the pruned regression tree model based on traffic density values (250-m radius). Blue points represent actual amphibian encounter rates for each of the 75 1-km road segments along the northern route.
Figure 6: Figure 6: Regression tree model results for ranid frogs vs. forest cover (2 km radius). The four predicted ranid encounter rates (green bars) from the regression tree are in the background, according to the relevant range in Forest Cover values. The raw encounter rate data (animals/100 km driven) for each road segment are superimposed as blue points.
Figure 7: Total amphibians encounter rates vs traffic density (250 m) and wetlands (250 m). The horizontal axis shows the percentage of a 250 m buffer around each of the 75 1-km road segments on our northern transect that is composed of wetlands. The vertical axis shows the traffic density value (cars per day per 30 m pixel) within the same buffers. The size of the blue circles indicates the relative magnitude of total amphibian encounter rates (scaled in terms of animals/100 km, with rates of "0" shown as the smallest points).
Figure 8: Total amphibians vs traffic density (250 m radius) at two levels of wetlands. Top graph shows only the 36 road segments with wetlands250 < 0.01 (low wetlands). Bottom graph shows the other 39 segments with wetlands250 > 0.01. Note the similar trend despite the 2x greater encounter rates in the lower graph (higher wetlands).
Figure 9: Regression tree model predictions for total amphibians vs. Average Daily Traffic (ADT; vehicles/day). The top graph shows the predicted total amphibian road encounter rates (live plus dead) as a function of different levels of traffic. The bottom graph shows the predicted trend in total amphibian mortality rates (% dead) as a function of ADT, using the same format as above.
Figure 10: Relationship between amphibian regression tree cross-validated R² and the scale at which the predictor variable (here impervious surface) was measured. Each amphibian group is represented by a different colored line (see legend on graph). There were 11 scales (30 m, 250 m, 500 m, 1 through 5 km, 6 km, 8 km, 10 km), each representing the radius of the buffers that were applied to the 75 1-km segments of the northern road transect. Hylidsnograytf = hylids without gray tree frogs, graytf = gray tree frogs only - these distinctions are not referenced in the text.
Figure 11: Projected Total Amphibian Road Encounter Rates - see text on map for details. Roads shown in red have the lowest predicted encounter rates (2.314 animals/100 km driven), whereas roads shown in green have the highest (37.94 animals/100 km driven). The large empty space in the center-right of the map is part of the Ft. Bragg military reservation. There are additional roads (primarily unpaved) in this area, but traffic information was not available.
Figure 12: Nocturnal snake encounter rates vs. traffic density (vehicles per day per unit area in the search radius) at a 1-km radius from the road segments of the northern transect (n=75, combined 2006-2008 data). Format follows above figures.
Figure 13: Nocturnal snake encounter rates vs. traffic density at a 1-km radius, for the 2007-only data for the southern route (07new90). Each point represents the encounter rate (animals/100 km driven) for a single 1-km road segment. The apparent outlier (high snake encounter rates at ~200 on the trafden1km axis) corresponds to a road segment that had low traffic volume itself, but was within 1 km of a busy highway.
Figure 14: Detection rates for total caprimulgids (all three spp. of nightjars) heard while driving the road transects, as a function of traffic density at a 2 km radius.
Figure 15: Average Quail Point Count Detection Rates as a function of impervious surface (%) at a 4 km radius from the road segments corresponding to each count station (n=75, data from the northern road transect 2007 only). Each blue point represents the detection rate (average birds per 3-minute count) for a single count station/road segment. The green bars in the background show the predicted detection rates from the regression tree model fitted to the same data. Note the striking decline that occurs at a very low threshold of urbanization (0.58%).
Figure 16: Total mesopredator mammal encounter rates (excluding dogs) as a function of traffic density at a 3-km radius. Each blue point represents the encounter rate (animals/100km driven) for a single 1-km road segment (n=75, data from the northern road transect 2006-8).
Figure 17: Native mesopredator mammal encounter rates (excluding cats and dogs) as a function of impervious surface (%) at a 250 m radius from the road segments. Each blue point represents the encounter rate (animals/100 km driven) for a single 1-km road segment (n=75, data from the northern road transect 2006-8).
Figure 18: Cat encounter rates (animals/100 km driven) as a function of protected area (managed area = "marea") at a 1-km radius (top) and 6-km radius (bottom) from the road segments of the northern route (n = 75, data = 2006-2008).
Figure 19: Trivariate plot showing mesopredator encounter rates (size of circles, smallest = 0) as a function of protected area (vertical axis) and traffic density (horizontal axis). Each circle corresponds to one of the 75 1-km segments of the northern road transect (data=2006-8). Note how the mesopredator rates decline sharply at the higher levels of protected area, which occur also at the lowest levels of traffic density.
Figure 20: Trivariate plots showing the relationship between an index of ground-nesting bird detection rates (size of circles, smallest = 0), traffic density (horizontal axis, at a 250 m radius), and mesopredator mammal encounter rates (top graph) and bird-eating snake encounter rates (bottom graph), with both predator rates in units of animals/100 km driven.
Figure 21: Nocturnal snake road encounter rates (animals/100 km) vs. the same rates for total mammalian mesopredators (excluding dogs, top) and cats-only (bottom). Each point represents one of the 75 segments along the northern road transect (n = 75, data = 2006-8).
Figure 22: Joint plot of the first two axes of the species-space ordination. Red arrows represent the combined correlation strengths for the environment variables with the two axes. For clarity only the variables at a 3-km scale are shown, and then only if their combined strength exceeded 0.20. The weighted average location of each wildlife group are shown as "+"s.
Figure 23: Joint plot of the first and third axes of the species-space ordination. Red arrows represent the combined correlation strengths for the environment variables with the two axes. For clarity only the variables at a 3-km scale are shown, and then only if their combined strength exceeded 0.20. The weighted average location of each wildlife group are shown as “+”s.
Figure 24: Joint plot of the second and third axes of the species-space ordination. Red arrows represent the combined correlation strengths for the environment variables with the two axes. For clarity only the variables at a 3-km scale are shown, and then only if their combined strength exceeded 0.20. The weighted average location of each wildlife group are shown as "+"s.
Figure 25: 3-dimensional joint plot showing all three axes of the species-space ordination simultaneously. The red arrows again represent only the 3 km scale variables that were most highly correlated with the different axes (forest cover pointing to the left, and traffic density and impervious surface pointing right). The blue x symbols connected by lines to the origin represent the weighted average scores for the wildlife groups. The line pointing up and away from the viewer corresponds with domestic cats, and the line pointing to the right = native mesopredators.
Figure 26: Comparison of the impervious surface conditions available across the broader Sandhills Region (left) and along the 75 segments of the northern road-cruising route (right). The histograms show the frequency distributions of impervious surface values within 1-km buffers of 1-km segments (16,000 for the Sandhills, 75 for the northern route).
# Tables

## Table 1: Survey Effort Details by Year

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### Table 2: Amphibian counts and encounter rates, by species and year (top) and by analysis group (bottom)

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(All rates = total animals encountered on road per 100km driven)
Table 3: Best scales comparison for single variable regression tree models.

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<td>impal</td>
<td>4</td>
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<tr>
<td></td>
<td>axiata</td>
<td>2</td>
<td>300</td>
</tr>
<tr>
<td></td>
<td>palmar</td>
<td>6</td>
<td>500</td>
</tr>
<tr>
<td></td>
<td>radula</td>
<td>3</td>
<td>500</td>
</tr>
<tr>
<td></td>
<td>wet</td>
<td>1</td>
<td>30</td>
</tr>
<tr>
<td>Ranaidae</td>
<td>overall</td>
<td>1.635.333</td>
<td>1.141</td>
</tr>
<tr>
<td></td>
<td>ADT05</td>
<td>for</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>impal</td>
<td>2</td>
<td>300</td>
</tr>
<tr>
<td></td>
<td>axiata</td>
<td>3</td>
<td>500</td>
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<tr>
<td></td>
<td>palmar</td>
<td>1</td>
<td>250</td>
</tr>
<tr>
<td></td>
<td>radula</td>
<td>7</td>
<td>500</td>
</tr>
<tr>
<td></td>
<td>wet</td>
<td>5</td>
<td>708.333</td>
</tr>
</tbody>
</table>

* p-values represent the results from Monte Carlo randomization tests based on 500 permutations of the observation data.

Table 4: Average Daily Traffic single variable models (ADT05, one scale only)

<table>
<thead>
<tr>
<th>Amphibian Group</th>
<th>n (seg)</th>
<th>x of splits</th>
<th>x-R^2</th>
<th>app-R^2</th>
<th>p-value</th>
<th>p-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bufo</td>
<td>68</td>
<td>1</td>
<td>0.037</td>
<td>0.147</td>
<td>0.108</td>
<td>0.034</td>
<td>0.056</td>
</tr>
<tr>
<td>Hyla</td>
<td>48</td>
<td>2</td>
<td>0.088</td>
<td>0.224</td>
<td>0.08</td>
<td>0.014</td>
<td>0.024</td>
</tr>
<tr>
<td>Ranidae</td>
<td>53</td>
<td>1</td>
<td>0.008</td>
<td>0.120</td>
<td>0.174</td>
<td>0.1</td>
<td>0.134</td>
</tr>
<tr>
<td>A. ocellatus</td>
<td>72</td>
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<td>0.265</td>
<td>0.07</td>
<td>0.008</td>
<td>0.004</td>
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*p-values represent the results from Monte Carlo randomization tests based on 500 permutations of the observation data.
Table 5: Best Overall Amphibian Models (including pruned-full and single-variable-only regression trees)

<table>
<thead>
<tr>
<th>Amphibian Group</th>
<th>n ( # segs)</th>
<th>variables included in best overall model</th>
<th># of splits</th>
<th>$\hat{R}^2$</th>
<th>$\text{app-R}^2$</th>
<th>p-value</th>
<th>p-value</th>
<th>p-value</th>
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<td>75</td>
<td>train250</td>
<td>2</td>
<td>0.528</td>
<td>0.577</td>
<td>&lt; 0.002</td>
<td>&lt; 0.002</td>
<td></td>
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<tr>
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<td>75</td>
<td>inrops250</td>
<td>2</td>
<td>0.277</td>
<td>0.449</td>
<td>&lt; 0.002</td>
<td>&lt; 0.002</td>
<td></td>
</tr>
<tr>
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<td>75</td>
<td>wet00</td>
<td>1</td>
<td>0.237</td>
<td>0.367</td>
<td>&lt; 0.002</td>
<td>&lt; 0.002</td>
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</tr>
<tr>
<td>tomatrampidos</td>
<td>75</td>
<td>train250</td>
<td>2</td>
<td>0.500</td>
<td>0.544</td>
<td>&lt; 0.002</td>
<td>&lt; 0.002</td>
<td></td>
</tr>
</tbody>
</table>

(note, best overall models chosen as those with the highest $\hat{R}^2$ for that amphibian group)

*p-values represent the results from Monte Carlo randomization tests based on 500 permutations of the observation data.*
<table>
<thead>
<tr>
<th>Common name</th>
<th>Species</th>
<th>2006 Count</th>
<th>2006 Rate</th>
<th>2007 Count</th>
<th>2007 Rate</th>
<th>2008 Count</th>
<th>2008 Rate</th>
<th>Combined 2000-8 Rate</th>
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</thead>
<tbody>
<tr>
<td>Nightjar</td>
<td>C. exoptilus</td>
<td>41</td>
<td>2.340</td>
<td>269</td>
<td>1.701</td>
<td>9</td>
<td>1.889</td>
<td>519</td>
</tr>
<tr>
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<td>C. exoptilus</td>
<td>18</td>
<td>0.999</td>
<td>131</td>
<td>1.131</td>
<td>1</td>
<td>0.188</td>
<td>150</td>
</tr>
<tr>
<td>whip-poor-will</td>
<td>C. exoptilus</td>
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<td>1.042</td>
<td>100</td>
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<td>592</td>
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<td></td>
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<td>0.261</td>
<td>30</td>
<td>0.299</td>
<td>1</td>
<td>0.188</td>
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<td>Coluber constrictor</td>
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<td>12</td>
<td>0.116</td>
<td>0</td>
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<td>0.123</td>
<td>12</td>
<td>0.116</td>
<td>1</td>
<td>0.188</td>
<td>20</td>
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<td>Elaphe guttata</td>
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<td>0.123</td>
<td>12</td>
<td>0.116</td>
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<td>Tantilla coronata</td>
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<td>0.104</td>
<td>2</td>
<td>0.019</td>
<td>1</td>
<td>0.188</td>
<td>9</td>
</tr>
<tr>
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<td>Lampropeltis calligaster</td>
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<td>0.052</td>
<td>5</td>
<td>0.048</td>
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<td>0.000</td>
<td>11</td>
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<tr>
<td>red-bellied water snake</td>
<td>Nerodia erythrostriga</td>
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<td>0.104</td>
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<td>0.019</td>
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<td>Nerodia abacura</td>
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<td>Nerodia fasciata</td>
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<td>0.000</td>
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<td>4</td>
<td>0.039</td>
<td>0</td>
<td>0.000</td>
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<td>Masticophis flagellum</td>
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<td>0.035</td>
<td>3</td>
<td>0.029</td>
<td>0</td>
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<td>0.000</td>
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<td>1</td>
<td>0.019</td>
<td>0</td>
<td>0.000</td>
<td>3</td>
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<td>Crotalus horridus</td>
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<td>1</td>
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<td>0.000</td>
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<td>0.000</td>
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</tr>
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<td>0.019</td>
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<tr>
<td><strong>Total Snakes</strong></td>
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</table>

(All rates = total animals encountered on road per 100km driven)
Table 7: Mammal Encounter Rates

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<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Mesopredator Mammals:</td>
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<td></td>
<td></td>
<td></td>
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<tr>
<td>domestic dog</td>
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<td>111</td>
<td>1.330</td>
<td>496</td>
<td>4.797</td>
<td>26</td>
<td>4.881</td>
<td>633</td>
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<td>0.996</td>
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<td>1.126</td>
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<td>0.106</td>
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<td>0.000</td>
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<td>Vulpes Vulpes</td>
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<td>0</td>
<td>0.000</td>
<td>9</td>
<td>0.054</td>
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<td>0.009</td>
<td>0</td>
<td>0.000</td>
<td>4</td>
<td>0.004</td>
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<td>coyote*</td>
<td>Canis latrans</td>
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<td>0.000</td>
<td>1</td>
<td>0.010</td>
<td>0</td>
<td>0.000</td>
<td>1</td>
<td>0.006</td>
</tr>
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<td>bobcat*</td>
<td>Felis rufus</td>
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<td>0.000</td>
<td>1</td>
<td>0.010</td>
<td>0</td>
<td>0.000</td>
<td>1</td>
<td>0.006</td>
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<tr>
<td><strong>Total Mesopredators</strong></td>
<td></td>
<td>169</td>
<td>2.338</td>
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<td>36</td>
<td>6.758</td>
<td>890</td>
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<td>58</td>
<td>1.308</td>
<td>179</td>
<td>1.731</td>
<td>10</td>
<td>1.877</td>
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<td>1.502</td>
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<td>10</td>
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</table>

(All rates = total animals encountered on road per 100km driven)

*coyotes and bobcats are included with the mesopredators, even though both species can also be viewed as potential top predators
### Table 8: Best overall regression tree models for snakes, birds, and mammals

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<tr>
<th>Animal group</th>
<th>predictor</th>
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<th>$t$-splits</th>
<th>$x$-R$^2$</th>
<th>$t$-splits</th>
<th>$x$-R$^2$</th>
<th>app-R$^2$</th>
<th>p-value</th>
<th>p-value</th>
<th>p-value</th>
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<td>birds</td>
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<td>&lt; 0.002</td>
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<td>&lt; 0.002</td>
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<td>2</td>
<td>0.197</td>
<td>0.354</td>
<td>0.050</td>
<td>&lt; 0.002</td>
<td>&lt; 0.002</td>
<td></td>
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</tr>
<tr>
<td>indexcaprim</td>
<td>trajlen3km</td>
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<td>0.644</td>
<td>0.018</td>
<td>&lt; 0.002</td>
<td>&lt; 0.002</td>
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<td></td>
<td></td>
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<tr>
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<td>impsl3km</td>
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<td>0.476</td>
<td>0.144</td>
<td>&lt; 0.002</td>
<td>&lt; 0.002</td>
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<tr>
<td>indexgroundbirds</td>
<td>impsl2km</td>
<td>1</td>
<td>0.505</td>
<td>0.527</td>
<td>0.110</td>
<td>&lt; 0.002</td>
<td>&lt; 0.002</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>indexwhips</td>
<td>impsl10km</td>
<td>4</td>
<td>0.281</td>
<td>0.461</td>
<td>&lt; 0.002</td>
<td>&lt; 0.002</td>
<td>&lt; 0.002</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>nightkts</td>
<td>impsl2km</td>
<td>2</td>
<td>0.182</td>
<td>0.355</td>
<td>0.042</td>
<td>&lt; 0.002</td>
<td>&lt; 0.002</td>
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</tr>
<tr>
<td>totexprim</td>
<td>trajlen2km</td>
<td>2</td>
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<td>0.438</td>
<td>0.026</td>
<td>&lt; 0.002</td>
<td>&lt; 0.002</td>
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<td></td>
</tr>
<tr>
<td>whoos</td>
<td>impsl6km</td>
<td>2</td>
<td>0.251</td>
<td>0.436</td>
<td>0.018</td>
<td>&lt; 0.002</td>
<td>&lt; 0.002</td>
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<tr>
<td>snakes</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>nocturnal</td>
<td>impsl2km, impsl5km, forsl4km</td>
<td>3</td>
<td>0.351</td>
<td>0.661</td>
<td>&lt; 0.002</td>
<td>&lt; 0.002</td>
<td>&lt; 0.002</td>
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<tr>
<td>nghtbirds</td>
<td>impsl8km</td>
<td>2</td>
<td>0.362</td>
<td>0.342</td>
<td>0.052</td>
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<td>0.002</td>
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<tr>
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<td>trajlen250</td>
<td>1</td>
<td>0.303</td>
<td>0.332</td>
<td>0.146</td>
<td>&lt; 0.002</td>
<td>0.012</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>mesopredators</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>cats</td>
<td>mcanat6km</td>
<td>1</td>
<td>0.072</td>
<td>0.235</td>
<td>0.064</td>
<td>0.010</td>
<td>0.030</td>
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<td>dogs</td>
<td>trajlen250</td>
<td>1</td>
<td>0.013</td>
<td>0.167</td>
<td>0.036</td>
<td>0.008</td>
<td>0.016</td>
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</tr>
<tr>
<td>mcanatcats</td>
<td>forsl8km</td>
<td>1</td>
<td>0.066</td>
<td>0.145</td>
<td>0.114</td>
<td>0.006</td>
<td>0.056</td>
<td></td>
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</tr>
<tr>
<td>mesopreds</td>
<td>impsl10km</td>
<td>1</td>
<td>0.085</td>
<td>0.078</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>

*Note: p-values represent the results from Monte Carlo randomization tests based on 500 permutations of the observation data.*
Table 9: Best overall predator models for birds and snakes.

<table>
<thead>
<tr>
<th>Prey group</th>
<th>Predator</th>
<th># of splits</th>
<th>x-R^2</th>
<th>app-R^2</th>
<th>p-value</th>
<th>p-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>birds:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>avgchucks</td>
<td>mesopredscb75t</td>
<td>2</td>
<td>0.199</td>
<td>0.278</td>
<td>&lt;0.002</td>
<td>0.012</td>
<td></td>
</tr>
<tr>
<td>avgquail</td>
<td>dogscb75t</td>
<td>0</td>
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<td>---</td>
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<td>---</td>
<td>---</td>
</tr>
<tr>
<td>avgwhips</td>
<td>dogscb75t</td>
<td>1</td>
<td>0.103</td>
<td>0.183</td>
<td>0.136</td>
<td>0.004</td>
<td>0.018</td>
</tr>
<tr>
<td>chucks</td>
<td>ratbirdsnakescb75t</td>
<td>1</td>
<td>0.207</td>
<td>0.107</td>
<td>0.064</td>
<td>0.03</td>
<td>0.042</td>
</tr>
<tr>
<td>indexcaprim</td>
<td>totsnakescb75t</td>
<td>4</td>
<td>0.148</td>
<td>0.349</td>
<td>0.01</td>
<td>&lt;0.002</td>
<td>0.002</td>
</tr>
<tr>
<td>indexchucks</td>
<td>ratbirdsnakescb75t</td>
<td>1</td>
<td>0.073</td>
<td>0.161</td>
<td>0.138</td>
<td>0.01</td>
<td>0.054</td>
</tr>
<tr>
<td>indexgroundbirds</td>
<td>mesopredscb75t</td>
<td>1</td>
<td>0.079</td>
<td>0.148</td>
<td>0.108</td>
<td>0.008</td>
<td>0.05</td>
</tr>
<tr>
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<td>dogscb75t</td>
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<td>0.032</td>
<td>0.207</td>
<td>0.076</td>
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<td>0.006</td>
</tr>
<tr>
<td>nightthrks</td>
<td>ratbirdsnakescb75t</td>
<td>0</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>totcaprim</td>
<td>ratbirdsnakescb75t</td>
<td>1</td>
<td>0.038</td>
<td>0.148</td>
<td>0.124</td>
<td>0.022</td>
<td>0.05</td>
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<tr>
<td>whips</td>
<td>mesoincatscb75t</td>
<td>0</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>snakes:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>noctsnakes</td>
<td>catscb75t</td>
<td>1</td>
<td>-0.019</td>
<td>0.047</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>ratbirdsnakes</td>
<td>mesopredscb75t</td>
<td>0</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>totsnakes</td>
<td>mesoincatscb75t</td>
<td>0</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
</tbody>
</table>

*note: p-values represent the results from Monte Carlo randomization tests based on 500 permutations of the observation data*
Table 10: Wildlife groups used in the NMS ordinations.

<table>
<thead>
<tr>
<th>Group</th>
<th>Abbreviation</th>
<th>Genera/Species Included (n of spp.)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Amphibians:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>toads</td>
<td>&quot;bstoads&quot;</td>
<td>Bufo (2), Scaphiopus (1)</td>
</tr>
<tr>
<td>treefrogs</td>
<td>&quot;hylids&quot;</td>
<td>Hyla (5)</td>
</tr>
<tr>
<td>true frogs</td>
<td>&quot;ranids&quot;</td>
<td>Rana (4)</td>
</tr>
<tr>
<td><strong>Snakes:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>large upland snakes</td>
<td>&quot;rbsnakes&quot;</td>
<td>Agkistrodon (1), Elaphe (2), Crotalus (1), Masticophis (1), Pituophis (1), Lampropeltis (2), Heterodon (1), Celuber (1), Thamnophis (1), Lampropeltis (1), Heterodon (1), Storeria (2), Carphophis (1), Cenophora (1), Tanilla (1), Diadophis (1), Virginia (1), Opheodrys (1)</td>
</tr>
<tr>
<td>small upland snakes</td>
<td>&quot;smsnakes&quot;</td>
<td>Agkistrodon (1), Nerodia (3), Farancia (1), Regina (1)</td>
</tr>
<tr>
<td>aquatic snakes</td>
<td>&quot;wssnakes&quot;</td>
<td></td>
</tr>
<tr>
<td><strong>Mammals:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>cats</td>
<td>&quot;cats&quot;</td>
<td>Felis catus (1)</td>
</tr>
<tr>
<td>native mesopredators</td>
<td>&quot;mesnocsats&quot;</td>
<td>Didelphis (1), Procyon (1), Urocyon (1), Vulpes (1), Canis (1), Felis (1)</td>
</tr>
<tr>
<td>dogs</td>
<td>&quot;dogs&quot;</td>
<td>Canis domesticus (1)</td>
</tr>
<tr>
<td><strong>Birds:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>chuck-will's-widows</td>
<td>&quot;idchucks&quot;</td>
<td>Caprimulgus carolinensis (1)</td>
</tr>
<tr>
<td>whip-poor-wills</td>
<td>&quot;idwhips&quot;</td>
<td>Caprimulgus vociferus (1)</td>
</tr>
<tr>
<td>nighthawks</td>
<td>&quot;nighthiks&quot;</td>
<td>Chordeiles minor (1)</td>
</tr>
<tr>
<td>bobwhite quail</td>
<td>&quot;quail&quot;</td>
<td>Colinus virginianus (1)</td>
</tr>
</tbody>
</table>
Table 11: Details on the Environmental Variables Used in all three data Chapters

<table>
<thead>
<tr>
<th>Variable</th>
<th>Units*</th>
<th>Abbreviation</th>
<th>Buffer Scales</th>
<th>Source**</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average Daily Traffic</td>
<td>vehicles/day</td>
<td>&quot;ADTUS&quot;</td>
<td>roads only</td>
<td>NC DOT</td>
</tr>
<tr>
<td>Traffic Density</td>
<td>(vehicles/day/km roads)/search are</td>
<td>&quot;tcdrn&quot;</td>
<td>30 m - 10 km</td>
<td>NC DOT</td>
</tr>
<tr>
<td>Impervious Surface</td>
<td>average percent within buffer</td>
<td>&quot;impse&quot;</td>
<td>30 m - 10 km</td>
<td>USGS</td>
</tr>
<tr>
<td>Forest Cover</td>
<td>percent of buffer</td>
<td>&quot;for&quot;</td>
<td>30 m - 10 km</td>
<td>USGS NLCD</td>
</tr>
<tr>
<td>Longleaf Pine Cover</td>
<td>percent of buffer</td>
<td>&quot;llp&quot;</td>
<td>30 m - 10 km</td>
<td>NC GAP</td>
</tr>
<tr>
<td>Protected/Managed Area</td>
<td>percent of buffer</td>
<td>&quot;mare&quot;</td>
<td>30 m - 10 km</td>
<td>NC DENR</td>
</tr>
<tr>
<td>Cropland Cove</td>
<td>percent of buffer</td>
<td>&quot;crop&quot;</td>
<td>30 m - 10 km</td>
<td>USGS NLCD</td>
</tr>
<tr>
<td>Grassland/Pasture Cove</td>
<td>percent of buffer</td>
<td>&quot;grsp&quot;</td>
<td>30 m - 10 km</td>
<td>USGS NLCD</td>
</tr>
<tr>
<td>Wetland Cover</td>
<td>percent of buffer</td>
<td>&quot;wet&quot;</td>
<td>30 m - 10 km</td>
<td>USGS NLCD</td>
</tr>
<tr>
<td>Water Cover</td>
<td>percent of buffer</td>
<td>&quot;wtr&quot;</td>
<td>30 m - 10 km</td>
<td>USGS NLCD</td>
</tr>
<tr>
<td>Relative Elevation</td>
<td>average (road elev. - average buffer elev)</td>
<td>&quot;relv&quot;</td>
<td>250 m - 10 km</td>
<td>USGS DEM</td>
</tr>
</tbody>
</table>

*all variables except ADT05 calculated using 30 m pixels in GIS, and buffer polygons of the specified widths extending from each 1 km road segment


Table 12: Non-metric multidimensional scaling results, 3-axis solution.

<table>
<thead>
<tr>
<th># of axes</th>
<th>Final Stress</th>
<th>p-value</th>
<th>Axis 1 R²</th>
<th>Axis 2 R²</th>
<th>Axis 3 R²</th>
<th>Cumulative R²</th>
<th>Axis 1 vs. 2 correlation</th>
<th>Orthogonality %</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>15.19</td>
<td>&lt;0.004</td>
<td>0.24</td>
<td>0.378</td>
<td>0.241</td>
<td>0.859</td>
<td>0.163</td>
<td>97.3</td>
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</tbody>
</table>

*p-values indicate the percentage of random permutation trials (n = 250) that achieved stress levels as low or lower than observed

*R²'s were adjusted for lack of orthogonality between the axes
Table 13: Correlation strengths and R²'s between the various wildlife groups and the three NMS axes.

<table>
<thead>
<tr>
<th>wildlife group</th>
<th>NMS Axis:</th>
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<th></th>
<th></th>
<th></th>
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</thead>
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<tr>
<td></td>
<td>group abbrev.</td>
<td>1</td>
<td>R²</td>
<td>2</td>
<td>R²</td>
<td>3</td>
</tr>
<tr>
<td>Amphibians:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>toads</td>
<td>bstoads</td>
<td>0.384</td>
<td>0.148</td>
<td>0.527</td>
<td>0.278</td>
<td>-0.04</td>
</tr>
<tr>
<td>tree frogs</td>
<td>hylids</td>
<td>0.238</td>
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<td>0.537</td>
<td>0.288</td>
<td>0.241</td>
</tr>
<tr>
<td>true frogs</td>
<td>ranids</td>
<td>0.135</td>
<td>0.018</td>
<td>0.477</td>
<td>0.228</td>
<td>0.213</td>
</tr>
<tr>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>large upland snakes</td>
<td>rbsnakes</td>
<td>0.494</td>
<td>0.244</td>
<td>0.424</td>
<td>0.18</td>
<td>0.086</td>
</tr>
<tr>
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<td>smsnakes</td>
<td>0.356</td>
<td>0.127</td>
<td>0.425</td>
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<td>wsnakes</td>
<td>0.14</td>
<td>0.02</td>
<td>0.39</td>
<td>0.152</td>
<td>0.12</td>
</tr>
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<td>Ground-nesting birds:</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>bobwhite quail</td>
<td>quail</td>
<td>0.236</td>
<td>0.056</td>
<td>0.4</td>
<td>0.16</td>
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<td>0.302</td>
<td>0.386</td>
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<td>0.437</td>
<td>0.191</td>
<td>-0.161</td>
</tr>
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<td>common nighthawks</td>
<td>nightlk</td>
<td>0.154</td>
<td>0.024</td>
<td>0.143</td>
<td>0.021</td>
<td>-0.369</td>
</tr>
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<td>Mesopredator mammals:</td>
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<td></td>
<td></td>
</tr>
<tr>
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<td>cats</td>
<td>0.04</td>
<td>0.002</td>
<td>-0.405</td>
<td>0.164</td>
<td>0.559</td>
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<tr>
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<td>dogs</td>
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<td>0.086</td>
<td>0.172</td>
<td>0.03</td>
<td>-0.054</td>
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<tr>
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<td>0.411</td>
<td>0.324</td>
<td>0.105</td>
<td>0.084</td>
</tr>
</tbody>
</table>
References


Stoddard, H. L. 1931. The bobwhite quail: its habits, preservation, and increase. Charles Scribner’s Sons, New York.


Biography

Ron Sutherland was born in Cary, North Carolina in 1976, at a time when the formerly bucolic Research Triangle region was just beginning its meteoric rise to becoming a major US metropolitan area. As a result, Ron quickly settled on his current career path, which is aimed at becoming a respected conservation biologist whose research and advocacy projects help to ensure the preservation of major wilderness areas for the benefit of humans and biodiversity alike. Ron received his B.S. degree in Biology from NC State University in 1999, then promptly married his high school sweetheart, Elizabeth Gatlin (now Elizabeth G. Sutherland). While at NCSU together, Ron and Beth ended up camping out on Crab Island, Australia (home of the world’s largest rookery of flatback sea turtles, and some rather large crocodiles) for nearly two months, without a radio, boat, or enough food. They survived and later (2002) both earned M.S. degrees in Conservation Biology and Sustainable Development at the University of Wisconsin, Madison. During the past 7 years, Ron has trained a pair of snake-hunting dogs (Pilot and Tessa), published over a dozen op-eds and over 30 letters to the editor in major newspapers, played water polo with three different local club teams, and, with the help of various teammates, won the Neuse River Sprint Triathlon down at the Duke Marine Lab on 5 separate occasions. Ron looks forward to enjoying similar adventures in the years to come, along with the love and friendship offered by his wife, his 2 brothers (Neil and David), and his parents (John and Anne).