HABITAT SELECTION AND MOVEMENT PATTERNS OF AMPHIBIANS IN ALTERED FOREST HABITATS

by

GABRIELLE JOY GRAETER

(Under the Direction of J. WHITFIELD GIBBONS)

ABSTRACT

I released adult southern leopard frogs (*Rana sphenocephala*), marbled salamanders (*Ambystoma opacum*), and southern toads (*Bufo terrestris*) on forest/clearcut edges to examine the effects of forest management on amphibian habitat selection and movement behavior. Salamanders selected habitat at random, toads preferred clearcuts, and frogs initially selected clearcuts but ultimately chose forests. All three species made more turns in clearcuts than forests, and toads and frogs moved farther in forests. Frogs and toads moved without regard to environmental conditions, but salamanders were influenced by soil moisture. I also examined the efficacy of fluorescent powder as an amphibian tracking technique and found that some colors were easier to detect when paths were long, that heavy rainfall truncated path length, and that effectiveness varied among species, habitat, and region. Such knowledge of individual and species-level responses to terrestrial habitat alteration will facilitate development of forest management plans that enhance persistence of amphibian populations.

INDEX WORDS: *Ambystoma opacum, Bufo terrestris, Rana sphenocephala*, marbled salamander, southern toad, southern leopard frog, habitat fragmentation, forest management, amphibians, movement, migration, habitat selection, permeability, fluorescent powder, tracking, clearcut, amphibian conservation

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Background on Amphibian Ecology and Conservation Issues

Place in Ecosystems

Amphibians are an important group of organisms for many reasons, including their role in transferring energy and nutrients between terrestrial and aquatic habitats, their high abundances in some areas, their integral role in food webs, and their usefulness as biological indicators of environmental degradation. Through the use of both terrestrial and aquatic habitats, as they move between the two for reproduction and in search of suitable habitat, many amphibians effectively transport nutrients and energy between the two environments (Wilbur 1980, Gibbons et al. in press). This transfer can have huge implications for the productivity and nutrient cycles of the adjoining habitats and for the survival and reproduction of other species within the food web (Wilbur 1980). Studies, both classic and recent, have shown that amphibians occur in remarkably high abundances in some areas (Burton and Likens 1975, Hairston 1987, Petranka and Murray 2001, Gibbons et al. in press). When amphibians exist in high biomass, it follows that they would play important ecosystem roles by providing a large amount of prey and nutrients to that particular locale (Petranka and Murray 2001). On a related note, amphibians are a critical link in many food webs because they provide a prey source for a wide variety of vertebrates including birds, snakes, mammals, and fish (Hairston 1987), and because they prey on invertebrates and other food items that are too small for many other organisms (Pough 1983). Lastly, their sensitivity to environmental changes renders amphibians particularly suitable as biological indicators of environmental health and integrity (Dunson et al. 1992, Blaustein 1994).

Habitat Use and Ecology

Most amphibians have biphasic life cycles and rely on both aquatic and terrestrial habitats during some portion of their life (Pough 2004). As ectotherms with highly permeable skin, amphibians usually have body temperatures that mirror their immediate surroundings; thus, they must adjust their behavior accordingly to regulate their body temperature and hydration levels (Duellman and Trueb 1994, Kam and Chen 2000). Not only do amphibians need adequate unaltered habitat, they also require specific habitat types at different life stages.

The United States has a diversity of isolated wetland types, including Carolina bays, cypress domes, desert wetlands, floodplain wetlands, karst wetlands, kettle-hole bogs, playas, pocosins, prairie potholes, sinkhole wetlands, and vernal pools (Tiner 2003). Many in the southeastern Coastal Plain are depression wetlands that fill from rainfall and dry seasonally. These ephemeral wetlands are particularly important for amphibian reproduction because the process of periodic drying and subsequent inundation excludes fish, which are significant predators on amphibian eggs and larvae (Semlitsch 2000, Teplitsky et al. 2003). The small size of these wetlands should not imply that they are less important; in fact, these small wetlands can be centers of great productivity and biodiversity (Russell et al. 2002a, Gibbons et al. in press).

However, as critical as these wetlands are, the time spent in these aquatic habitats is only a small portion of most amphibians' life cycles because the majority of time is spent in the terrestrial landscapes surrounding these wetlands (Semlitsch 1998, Gibbons 2003). Most amphibians that use these wetlands only return to breed and many species will skip breeding in years when conditions are not suitable for reproduction (Bailey et al. 2004). Recently, numerous studies have emphasized the significance of the terrestrial component of amphibian life cycles and the necessity of protecting both the aquatic and terrestrial habitats (Gibbons 2003, Semlitsch and Bodie 2003, Porej et al. 2004). Information has been compiled for individual species on terrestrial habitat needs, and several alternative strategies for protection of terrestrial buffers around wetlands have been suggested as means to protect amphibians from environmental threats (Bulger et al. 2003, Semlitsch and Bodie 2003, Schabetsberger et al. 2004).

Conservation Status

Amphibian populations are declining worldwide (Blaustein et al. 1994, Gibbons et al. 2000, Stuart et al. 2004) and these declines are attributed to many different causes, including introduced exotic species, disease, ultraviolet radiation, and environmental contaminants (Blaustein and Kiesecker 2002). Although these causes are probably interacting synergistically, habitat degradation and loss is considered by most amphibian ecologists to be the primary cause of these declines (Alford and Richards 1999). Amphibians are facing these same threats in the southeastern United States (Means et al. 1996). While large-scale amphibian population crashes have not yet occurred in the Southeast as they have elsewhere, many species are considered to be declining or at risk (Dodd 1997, Means 2005). In fact, of the 77 amphibian species native to the Coastal Plain, 15 (19%) have been ranked G-1 (critically imperiled) to G-4 (apparently secure, but not demonstrably widespread, abundant, and secure) by The Nature Conservancy (Means 2005).

It seems apparent that as the pressures and consequences of human population growth escalate, amphibians in the Southeast will be increasingly more at risk unless positive changes are made. Between 2000 and 2004, human population has increased by 6.6% in the South Atlantic states and by 4.6% in South Carolina (U.S. Census Bureau 2004). This rate of human population increase is predicted to result in greater rates of urbanization (Wear 2002) and an intensification of forest management and productivity on existing timberland (Prestemon and Abt 2002).

Forest Management in the Southeast

According to a report by the United States Forest Service (Prestemon and Abt 2002), the Southeast produces more timber than any single country in the world and produces about 60 percent of the timber products in the United States, almost all of which is from privately owned forests. The Southeast is projected to retain this status for decades to come (Prestemon and Abt 2002). In fact, prices for timber are expected to increase over the next 40 years, and this is anticipated to serve as an incentive to private timber companies to improve their productivity and invest in more intensive forest management (Prestemon and Abt 2002). The amount of land in the South managed as pine plantations is projected to increase continuously, resulting in a 67 percent increase (from 33 to 54 million acres) over a 45 year period, between 1995 and 2040 (Prestemon and Abt 2002).

Forest management for timber production is not only a prevalent practice throughout the southeastern United States, it is also of considerable importance to the economy. In 1997, the direct overall economic gain from the different sectors of the timber industry (includes timber, logging, sawmills, wood furniture, pulp and paper, and all other wood products) in the South was more than \$40 million (Abt et al. 2002). In the same year, the wood products sectors contributed over 770,000 direct jobs to the southern economy, \$120 billion in total industry output, and over \$40 billion in Gross Regional Product (Abt et al. 2002).

Although the management methods vary within the different regions in the Southeast, the majority of timber production in the Coastal Plain is derived from a combination of pine plantations and mixed hardwood stands (Conner and Hartsell 2002). Throughout the lower Coastal Plain, loblolly (*Pinus taeda*) and short-leaf pine (*Pinus echinata*) are the predominant species in planted pine forests (15 million acres), with a lesser amount (12.5 million acres) planted in slash (*Pinus elliottii*) and long-leaf pine (*Pinus palustris*, Conner and Hartsell 2002). In addition, oak-pine (8.2 million acres), oak-hickory (8.9 million acres), and oak-gum-cypress (13.9 million acres) forests make up a major portion of managed Coastal Plain forests (Conner and Hartsell 2002).

The timber industry in South Carolina typically mirrors the overall trends in the Southeast. Between 1952 and 1999, South Carolina experienced a large increase in the area of planted pine forests (from 233,000 to 2.7 million acres) and a simultaneous decrease in land area with natural pine forests (from 5.9 million to 2.8 million acres, Conner and Hartsell 2002). In fact, a recent inventory discovered that more land in South Carolina is planted in pine plantations than natural pine forests; as of 2001, the 3.1 million acres of planted pine stands outnumbered natural pine by 150,000 acres (Conner et al. 2004). One pine species, loblolly pine, made up 94 percent of pine plantation acres as of 2001 (Conner et al. 2004). In terms of economic input, South Carolina's economy receives \$14.7 billion annually from

forestry, logging, wood products, and furniture manufacturing (Conner et al. 2004). Additionally, over 40,000 South Carolinians are directly or indirectly employed in one of these sectors, and collectively receive an income of \$1.7 billion (Conner et al. 2004).

Clearly, timber production is a significant source of economic income for the southeastern United States and South Carolina. The combination of a huge economic drive behind the timber industry and a vast amount of land area under intensive forest management in the South suggests that the environmental costs of these practices could be extensive. Since most amphibians in the Coastal Plain region rely on terrestrial habitats for the majority of their life cycles and have to migrate in order to reach breeding ponds, they are particularly vulnerable to the changes that occur when land is altered for timber production purposes. However, given that timber production will continue because of consumer demand, there is merit in seeking a balance between these competing interests. In fact, managed forests have the potential to support wildlife and provide suitable habitat, but the degree to which they succeed at this depends on how the forests are managed. Initiatives promoting sustainable forestry have been gaining approval and support from professionals in a broad range of fields and sectors (NCSSF 2005). These initiatives encourage forest managers to integrate modern forest science for wood production with a protection of biological diversity and conservation of habitat (NCSSF 2005). By adopting these sustainable forestry practices, forest managers may be able to simultaneously produce timber and provide suitable habitat for amphibians.

Summary of Previous Research on Amphibian Responses to Forest Management

Many studies have been conducted to assess the effects of forest management on amphibians and most have focused on the implications for amphibian abundance, species richness, and diversity. A review by deMaynadier and Hunter (1995) compiled and summarized the findings of 18 such studies. In most, forest clearing resulted in an overall decline in amphibian abundance, and in some cases species richness also decreased (deMaynadier and Hunter 1995). Specifically, they reported a median value of 3.5 times more amphibians on control plots than on clearcut plots in these 18 studies (deMaynadier and

Hunter 1995). For instance, in western North Carolina, Petranka et al. (1993) found that capture rates were five times higher in controls than in recent clearcuts. Similarly, in a deciduous forest in central New York State, complete removal of the forest canopy resulted in declines of the red-backed salamander (*Plethodon cinereus*) and conifer plantations contained very low densities of salamanders (Pough et al. 1987). In a study examining the distribution of populations along silvicultural edges in Maine, amphibian abundance was lower in clearcuts and plantations and salamander richness was lower in clearcuts than in forests; also, some amphibian species were found to be more sensitive to intensive forest management than others (deMaynadier and Hunter 1998). Several studies have demonstrated that it can take a long time for species to recover to pre-harvest abundance and diversity (Petranka et al. 1993, Herbeck and Larsen 1999). However, exceptions to this pattern of decreased species abundance and richness in clearcuts exist and are mentioned in the deMaynadier & Hunter review paper (1995). Most of the studies mentioned in the review that reported effects of forest management on amphibians were from regions outside of the southeastearn Coastal Plain.

Amphibian Population-Level Responses to Forest Management in the Southeastern Coastal Plain

Studies conducted on the effects of forest management on amphibians within the southeastern United States have shown contradictory results. For example, in a study with three upland forest habitats around a restored Carolina Bay (Sharitz 2003) in South Carolina, most measures, especially capture rate, indicated that the mixed hardwood forest was the most suitable amphibian habitat (Hanlin et al. 2000). Similarly, Means et al. (1996) claimed that the most probable reason for an abrupt decline in the flatwoods salamander at one site in Florida was the conversion of longleaf pine savanna into mechanically prepared slash pine forest. However, two studies did not detect any major effects on the amphibian populations in question; one had inadequate replication and the amount of coarse woody debris in the clearcut may have mitigated the negative effects (Chazal and Niewiarowski 1998) and the other, while finding no effects on the amphibians there, found that the ambystomatids were absent from all five

sites, suggesting that forest management may have had an effect previously (Russell et al. 2002a, Russell et al. 2002b).

The results of several other studies in the Southeast also demonstrate that interpreting the effects of forest management on amphibians in this region is not straightforward. In a study looking at the response of herpetofauna to skidder traffic and group-selection harvesting, negative effects were observed only in salamanders (Cromer et al. 2002), and in another study the amphibians that had less pine litter for cover exhibited behavior that may have put them more at risk of predation (Moseley et al. 2004). At a site in the North Florida flatwoods, a decrease in amphibian abundance from forest management was observed, but the populations appeared to recover after three years, possibly due to the heterogeneity and small size at this particular site (Enge and Marion 1986). Thus, while the effects of forest management on amphibians in the Southeast have not been confirmed definitively, it is obvious that some species are responding to certain forest conditions. This emphasizes the need to identify which species are negatively affected, what forest management conditions they are affected by, and how to mitigate these situations.

Movement Responses of Individual Amphibians to Forest Management

Relevance of Movement Behavior

Initial studies have provided critical information by focusing on the patterns, such as amphibian abundance and richness, of the effects of forest management on amphibians, (deMaynadier and Hunter 1995). However, a need exists for properly replicated, well-designed, experimental studies that look beyond measures of abundance and richness to investigate the causal processes behind the patterns observed. In particular, studies are needed on how forest management may affect amphibian survival, growth, and predation as well as disease prevalence, reproductive success, microhabitat selection, and movement patterns. For example, when an experiment reports a decrease in abundance or species richness, what are the reasons for these decreases? Are the amphibians dying during the logging event or sometime shortly afterwards (Petranka et al. 1993)? Or are they able to traverse areas that have been clearcut or modified extensively and select more suitable habitat (Ash 1997)?

One way to answer these questions is to examine, with a species-specific approach, how, when, and why amphibians adjust their movement patterns and behaviors in altered habitats. Since most studies in the Southeast have focused their methodology on relative capture rates from pitfall traps, using alternative methods, such as tracking individual amphibian's movements, may elucidate patterns that were not apparent from other methods due to technique-specific biases. Modified movement patterns by juvenile or adult amphibians in response to an altered landscape could be responsible for the observed declines in abundance and richness in a study. For example, animals could migrate out of a disturbed area (Ash 1997), or they might move faster or more often (Rosenberg et al. 1998, Moseley et al. 2004) and be at greater risk of predation. Alternatively, they could move less and have a decreased prey supply (Rohr and Madison 2003) or more stressful temperature-moisture regime (Johnston and Frid 2002).

Studies of movement behavior can provide information for scaling up from individual to population level. For example, a study by Haddad et al. (1999) on butterfly behavior at habitat edges demonstrated that simple behaviors can be used instead of detailed dispersal studies to predict how corridors will affect movement between habitat patches. In other words, individual movement decisions and behaviors, in combination with landscape characteristics, can influence distribution patterns (Johnson et al. 1992).

Habitat Selection

Many amphibians preferentially select forested areas over cleared areas, but this preference differs by species and among studies. Amphibians have shown a preference for forested habitat over open disturbed habitat in both the juvenile (deMaynadier and Hunter 1998, Sjogren-Gulve 1998, Rothermel and Semlitsch 2002, Vasconcelos and Calhoun 2004) and adult (Gibbs 1998, Chan-McLeod 2003, Rittenhouse et al. 2004, Vasconcelos and Calhoun 2004) life stages in a wide range of amphibian species from different regions of North America and the world. Individual amphibians were found to either move into forested habitats rather than cleared habitats or to avoid movement into the cleared habitats. Red-spotted newts (*Notophthalmus viridescens*) in Connecticut behaviorally avoided forest

edges and open areas and were captured most often within interior forest habitat (Gibbs 1998). Similarly, a strong directional movement towards old-growth forest was demonstrated by Italian crested newts (Triturus carnifex) as they emigrated from an ephemeral lake in the Alps (Schabetsberger et al. 2004). At breeding pools in Maine, wood frog (*Rana sylvatica*) and spotted salamander (*Ambystoma maculatum*) juveniles dispersed toward and adults migrated from and toward closed canopy forested habitat (Vasconcelos and Calhoun 2004). This type of habitat preference has also been tested in the laboratory with spotted salamanders, such that when given a choice between forest substrate and grassland substrate, salamanders selected forest substrate more often (Rittenhouse et al. 2004). In a field experiment, Ensatina eschscholtzii chose to move through naturally vegetated corridors more often than they chose corridors with bare soil (Rosenberg et al. 1998). Sometimes, movement responses to forest management can be sex-dependent. For example, Bartelt et al. (2004) found that female western toads (Bufo boreas) moved further than males and selected open forests and soft forest edges over clearcuts and forests with closed canopies. Likewise, in a radio-tracking study on Vancouver Island of 120 red-legged frogs (R. a. aurora), Chan-McLeod (2003) concluded that 86% of the frogs were moving almost exclusively within the old-growth forest and behaviorally avoiding the clearcut. These studies demonstrate that a broad range of amphibian taxa from many geographic ranges have shown a preference for intact or forested habitat over disturbed or open habitat. Habitat preferences and altered movement patterns in response to changes in the landscape can have effects beyond the individual amphibian level. In particular, effects observed at the individual level, such as habitats acting as barriers to amphibian movement, can actually translate into population level consequences, including decreased survival, growth, and reproductive success.

On the other hand, some studies have shown no effect of land-use changes on amphibian movement. When red-legged frogs (*R. a. draytonii*) made long-distance migratory movements overland from terrestrial areas to breeding ponds in California, most of them moved in fairly straight paths without any perceived regard for the surrounding topography or vegetation types (Bulger et al. 2003). A recent radio-telemetry study found that adult wood frogs (*R. sylvatica*) showed no preference for either clearcuts or forests (T. Rittenhouse pers. comm. 2005). A lack of effects on movement could be interpreted in several ways. First, the species could be relatively robust to forest changes. However, effects may be present, but not exhibited as effects on movement patterns or behavior of the animals. It is also possible that the forest management practices in these studies negatively influence the amphibians, but that effects are not detected at the scale or detail of the research question. For example, a radio-tracking study may be looking for effects on large-scale landscape level movements and not be able to detect the differences present on a finer scale, such as how often an individual changes location on a micro-habitat scale. Furthermore, costs such as increased risks of predation, desiccation, and disease and decreased growth rate and reproductive success may be experienced even if no movement differences are perceived (e.g., T. Rittenhouse pers. comm. 2005, differences in water loss rate in *R. sylvatica*). Once again, these indirect fitness consequences can ultimately translate into effects on population dynamics.

Very few studies have done a multi-species comparison of the effects of forest management practices on the movement of amphibians (but see Gibbs 1998, Rothermel and Semlitsch 2002). Despite the paucity of studies, information comparing species movement responses is greatly needed in the conservation and land management fields. By comparing three juvenile amphibian species, Rothermel and Semlitsch (2002) discovered that two species (spotted salamander, *A. maculatum*; American toad, *B. americanus*) oriented towards forest and the movements of a third species (small-mouthed salamander, *A. texanum*) did not differ from random expectations. In a study looking at multiple amphibian species' movement responses to a variety of types of forest edges, some species' movements were influenced by these different landscapes and others did not appear to be (Gibbs 1998). In this case, the capture rates of two species at drift fences at different distances from edges were influenced by forest edges (red-spotted newts, *N. viridescens*; marbled salamander, *A. maculatum*; redback salamander, *P. cinereus*; wood frog, *R. sylvatica*). Having this type of species-specific data is invaluable for making informed and appropriate forest management decisions because in many cases effects are observed with some species but not others and responses are variable.

Factors Influencing Fine-Scale Movement Behavior

When amphibians find themselves in modified habitats, sometimes they adjust their movement behavior. They may change the directionality, timing, frequency, or rate of movement, or keep closer to cover within that habitat. In actuality, amphibians can probably alter their movement in innumerable ways. Movement and habitat choice within a landscape are complex decisions based on multiple factors, including a need to travel quickly, expend the least amount of energy, find suitable prey, and reduce the risks of predation and desiccation. For example, logging affected the movements of Pacific giant salamanders (*Dicamptodon tenebrosus*) at sites in southwestern British Columbia with three different forest management histories: forested, clearcut with riparian buffers, and clearcut to the stream edge; the radio-telemetry data revealed that the salamanders in clearcuts had smaller home ranges, stayed closer to the stream, and spent more time in subterranean refuges than those at forested sites (Johnston and Frid 2002). Thus, it appears that the salamanders in the clearcuts had to adjust their overall behavior and movement behavior in order to compensate for the conditions within the altered habitat. Similarly, in the field experiment where *E. eschscholtzii* selected between and migrated within different corridor pathway types, Rosenberg et al. (1998) found that the salamanders that moved into the bare corridors had shorter residency times and higher movement rates than those in the vegetated corridors.

Several other studies have revealed similar results, that amphibians frequently adjust their behavior and movement patterns in response to altered habitats. For example, displaced northern green frogs (*R. clamitans*) released at locations on golf courses where tall grass, short grass, and forest converged exhibited adjusted movement behaviors (Birchfield and Deters 2005). The frogs preferentially moved through the short grass, but stayed close to the taller grass, presumably for cover; this was interpreted as a choice for the habitat with the least resistance that had sheltering habitat nearby (Birchfield and Deters 2005). The vegetation type and forest management history of the areas around breeding ponds can also affect the timing of emigration. For instance, tiger salamanders (*A. tigrinum*) at the pond surrounded with the most forest, and therefore the most local refuges, tended to delay or even

postpone their emigration, whereas those in more exposed ponds emigrated sooner and did not settle in the immediate surrounding terrestrial areas (Madison and Farrand 1998).

Amphibians have also been known to alter their movements by reversing their direction in a clearcut or behaviorally avoiding movement through an area. As an example, juvenile spotted salamanders (*A. maculatum*) made more reversals of direction as they dispersed through open fields (4 out of 5 individuals) than when they moved through forests (none) (Rothermel and Semlitsch 2002). In the study on Vancouver Island, Chan-McLeod (2003) also examined reversals of direction in red-legged frogs (*R. a. aurora*); she found that of the frogs that ventured out into clearcuts, 19 out of 36 reversed direction and moved back into the forest.

The effects of forest management practices on amphibian movement can be season or weather dependent, meaning that the differences in movement may only be evident during certain weather conditions. For example, the red-legged frogs tracked on Vancouver Island preferred the forests, but this association was not as tight during periods with high precipitation (Chan-McLeod 2003). More specifically, the probability that a frog would enter a clearcut was strongly determined by the amount of precipitation (Chan-McLeod 2003). Weather can also affect the way that amphibians move within differently managed forests and clearcuts. During a year with less precipitation, Pacific giant salamanders (*D. tenebrosus*) in clearcuts were more dependent on rainfall for their movements than those in forested habitats (Johnston and Frid 2002).

Defining Permeability for Amphibians

Throughout the literature on amphibian movement, a common concept, under the guise of various terminologies, has emerged: permeability. Permeability is known in a general sense as the extent to which an altered landscape impedes or acts as a barrier to movement by organisms. Many different applications and interpretations and a varied vocabulary exist for describing the phenomenon of landscape permeability. An assessment of the use of this term in amphibian ecology reveals two closely related but distinct types of permeability, which I will term "edge permeability" and "habitat permeability." I will

define and provide examples of both edge and habitat permeability, in an attempt to clarify their differences and their applications in the field of amphibian ecology.

The original use of the permeability concept in amphibian ecology was one of edge permeability, which is the probability of entering a certain patch type (Stamps et al. 1987). Edge permeability has been defined by Gibbs (1998) as "the magnitude of reduction or increase in amphibian movement at ecosystem edges relative to continuous forest." Habitat permeability, in contrast, is the probability of successfully traversing a given patch, and is focused on how easily an individual moves through an area. For the purpose of clarity, I define habitat permeability as the relative decrease or increase in magnitude of amphibian movement through different habitats.

Edge permeability has been referred to as the degree to which a habitat acts as a barrier to movement or results in behavioral avoidance by an amphibian. It is the relative tendency for individuals to enter different habitats. For example, Gibbs (1998) looked at the permeability of forest edges to amphibian movement and found a range of relative permeability to forest edges among six amphibian species, with certain landscape edges being more of a hindrance to movement for some species. Barrier effects were also observed in a radio-telemetry study on red-legged frogs (*R. a. aurora*), particularly during hot and dry conditions (Chan-McLeod 2003). Similarly, Richter et al. (2001) indicated that dispersal distances of the dark gopher frog (*R. sevosa*) may have been constrained by a clearcut on adjoining land; though this clearcut was well within their dispersal range, none moved into the area and several were observed to move along the edges.

Habitat permeability, on the other hand, is a question about what happens after an amphibian enters the altered habitat. This concept has also been termed "landscape resistance" or "landscape impedance" and is considered the degree to which the landscape impedes movement. It is basically the relative ease of travel through different habitats, which is a function of both behavioral and physiological costs. It is more difficult to measure because it requires more information on the animals' condition. For example, Rothermel and Semlitsch (2002) noted that old-field habitats may have greater landscape resistance for some species of dispersing juveniles such that they moved shorter distances and

experienced higher dehydration rates in old-field habitats than in forest. Distance traveled, rate of movement, and degree of dispersal success are also measures of the habitat permeability of an altered landscape. For example, a study on red-backed salamanders (*P. cinereus*) that were displaced at different distances in an old-field from a forest edge found that, although the salamanders could traverse the open fields, their return rate declined with distance from the edge (Marsh et al. 2004). In some cases, when amphibians move into an area with a low permeability, they may be affected beyond a simple adjustment of their movement; direct consequences on their migratory success or even survival in an area may become apparent. For instance, less than 15% of dispersing juvenile amphibians reached the forest from pools in old-fields 50 m from a forest edge, possibly because of high mortality (Rothermel 2004).

Although I have separated these two permeability concepts, many researchers are simultaneously examining the extent to which an altered area acts as an outright barrier to movement (edge permeability) and the degree to which movement is modified as individuals move through an altered habitat (habitat permeability).

Objectives of Study

The goal of the current study was to assess the efficacy of tracking amphibian movements with fluorescent powder and to quantitatively compare the habitat choice and movement patterns of three amphibian species, southern leopard frog (*R. sphenocephala*), southern toad (*B. terrestris*) and marbled salamander (*A. opacum*) in relation to forest management practices. In the first chapter, I address three topics: First, I experimentally tested and compared the habitat choice and movement patterns (using a Geographic Information System, GIS) of these amphibian species when released on forest/clearcut edges. Second, I determined if the habitat choice and movement patterns documented could be explained by any amphibian characteristics (e.g., sex, body size) or environmental conditions (e.g., precipitation, relative humidity, air temperature). Lastly, I investigated if *R. sphenocephala* preferentially selected certain microhabitat features, such as herbaceous plants or coarse woody debris, or moved independently of microhabitat characteristics. In the second chapter, I determined the effectiveness of using fluorescent

powdered pigments for tracking the movements of amphibians. The ultimate goal was to provide information that land managers and conservationists could use to make informed and appropriate forest management decisions for these three species, as well as species that would be expected to have similar responses to forest management.

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CHAPTER 2

HABITAT SELECTION AND MOVEMENT PATTERNS OF THREE AMPHIBIAN SPECIES (RANA SPHENOCEPHALA, AMBYSTOMA OPACUM, BUFO TERRESTRIS) IN ALTERED FOREST HABITATS IN THE UPPER COASTAL PLAIN OF SOUTH CAROLINA¹

¹Graeter, G. J. To be submitted with modifications to *Journal of Wildlife Management*.

INTRODUCTION

Amphibians are declining globally from a variety of causes, including disease, environmental contaminants, invasive species, and habitat loss (Blaustein 1994, Blaustein and Kiesecker 2002, Semlitsch 2003, Stuart et al. 2004). Although these forces may act synergistically to cause declines, habitat degradation and loss are considered the primary causes of amphibian declines (Alford and Richards 1999). As alteration of forested land is increasing at an alarming rate in many regions, habitat loss and forest fragmentation are increasingly urgent threats to amphibians (Semlitsch 2000). Forest management for timber production is prevalent throughout the Southeast; the timber industry is an important player in the region's economy (Abt et al. 2002), and the region produces more timber than any single country in the world (Prestemon and Abt 2002). Timber production on such a large scale has the potential to negatively affect amphibians that use and live in these habitats.

A review of the effects of forest management on amphibians found that in most studies, forest clearing resulted in an overall decline in amphibian abundance (deMaynadier and Hunter 1995). In the Southeast, the results are less clear, with studies finding negative effects, no effects, or effects only under some conditions (Russell et al. 2004). These initial studies have provided critical information by focusing on amphibian abundance and richness patterns that result from forest management. However, experimental studies that go beyond measures of abundance and richness are needed to determine the causal processes that underlie observed patterns. One way to address the causal processes is to examine, using a species-specific approach, how, when, and why amphibians adjust their movement behaviors and habitat selection in altered habitats. Studies of the movement behavior of individuals are particularly valuable because they can provide information for scaling up from the individual to the population level (Lima and Zollner 1996, Haddad 1999) and can help predict amphibian habitat use and needs (Gibbs 1998).

Many amphibians preferentially select forested areas over cleared areas (Rothermel and Semlitsch 2002, Chan-McLeod 2003, Vasconcelos and Calhoun 2004), but this preference differs by species and among studies. In many cases, amphibians have been found to adjust their behavior and

movement in response to altered habitats (Madison and Farrand 1998, Johnston and Frid 2002, but see Bulger et al. 2003). A change in permeability, defined generally as the extent to which a particular habitat type impedes or acts as a barrier to movement by amphibians, is one way that amphibians can be influenced by forestry practices or other land uses. An assessment of the use of this term in amphibian ecology reveals two closely related but distinct types of permeability, which I will term "edge permeability" and "habitat permeability." Edge permeability, as defined by Gibbs (1998), is "the magnitude of reduction or increase in amphibian movement at ecosystem edges relative to continuous forest." I define habitat permeability as the relative decrease or increase in magnitude of amphibian movement through different habitats.

Reduced habitat permeability in altered habitats and an inability to differentiate between habitats can potentially have both individual costs and population-level implications for amphibians. Individuals can experience direct physiological costs and reduced reproductive success from spending time in and moving through unsuitable habitat (Schwarzkopf and Alford 1996). If a species' survival or reproductive success is reduced below a certain threshold, a population may decline or go locally extinct. Furthermore, if some areas in a landscape have decreased edge or habitat permeability or become outright movement barriers to a species, connectivity between different habitats in the landscape could decrease. Thus, a population may become isolated in a fragmented landscape (Hanski 1999), and be unable to reach its breeding, foraging, or over-wintering habitats. When populations are unable to interact and exchange genes, harmful genetic consequences are possible at the local level (Frankham et al. 2002, Davis and Verrell 2005). Small, isolated populations suffer increased susceptibility to perils of small population size, including genetic drift, inbreeding depression, and reduced resilience to demographic and environmental stochasticity, environmental change, and disease (Davis and Verrell 2005). Furthermore, decreased permeability can reduce a population's chance of being rescued through immigration (Semlitsch 2000, Joly et al. 2001). These potential population-level consequences for amphibians in disturbed habitats highlight the importance of studying amphibian movement and habitat selection in altered habitats, especially considering concerns for amphibian declines.

The objective of my study was to quantitatively compare the habitat choice and movement patterns of three amphibian species, southern leopard frogs (*Rana sphenocephala*), marbled salamanders (*Ambystoma opacum*), and southern toads (*Bufo terrestris*), in four types of forest management plots. First, I experimentally tested and compared the habitat choice and movement patterns (using a Geographic Information System, GIS) of these three amphibian species by releasing them on forest/clearcut edges. Taking physiological differences into account, I hypothesized that *R. sphenocephala* and *A. opacum* would preferentially select forest, but that *B. terrestris* would have less affinity for forest habitats. Second, I determined if the habitat choices and movement patterns could be explained by any within-species characteristics (e.g., sex, body size) or environmental factors (e.g., precipitation, relative humidity, air temperature). Because amphibians have permeable skin and are susceptible to desiccation, they generally prefer moist, humid environments (Duellman and Trueb 1994). Thus, I predicted that the amphibians would use environmental cues, particularly soil moisture and relative humidity, as indicators of habitat suitability. Lastly, I investigated whether *R. sphenocephala* preferentially selected certain microhabitat features or moved independently of them.

MATERIALS AND METHODS

Study Sites and Experimental Design

My research was conducted as part of the LEAP (Land-use Effects on Amphibian Populations) project, a large-scale, collaborative, and experimental study focused on the processes through which forest alteration affects terrestrial amphibian populations. LEAP has been experimentally manipulated and replicated at the regional (Maine, Missouri, and South Carolina) and local site scales. My research took place in west-central South Carolina within the US Department of Energy's Savannah River Site National Environmental Research Park (SRS-NERP). About 95% of the 803-km² SRS-NERP consists of forested habitats, including second-growth hardwood forests, planted pine forest, and other terrestrial and aquatic habitats (Gibbons et al. 1997).

The LEAP study design in South Carolina consists of four sites, each configured with an isolated seasonal wetland surrounded by four upland forest management treatments; the forest is predominantly pine (e.g., longleaf, loblolly, slash pine), but has hardwoods interspersed throughout (e.g., oaks, maple, hickories, dogwood, sweetgum). I used three of the LEAP sites (1000, 37, 119); each site is approximately 7 km from the others. The wetlands at these three sites are all approximately 1.3 ha, but water levels and areal coverage fluctuate with the season and amount of rainfall. These seasonal wetlands typically fill via rainfall in the winter months, between November and March, and dry out in the summer months (Sharitz 2003).

The four forest management treatments around each wetland are: (1) a clearcut with the coarse woody debris (CWD) retained (CC-retained), (2) a clearcut with the CWD removed (CC-removed), (3) a partial cut in which canopy cover was reduced by approximately 15% relative to the control treatment, and (4) an unharvested forest control (Figure 2.1). The treatments were randomly assigned with the prerequisite that the two clearcuts are always situated opposite each other. These areas have been managed for timber in the past, but all of the forests are currently mature (> 25 years old), with the exception of a younger (8-yr old) stand in the partial treatment at 119 (approximately 1/3 of partial). Site 119 also has a man-made ditch along the edge between the control and CC-retained treatments. Small, unpaved access roads, covered in soil and leaf litter, lead up to and partially through all three sites.

For my study, 12 amphibian release locations were designated along the habitat edges at each site (Figure 2.1). Three release points were situated on each edge at each site, with the first release point at least 50 m from the wetland, the middle point approximately 25 m from the other two release locations, and the third point between 50-72 m from the outer boundary (Figure 2.1). These distances were selected to eliminate confounding effects from the other forest edges at the wetland and the outer boundary. Furthermore, I set all release points a minimum of 25 m from the small access roads. At each release point, I cleared a circular area (diameter of 1 m) of all vegetation and roots to create a uniform area. In addition, I made sure that all release points had a relatively level surface and were free of major obstructions in the immediate vicinity.

Study Species

Southern leopard frogs (Rana sphenocephala)

The southern leopard frog (Rana sphenocephala) has a pointed snout, long legs, a green and/or brown coloration with dark rounded spots on its back, and a white underside (Martof et al. 1980, Conant and Collins 1998). Leopard frogs range in size from 50-90 mm snout-vent length (SVL), and males are usually smaller than females (Martof et al. 1980). Breeding generally occurs in the winter or early spring, but has been known to take place in the fall in some areas (Martof et al. 1980). This species is common in shallow, freshwater habitats throughout the Southeast (Martof et al. 1980, Conant and Collins 1998), and is relatively widespread on the SRS (Gibbons et al. 1976, Gibbons and Semlitsch 1991, Buhlmann et al. 2005). Studies on the terrestrial migration of a few closely related species provide some indication as to the terrestrial habitat use and movement behavior of R. sphenocephala. For example, five individual frogs of a related species, R. clamitans, migrated a mean distance of 485 m (range: 321-570 m) in Missouri (Birchfield and Semlitsch in review) and a Florida population of *R. capito* moved 280-480 m from a breeding site (Greenberg 2001). However, little is known of the non-breeding season activity and habitat use of *R. sphenocephala*. This species forages terrestrially and can move long distances overland, especially in the summer (Martof et al. 1980, Conant and Collins 1998), but the details about this movement are lacking, including migration distance, the terrestrial habitats selected, and whether they spend the non-breeding season primarily in aquatic or terrestrial habitat. On the SRS, we know that this species' terrestrial habitat use includes upland, mixed pine, and hardwood forests in mesic conditions (Buhlmann et al. 2005). This information suggests that they could be negatively affected by forest alteration. Although *R. sphenocephala* occur at our LEAP sites, none of the sites had a breeding population in 2004-2005 (Gibbons et al. unpublished data).

Marbled salamanders (Ambystoma opacum)

The marbled salamander (*Ambystoma opacum*) has white or light gray irregularly shaped crossbands on the head, back, and tail on a black background (Petranka 1998). This species has a wide

range within the eastern deciduous forests, existing from southern New England to northern Florida and as far west as the tallgrass prairie (Petranka 1998). The adults are medium-sized (77-127 mm TL) with a stout body (Conant and Collins 1998, Petranka 1998). In South Carolina, the adults breed in the late fall, with breeding concentrated in October-December (Krenz and Scott 1994). Like other ambystomatids, this species is mostly fossorial, with above-ground movement primarily during warm rainy weather in the summer and fall, and also in the winter months in more southern climes (Petranka 1998). They have been known to migrate into the surrounding upland habitat as far as 450 m from the breeding site (Williams 1973); reported mean migration distances are 30 m (Douglas and Monroe 1981) and 194 m (Williams 1973). However, very little is known about their terrestrial life stages relative to the amount of information on their aquatic ecology. A study on amphibian response to forest gap creation concluded that Ambystoma were negatively affected by areas with open canopy (Cromer et al. 2002). Ambystoma opacum may be more sensitive to environmental changes than the two other Ambystoma species present at my sites, the mole salamander (A. talpoideum) and tiger salamander (A. tigrinum), in part because A. opacum are not as adept at burrowing underground (Semlitsch 1983). Petranka (1998) proposed that habitat loss, of both breeding sites and terrestrial habitat, is probably the greatest threat to this species. Thus, I included this species in my study because of its unique life history and presumed sensitivity to habitat alteration. Ambystoma opacum have breeding populations at both site 37 and 119, so I captured salamanders at these two sites, and used them in the experimental releases at their original sites.

Southern toads (Bufo terrestris)

The southern toad (*Bufo terrestris*) is common throughout the Coastal Plain, including the SRS (Gibbons et al. 1976, Buhlmann et al. 2005), and especially in areas with sandy soils (Conant and Collins 1998). Southern toads range in size from 41-98 mm SVL and dorsal coloration is often brown, but varies from red to black (Martof et al. 1980, Conant and Collins 1998). Females are generally larger than the males (Martof et al. 1980). The toads breed in shallow water from March to October (Conant and Collins 1998) throughout their range, with the breeding peak from April to June at my research sites (pers. obs.).
They are generally active at dusk and well into the night (Conant and Collins 1998), but are sometimes active during the daylight hours (pers. obs.). Although no one has documented terrestrial migration distances of *B. terrestris* directly, one study of a closely related species, *B. americanus*, demonstrated movements of 23-480 m (n=176) from the breeding site (Oldham 1966). It is surprising that there is so little basic natural history knowledge for *B. terrestris*, but as with *R. sphenocephala*, individual-based movement studies simply have not been conducted on even the most common amphibian species. This species is often considered a generalist species because of its greater tolerance to water loss (Hillyard 1999) and widespread occurrence in many habitat types (Bennett et al. 1980, Gibbons and Semlitsch 1991, Hanlin et al. 2000, Buhlmann et al. 2005). I included the southern toad in this three-species comparison because, relative to the other two species, it is considered to be somewhat resilient to habitat alteration. Since *B. terrestris* had a breeding population at both site 37 and 119, toads for my experiment were captured at these two areas and released at their original site.

Amphibian Collection and Holding Techniques

I captured 48 adult *R. sphenocephala* by hand and using aquatic minnow traps, pitfall traps, and box funnel traps in May-August 2004 at a nearby wetland, Ellenton Bay (approximately 15 km from site 37 and 22.3 km from site 1000). I was unable to use frogs from the LEAP wetlands because the wetlands dried up earlier than expected, and I did not capture enough for this experiment. I kept the frogs outdoors in shaded 847-liter cattle tanks with moist soil, a water source, and ½-inch crickets. Males and females were kept in separate holding tanks. Most frogs were used in the experimental releases within 1-9 days from the date of capture, although a few were held for up to two weeks.

Adult *A. opacum* were captured in pitfall traps from late October to November 2004 as they entered the wetlands at sites 37 and 119. Initially I kept the salamanders in terrestrial cattle tanks with soil, leaf litter, coverboards, and grass sod and black mesh lids for shade, and allowed them to breed. In mid-December 2004, the salamanders were transferred indoors to site-specific containers in a climate-controlled room (21.1 C \pm 2.8 C and approximately 10% relative humidity) in the animal care facility at

the Savannah River Ecology Laboratory (SREL). They were kept in containers lined with clean moist paper towels and fed ¹/₄-inch crickets regularly. I transferred the salamanders to containers at the release sites at least 24 hours in advance (max of 4 nights) to allow them to acclimate to their original site. The containers were 48 cm long x 38 cm wide x 16 cm high with mesh on all four sides and located at the edge of the wetland in a dry shady area; I filled the containers with moist soil and leaf litter. Both air and some rain could enter through the mesh and presumably the salamanders could see out of the container. Males and females were kept in different containers adjacent to each other at each site. All salamanders survived this acclimation period and appeared to be in good condition at the time of release. The salamanders were released during the post-breeding migratory period when *A. opacum* are normally active in the terrestrial habitat (Gibbons et al. unpublished data).

I captured adult *B. terrestris* in pitfall traps from late March to early May 2005, at sites 37 and 119. The longest time an individual was held was 11 days. I held the toads in the same outdoor holding tanks that were used previously for *R. sphenocephala*, and kept them separate by site and sex. I provided the toads with water, moist soil, cover objects, shade, and a regular supply of ½-inch crickets.

Experimental Releases

I conducted experimental releases in May-August 2004 (*R. sphenocephala*) at 37 and 1000, February-March 2005 (*A. opacum*) at 37 and 119, and March-May 2005 (*B. terrestris*) at 37 and 119. I released animals at both sites on each night and randomized the release point assignment and order of release within each site. To track their movements, I applied non-toxic fluorescent powder by dipping the lower 2/3 of each individual's body into orange, pink, chartreuse, or green powder (Series T1 from Radiant Color, Richmond, CA). The application process took less than 30 seconds. Prior to release, I placed each powdered amphibian under a black bucket for a 5-minute acclimation period. Then, I lifted the bucket using a 5 m pole, and departed along the edge with only the aid of a dim red light.

Release methods were standardized across species with a few exceptions. For *R. sphenocephala*, I generally released one frog per edge at each site for a total of eight per night. A total of 48 frogs (22

females; 26 males) were released. In August, however, I released nine frogs on one night and five on a second night to compensate for the loss of several powder trails from heavy rain. I released adult *A*. *opacum* on five different nights; during the first trial I released eight salamanders and on subsequent release dates, nine were released per night. The total number of salamanders released was 44 (22 females; 22 males), with half of those at each site and equal sex ratios during each release. For *B*. *terrestris*, I released a total of 36 post-breeding toads, with 24 males and 8 females released at site 37, and 4 males released at site 119. Ten toads were released per night on two nights, six were released on another night, and five were released on two nights. I released more toads at site 37 because of an unexpectedly low number of post-breeding toads captured at site 119.

Environmental Data

On each release night, I noted the moon phase (1=new moon, 2=crescent, 3=quarter, 4=gibbous, 5=full moon), wind (Beaufort wind scale) and weather (0=mostly cloudy, 1=partly cloudy, 2=clear) conditions, and the pre- and post-release precipitation, as well as anything that could potentially affect movement, such as the presence or absence of anurans calling from a wetland. I created a sky brightness and condition index by summing the moon phase and weather codes, so that sky condition index values ranged from 1 (darkest sky and most cloud cover) to 7 (brightest and clearest sky).

Immediately before releasing each individual, I recorded environmental data at two locations 10 m from the release point, one in each of the adjacent treatments. I recorded relative air humidity to the nearest 1% (Bacharach Pocket-Size Sling Psychrometer, Forestry Suppliers Inc.), soil moisture accurate to 0.5% (TH₂0 Soil Moisture Meter, Dynamax Inc. Houston, TX), and air temperature to 0.5 C degrees for all three species (*R. sphenocephala*: iButtons, Dallas Semiconductor/Maxim, Dallas, Texas; *A. opacum* and *B. terrestris*: digital Hygro-thermometer, Forestry Suppliers, Inc.). I took air temperatures and relative humidity approximately 0.5 m off the ground and soil moisture in the top 8 cm of soil. In addition, I recorded soil temperatures for the *R. sphenocephala* experiment by placing iButtons 2 cm below the soil surface.

Tracking and Delineating Movement Paths

I used a Portable Rechargeable UV Lamp (UVL-26P, Fisher Scientific International) to track individuals approximately 24 hours after they were released. As the powder was located, I laid string down on top of the powder trail to mark each individual's route. I recorded the path as ended either when I found the individual or was unable to find any more powder. When I did locate an individual, I recorded what type of cover it had selected. A Global Positioning System (GPS) Trimble Pro-XR backpack unit was used to create a file for each individual amphibian's movement path. A GPS point was taken whenever an individual made a >10-degree turn with a length \geq 1 m. I downloaded the GPS data and imported it into a Geographic Information System (GIS) for analysis of movement paths.

Microhabitat Use by Rana sphenocephala

For the *R. sphenocephala* powder trails, I recorded microhabitat data at regular intervals along each frog's path (at 5-m intervals for the first 20 m and subsequently at 10-m intervals). A $1-m^2$ plot was centered over each sampling location and the percent ground cover was estimated for 6 variables: (1) bare exposed soil, (2) leaf and pine litter, including twigs < 2 cm in diameter, (3) herbaceous plants and creeping ground vines, (4) all woody plants that had a stem diameter < 7.62 cm, (5) fine woody debris of 2-10 cm diameter, (6) coarse woody debris of > 10 cm diameter (Bartelt et al. 2004). I used a percent cover class scheme for visually estimating percent cover: Class 1: (0-5%), Class 2: (6-25%), Class 3: (26-50%), Class 4: (51-75%), Class 5: (76-95%), Class 6: (96-100%, Mueller-Dombois and Ellenberg 1974).

In addition to the ground cover sampling, I used two metrics to assess the presence of trees at each interval along each frog's path: a count of trees and the percent canopy cover. The tree tally consisted of recording the number of living over- and under-story hardwood and pine trees with a diameter at breast height (DBH) \geq 7.6 cm within a 5-m radius of the center of the 1-m² plot. I also recorded the percent canopy cover from the center of each plot using a spherical crown densiometer (Forestry Suppliers Inc., Lemmon 1956).

Microhabitat Availability

From October 19-26, 2004, before leaf-fall, I recorded data on the microhabitat available at all four treatments at sites 1000 and 37. These data were collected in an effort to compare the microhabitat used by *R. sphenocephala* to the microhabitat available. To accomplish this, I measured microhabitat (as described above) at 50 sampling points per quadrant, along five non-overlapping transects radiating out from the wetland (Figure 2.2). Data were recorded at 10-m intervals along these transects (10 points/transect). This systematic sampling design was selected because it ensured even distribution of sampling points throughout each quadrant.

Data Analyses

Habitat Selection

I hypothesized that amphibians would select forests more frequently when released on a forest/clearcut edge. To test this hypothesis, I calculated binomial probabilities of the observed outcomes, and confidence intervals around the maximum likelihood estimate for each movement parameter. For this study, selection of forest (either control or partial) was labeled as a "success." I noted each individual's location within the experimental array at selected distances from the release point (*R. sphenocephala:* 5 m, 30 m, 60 m, 90 m; *B. terrestris:* 5 m, endpoint; *A. opacum:* 2 m, endpoint). The maximum likelihood parameter for the binomial proportion is the number of successes, *k*, divided by the number of trials, *n*, which is the number of individuals that still had a visible path at each selected distance. I calculated binomial confidence intervals using the method proposed by Wilson (1927) and found in later studies to be superior (Agresti and Coull 1998, Brown et al. 2001, Henderson and Meyer 2001) to both the normal approximation, which cannot generally be used for small sample sizes, and the commonly used method of Clopper and Pearson (1934). The 95% confidence intervals were calculated for each of the four edge types (Figure 2.1) and distances for each species. Lastly, I calculated the confidence intervals for a comparison of clearcut versus forest selection, whereby the control and partial were combined as "forest" and CC-removed and CC-retained were combined as "clearcut."

Movement Path Analysis

To assess how forest management affects amphibian movement patterns, I used ArcView 3.3 with the Spatial Analyst (Environmental Systems Research Institute, Redlands, Calif.) and Animal Movement extensions (Hooge and Eichenlaub 1997) to calculate several movement path features, including total path length, number of turns, and path linearity (net distance divided by total distance; a value of 1 is completely straight). I used Rayleigh's z-test to examine path directionality (Batschelet 1981). I also examined the number of individuals from each species that moved into clearcuts initially and then promptly (in < 40 m) reversed direction toward forested habitat because reversal behavior is an indication of reduced habitat permeability.

I conducted analyses with SAS (SAS Institute 2000) to compare total path length, number of turns per 10 m, and path linearity among species and treatment types. First, I ran a separate univariate ANCOVA using PROC GLM for each of the path characteristics (total path length, number of turns/10 m, and path linearity) to compare among the three species. I used the percent of each path in a clearcut as a covariate and the type III sums of squares as the basis for the F-test. To compare among the four treatment types I used a multivariate analysis of variance (MANOVA) for each species, combining path length, number of turns/10 m, and linearity into a multivariate movement response. When a path went into more than one treatment, I separated it into segments and only included the longest path segment (minimum of 10 m) for each individual in the treatment comparison to ensure all observations were independent. I also performed a MANOVA for each species with only two treatment levels (forest: control and partial; clearcut: CC-removed and CC-retained) and added site and a site-treatment interaction as effects.

Influence of Amphibian and Environmental Variables

I conducted stepwise logistic regression (α =0.05) in SAS (PROC LOGISTIC, SAS Institute 2000) to determine if amphibian (sex, SVL) and/or environmental conditions (relative humidity, soil temperature, air temperature, precipitation, soil moisture, wind, sky condition) influenced the habitat

choices of each individual. I ran this analysis separately for all three species at each distance from the release point.

Microhabitat Availability versus Use by R. sphenocephala

To determine the strength of the evidence that forest treatment and habitat availability influence habitat use by *R. sphenocephala*, I condensed the microhabitat availability and use data into ecologically meaningful composite variables. The three composite variables measured the degree of (1) ground-level openness: sum of the class midpoint values (Mueller-Dombois and Ellenberg 1974) for percent bare ground, leaf litter, and herbaceous vegetation, (2) ground-level cover: sum of the midpoint values for percent woody vegetation, woody debris 2-10 cm diameter, and woody debris greater than 10 cm diameter, and (3) tree density: sum of the number of understory hardwoods, understory pines, overstory hardwoods, and overstory pines. I reasoned that each of these three composite variables could potentially influence the frogs' movement patterns and microhabitat selection. The composite variables were unimodally distributed and not strictly categorical.

Based on basic amphibian ecology, I created a set of models relating frog microhabitat use of each composite variable to forest treatment, accounting for potential effects of habitat availability and individual sex and SVL. I used an information-theoretic and model selection approach to evaluate these a priori models for frog use of each composite variable (Franklin et al. 2001). I tested effects of treatment type and availability of the composite variable, singly and in combination (3 models), to examine their influence on habitat use. I then asked whether characteristics of individuals (sex, SVL) provided bettersupported models of habitat use than treatment and habitat availability (3 models). I thought sex might be a stronger predictor than SVL because several studies have found gender differences in habitat use (Bartelt et al. 2004) and because I used a relatively narrow size range of individuals in trials. Thus, I tested whether sex alone or SVL and sex improved models based on treatment and availability (2 models); I also evaluated models based on availability and sex for ground-level openness, and availability, sex, and SVL for the other two variables. Including the null model (no predictor variables).

these different combinations resulted in 10 candidate models for "ground-level openness" recorded along each frog's path, and 11 each for "ground-level cover" and "tree density."

I used Akaike's Information Criterion corrected for small sample sizes (AICc) with the maximum likelihood method (Snijders and Bosker 1999) to evaluate and rank the alternative models (Franklin et al. 2001). I fit each candidate model as a mixed model with fixed and random effects using PROC MIXED (Singer 1998, SAS Institute 2000). I included the following random effects in all models: (1) variation among observations within a frog, (2) variation among frogs (nested within sites), and (3) variation among the eight sites. The model in each composite variable set carrying the lowest AICc value, the lowest Δ_i value ($\Delta_i = AICc_i - AICc_{minimum}$), and the highest Akaike weight ($w_i=\exp(-\Delta_i/2)/\sum_{r=1}^{R}\exp(-\Delta_r/2)$) is the model that best approximates the data (Franklin et al. 2001). To determine the amount of variance explained by the fixed effects in the best model relative to the null model, I compared the covariance parameter estimates for the random effects for each composite variable. If several models are closely weighted, the rule of thumb for determining how much evidence there is for each model is that models with a $\Delta_i \leq 2$ have substantial support, those with $4 \leq \Delta_i \leq 7$ have considerably less support, and those with $\Delta_i > 10$ have no support (Burnham and Anderson 2004).

RESULTS

Habitat Selection

The results of a binomial probability test are considered significantly different from random if the confidence intervals do not include the value 0.5. Thus, *R. sphenocephala* selected habitat non-randomly only at distances of 5 m from the release point (Table 2.1). At three out of four edge types, the frogs selected clearcut significantly more than forest at 5 m (Table 2.1). When I pooled the data for the two forested treatments and for the two clearcuts, only 7 out of 44 frogs selected forests at 5 m, which is significantly different from random selection (Table 2.2). None of the other distances in the two-treatment analysis for *R. sphenocephala* had a confidence interval that differed from random (Table 2.2), but the overall trend was that an increasingly larger proportion of the individuals were in forest as the

frogs moved further from the release point (Figure 2.3). Thus, most of the frogs had selected clearcut at 5 m, but at the intermediate distances (30 and 60 m) about half of the frogs were in forest, and at 90 m the majority (10 out of 14) were in forest (Figure 2.3).

All of the *A. opacum* binomial confidence intervals for the four edge types and the overall forestclearcut comparison included the value 0.5, meaning that habitat selection did not differ from random at either 2 m or the endpoint (Table 2.1 and 2.2), which ranged from 2.8 to 44.1 m from the release points. Approximately half of the salamanders selected forest at both 2 m and at the endpoint (Figure 2.4).

I found evidence of nonrandom habitat selection for *B. terrestris* at the 5-m distance, but not at the endpoint, which ranged from 5.8 to 324.3 m from the release point. At two edge types, control/CC-retained and partial/CC-removed, the toads selected clearcut significantly more often than forest (Table 2.1). A similar pattern existed for the two-treatment comparison in that the toads initially (at 5 m) selected clearcuts significantly more often than forests (Table 2.2, Figure 2.5). At the endpoint, the ratio of toads in forests and clearcuts was more even, but more toads were still selecting clearcuts (Figure 2.5).

Movement Path Analysis

I superimposed the movement paths for the three species onto a GIS layer of the LEAP sites using ArcView 3.3 to create a map for each species at each site (Figures 2.6-2.8). At least one *B. terrestris* and one *R. sphenocephala* traversed successfully across a clearcut and moved outside of the LEAP array within the 24 hours (Figures 2.6b, 2.7a). Although field observations suggested that *R. sphenocephala* exhibited a high frequency of reversals out of clearcuts (11 of 37; 29.7%) within 40 m of movement, a similar percentage of individuals reversed out of forests (2 of 7; 28.6%) and into clearcuts. Likewise, there was no indication or pattern of reversal behavior apparent in the movements of the other two species.

As is evident from the movement path maps, clear differences in path characteristics exist among the three species. The path length differed significantly among the three species ($F_{2,118}$ =23.03, p < 0.0001; Figure 2.9), and the covariate, percent of path in clearcut, was also significant ($F_{1,118}$ =7.04,

p=0.0091), suggesting that the treatment type influenced the length of the path. The minimum path length was similar among species, with all three species having at least one individual that moved a very short distance (Figure 2.10). The maximum path length was similar among *R. sphenocephala* and *B. terrestris*, but much shorter for *A. opacum* (Figure 2.10). The number of turns per 10 m also differed significantly among species ($F_{2,118}$ =26.99, p < 0.0001; Figure 2.11), and again, the covariate was significant ($F_{1,118}$ =6.55, p=0.0118). The three species also differed in their path linearity ($F_{2,118}$ =9.38, p=0.0002; Figure 2.12), but this time the covariate was not important ($F_{1,118}$ =0.62, p=0.4339). Almost all of the *R. sphenocephala* (95.5%) had significantly directional movement, according to the Rayleigh's z-test, whereas smaller proportions of *B. terrestris* and *A. opacum* had directional movement (77.1 and 58.1%, respectively).

The multivariate movement response did not differ among treatments when all four treatment levels were considered (*R. sphenocephala*: Wilk's λ =0.7114; F_{9,93}=1.55, p=0.1437; *A. opacum*: Wilk's λ =0.7970; F_{9,90}=0.98, p=0.4626; *B. terrestris*: Wilk's λ =0.7405; F_{9,71}=1.03, p=0.4234). However, movement response differed among treatments and between sites for *R. sphenocephala* when only two levels were considered (Table 2.3). *Rana sphenocephala* and *B. terrestris* had longer path lengths in forests than in clearcuts, but no difference in path length was discernible for *A. opacum* (Figure 2.13). All three species took more turns per 10 m in the clearcut than in the forest, although this relationship appears strongest in *B. terrestris* and *R. sphenocephala* (Figure 2.14). Path linearity was similar in forests and clearcuts (Figure 2.15). Note that the distribution of fluorescent powder colors used was similar across all treatment types, and thus, there was no potential bias based on the detectability of color (see Chapter 3).

Influence of Amphibian and Environmental Variables

None of the amphibian or environmental variables explained the treatment choices made by *R*. *sphenocephala* or *B. terrestris* at any of the distances from the release point. None of these variables met the 0.05 significance requirement by logistic regression's stepwise selection for entry into the model. However, the model for initial habitat selection (at 2 m) by *A. opacum* included mean soil moisture, an

average of soil moisture values taken 10 m into each treatment from the release point (Wald $X^2=8.2013$, p=0.0042). The odds ratio estimate for soil moisture (1.277) implies that there is a 27.7% greater chance that the salamanders will select a clearcut for every 1% increase in the soil moisture. None of the amphibian or environmental variables explained the *A. opacum* treatment choices at the endpoint.

Microhabitat Availability versus Use by Rana sphenocephala

The highest ranked model for the amount of ground-level openness used by the frogs included the treatment type (Table 2.4), with treatment explaining 42% of the random among-site variation. The model including treatment and availability is the next highest weighted model and also has considerable support (Table 2.4). Relative to the CC-retained, the frogs used 7% more ground-level openness in the control, 10% more in the partial, and 6% more in the CC-removed (Table 2.5), according to estimates from the highest ranked model. Although the standard error values are relatively high, the 95% confidence limits for the partial treatment do not include zero, so there is support for the partial being different from the CC-retained (Table 2.5). Although openness was lowest in the CC-retained, the model based only on availability had about 1/3 the weight of the model based on treatment (Table 2.4). This reflects the greater use of openness in the partial than in the other treatments, even though availability was similar to that in the control and CC-removed (Figure 2.16), and the high occurrence of frogs in open patches relative to availability in the CC-retained.

Six models for ground-level cover were similarly weighted and had similar support ($\Delta_i \leq 2$; Table 2.6); in fact, the second highest weighted model for ground-level cover was the null model. The best model for ground-level cover included availability and sex (Table 2.6), with these variables accounting for 10% of the random among-frog variation and none of the among-site variation. The standard error was high for availability (Table 2.5), so the evidence that this variable influenced habitat use was low. However, the effect of sex on habitat choice had some support; females were predicted to use cover 4.7% more than males (Table 2.5). In some quadrants, ground-level cover use was higher than availability, but frogs used remarkably less cover in CC-retained (Figure 2.17); each percent increase in availability

resulted in a small (almost 0) predicted increase in use (Table 2.5), suggesting that availability had little influence on frog use of ground-level cover.

Six models are similarly supported for tree density and most include treatment or availability or both (Table 2.7), indicating that these factors may have some influence on habitat use. As tree density was simply a count of the number of trees, and the forest management treatments were designed to have different amounts of trees and canopy cover, a close correlation between treatment and tree density availability was expected. The best model for frog use of tree density included treatment type and tree density availability (Table 2.7), with these variables explaining almost 100% of the random among-site variation. Some support exists for treatment having an influence above and beyond the effect of availability (Table 2.5); for every tree added as available, the frogs "used" an extra tree, but this association is not as strong for the control as for the other treatments (Figure 2.18). In general, the frogs seemed to use lower tree density in the control and higher tree density in the partial and clearcuts relative to what was available (Figure 2.18). The use of higher tree density by frogs than what was available in the clearcuts was because they were released on the edges.

DISCUSSION

My results confirm that habitat selection and movement are complex phenomena, that forest management may influence amphibian movement in a variety of ways, and that responses may differ greatly among species. Specifically, the three species in my study differed in their capability to perceive and select among different habitats and in their behaviors when moving in forests versus clearcuts. These inter- and intraspecific differences presumably have varying effects on an individual's physiological functions, survival, and reproduction, and those, in turn, translate into population-level consequences.

The goals of my study can be reduced to three major questions: 1) do amphibians exhibit behavioral avoidance of clearcuts? 2) are clearcuts less permeable to amphibians, relative to forested habitat? 3) what are the potential consequences for amphibians of habitat selection choices and diminished habitat permeability? The more we understand how each species' response varies with respect to site, season, and regional factors, the better equipped we will be to accommodate each species' needs in managed forests. Although I observed variation among individuals and species at a site, variation in response can also occur seasonally and between the same species in different regions (deMaynadier and Hunter 1995, Russell et al. 2004) and probably even in different habitats within a region.

Each species may use a unique set of cues for selecting habitats that allow them to move efficiently, avoid predators, and reduce the risk of desiccation. As habitat loss and fragmentation increase in the landscape, the survival and persistence of amphibian species and populations may depend increasingly on their ability to distinguish between habitats and act accordingly. Knowledge of species responses to habitat alteration will enable land managers and conservationists to account for these differences in their forest management plans.

Habitat Selection

Rana sphenocephala

As anticipated, habitat selection varied among *R. sphenocephala*, *A. opacum*, and *B. terrestris*. However, the differences observed were not always as I had predicted. For example, I expected *R. sphenocephala* to select forests, and ultimately they did, but only after an initial preference for clearcuts. More frogs were in forests at 90 m, but the small sample size at that distance makes it difficult to detect a significant difference using the binomial test. The percentage of frogs in forest at 90 m suggests that they may ultimately prefer forests, but this could be an artifact of the technique used (see Chapter 3); if the fluorescent powder was less effective in the clearcuts, then fewer individuals in the clearcuts would have intact paths at 90 m. Thus, further research is necessary to determine if the technique works equally well in differing habitats. Nonetheless, the fact that the frogs did make a choice at 5 m shows that they were using cues and making informed decisions. Although some studies have found that *R. sphenocephala* prefer forests (e.g., Enge and Marion 1986), other studies have not detected any negative effects of clearcuts on this species (e.g., Russell et al. 2002b).

Several possible explanations exist for the frogs' initial movement into clearcuts and eventual selection of forests. First, since the frogs were originally from a grassy non-forested Carolina bay wetland, they may have initially moved into the clearcut because they associated a large open area with water. Other investigators have found that amphibians orient towards wetlands and other water sources when in an unfamiliar habitat (Oldham 1967, Sinsch 1992), so this explanation has merit. Another possibility is that the frogs initially took the path of least resistance and later began to select more sheltering habitat. Similarly, a study of displaced green frogs (R. clamitans) on a golf course found that the frogs chose the habitat that allowed the fastest rate of movement (short grass) and preferred areas immediately adjacent to more sheltering habitat (Birchfield and Deters 2005). In contrast, adult R. sylvatica migrated preferentially toward closed-canopy forested habitat and avoided open clearings at a study site in Maine (Vasconcelos and Calhoun 2004). The behavioral differences observed between R. sylvatica in Maine and R. sphenocephala in my study may be due to regional, species, or environmental differences, among others. A third feasible explanation for the movement behavior of *R. sphenocephala* is that the environmental gradient between the treatments, while inconsequential at night, can be quite large during the day; thus, the frogs that spent a day in a clearcut may have moved into forest after nightfall but before I tracked their movement 24 hours after release. These three explanations are not mutually exclusive; they could all potentially have influenced the frogs' movements.

Ambystoma opacum

I expected *A. opacum* to select forests more than clearcuts, but instead they appeared to move at random when released on forest/clearcut edges. This differs from the nonrandom movement observed by adult *A. maculatum* as they exited breeding pools in Maine; these individuals migrated preferentially towards closed-canopy forests and avoided open clearings (Vasconcelos and Calhoun 2004). However, a study in Connecticut found that *A. opacum* had the highest forest-edge permeability out of six amphibian species, suggesting that this species will attempt to cross open areas (Gibbs 1998). Perhaps *A. opacum* are willing to move through clearcuts or similar open habitat when moisture and temperature conditions

are favorable. If that is the case, the *A. opacum* in my experiment may have moved at random simply because they did not need to be selective under the relatively mild conditions at the time of release. Alternatively, since they are a slower moving species, it is possible that individuals may not have had enough time to select ideal habitat; it could take them more than 24 hours to select suitable habitat. The salamanders were probably not making a migratory movement since they did not move very far relative to the much lengthier migration distances recorded previously for this species (Williams 1973); instead it seems that they were focused on securing cover. Most likely, the apparent random movement by *A. opacum* is a combination of little pressure to be selective given the environmental conditions when released and of limited time to sufficiently sample the habitats and select an ideal area.

Bufo terrestris

Bufo terrestris appeared to prefer clearcuts, which is consistent with their prevalence throughout most types of habitat on the Savannah River Site (Gibbons and Semlitsch 1991, Buhlmann et al. 2005) and the preference of some toads for areas with sandy or bare soil (Bartelt et al. 2004). Several researchers have concluded that toad abundance does not differ in clearcuts and forests (Enge and Marion 1986, Perison et al. 1997) and others have found that *B. terrestris* are ubiquitous in most habitats and readily occupy open grassy habitats (Phelps and Lancia 1995, Hanlin et al. 2000). Spadefoot toads (*Pelobates fuscus*) at a research site in France preferentially used areas that had bare soil and shorter vegetation and avoided shrub-covered areas (Eggert 2002), which is similar to the initial movement patterns I observed for *B. terrestris*. The toads, once given time to move further, may not have shown a preference for clearcuts, but research on western toads (*B. boreas*) has highlighted the importance of sun exposure to toads (Bartelt et al. 2004). *Bufo boreas* generally preferred habitat, such as open forests and habitat edges, which provided some cover but also allowed a reasonable amount of light to penetrate to the ground for the purposes of basking (Bartelt et al. 2004). Thus, *B. terrestris* may be capable of using multiple habitat types and might not find the environmental conditions in clearcuts problematic, providing that the moisture level is adequate, cover is available, and there is no shortage of prey.

Habitat Differentiation

The current study revealed that *R. sphenocephala* and *B. terrestris* could differentiate between forests and clearcuts, but *A. opacum* were unable to differentiate, lacked the incentive to be selective, or truly had no preference during migration. The initial selection of clearcut by *R. sphenocephala* demonstrates that they recognized it as different from the forest. That the majority of frogs at the 90 m distance were in forests suggests that they are capable of distinguishing between differing habitats and then selecting the most suitable habitat type. Even though the toads preferred clearcuts, the fact that they recognized a difference in the clearcut and forest implies that they would be capable of moving into the forest if conditions were unsuitable for them in the clearcut.

The salamanders' inability or decision to be non-selective when released could pose some serious problems for this species, especially in the long term. If they are unable to initially differentiate between the habitats, then the high soil moisture and apparently suitable conditions of a clearcut on a night in early spring could create a situation where the clearcut acts an ecological trap or habitat sink (Chan-McLeod 2003, Rittenhouse et al. 2004, Rothermel 2004). Species with low mobility or an inability to distinguish between habitats may initially enter a seemingly suitable area and then not be able to leave when conditions worsen. Some species are known to wait for a rainy night to move (Shoop 1974, Johnston and Frid 2002); thus, if it does not rain for an extensive amount of time, they will likely face a high risk of desiccation. Therefore, a poor initial decision may carry great consequences for survival.

The range of responses and behaviors from these three species reinforces that habitat choice is species-specific (Russell et al. 2004) and likely depends on regional (deMaynadier and Hunter 1995), seasonal (Seebacher and Alford 2002), and habitat differences (Russell et al. 2004). Habitat choice is a complex decision precisely because it is influenced by multiple factors, including a need to travel quickly, to expend the least amount of energy, and to reduce the risks of predation and desiccation.

Movement Path Analysis

The results from the movement path analysis indicate that the manner in which amphibians move can vary greatly among species and habitat types. Other investigators have found differences in movement patterns among species (Sjogren-Gulve 1998, Rothermel and Semlitsch 2002), but to my knowledge no one else has quantified movement path characteristics among multiple species and different habitat types. Understanding individual amphibian movement behavior and habitat use is critical for modeling and predicting the habitat needs and movements of amphibians in fragmented and altered landscapes (Gibbs 1998, Semlitsch 2000). In fact, I am more interested in estimating the values for the movement parameters, regardless of statistical significance, because these estimates are crucial for modeling and reasoned conservation planning. The underlying reason for gathering this type of information is that these movement pattern differences could presumably have implications for individual-level fitness and ultimately have population-level effects (Lima and Zollner 1996).

The maximum and average path length provide measures of a species' potential mobility; *R. sphenocephala*, with a higher mean path length, were most mobile, while *B. terrestris* were capable of being as mobile (similar maximum path length), but traveled shorter distances on average. *Ambystoma opacum* on the other hand, seemed unable or unwilling to move long distances in a single night. Increased wandering or searching behavior in exposed areas could make a species more vulnerable to predation (Rosenberg et al. 1998), and possibly decrease chances of successfully traversing large tracts of unsuitable habitat. For example, *B. terrestris* took more turns per 10 m and had less linear movement than the other species. *Ambystoma opacum* also made more turns per 10 m than *R. sphenocephala*, and fewer individuals had directional movement, suggesting that they did relatively more searching. However, a shorter mean movement distance for *A. opacum* indicates that the salamanders may have been initially searching for cover. These differences in mobility and movement patterns could lead to large interspecific differences in individual survival and population viability in altered landscapes (Johnston and Frid 2002).

Amphibians need to move efficiently (Zollner and Lima 2005), so increased searching behavior (e.g., more turns/10 m) would presumably require more energy than moving in a more direct manner. Likewise, when amphibians alter their movement patterns in response to altered habitats, they may also be putting themselves more at risk to predation and desiccation (Moseley et al. 2004). Thus, the fact that all three species made more turns in clearcuts than in forests suggests that movement in these habitats incurs physiological costs. Both *R. sphenocephala* and *B. terrestris* moving farther in forests could mean that when the habitat allows, these species prefer to move longer distances. However, further research on the relative suitability of differing habitats needs to be conducted to fully understand this behavior. *Ambystoma opacum* did not move farther in forests, which supports that they were simply searching for cover, at least within the first 24 hours after being released. Another possibility is that the short length of the *A. opacum* trails could make it difficult to detect treatment differences in path characteristics.

The percent of path in clearcut influenced path length and the number of turns per 10 m but not linearity in the among-species comparison of path characteristics. This suggests that a treatment effect exists for some of these movement variables and supports the claim that some amphibian species, under certain conditions, may alter their movement behavior in response to forest management.

The significant site effect for *R. sphenocephala* is not surprising because site differences often exist in amphibian studies (Russell et al. 2002a, Chan-McLeod 2003). Site differences that may have influenced the frogs' behavior include variation in topography, vegetation, and moisture, as well as off-site areas of interest to the amphibians, among many others. However, not enough is known about how these species orient and what their primary cues are to state with certainty the particular site differences that affected the frogs' movement patterns.

Edge and Habitat Permeability

Edge and habitat permeability have the potential to influence individuals and have populationlevel effects. Because none of the species exhibited strong behavioral avoidance of the clearcuts and all three species successfully moved across the forest/clearcut edges, edge permeability is probably not a serious problem for these species. However, the permeability of an edge has been shown to vary by season and with the weather conditions in some cases (Chan-McLeod 2003), so it is possible that some species may experience decreased edge permeability in another season. For example, *R. a. aurora* are more likely to avoid moving across habitat edges and into clearcuts in hot and dry weather (Chan-McLeod 2003). Salamanders have a relatively higher risk of desiccation than most anurans (Duellman and Trueb 1994), so seasonal changes in edge permeability may be most applicable to *A. opacum*.

The time-scale of my study does not provide enough information about habitat permeability to definitively state its influence on these three species, but my results suggest that habitat permeability is also not a major issue. *Rana sphenocephala* seemed fully capable of moving across large sections of a clearcut, so perhaps habitat permeability was not reduced for this species. However, quite a few of the frogs reversed direction out of clearcuts, indicating that they may have found the clearcuts unsuitable. *Bufo terrestris* also seemed capable of traversing a clearcut within 24 hours and their movements showed little indication of diminished habitat permeability in clearcuts. In fact, the toads may be able to tolerate the extreme daytime conditions in clearcuts better than the other two species, especially if the toads can find suitable cover and moisture (Bartelt et al. 2004, G. Graeter unpubl. data). Spending time in clearcuts could incur other costs for *B. terrestris*, such as behavioral modifications or increased predation risk, but the clearcuts do not seem to act as barriers to their movement.

Although I did not detect treatment-related differences in habitat selection or movement for *A*. *opacum* during the first 24 hrs after release, clearcuts may still pose reduced permeability for this species on longer time-scales or under harsher environmental conditions. *Ambystoma opacum* may experience reduced permeability in the clearcuts because they are a less mobile species and face greater risks of desiccation (deMaynadier and Hunter 1998). Other investigators have found significantly decreased habitat permeability in closely related species (C. Conner pers. comm. 2005, B. Metts unpubl. data, Rothermel and Semlitsch 2002, Rothermel 2004), so a reasonable assumption is that *A. opacum* may be affected comparably because they share a similar physiology and movement ability. Tracking *A. opacum* for multiple days or under weather conditions that are less ideal for this species may have produced

different results. Further research is needed to more fully understand the role that permeability plays in amphibian movement and population dynamics in altered habitats.

Influence of Amphibian and Environmental Variables

Rana sphenocephala and *B. terrestris* did not select habitat relative to environmental cues or according to amphibian characteristics, including SVL and sex. This suggests that these two species moved without regard to the observed environmental conditions, including soil moisture and temperature, relative air humidity and temperature, and sky condition. Alternative cues, such as olfactory or auditory cues, may be particularly important during habitat selection when temperature and moisture levels do not differ among otherwise drastically different habitats (Rittenhouse et al. 2004). Thus, when environmental conditions are suitable, as they presumably are on a warm, moist night, the frogs and toads may not use environmental conditions to orient because there is no pressure to do so. Furthermore, the time scale during which amphibians sample environmental conditions and make decisions about habitat selection could be much longer than the time course of my experiment.

Habitat selection of *A. opacum* was correlated with mean soil moisture, with salamanders being more likely to go into clearcuts if soil moisture content was higher. Perhaps a species that is highly vulnerable to desiccation, like *A. opacum*, is more likely to use environmental cues to make habitat selection decisions than less vulnerable species, even on nights when environmental conditions are tolerable. *Ambystoma opacum* may use these cues more because they are less mobile and possibly less capable of successfully leaving an unsuitable area. A lab experiment on a closely related species, *A. maculatum*, on substrate selection confirmed that salamanders preferred soil with higher moisture (Rittenhouse et al. 2004). Field studies have also found that ambystomatid salamanders prefer habitats with higher moisture levels (Naughton et al. 2000, Moseley et al. 2004), presumably because the high ambient air temperatures and low soil moisture levels that often exist in exposed disturbed areas have been shown to cause dehydration (Petranka et al. 1993). Rittenhouse et al. (2004) also found that *A. maculatum* preferred habitat with leaf litter over bare soil; thus, if leaf litter and moisture were sufficient,

the salamanders in my study may have considered the clearcuts to be suitable habitat. However, because I did not track them for multiple days, I do not know whether they would stay in the clearcuts and if they would experience negative consequences of that choice in the long term.

Microhabitat Availability versus Use by Rana sphenocephala

I condensed several variables (bare ground, leaf litter, and herbaceous vegetation) into one variable representing ground-level openness. The inclusion of only the treatment variable in the highest weighted model for ground-level openness implies that forest treatment influenced use of openness by the frogs independent of differences in availability. The mean use and availability values for each treatment at the two sites also support the influence of treatment on use of openness. The general trend was that frogs used more openness in forests and less in clearcuts than was available, suggesting a preference for a level of openness suitable for efficient movement but without too much exposure (Birchfield and Deters 2005). Most likely, some characteristic or feature beyond what I measured for availability influenced use from one treatment to another. One possible explanation for the importance of treatment to use of openness is that the frogs may have preferred more openness, but had a harder time using openness in the CC-retained. The frogs' behavior also may have been affected by treatment-specific features, such as the amount of overhead canopy, the topography, or olfactory cues; other investigators have suggested that these types of cues have the potential to influence amphibian habitat use and movement (Oldham 1967, Dole 1972, Rittenhouse and Semlitsch in review).

The composite variable for ground-level cover was created by combining the woody vegetation and woody debris variables. Since six models for ground-level cover were equally weighted by AIC, I cannot state conclusively whether any of the variables influenced frog use of ground-level cover. The highest weighted model had little support for the availability variable because of high standard error, but the frog gender variable had slight support, indicating that frog use of cover may have differed by sex to some degree. Female *R. sphenocephala* may have used more cover than males, which mirrors the findings of a study on *B. boreas* (Bartelt et al. 2004). One obvious trend is that the frogs in the CC-

retained used less cover than was available; this behavior reinforces that the frogs were focused on movement, rather than on selecting suitable cover. In general the frogs may have preferred to use a similar amount of cover regardless of how much was available and of which treatment they were in; in that scenario, frogs might prefer to move through relatively open areas because it is the most efficient use of energy and time. Again, this behavior parallels the results of the study on *R. clamitans* on a golf course, where the frogs chose to move in the shortest grass, presumably because it allowed the greatest rate of movement (Birchfield and Deters 2005).

The tree density composite variable was created by summing the number of trees in four categories (understory hardwoods, understory pines, overstory hardwoods, overstory pines). Six models were similarly weighted for tree density, but the fact that availability or treatment or both were in all of these models implies that these two variables likely have some influence on habitat use of tree density. Thus, the frogs used habitat relative to availability in some cases, but even after accounting for differences among treatments in availability, treatment still influenced behavior. The frogs associated with higher tree density than was available except in the control treatment, implying that they prefer to keep close to trees to a certain extent. In fact, the frogs appeared to use higher tree density than was available in the clearcuts (i.e., tree density availability = 0), but this is only because they were initially released into edge habitat.

In general, *R. sphenocephala* used microhabitat relative to what was available, except when it obstructed their movement (e.g., large amounts of CWD in the CC-retained treatment). Rather than selecting cover, the frogs seemed to select habitat that would ease their movement. Microhabitat use appeared to be a complex process whereby the frogs moved through an area and simultaneously drew on different types of information to make selection choices. Sometimes they may have simply moved a certain direction, avoiding large amounts of CWD or shrubs along the way. At other times they may have used cues from something I was unable to capture in my measurements, such as olfactory cues, topography, or distant sounds or landscape features (e.g., frog choruses, tree-lines, wetlands).

Despite other factors that may have influenced habitat use, my study demonstrates that amphibian habitat use is affected by forest alteration; this could have individual and population-level consequences for amphibians, such as increased risks of predation and desiccation, if an individual is unable to adjust as needed. I found that body size and sex had little influence on habitat use, although females may have used slightly more cover than males. I also found that treatment type influenced the use of ground-level openness and that both availability and treatment had some influence on use of tree density, but neither availability nor treatment had a strong influence on use of ground-level cover. In summary, the leopard frogs preferentially used more open areas, avoided those areas with excess cover that could impede movement, and often associated with greater tree density than was available.

CONCLUSIONS AND IMPLICATIONS

The experimental releases on forest/clearcut edges demonstrated that, over 24 hrs, *A. opacum* selected habitat at random, *B. terrestris* preferred clearcuts, and *R. sphenocephala* initially selected clearcuts, but may have ultimately preferred forests. The choices these species made indicate that while both *B. terrestris* and *R. sphenocephala* are capable of differentiating between habitat types, *A. opacum* may not be able to. I also found that the manner in which amphibians move can vary greatly among species and different habitat types. Whereas the frogs exhibited long-distance, directional movement with few turns, the toads exhibited more searching and wandering behavior, and the salamanders seemed to be focused primarily on locating cover. All three species made more turns in clearcuts than forests, and *B. terrestris* and *R. sphenocephala* moved farther in forests. *Rana sphenocephala* and *B. terrestris* did not select habitat relative to environmental cues or according to amphibian characteristics, but *A. opacum* were more likely to go into clearcuts if soil moisture content was higher. *Rana sphenocephala* often selected microhabitat with more openness than was available, avoided excess cover that would obstruct movement, and used higher tree density than was available in all treatments except the control.

One should consider the results of this study in the context of the experiment's time scale and seasons. For example, each individual was given only 24 hours to select habitat and move. For some

species, such as *A. opacum*, this may not be enough time to select their ultimate habitat choice. Similarly, each species' response could differ according to season (Schlaepfer and Gavin 2001, Watson et al. 2003). Thus, although *A. opacum* did not make a clear choice of either clearcut or forest in late winter/early spring, the harsher conditions of other seasons may provide incentive to be more selective, especially if the conditions in the clearcut are more severe. Likewise, *R. sphenocephala* might show a stronger preference for forests if released under less ideal conditions or if given more time. Furthermore, some species are relatively sedentary during the non-breeding season (e.g., *A. opacum*) and others are more nomadic (e.g., *B. terrestris*); these differences could affect how their behavior is interpreted and the potential consequences each species experiences.

Because all three species were released in their respective post-breeding seasons, individuals may have been in a migratory mode, where they are simply focused on moving away from the breeding pond and towards their non-breeding season habitat, rather than selecting suitable habitat along the way (Bulger et al. 2003, Rittenhouse and Semlitsch in review). However, it seems that this operating system best fits the movement behavior and habitat selection of *R. sphenocephala* since they moved relatively directionally with few turns and without regard to environmental conditions at distances relevant to migratory movement, and generally preferred to move in more open areas, avoiding habitat types that obstructed movement. *Ambystoma opacum*, on the other hand, traveled short distances, were often found under cover, and probably used soil moisture cues, indicating that the salamanders were more focused on locating suitable cover rather than on migratory type movements. *Bufo terrestris* seems to hold an intermediate position; whereas some of the toads moved distances that were relevant to migratory movements, without regard to environmental conditions, others moved only a short distance and immediately took refuge under cover. Furthermore, the toads exhibited more wandering and searching behavior, as was evident from their relatively high number of turns and less directional movement.

The results of my study help explain and support the findings of several previous studies that examined the effects of forest management on amphibian abundance in the Southeast. For example, that the *A. opacum* I studied seemed unable or unwilling to differentiate between the habitats could mean that

the clearcuts were ecological traps for this species and this behavior could help explain the reduced abundance observed for *Ambystoma* species in forest clearings (Means et al. 1996, Cromer et al. 2002). Similarly, previous studies have found that *B. terrestris* are present in high abundances in a variety of different habitats (Bennett et al. 1980, Hanlin et al. 2000) and my findings demonstrate that this may be because they prefer clearcuts and do not avoid movement into them. Likewise, the ultimate preference for forest habitat by *R. sphenocephala* helps clarify the patterns previously observed, that this species sometimes exists in higher abundances in forests than in clearcuts (Bennett et al. 1980). Furthermore, the costs, such as higher risks of predation and desiccation, that are presumably associated with an increased turning frequency in the clearcuts could account for the slightly lower abundances recorded for *R. sphenocephala* and *B. terrestris* in clearcuts (Bennett et al. 1980, Hanlin et al. 2000).

The ability of some amphibian species to distinguish between habitats or successfully traverse a clearcut does not mean that an area meets that species' habitat needs or that there are no costs to moving through those areas. A study on red-legged frogs (*R. a. draytonii*) found that most migrating frogs moved overland in approximately straight lines to target sites without apparent regard to vegetation type or topography (Bulger et al. 2003). These results parallel my observation on *R. sphenocephala* in that some of them successfully traversed an altered habitat. However, it is possible to move through an area but experience consequences of that movement; for example, a recent radio-telemetry study observed no difference in *R. sylvatica* movement in different habitats, but did find differences in water loss rates between clearcuts and forests (T. Rittenhouse pers. comm. 2005).

Reduced habitat permeability in clearcuts and an inability to differentiate between habitats can potentially have both individual costs and population-level implications for amphibians. Individuals can experience direct physiological costs from spending time in and moving through unsuitable habitat (Schwarzkopf and Alford 1996). Amphibian body temperature, a function closely linked to water loss, is dependent on environmental temperatures and can therefore become disrupted in unsuitable habitats. For example, an individual's water budget can become unbalanced so that it experiences elevated rates of evaporative water loss (Schwarzkopf and Alford 1996, Rothermel and Luhring in press), which can lead

to dehydration or even death through desiccation (Rothermel and Luhring in press). All three species in this study took more turns in clearcuts than in forests, which could potentially require more energy per distance covered and affect water loss rates and body temperature. Even if an individual does not reach its critical thermal limit, it can still experience sublethal effects associated with an elevated body temperature (e.g., dehydration, decreased ability to capture prey, Preest and Pough 1989, 2003). Furthermore, physiologically related stress can potentially result in impaired immune functions and thus, an elevated susceptibility to parasites and pathogens (Carey 1993, Daszak et al. 2003). Finally, spending more time in clearcuts where exposure is greater, as *B. terrestris* may do, could make an individual more vulnerable to predation (Moseley et al. 2004).

An amphibian's reproductive success can also be influenced by spending time in suboptimal habitat or by a decrease in habitat permeability. For example, body mass in amphibians is directly related to female fecundity (Scott and Fore 1995), and an inability to adequately meet energetic demands can reduce fat stores and decrease egg production. A decrease in reproductive success can also result from movement-related causes. Decreased habitat permeability can make it more difficult for an individual to move successfully through a clearcut to reach a breeding site. Alternatively, an individual may arrive at the breeding pond, but if fewer individuals have successfully traversed a clearcut, it could be more difficult to find a mate. All of these individual-level costs can translate into population-level consequences, such as genetic problems and reduced functioning of metapopulation dynamics.

Having a solid understanding of how a particular species responds to certain forest management practices in different seasons, under different weather conditions, and at different sites is important for making relevant, informed, and species-specific management decisions. With species-specific knowledge, land managers can begin to implement measures that minimize negative effects associated with forest management for the amphibians in an area. My results suggest that a forested buffer around a wetland may benefit some amphibian species, particularly those for which clearcuts may act as an ecological trap (e.g., *A. opacum*) and for those that encounter decreased permeability in clearcuts (e.g., possibly *R. sphenocephala*). Leaving a buffer of intact forest around a wetland will increase the

likelihood that sufficient habitat is present to meet the needs of each species and to facilitate successful movement to and from the breeding site (Semlitsch and Bodie 2003). My research suggests that a small clearcut (4.1 ha) may not be a serious problem in terms of migration for some species. Presumably, larger clearcuts could be more problematic for amphibians than smaller ones because they may be more likely to impede movement or even become a complete barrier. An amphibian's ability to successfully move through an altered area can decrease with distance traveled (Marsh et al. 2004). At present I do not have enough information to make a specific recommendation about the size of clearcuts.

Forest management can be conducted in a manner that potentially minimizes the impacts on amphibians. Sustainable forestry, which strives to maintain habitat quality and biodiversity, is slowly gaining support and being used more frequently (NCSSF 2005). This type of forestry may offer a suitable balance between the economic demand for forest products and the need for wildlife conservation, primarily because sustainable forestry considers the whole forest ecosystem. For example, timing management activities in coordination with amphibian habitat selection abilities and habitat permeability characteristics, including how they differ seasonally and among species, may result in fewer detrimental effects of forest management activities on amphibians. When managing an area for an amphibian species, consider whether individuals can differentiate between habitats, the costs of movement and spending time in disturbed habitats, and a species' short and long term non-breeding habitat preferences. Whereas management of a *Rana* species may require relatively small clearcuts with forested habitat in the vicinity of a breeding site, management for a *Bufo* species may require a mix of forested and open habitats containing plenty of suitable cover (e.g., leaf litter and coarse woody debris). Amphibians, especially salamanders, require leaf litter and loose soil for cover, so any techniques that minimize soil compaction and removal of leaf litter are beneficial. Lastly, forests should be managed so that they have structural diversity and allow sufficient light intensity in the forests. This is particularly an issue in managed pine plantations, where structural diversity and ground floor vegetation are lacking, and light penetration is minimal (Means et al. 1996, Means 2005).

Future research should investigate the ultimate habitat selection and response of A. opacum under less ideal environmental conditions in which the consequences of making a poor choice detrimentally affect survival and reproductive success. As amphibian tracking technology advances, it may become possible to track small amphibians, such as A. opacum, for longer periods of time with minimal disturbance to the animal and its behavior. The use of fluorescent powder for tracking amphibians may be a particularly useful technique for studying endangered or threatened species (e.g., flatwoods salamander, A. cingulatum), especially when basic information on the species, such as their habitat use or movement patterns, is lacking. More research is needed to identify and understand the physiological costs that amphibians experience from movement through different forest management types. A comparison of the effects of forest management on amphibians among differently sized clearcuts is needed so that recommendations can be made for the size of clearcuts. A closer look at the effects of permeability on amphibians in differing habitats is much needed, particularly in the Southeast because little research has been done on this topic in this region. In terms of population-level effects, the ability of a species to persist in the long term also depends on the dispersal ability of juveniles. Others are already investigating some of these movement issues from the perspective of juvenile amphibians (B. Metts pers. comm. 2005, Gibbons et al. unpubl. data). Lastly, longer term studies of movement are needed to improve our understanding of basic habitat use by these species and to reveal any seasonal differences in their habitat selection and movement behavior in altered forests.

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Table 2.1. Binomial probability results for *R. sphenocephala*, *A. opacum*, and *B. terrestris* by edge type. Sample size (n) for each species at each of the selected distances from the release point, number of individuals that selected forest (control or partial; k), and the lower (L) and upper (U) limits of Wilson's 95% confidence interval (C.I.) are listed for each of the four edge types (CON/REM: control/CC-removed; CON/RET: control/CC-retained; PAR/REM: partial/CC-removed; PAR/RET: partial/CC-retained). Confidence intervals that do not include the value 0.5 (in bold) indicate that the sample varies from random habitat selection.

Edge Type																		
		CON/REM					CON/RET				PAR/REM				PAR/RET			
	-		C.I.				C.I.			C.I.				C.I.				
Species	Distance	n	k	L	U	n	k	L	U	n	k	L	U	n	k	L	U	
R. sphenocephala	5 m	12	1	0.01	0.35	11	2	0.05	0.48	11	3	0.10	0.57	10	1	0.02	0.40	
	30 m	9	2	0.06	0.55	9	5	0.27	0.81	11	5	0.21	0.72	9	4	0.19	0.73	
	60 m	8	3	0.14	0.69	4	3	0.30	0.95	8	4	0.22	0.78	8	2	0.07	0.59	
	90 m	3	1	0.06	0.79	4	3	0.30	0.95	4	3	0.30	0.95	3	3	0.44	1.00	
A. opacum	2 m	11	5	0.21	0.72	11	5	0.21	0.72	11	3	0.10	0.57	11	5	0.21	0.72	
	End	6	3	0.19	0.81	9	5	0.27	0.81	9	3	0.12	0.65	9	4	0.19	0.73	
B. terrestris	5 m	10	3	0.11	0.60	8	0	0.00	0.32	8	1	0.02	0.47	8	4	0.22	0.78	
	End	8	4	0.22	0.78	7	2	0.08	0.64	7	3	0.16	0.75	7	3	0.16	0.75	
Table 2.2. Binomial probability results for *R. sphenocephala*, *A. opacum*, and *B. terrestris*, with data condensed into two treatments, Forest v. Clearcut. Sample size (n) for each species at each of the selected distances from the release point, number of individuals that selected forest (control or partial; k), and the lower and upper limits of Wilson's 95% confidence interval are listed. A confidence interval that does not include the value 0.5 (in bold) indicates that the sample varies from random habitat selection.

Species	Distance	n	k	Lower C.I.	Upper C.I.
R. sphenocephala	5 m	44	7	0.08	0.29
	30 m	38	16	0.28	0.58
	60 m	28	12	0.27	0.61
	90 m	14	10	0.45	0.88
A. opacum	2 m	44	18	0.28	0.56
	End	33	15	0.30	0.62
B. terrestris	5 m	34	8	0.12	0.40
	End	29	12	0.26	0.59

Table 2.3. Results of multivariate analysis of variance of the effects of treatment (clearcut v. forest), site, and their interaction on each species' movement path characteristics (path distance, # turns/10 m, and linearity).

Species	Source of variation	df	Wilks' λ	F	р
R. sphenocephala	Treatment	3,38	0.7473	4.28	0.0106
	Site	3,38	0.8046	3.08	0.0390
	Treatment x site	3,38	0.9467	0.71	0.5502
A. opacum	Treatment	3,37	0.9544	0.59	0.6261
	Site	3,37	0.9435	0.74	0.5354
	Treatment x site	3,37	0.9865	0.17	0.9164
B. terrestris	Treatment	3,29	0.8410	1.83	0.1642
	Site	3,29	0.9708	0.29	0.8318
	Treatment x site	3,29	0.9046	1.02	0.3985

Model	Δi	Akaike weights
$y=\beta_0+\beta_1(trt)$	0.00	0.37
$y=\beta_0+\beta_1(trt)+\beta_2(avail)$	1.90	0.14
$y=\beta_0+\beta_1(avail)$	2.30	0.12
$y=\beta_0+\beta_1(sex)+\beta_2(avail)$	3.00	0.08
$y=\beta_0 + \beta_1(sex) + \beta_2(trt) + \beta_3(avail)$	3.00	0.08
y=β ₀	3.30	0.07
$y=\beta_0+\beta_1(sex)$	3.80	0.06
$y=\beta_0+\beta_1(sex)+\beta_2(svl)$	4.80	0.03
$y=\beta_0+\beta_1(svI)$	5.30	0.03
$y=\beta_0 + \beta_1(sex) + \beta_2(svl) + \beta_3(trt) + \beta_4(avail)$	6.50	0.01

Table 2.4. Ground-level openness candidate models showing fixed effects, model Δi values, and Akaike weights.

Table 2.5. Fixed effects coefficient estimates for the highest ranked models for each composite variable.

Composite Variable	Variables in Best Model	Subcategory	Coefficient Estimate	Standard Error
Ground-Level Openness	treatment	CON	7.2672	4.6446
		PAR	10.2584	4.5294
		REM	5.8507	4.3298
		RET	0	-
Ground-Level Cover	availability		0.1329	0.1431
	sex	female	4.6785	2.6206
		male	0	-
Tree Density	availability		1.0249	0.547
	treatment	CON	-1.1265	2.453
		PAR	0.2402	1.2265
		REM	0.1542	0.2855
		RET	0	<u>-</u>

Model	Δί	Akaike weights
$y=\beta_0+\beta_1(avail)+\beta_2(sex)$	0.00	0.20
y=β ₀	0.30	0.17
$y=\beta_0+\beta_1(avail)$	0.80	0.14
$y=\beta_0 + \beta_1(avail) + \beta_2(sex) + \beta_3(svl)$	1.20	0.11
$y=\beta_0 + \beta_1(sex)$	1.30	0.11
$y=\beta_0+\beta_1(svI)$	2.00	0.07
$y=\beta_0 + \beta_1(sex) + \beta_2(svl)$	2.60	0.06
$y=\beta_0 + \beta_1(trt)$	2.70	0.05
$y=\beta_0 + \beta_1(avail) + \beta_2(trt) + \beta_3(sex)$	3.30	0.04
$y=\beta_0+\beta_1(trt)+\beta_2(avail)$	4.10	0.03
$y=\beta_0 + \beta_1(avail) + \beta_2(trt) + \beta_3(sex) + \beta_4(svl)$	4.40	0.02

Table 2.6. Ground-level cover candidate models showing fixed effects, model Δi values, and Akaike weights.

Table 2.7. Tree density candidate models showing fixed effects, model Δi values, and Akaike weights.

Model	Δi	Akaike weights
$y=\beta_0+\beta_1(trt)+\beta_2(avail)$	0.00	0.26
$y=\beta_0 + \beta_1(avail) + \beta_2(trt) + \beta_3(sex)$	0.30	0.22
$y=\beta_0+\beta_1(avail)$	1.40	0.13
$y=\beta_0 + \beta_1(trt)$	1.70	0.11
$y=\beta_0 + \beta_1(avail) + \beta_2(sex)$	1.80	0.10
$y=\beta_0 + \beta_1(avail) + \beta_2(trt) + \beta_3(sex) + \beta_4(svl)$	2.00	0.09
$y=\beta_0 + \beta_1(trt) + \beta_2(sex)$	2.10	0.09
y=β ₀	25.40	0.00
$y=\beta_0 + \beta_1(sex)$	25.50	0.00
$y=\beta_0 + \beta_1(sex) + \beta_2(svl)$	27.10	0.00
$y=\beta_0+\beta_1(svl)$	27.20	0.00



Figure 2.1. Diagram of a LEAP array showing the arrangement of the four forest management treatments [control (CON), partial cut (PAR), clearcut with coarse woody debris (CWD) retained (RET), and clearcut with CWD removed (REM)]. The four edge types (CON/RET, PAR/RET, PAR/REM, CON/REM) and 12 release points (3 per edge) are labeled. Each treatment is approximately 4.1 ha and each edge is approximately 178 m from the wetland to the outer boundary.



Figure 2.2. Diagram of microhabitat availability transects in one quadrant. Each transect was 90 m, with data recorded at 10 points at 10-m intervals. A total of 50 points were taken in each quadrant at each site.



Figure 2.3. Percentage of *R. sphenocephala* in clearcut v. forest at selected distances (5 m, 30 m, 60 m, and 90 m) from the release point on forest/clearcut edges.



Figure 2.4. Percentage of *A. opacum* in clearcut v. forest at 2 m and endpoint from the release point on forest/clearcut edges.



Figure 2.5. Percentage of *B. terrestris* in clearcut v. forest at 5 m and endpoint from the release point on forest/clearcut edges.



Figure 2.6. Movement paths of *R. sphenocephala* at (A) site 1000 and (B) site 37. Paths are color-coded by the date the frogs were released. The black outline represents the treatment and wetland boundaries.



Figure 2.7 Movement paths of *B. terrestris* at (A) site 37 and (B) site 119. Paths are color-coded by the date the toads were released. The black outline represents the treatment and wetland boundaries.



Figure 2.8. Movement paths of A. *opacum* at (A) site 119 and (B) site 37. Paths are color-coded by the date the salamanders were released. The black outline represents the treatment and wetland boundaries.



Figure 2.8C. A close-up of the A. opacum movement paths on the control/CC-removed edge at site 37.



Figure 2.9. Mean path length for each species. Values shown are least-squares means ± 1 standard error.



Figure 2.10. Minimum and maximum path lengths for each species.



Figure 2.11. Mean number of turns per 10 m for each species. Values shown are least-squares means ± 1 standard error.



Figure 2.12. Mean path linearity for each species. Values shown are least-squares means ± 1 standard error. A linearity value of 1 represents a path that is completely straight.



Figure 2.13. Mean path length in forests v. clearcuts for each species. Values shown are least-squares means ± 1 standard error.



Figure 2.14. Mean number of turns per 10 m in forests v. clearcuts for each species. Values shown are least-squares means ± 1 standard error.



Figure 2.15. Mean path linearity in forests v. clearcuts for each species. Values shown are least-squares means ± 1 standard error. A linearity value of 1 represents a path that is completely straight.



Figure 2.16. Mean values for ground-level openness availability v. ground-level openness use by *R*. *sphenocephala* by treatment type (control, partial, CC-retained, CC-removed) and site (37 and 1000).



Figure 2.17. Mean values for ground-level cover availability v. ground-level cover use by *R*. *sphenocephala* by treatment type (control, partial, CC-retained, CC-removed) and site (37 and 1000).



Figure 2.18. Mean values for tree density availability v. tree density use by *R. sphenocephala* by treatment type (control, partial, CC-retained, CC-removed) and site (37 and 1000).

CHAPTER 3

THE USE OF FLUORESCENT POWDERED PIGMENTS AS AN EFFECTIVE TECHNIQUE FOR TRACKING AMPHIBIANS¹

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INTRODUCTION

Researchers often use thread-trailing devices or radio-telemetry to study amphibian movement and terrestrial habitat use (Sinsch 1988, Madison and Farrand 1998, Schwarzkopf and Alford 2002, Watson et al. 2003). Fluorescent powdered pigments, used predominately for tracking small mammals, reptiles, and insects (Johansson 1959, Lemen and Freeman 1985, Fellers and Drost 1989, Blankenship et al. 1990, Dodd 1992, McCay 2000, Sujii et al. 2000), have recently been used successfully to track the terrestrial movements of amphibians (Eggert 2002, Birchfield and Deters 2005). The small size and sensitive skin of amphibians can make tracking their movements problematic, if not impossible, with some methods. Fluorescent powder has several major advantages as a tracking method, including being relatively inexpensive and harmless to amphibians (Rittenhouse et al. in review) and being suitable for use on juveniles and small species. Lastly, powder tracking is particularly useful for obtaining detailed information about an amphibian's movement, behavior, and microhabitat use over a short time period.

Powder tracking is beginning to be recognized as an underutilized amphibian tracking method that has great potential and may actually be the preferred method under certain circumstances (Rittenhouse et al. in review). However, the effectiveness and limitations of this method with multiple amphibian species under varying field conditions have not yet been explored. I present data from an experimental field study of three species, marbled salamander (*Ambystoma opacum*), southern toad (*Bufo terrestris*), and southern leopard frog (*Rana sphenocephala*) to demonstrate the potential success and specific limitations of powder tracking as a technique for amphibians. Because little is known about the relative distances different species can be tracked with powder, my data on powder path distances for multiple species provides a reference that will help determine if powder tracking is the right technique for certain species and research questions. My results also shed light on the effects of precipitation on path length and the effectiveness of different powder colors. Lastly, I provide general recommendations regarding the appropriate circumstances for using this technique with amphibians and how to maximize its effectiveness.

MATERIALS AND METHODS

I released 44 adult *A. opacum* (February-March 2005), 36 adult *B. terrestris* (March-May 2005), and 48 adult *R. sphenocephala* (May-August 2004) on forest/clearcut edges on the Savannah River Site (SRS) in the Coastal Plain of South Carolina. The clearcuts were created in spring of 2004 as part of the LEAP (Land-use Effects on Amphibian Populations) study. Methods used in this experiment and the LEAP study are discussed in more detail elsewhere (see Chapter 2).

Prior to release, I applied fluorescent powder (\$12/lb, Radiant Color Series T1, Richmond, CA; now DayGlo Color Corporation, Cleveland, OH) to each individual by dipping the lower 2/3 of its body into powder, taking care to prevent powder from coming in contact with the animal's eyes or mouth. Handling time was kept to less than 30 seconds. Approximately 24 hours after I released the individuals, I tracked the path of each using a Portable Rechargeable UV Lamp (UVL-26P, Fisher Scientific International) until I either located the animal or could not find any more powder. I used a Global Positioning System (GPS) Trimble Pro-XR backpack unit to record each path from start to end. Then I downloaded the GPS data and imported it into a Geographic Information System (GIS) to determine the length of each powder path.

I used ArcView 3.3 (Environmental Systems Research Institute, Redlands, Calif.) and the Animal Movement extension (Hooge and Eichenlaub 1997) to calculate powder path lengths for each species. To assess how path length varied among the four powder colors, I tested the effects of powder color and species on path length using a two-way ANOVA (Proc GLM, SAS Institute 2000). I used Tukey-Kramer's test to determine which colors differed from each other. I used the Type III sum of squares because I had unequal sample sizes. Lastly, I assessed the effect of precipitation on powder path length by examining changes in mean and maximum path length for each species with different amounts of post-release precipitation. For this analysis, I classified rainfall based on three different precipitation classes: 0 mm, light (< 10 mm), and heavy (> 10 mm).

RESULTS

Path length differed significantly among species in the two-way ANOVA ($F_{species 2,120}=17.52$, p<0.0001). The mean path length was shortest for *A. opacum* and longest for *R. sphenocephala* (Figure 3.1). The minimum distance an individual traveled was similar among the three species (1.9 – 3.5 m; Figure 3.1). The maximum distance traveled by *B. terrestris* and *R. sphenocephala* was similar, but *A. opacum* moved a shorter maximum distance (Figure 3.1). Similar data collected by LEAP collaborators provide insight into the variation in efficacy of this technique among species, regions, and varying climatic conditions (Figure 3.1). At a site in central Missouri, adult ringed salamanders (*A. annulatum*) were tracked farther (3 hrs post-release; n=60) on average than the *A. opacum* in my study, but far shorter distances than both *B. terrestris* and *R. sphenocephala* (Chris Conner pers. comm. 2005, Figure 3.1). In east-central Maine, tracking (4 hrs post-release; n=10) the movement of adult wood frogs (*R. sylvatica*) using fluorescent powder yielded fairly short paths (Sean Blomquist pers. comm. 2005, Figure 3.1).

Path length also varied among powder colors ($F_{powder color 3,120}=2.63$, p=0.0536). Chartreuse paths were the longest, pink the shortest, and green and orange were intermediate in path length (Figure 3.2). Chartreuse and pink path lengths differed significantly from each other (p=0.0596) based on a Tukey-Kramer test. Path length did not appear to differ among powder colors for *A. opacum*; however, chartreuse path lengths were still longest for both *B. terrestris* and *R. sphenocephala* (Figure 3.3).

The amount of post-release rainfall affected powder path length. Because there was no postrelease precipitation during the *B. terrestris* powder tracking season, I could not look at the effects of rainfall on path length for this species. Light amounts of precipitation (< 10 mm) did not seem to make detection of powder more difficult (Figure 3.4a and 3.4b). However, heavy rainfall (> 10 mm) slightly decreased the mean path length for *R. sphenocephala*. Most importantly, the maximum path length for *R. sphenocephala* was greatly reduced after heavy rains (Figure 3.4a). Shorter paths, such as those created by *A. opacum*, are apparently not negatively affected by light rainfall (Figure 3.4a)

DISCUSSION

Fluorescent powder tracking can be used successfully with a broad range of amphibian taxa, but the effectiveness of the technique depends greatly on a species' habitat use and movement range, weather conditions, and scale of the research question. I found that amphibians can be tracked long distances (> 350 m) within a 24-hr time period under ideal conditions. The ability to detect fluorescent powder varies, however, by powder color, especially when paths are long; when the flecks of powder become infrequent along the powder path, some colors (e.g., chartreuse) appear brighter and are more easily detected. I also found that fluorescent powder trails made by amphibians persisted under light rainfall, but were shortened considerably by heavier rainfall.

The comparison of mean path lengths of *A. opacum* and *A. annulatum* confirms that this technique has the potential to be equally successful with two closely related species in different geographic regions (C. Conner pers. comm. 2005). However, differing environmental conditions and the specific natural history of a species can make this technique less successful. For example, *R. sylvatica* were more difficult to track with fluorescent powder than *R. sphenocephala* because of the wet ground conditions at the research site in Maine (S. Blomquist pers. comm. 2005).

Some powder colors are difficult to distinguish under UV light (Stark and Fox 2000, Birchfield and Deters 2005). I found that the pink and orange powder looked similar, as did chartreuse and green. However, this problem could often be remedied by looking closely at the powder under a white light; when the speck of powder was large enough, the colors could be differentiated through close examination. Likewise, some colors are simply more difficult to detect (Stark and Fox 2000, Birchfield and Deters 2005). This study is the first to quantify a difference in amphibian path length among powder colors. The mean values for the path lengths of the four powder colors were as expected based on my experience in the field; when there were small amounts of powder, chartreuse and green paths were easiest to detect, followed by orange. Conversely, pink was the most difficult color to detect because it was the least bright under the UV light. The effect of powder color on path length was only detectable for the relatively long paths I obtained with *B. terrestris* and *R. sphenocephala*; as path length increased, certain colors became increasingly more difficult to detect than others. With relatively short path lengths or slow-moving animals (e.g., *A. opacum*), the powder trails were heavy and color had little effect on detectability, as found in previous studies (Birchfield and Deters 2005). Thus, although observer detection varies by color, this probably is not a problem unless animals travel long distances.

Just as powder works better for tracking some lizard species than others because of their scale type (Dodd 1992, Stark and Fox 2000), differing skin types in amphibians presumably affect how well the powder clings to the skin, and thus, the efficacy of this technique with a particular species. For example, powder stayed on *B. terrestris* better than *A. opacum*, presumably because *B. terrestris* has more surface area and uneven skin that powder clings to more readily. Thus, I found that certain techniques seemed to improve application and retention of the powder. Like many salamanders, *A. opacum* squirmed while being handled, causing the powder to wipe off; thus, I suggest minimizing handling time and keeping the powder in a small plastic container to ease application. *Rana sphenocephala* can also be difficult to handle so I recommend holding the frog by its front legs with its snout in the palm of your hand while applying powder. Lastly, the powder clung best to *B. terrestris* if loose soil was brushed off and the animal's skin was slightly moist.

The majority of the powder had usually brushed off the amphibians within 1-2 days and only small remnants of powder were still visible on their skin. Of the *B. terrestris* and *A. opacum* I examined in the days following powder application, most had very little powder clinging to them. I only saw *R. sphenocephala* on one occasion during the post-application period, so I do not know for certain how much powder was retained by this species. However, considering how far the *R. sphenocephala* moved and that their skin has a smooth texture, the powder probably had a similar retention time to the other two species. In a laboratory setting, where there was less opportunity to brush the powder off on natural objects (Rittenhouse et al. in review), amphibians lost powder at a rate comparable to what I observed.

Others have suggested that precipitation tends to reduce the visibility of the powder trail and even obliterate it entirely (Lemen and Freeman 1985, Blankenship et al. 1990), but to my knowledge no one has tested how different amounts of rainfall affect the mean and maximum lengths of amphibian paths. I found that light rainfall did not affect the maximum path length of *R. sphenocephala*, but that heavy rainfall greatly truncated the maximum path length; thus, I demonstrated that fluorescent powder tracking can be successful even with some precipitation.

Fluorescent powder, while non-toxic, is fairly persistent in the landscape (Halfpenny 1992), particularly if there is little moisture or precipitation. Thus, in a small area, a heavy rainfall will be necessary before powder of the same color can be used again (Stark and Fox 2000). Sometimes, powder can remain for weeks, even after a rain, especially where powder is thickly deposited. However, the powder is persistent in that specks of powder were found scattered throughout the study area, but the path itself was not discernable for more than a few meters. Wind can also affect the persistence and location of the powder (Eggert 2002); however, I only found the wind problematic when already sparse powder became scattered and when two or more paths of similar color crossed one another.

Recommendations

Before deciding to use fluorescent powder for tracking amphibians, several points should be considered. First, because powder paths usually persist only 1-2 days from application, this technique is most effective in answering questions about fine-scale movement and microhabitat use. For example, I could discern whether an individual had rested on woody debris or moved under it, the type of vegetation they had traveled through or avoided, and what type of cover they selected. If one were interested in answering long-term questions, powder could be reapplied, but this has the obvious disadvantage of influencing the animal's behavior. The success of this technique can also be influenced by the natural history of a species. For example, if the species periodically spends time in an aquatic or moist environment or burrows underground, it will be more difficult to track with powder (S. Blomquist pers. comm. 2005, Eggert 2002). In addition, the distance a species moves can affect the ease of detecting the

powder and differentiating between multiple paths. For instance, if a species' movements are concentrated within a small area, it can be difficult to follow the path when powder trails cross (Stark and Fox 2000).

Weather conditions, as well as site and regional differences, can also affect the suitability of fluorescent powder as a tracking technique for amphibians. For example, in areas where field conditions are typically moist, as they are at the LEAP study area in Maine (S. Blomquist pers. comm. 2005), powder tracking may not be as informative or useful as it is in drier regions. Similarly, some studies have suggested that vegetation type can affect how well the technique works (Mullican 1988, Eggert 2002), which obviously varies among research locations. Finally, in situations where paths are unlikely to overlap (e.g., individuals are being tracked in separate locations) and only one powder color is needed, chartreuse may be the optimum color to use.

My research has demonstrated that fluorescent powder tracking can be very effective at obtaining detailed movement and habitat use data for a variety of amphibian species. For example, it can be used to look at detailed movements, to assess whether certain habitats have been sampled, to test the effectiveness of other research methods, and as a supplement to other amphibian research techniques. However, the usefulness of this technique may vary by region, by the particular environmental conditions of a research site, and by the habitat use and movement behavior of the study species.

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🗆 Mean 🔳 Minimum 🖾 Maximum

Figure 3.1. Mean, minimum, maximum path lengths of *A. opacum*, *B. terrestris*, and *R. sphenocephala* in S.C. (this study), *A. annulatum* in M.O. (C. Conner pers. comm. 2005), and *R. sylvatica* in M.E. (S. Blomquist pers. comm. 2005). Mean path length values have ± 1 standard error.



Figure 3.2. Mean path length for the four fluorescent powder colors. Values are least squares means ± 1 standard error from the two-way ANOVA with species and powder color as effects.



Figure 3.3. Mean path length for powder color, specific to species. Values are least squares means ± 1 standard error.





B. Ambystoma opacum



Figure 3.4. Relationship between post-release precipitation and mean and maximum powder path length in (A) *R. sphenocephala* at three different precipitation levels and (B) in *A. opacum* at two different precipitation levels. No rainfall greater than 10 mm was recorded during the *A. opacum* releases, thus, that category is not included.

CHAPTER 4

CONCLUSION

In this study, I examined the effects of forest management on habitat selection and movement behavior of adult amphibians and evaluated the efficacy of the fluorescent powder tracking technique for amphibians. Using the experimental releases on forest/clearcut edges, I demonstrated that marbled salamanders (*A. opacum*) selected habitat at random, southern toads (*B. terrestris*) preferred clearcuts, and southern leopard frogs (*R. sphenocephala*) initially selected clearcuts, but may have ultimately preferred forests. These results indicate that both *B. terrestris* and *R. sphenocephala* are capable of differentiating between habitat types and do not necessarily avoid recently cleared areas. *Ambystoma opacum* may not be able to differentiate between habitats or require more time (> 24 hrs) to select non-breeding habitat.

I also found that the manner in which amphibians move can vary greatly among species and habitat types. Whereas leopard frogs exhibited long-distance, directional movement with few turns, southern toads exhibited more searching and wandering behavior. Marbled salamanders seemed to be focused primarily on locating cover. All three species made more turns in clearcuts than forests, and *B. terrestris* and *R. sphenocephala* moved farther in forests. None of the environmental cues or individual characteristics I measured appeared to influence habitat selection by *R. sphenocephala* or *B. terrestris*. *Ambystoma opacum* were more likely to enter clearcuts if soil moisture content was higher. *Rana sphenocephala* generally used microhabitat relative to what was available, but avoided microhabitat, such as the large amounts of debris in the clearcuts with CWD retained, that might obstruct movement. Amphibian habitat selection and movement behavior and the differences among species are important because they affect individual fitness and even population dynamics.

My examination of the efficacy of fluorescent powdered pigments for tracking amphibian movement demonstrated some important differences. First, the efficacy of this technique varied among species, regions, and varying climatic conditions. The technique tended to be more effective in pine habitat in South Carolina (this study) and mixed hardwood habitat in Missouri (data from C. Conner 2005) than in the mixed hardwood habitat in Maine (data from S. Blomquist 2005) where the ground moisture was high. I found that while the powder colors gave comparable path lengths when animals moved short distances in my study, certain powder colors (i.e., chartreuse) were easier to detect when paths were long and the powder began to wear off. Lastly, I demonstrated that heavy rainfall truncated paths, but light rainfall had no negative effect on path length.

This study highlights the importance of species-specific information when it comes to assessing the effects of habitat disturbance on amphibians; information of this type is greatly needed for modeling amphibian habitat use and movements in order to make more informed conservation decisions. I also demonstrated that fluorescent powder tracking can be used successfully with a broad range of amphibian taxa, but the effectiveness of the technique depends greatly on a species' habitat use and movement range, and the weather conditions and scale of the research question. Knowledge of individual species' responses to forest alteration enables land managers and conservationists to make relevant speciesspecific forest management decisions.