EFFECTS OF FOREST HARVESTING ON REPTILES AND AMPHIBIANS OF THE

SOUTHEASTERN UNITED STATES

by

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(Under the Direction of J. Whitfield Gibbons)

ABSTRACT

Reptiles and amphibians are currently experiencing population declines that are attributed to several causes. Habitat loss, including conversion, degradation, and alteration, is the single greatest factor threatening reptile and amphibian populations. Forest harvesting represents one prominent form of land-use that may result in habitat loss for reptiles and amphibians and contribute to ongoing declines. There are few studies of the effects of forest harvesting on reptiles and results are often conflicting, suggesting a strong need for more detailed studies of reptile responses to forest harvesting. In contrast, amphibians generally exhibit declines in abundance and richness following forest harvesting, particularly after clearcutting. Therefore, there is an increased need to understand which mechanisms underlie observed changes in amphibian abundance in richness in response to forest harvesting.

I conducted studies on the responses of reptiles and amphibians to forest harvesting on the Savannah River Site, Aiken, SC by creating 4 experimental treatments representing a range of forest harvesting intensities: (1) unharvested control (> 30 years old); (2) partially thinned stand in which the canopy was thinned to approximately 85% of that in the control (thinned

forest); (3) clearcut with coarse woody debris retained; and (4) clearcut with coarse woody debris removed.

I found that the relative abundance of small-bodied snakes was lower after clearcutting compared with unharvested controls of second-growth planted pines. I also found that the relative abundance of small-bodied snakes was greater in partially thinned forest stands compared with unharvested controls. In a second study I found that forest clearcutting can lead to decreased growth and survival of southern toads (*Bufo terrestris*) in field enclosures despite having no effect on their relative abundance between clearcuts and unharvested forests. In a third study, I found that survival of juvenile marbled salamanders (*Ambystoma opacum*) in field enclosures was greatly reduced in all harvested treatments compared with unharvested controls but adults only exhibited reduced survival in clearcut treatments. In a final study, I found that fewer amphibians migrated through clearcut treatments than forested treatments, particularly when emigrating from reproductive wetlands. Also, salamanders had a greater affinity for migrating through forests than did frogs.

INDEX WORDS: conservation, landscape ecology, wetlands, herpetofauna, herpetology, snakes, amphibians, reptiles, frogs, salamanders, forestry, logging, clearcutting.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Reptiles and amphibians are under-appreciated components of many ecosystems (Gibbons 1988). Because they are ectothermic, they convert large proportions of consumed energy into biomass compared with endotherms which expend substantial energy on homeothermy (Pough 1980). Subsequently, many ecosystems are capable of supporting great densities of reptiles and amphibians which exceed densities of most endothermic vertebrates (Burton and Likens 1975; Fitch 1975; Godley 1980). Reptiles and amphibians also have diverse roles in many ecosystems and serve as both predators and prey at multiple trophic levels (Campbell and Campbell 2001). Their diverse roles and great densities likely make them instrumental in the trophic movement of energy in many systems; in some cases, amphibians have been shown to affect ecosystem processes by exerting top-down control in a food web (Wyman 1998).

Recently, the widespread decline of amphibians has generated considerable interest in documenting the global abundance and status of amphibians and causes of their declines (Houlahan et al. 2000, Collins and Storfer 2003, Stuart et al. 2004). Whereas the status of reptile populations has received comparatively less attention, there is growing concern over similar declines reported for many reptiles (Gibbons et al. 2000; Winne et al. 2007). Habitat loss and alteration are major factors in all faunal declines, including those of reptiles and amphibians (Blaustein et al. 1994, Alford and Richards 1999, Gibbons et al. 2000, Collins and Storfer 2003,

Stuart et al. 2004). Forest loss due to agriculture, urban development, or logging is a leading form of habitat loss that affects faunal populations globally and is also widespread in the US.

The United States is the world's leading producer of lumber, wood products, and pulp fiber with a total industry harvest of just over 20 billion ft^3 of softwood and hardwood timber in 2001 (Kincaid 2002). In fact, the Southeast, America's most productive forest region, produces more timber than any other single country and contributes about 60% of the timber products in the US alone (Prestemon and Abt 2002).This production results in the managed harvest of large tracts of both public and private forest. Forest harvesting such as clearcutting is one form of habitat alteration that may decrease the suitability of the terrestrial environment for reptiles and amphibians. Clearcutting results in increased air and soil temperatures and a reduction in ground litter, factors that may reduce survival or behavior of small-bodied, desiccation-prone animals (Rothermel and Semlitsch 2002, Rothermel 2004). Clearcutting also creates a mosaic of patchwork habitats that fragments the environment and may lead to changes in connectivity of local populations by creating barriers to movement (deMaynadier and Hunter 1999, Chan-McLeod 2003). In practice, the effects of forest harvesting on reptiles and amphibians seldom lend themselves to generalization because of important differences in the biology, physiology, and behavior of reptiles and amphibians.

In general, the responses of reptiles to forest harvesting have received limited attention. Based on some studies, it has been suggested that reptiles may benefit from the early successional habitats created by forest management (Campbell and Christman 1982; Welsh and Lind 1991; Greenberg et al. 1994). However, one study has identified short-term declines in reptile populations resulting from forest harvesting and associated site preparation (Russell et al. 2002). Additionally, declines of some southeastern snake species, including the southern

hognose snake (*Heterodon simus*; Tuberville et al. 2000) and the eastern kingsnake (*Lampropeltis getula*; Winne et al. 2007), have occurred concomitant with pervasive even-aged forest management and the loss of historic longleaf pine forests. Unfortunately, there too few studies examining the effects of forest harvesting on reptiles and even fundamental comparisons of capture rates or relative abundances between clearcuts and unharvested forests are scarce.

In contrast to reptiles, we know considerably more about the effects of forest harvesting on the relative abundance and richness of amphibians. In a majority of comparative studies, relative abundance of amphibians has been strongly associated with forest cover and negatively associated with clearcutting and other types of harvesting, although there are occasional exceptions (reviewed in deMaynadier and Hunter 1995). For the most part, amphibian abundance and richness is greater in forests than in harvested habitats, suggesting that environmental quality, or at least the ability of the environment to sustain amphibian life, declines as forest is lost and converted. In many cases, salamanders are more likely to decline in relative abundance due to forest loss than are frogs. Additionally, it is generally assumed that the causes of declines in relative abundance of amphibian result from several underlying mechanisms. For example, animals may evacuate altered habitats, reduce activity and retreat underground, experience reduced birth rates, or suffer greater mortality, any or all of which could cause the observed reductions of relative abundance in clearcuts. Thus, relative abundance has been criticized as measure of the effects of habitat alteration on amphibian populations. Studies of changes in vital rates of amphibian populations (e.g., survival, reproduction, migration) are therefore a better measure of habitat suitability (Armstrong 2005), but they are generally lacking.

Clearly, a significant need exists for experimental inquiry into the underlying processes that contribute to post-harvest changes in amphibian populations for at least two reasons. First,

the ability to provide actionable information to land managers requires a more complete understanding of the processes underlying post-harvest population change. Development of effective management strategies and recommendations for sustaining amphibian populations in managed forests requires that we understand the different demographic responses of amphibians to increasing intensities of forest alteration. Second, it is necessary to obtain specific demographic data (e.g., survival or migratory success) to provide parameters for future modeling efforts that estimate responses of amphibian species to forest clearing (Halley et al. 1996; Griffiths and Williams 2000).

The primary goal of my study is to increase our understanding of reptile and amphibian responses to forest harvesting. In Chapter 2, I present the results of a three-year study examining the effects of different forest harvesting practices on the relative abundance of small-bodied snakes. In Chapter 3, I compare abundance indices with vital rates for use in determining the suitability of altered habitats for amphibians. In Chapter 4, I examine the survival of marbled salamanders (*Ambystoma opacum*) under different forest harvesting practices. Finally, in Chapter 5 I examine the effects of upland forest harvesting on migrating amphibians to examine their movements through terrestrial habitats in response to habitat alteration.

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CHAPTER 2

RESPONSE OF A REPTILE GUILD TO FOREST HARVESTING[1]

INTRODUCTION

Loss of habitat and conversion of natural habitat to other forms of land-use are often suggested as the leading causes of imperilment for many fauna. Timber harvesting (i.e. logging) is one of the more prominent forms of habitat alteration that shapes plant and animal communities, and forest loss or conversion is widespread on most continents. The southeastern United States is the leading timber-producing region in the country, surpassing most other individual countries (Prestemon and Abt 2002). Timber stands in the Southeast are typically maintained as even-aged, planted pine forests, and there are 13.8 million ha of such systems in the Southeast (Siry 2002). This forest type has largely replaced the historic and previously extensive longleaf pine (*Pinus palustris*) system, a habitat that has been reduced by as much as 90% by logging, conversion to pine plantations, and other development (Noss 1989). Many floral and faunal species associated with longleaf pine ecosystems have subsequently declined, leading to the designation of several species as endangered (Means and Grow 1985; Noss 1988).

Even-aged, managed pine forests that currently dominate the southeastern United States are often different from natural forest ecosystems. In particular, stand density in mature longleaf pine and mixed pine-hardwood forests is lower than in even-aged pine stands in which timber production is maximized through dense planting of commercial species (Means 2005). Commercially managed forests typically have closed canopies, deep litter beds, and sparse understory vegetation rather than the open canopies and grassy understories characteristic of longleaf pine ecosystems (Means 2005). Additionally, harvesting of even-aged forests is done predominantly through forest clearcutting which occurs annually on an estimated 810,000 ha in the Southeast (Siry 2002). In general, clearcutting and the use of heavy equipment during timber harvesting and subsequent site preparation eliminate canopy and alter litter and soil structure

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(Chen et al. 1999; Zheng et al. 2000). Leaf litter and coarse woody debris decrease in clearcuts, the amount of bare ground increases, and drier microclimates proliferate (Hunter 1990; Greenberg et al. 1994; deMaynadier and Hunter 1995). Therefore, even-aged pine plantations represent a considerable departure from the historic forests in this area. Importantly, managed pine forests may negatively affect fauna because of the forests' artificially high stand densities or the accompanying use of clearcutting harvest methods.

The unique life histories of snakes and their roles in food webs make them diverse and important components of many ecosystems (Campbell and Campbell 2001). Recognition of this importance coupled with growing concerns over population declines (Gibbons et al. 2000; Winne et al. 2007) have prompted increased interest in preventing the disappearance of these critical, and often hidden, elements of biodiversity. In forest systems, timber harvesting has been implicated in declines of amphibians (deMaynadier and Hunter 1995; Todd and Rothermel 2006). Fewer investigations have focused specifically on the response of reptiles to forest management (Gardner et al. 2007), despite the enormous scale of timber harvesting and its potential impact. A small number of researchers have proposed that forest clearcutting may benefit reptiles by creating early successional habitats (e.g., Campbell and Christman 1982; Greenberg et al. 1994), but it is unclear whether such generalizations are broadly applicable to all reptiles and whether other intensities of timber harvest affect reptiles.

We initiated this study to determine the effects of 2 types of timber harvesting on small-bodied snakes (<25 cm) in an even-aged pine plantation: clearcutting and partial stand thinning. Small snakes are often incredibly abundant (Fitch 1975; Willson and Dorcas 2004), consume and produce large amounts of biomass (Godley 1980), and have small home ranges and low vagility (Barbour et al. 1969), which makes them useful indicators of the effects of localized habitat

alteration on a reptile guild. We hypothesized that relative abundances of small snakes would be lower in forest clearcuts than in unharvested controls due to the environmental conditions and subsequent physiological or behavioral constraints imposed on them by this highly-altered habitat, despite possible life-history differences among species. We also hypothesized that the relative abundance of small snakes would be greater in thinned canopy stands than in unharvested controls for 2 reasons. First, the most common small snake species in the region (*Tantilla coronata*) is widely distributed in formerly longleaf pine habitat and should presumably respond favorably to partial canopy reduction. Second, by thinning a planted pine forest, the forest floor becomes more insolated and there is a corresponding increase in understory productivity that may promote an increase in the abundance of small snakes. In addition to testing the effects of timber harvesting on a reptile community, we compared microhabitat characteristics of managed pine treatments to document the effects of even-aged pine management and timber harvest methods on forest habitat and to determine which habitat characteristics most affected the relative abundances of small snakes.

METHODS

Study site

The U.S. Department of Energy's Savannah River Site (SRS) in South Carolina (U.S.A.) occupies approximately 780 km^2 of the Atlantic Coastal Plain physiographic province. The surrounding uplands were longleaf pine forest up to as recently as the 1880s (Hammond 1883). Fire suppression, logging, and conversion of land for agricultural use reduced much of the upland longleaf pine habitat in the immediate region prior to site establishment in 1951 (Kilgo and Blake 2005). After establishment of the SRS, the U.S. Forest Service began managing the remaining forested areas and replanted much of the SRS with commercial pine species such as

slash pine (*Pinus elliottii*) and loblolly pine (*P. taeda*) (Kilgo and Blake 2005). By 2001 nearly all the SRS was forested and 72% of the forest stands were over 30 years old (Kilgo and Blake 2005). Much of the current land on the SRS is managed as even-aged planted pine forests with prescribed burning on a 3-year cycle.

Experimental arrays

We selected 4 forested sites on the SRS for study (see also Rothermel and Luhring 2005; Todd and Rothermel 2006). These sites were second-growth, managed-pine forests of loblolly pine (*P. taeda*). Where present, understory consisted of sweetgum (*Liquidambar styraciflua*), wax myrtle (*Morella cerifera*), and holly (*Ilex opaca*), with ground cover dominated by Carolina jessamine (*Gelsemium sempervirens*) and grasses.

We centered each of the 4 circular experimental sites on isolated, seasonal wetlands that hold water during winter and early spring. The circular sites extended outward from the wetland boundaries for 168 m. We divided each circular site into 4, 4-ha quadrants delineated by 2 perpendicular transects that intersected at the center of the wetland (Fig. 2.1). Each quadrant was assigned randomly to 1 of 4 treatments: (1) unharvested control (> 30 years old); (2) partially thinned stand in which the canopy was thinned to approximately 85% of that in the control (thinned forest); (3) clearcut with coarse woody debris retained (CC-retained); and (4) clearcut with coarse woody debris removed (CC-removed). The 2 forested plots were opposite each other (Fig. 2.1). The isolated wetlands in the interior of the experimental arrays were unharvested. Logging commenced in February 2004 and was completed at the sites in April 2004. We did not perform any additional site preparation such as replanting, harrowing, burning, or the application of herbicides.

In April 2004, we installed 9, 15-m sections and 1, 45-m section of drift fence in each quadrant at all 4 experimental sites (16 total quadrants). The 45-m section of drift fence was located closest to the isolated wetland in each quadrant and the 9, 15-m sections were located in the surrounding xeric uplands 50, 100, and 150 m from the wetland (Fig. 2.1). We placed 6, 8-L pitfall traps (24 cm in diameter and 18 cm high) paired on opposite sides of each 15-m drift fence (54 pitfall traps per quadrant). We also placed 12, 19-L pitfall traps (31 cm in diameter and 24 cm high) paired on opposite sides of each 45-m section of drift fence. Pitfall traps contained 1–3 cm of standing water and floating sponges in the bottom to prevent drowning or desiccation of captured animals. The drift fences of aluminum flashing were buried 15 cm into the ground and extended 45 cm above the ground (Gibbons and Semlitsch 1982).

Data collection

We checked drift fences every 1-2 days from 1 April 2004 through 28 July 2006 but removed pitfall traps each August. Sampling effort among habitats was always equal and contemporaneous whenever traps were open, eliminating biases from treatment comparisons. Additionally, sampling effort was concentrated during periods of the year when small-bodied snakes are most active (April to November; Semlitsch et al. 1981; Gibbons and Semlitsch 1987), excluding August.

We recorded capture date and location of all snakes. We measured snout-to-vent length (SVL) and tail length in the laboratory. We recorded mass to the nearest milligram with an electronic scale and determined the sex of snakes by cloacal probing. Each snake was given a unique identifying mark (ventral-scale heat branding; Winne et al. 2006). We determined clutch size in females through manual palpation or visual inspection of the venter. We maintained all snakes indoors at room temperature in small containers with moistened paper towels and

released them at their original points of capture within 2–4 days. We did not collect any

pretreatment data on relative snake abundances. Instead, we relied on replication and

randomization of treatments to allow comparisons of treatment effects on relative snake

abundance.

In July 2004, we established permanent habitat-sampling points at all 9, 15-m drift fences

in each quadrant. We positioned the permanent sampling points 15 m toward the wetland from

each drift fence. We collected habitat data 2 m from each permanent point at 2 randomly chosen

bearings. At both random secondary points, we centered a 1-m^2 quadrat on the point and visually

estimated bare soil, litter, coarse woody debris (logs over 10 cm in diameter, hereafter CWD),

and understory vegetation in each quadrat to the nearest 5%. We defined understory vegetation

as forbs, grasses, and woody vines <1 m tall. We excluded large trees. We measured litter depth

with a ruler in each corner of the quadrat. In the center of each quadrat, we faced each cardinal

direction and measured canopy cover with a spherical densiometer. We deployed iButton data

loggers (Maxim Integrated Products, Sunnyvale, California) at 4 randomly chosen primary

points in each quadrant to record near-ground air temperatures continuously from September

2004 to October 2005. We fastened the data loggers on stakes 25 cm above the soil and shaded

them from direct sunlight.

We sampled all 4 quadrants at an experimental site in 1 day, and all 4 experimental sites

within 1 week. Sampling was conducted only on days with no rain in the previous 24 hours. We

collected the aforementioned habitat data in July 2004, August 2005, and August 2006. We

calculated mean habitat characteristics for each permanent point on the basis of data collected at

the 2 random secondary points. Means from primary points were then used to calculate quadrant

means for use in all statistical analyses. In March 2006 we measured CWD along 25-m line

transects in 7 of the permanent primary-habitat sampling points in each quadrant along randomly

chosen directions (Pickford and Hazard 1978). We calculated the mean CWD volume along

transects for each quadrant and mean log densities per hectare for each quadrant. We used means

from each quadrant to make statistical comparisons among habitats.

Statistical analyses

We excluded captures from the 6 pitfall traps along the inside of each 45-m drift fence

closest to the wetland from analyses. We limited our analyses to only small-bodied snake species

because (1) large snakes have greater home ranges and are probably less affected by our 4-ha.

treatments, (2) large snakes can move long distances and may be exposed to multiple treatments

during the study, and (3) pitfall traps do not effectively capture many large-bodied snakes (Todd

et al. 2007). Thus, we focused our analyses on 6 small-bodied snakes: scarlet snakes

(*Cemophora coccinea*), ringneck snakes (*Diadophis punctatus*), scarlet kingsnakes

(*Lampropeltis triangulum*), redbelly snakes (*Storeria occipitomaculata*), southeastern crowned

snakes (*T. coronata*), and smooth earth snakes (*Virginia valeriae*).

We pooled all captures of the 6 focal species across years and sites and used a chi-square

test to determine whether the total number of small snakes captured during the study varied

among treatments. For *T. coronata* and *V. valeriae*, we used repeated-measures multivariate

analyses of variance (MANOVA) with experimental sites as blocking factors to test for treatment

effects on the number of animals captured after adjusting for trapping effort. We limited our

analyses to animals captured from 10 May through 31 July each year to standardize counts and

trapping effort among years for use as repeated measures. We normalized count data using

square-root transformations (Zar 1998). We pooled captures of *T. coronata* across years and

separated males from non-gravid females and used analyses of covariance (ANCOVA) to

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determine whether size-specific body mass was affected by treatment, using log-transformed lengths as covariates and log-transformed masses as response variables. We pooled captures across years and used ANCOVA to determine whether size-specific fecundity in female *T. coronata* varied among treatments, using log-transformed lengths as covariates and log-transformed counts of clutch size as response variables. We excluded all recaptures from statistical analyses. We examined all data prior to analyses to ensure that analytical assumptions were met (Zar 1998).

We compared mean litter depth, canopy density, bare soil coverage, litter coverage, and understory vegetation coverage with repeated measures MANOVA with experimental sites as blocking factors and each year of study as a repeated measure. We compared minimum and maximum air temperatures among treatments each month from September 2004 to October 2005 with a repeated measures MANOVA with experimental sites as a blocking factor and months as repeated measures. To compare density and volume of CWD among treatments, we used 2-way analyses of variance (ANOVA) with experimental sites as blocking factors. Again, we examined data for assumptions prior to analyses and used log or arcsine square-root transformations where needed to correct for nonnormality or heteroscedasticity. Lastly, we used a canonical correlation analysis to determine which habitat characteristics most affected small snake abundance. We included mean litter depth, canopy density, bare soil coverage, litter coverage, understory vegetation coverage, and coarse woody debris coverage of each treatment in each year as independent variables and the number of *T. coronata* and *V. valeriae* captured in each treatment each year as dependent variables. We used normalized data in the analysis as described previously. We performed all statistical analyses with SAS (version 9; SAS Institute 2000).

Effects on the snake community

Among our 6 focal species, *T. coronata* were captured most frequently, representing 78% of all captures (447 of 573 total captures). The number of small snakes captured was highest in the thinned forests and significantly lower in the 2 clearcut treatments ($\chi^2 = 46.24$, *df* = 3, *p* < 0.001; Fig. 2.2). Additionally, captures of 4 of the 6 focal species were fewest in the most altered treatment, CC-removed (*L. triangulum*, *S. occipitomaculata*, *T. coronata*, and *V. valeriae*; Fig. 2.2).

Treatment significantly affected the number of *T. coronata* captured (MANOVA: $F_{3,9}$ = 4.18; *p* = 0.041; Fig. 2.3a) and there was a marginal interaction of treatment with time (MANOVA: $F_{6,18}$ = 2.53; *p* = 0.06). Generally, we captured the fewest *T. coronata* in the 2 clearcut treatments and the most in the thinned forest treatment, but a difference in captures among treatments was less obvious in the second year compared with the first and third years. Treatment did not affect size-specific body mass of *T. coronata* for males (ANCOVA: $F_{3,87}$ = 0.61; *p* = 0.612) or non-gravid females (ANCOVA: $F_{3,48}$ = 1.58; *p* = 0.208). Similarly, treatment did not affect clutch size of gravid females (ANOVA: $F_{3,35}$ = 0.13; *p* = 0.942). Although captures of *V. valeriae* were fewest each year in the CC-removed quadrants and greatest in thinned forest quadrants, we observed variation in captures both among treatments and within treatments. Subsequently, there was no significant effect of treatment on number of *V. valeriae* captured (MANOVA: $F_{3,9}$ = 1.01; *p* = 0.432; Fig. 2.3b) and no time-by-treatment interaction (MANOVA: $F_{6,18}$ = 0.84; *p* = 0.58).

We recaptured 4 *T. coronata*, 1 *L. triangulum*, and 1 *C. coccinea* during the study. In general, we recaptured animals at their original point of capture or in adjacent traps from 17 to

681 days later. The greatest known travel distance was 40 m by a *T. coronata*, whereas all other recaptured snakes were within 10 m of their original capture location. All snakes were recaptured in the same treatment as their initial capture, 4 in CC-removed and 2 in thinned forests.

Effects on forest habitat

In general, litter depth and ground coverage were highest in unharvested forests and decreased progressively with increasing forest disturbance (litter depth: $F_{3,9} = 7.87$, $p = 0.007$; litter coverage: $F_{3,9} = 16.5$, $p < 0.001$; Table 2.1). In contrast, there was no exposed soil in unharvested controls and only 1-3% of the ground was exposed in thinned forest stands. In the 2 clearcut treatments, exposed soil was significantly greater and averaged 9-15% of the forest floor ($F_{3,9} = 5.72$, $p = 0.018$; Table 2.1). Canopy was nearly eliminated in the 2 clearcut treatments and reduced in the thinned forest treatment compared with the unharvested pine stands ($F_{3,9} = 327.1$, $p < 0.001$; Table 2.1). Understory vegetation increased significantly in clearcuts and thinned stands compared with unharvested controls ($F_{3,9} = 7.51$, $p = 0.008$; Table 2.1). Lastly, the proportion of ground covered by coarse woody debris was highest in the CC-retained treatment, followed by the thinned stand, and was reduced in the unharvested control and CC-removed ($F_{3,9}$ $= 4.0$, $p = 0.045$; Table 2.1). None of the time by treatment interactions in the multivariate analyses of variance that compared habitat differences among treatments was significant ($p >$ 0.05). In the CC-retained treatments, there were significantly more logs per hectare than in all other treatments (ANOVA: $F_{3,9} = 29.61$, $p < 0.001$). Similarly, the volume of CWD along transects was greater in CC-retained treatments than in other treatments (ANOVA: $F_{3,9} = 4.67$, p $= 0.031$).

Monthly maximum air temperatures were significantly warmer in the clearcuts, intermediate in the thinned forest, and coolest in the unharvested forest ($F_{3,9} = 63.97$, $p < 0.0001$;

Fig. 2.4). The trend was reversed for monthly minimum air temperatures where overnight minima were reduced in clearcuts, intermediate in thinned forests, and warmest in unharvested forests ($F_{3,9} = 74.8$, $p < 0.0001$; Fig. 2.4).

Correlates of habitat and small snake abundance

Canonical correlation analysis revealed that only one of the two canonical dimensions was statistically significant ($F_{12,80} = 2.2$, $p = 0.02$). Dimension 1 had a canonical correlation of 0.63 between the sets of variables. Litter coverage and vegetation coverage were the greatest contributors to the habitat axis of dimension 1. Of the response variables, the number of *T. coronata* captured was a greater contributor to the small snake axis of dimension 1 than was the number of *V. valeriae* captured. Litter coverage was positively correlated to small snake abundance and vegetation coverage was negatively correlated to small snake abundance.

DISCUSSION

Although some authors suggest that clearcutting may create favorable habitats for reptiles (Campbell and Christman 1982; Greeberg et al. 1994), our results reveal that responses of reptiles to forest harvesting may be more complex than previously assumed. Because clearcutting, by definition, results in the complete removal of canopy cover, daily thermal maxima increase and nighttime minima decrease. Additionally, forest clearcutting affects the understory and can change the availability and distribution of ground cover, simultaneously eliminating the source of future litter inputs. The loss of ground litter and increase in exposed soil that we observed in clearcuts are consistent with results found in other studies (Hunter 1990; Greenberg et al. 1994; deMaynadier and Hunter 1995).

For reptile assemblages adapted to open spaces, habitat edges, or hot, dry conditions (e.g., some lizards), clearcutting may have no deleterious consequences and may benefit some

species (e.g., Greenberg et al. 1994). However, small-bodied, leaf litter snakes are unlikely to benefit from habitat alteration that eliminates ground litter. In fact, our canonical correlation analysis revealed that the proportion of forest floor covered in leaf litter was strongly correlated with small snake abundance. This was further evidenced by the decreased relative abundance of small snakes in clearcuts which had highly reduced ground litter, despite some successional regrowth of vegetation in clearcuts. Similarly, other authors have documented decreased abundance of small snakes in forest clearcuts. For example, despite finding increased reptile abundance and species richness in clearcuts adjacent to bottomland hardwood stands, Perison et al. (1997) found a small snake species, *D. punctatus*, more abundant in unharvested forests. Short-term decreases in snake abundance appear to result from clearcutting, even for one large-bodied snake (*Coluber constrictor*) (Russell et al. 2002).

Of the 2 types of clearcuts we studied, captures of small snakes were fewer in the more-altered clearcut, where CWD was not retained. Coarse woody debris may be an important microhabitat for amphibians and reptiles (deMaynadier and Hunter 1995; Russell et al. 2004), and small, forest-floor-dwelling snakes may rely heavily on CWD for daytime refugia or other purposes (e.g., foraging or nesting). Total captures of the 6 small snake species and captures of *T. coronata* and *V. valeriae* were generally greater where CWD was retained than where it was removed, but both clearcut treatments still had fewer captures than unharvested forest controls. Enge and Marion (1986) found that intensive site-preparation practices that produce highly disturbed habitats similar to our clearcuts where coarse woody debris was removed, have a negative effect on overall reptile numbers in north Florida flatwood forests. Although CWD was available in our thinned forest stands where small snake abundance was greatest, the amount of forest floor covered by CWD was not found to be a significant contributor per se to small snake

abundance in our canonical correlation analysis. We recommend additional studies to determine the relative importance of CWD to snakes and other reptiles in forest habitats.

We predicted that partially thinned forests would have greater relative abundances of small snakes than unharvested controls. Indeed, the abundance of small snakes was greatest in the thinned-canopy forests relative to all other treatments. At sites with open canopy gaps in southern Appalachian forests, 3 small snake species (*Carphophis amoenus*, *D. punctatus*, and *S. occipitomaculata*) are more abundant there than in completely forested sites (Greenberg 2001). These responses are consistent with the view that reptiles respond favorably to the warmer microhabitats and habitat heterogeneity produced by some methods of forest management, provided that animals retain access to adequate refuge from harsh environmental conditions, which is unlikely in clearcuts. Partially thinned forests in our study maintained ground litter with limited exposed soil, factors likely critical for the persistence of litter-dwelling species. Additionally, canopy cover was still present in the thinned forests, preventing daytime temperatures from reaching the high maxima that occurred in clearcuts and that can cause mortality among small-bodied ectotherms (e.g., Rothermel and Luhring 2005). A partially thinned forest likely provides an acceptable tradeoff that maintains adequate refugia and ground litter while providing sunny open areas favorable for thermoregulation by ectotherms.

Modern managed-pine forests of the Southeast differ from longleaf pine forests for a few key reasons. Because of their open canopy structure, the floor of longleaf pine forests receives greater insolation, which in turn supports dense understory grasses and greater productivity (Noel et al. 1998; Means 2005). Arthropod densities increase as stand density of longleaf pine stands decrease (Hanula et al. 2000). Arthropods and other macro-invertebrates are key prey items for some small snake species (e.g., *T. coronata*) and also support many amphibians and

lizards that are in turn preyed upon by other small snakes (e.g., *C. coccinea, D. punctatus, L. triangulum*). Thus, thinned pine forests may be more capable of supporting small snakes than are densely planted pine forests. Additionally, our most commonly captured snake, *T. coronata*, is widely distributed in historically longleaf pine regions of the Southeast, and its closely related congener, *T. relicta*, is likewise abundant in open-canopy sandhills of Florida (Mushinsky 1985). Campbell and Christman (1982) suggest that herpetofaunal assemblages respond to physical and biotic factors more so than to ecosystem types. We suggest that the open canopy formed by partial forest thinning may benefit small snakes because it acts as a surrogate to the open-canopied forests to which some of these species are historically adapted. Unfortunately, no published studies compare reptile communities in longleaf pine forests with those in differently managed planted-pine forests.

The difference we observed in the abundance of small snakes among forest treatments can occur through several mechanisms, including changes in survival and fecundity, mortality incurred during harvesting, or emigration and habitat selection or avoidance. Reduced habitat quality can manifest in reduced body conditions in animals due to evaporative water loss, low prey abundances, or poor feeding success, which can in turn reduce fecundity (Aldridge and Semlitsch 1992). However, we found no evidence of treatment effects on body condition or clutch size in *T. coronata*. Additionally, no small snakes were ever recaptured in a habitat other than that of their initial capture. Small-bodied snakes have small home ranges (ca. 250 m^2 for *Carphophis amoenus*, Barbour et al. 1969) and movement distances are low. Our results on minimum movement distances are consistent with previous findings and indicate that emigration and immigration likely had a minimal effect on snake abundance in the treatments.

Differences in survival due to variation among treatments in predation risk, prey availability, or environmental conditions most likely had the greatest impact on snake abundance. For example, maximum temperatures recorded in free-ranging small snakes, such as *D*. *punctatus*, *L*. *triangulum*, and *S*. *occipitomaculata*, do not exceed 32 $^{\circ}$C (Table 3 in Brattstrom 1965), a temperature exceeded daily near the forest floor during the summer in the clearcuts we studied. Moreover, we found that leaf litter was positively correlated to small snake abundance. Loss of leaf litter may increase predation and desiccation risk by eliminating refugia and exposing small snakes to direct sun, leading to increased mortality.

CONCLUSIONS

Several snake species are reportedly declining in the southeastern United States (e.g., *Crotalus adamanteus*, Martin and Means 2000; *Heterodon simus*, Tuberville et al. 2000; *Lampropeltis getula,* Winne et al. 2007). In contrast, there are no reports of the status of small-bodied southeastern snakes which remain largely ignored. Our results demonstrate one possible mechanism of population decline in small-bodied snakes resulting from forest clearcutting. Although the 4-ha clearcuts in our study were large enough to negatively affect small snakes, the sizeable scale at which clearcutting typically occurs (50-200 ha) may negatively impact larger snake species as well. Thus, we recommend that future studies more carefully examine the effects of land use and forest management practices on snake species and other reptiles in general. Additionally, the effects of clearcutting on snakes may be greater in practice than demonstrated in our study due to the extensive site preparation and replanting that accompanies much traditional forest management. Raking, harrowing, roller-chopping, bedding, replanting, and the use of herbicides may additively affect snake populations (Enge and Marion 1986).

The extensive loss of open-canopy forest, due in part to the reduction of open forest habitats, fire suppression, and conversion to cultivated pine stands, is of foremost concern for the conservation of many southeastern reptiles. To properly manage snake populations, we recommend that land managers maintain open-canopy stands within larger tracts of managed forests, possibly by staggering stand age in plantations, implementing prescribed burns that prevent canopy closure, or otherwise adjusting management activities so that thinned- or open-canopy habitats remain available in the landscape. There is an urgent need for studies of longleaf pine habitats and cultivated pine forests that compare habitat characteristics and reptile assemblages because they could inform sustainable forest-management practices.

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Table 2.1 Mean (SE) habitat characteristics of the 4 treatments: unharvested control, thinned forest, CC-retained (clearcut with coarse woody debris retained), and CC-removed (clearcut with coarse woody debris removed).

	Unharvested control	Thinned forest	CC-retained	CC-removed
Litter depth (cm)	4.2 (0.4)	3.1 (0.4)	2.8 (0.3)	2.1 (0.3)
Percent canopy cover	92.8 (1.2)	81.4 (2.1)	6.9 (1.8)	6.8 (2.2)
Percent bare soil	0	1.4 (0.5)	7.9 (2.5)	8.3 (1.3)
Percent litter cover	67.7 (3.7)	64.0 (3.7)	34.8 (4.6)	28.6 (5.2)
Percent understory vegetation cover	31.7 (3.7)	32.6 (3.7)	52.7 (6.2)	62.6 (5.8)
Percent coarse woody debris	0.8 (0.3)	2.2 (0.5)	4.8 (1.4)	0.9 (0.4)
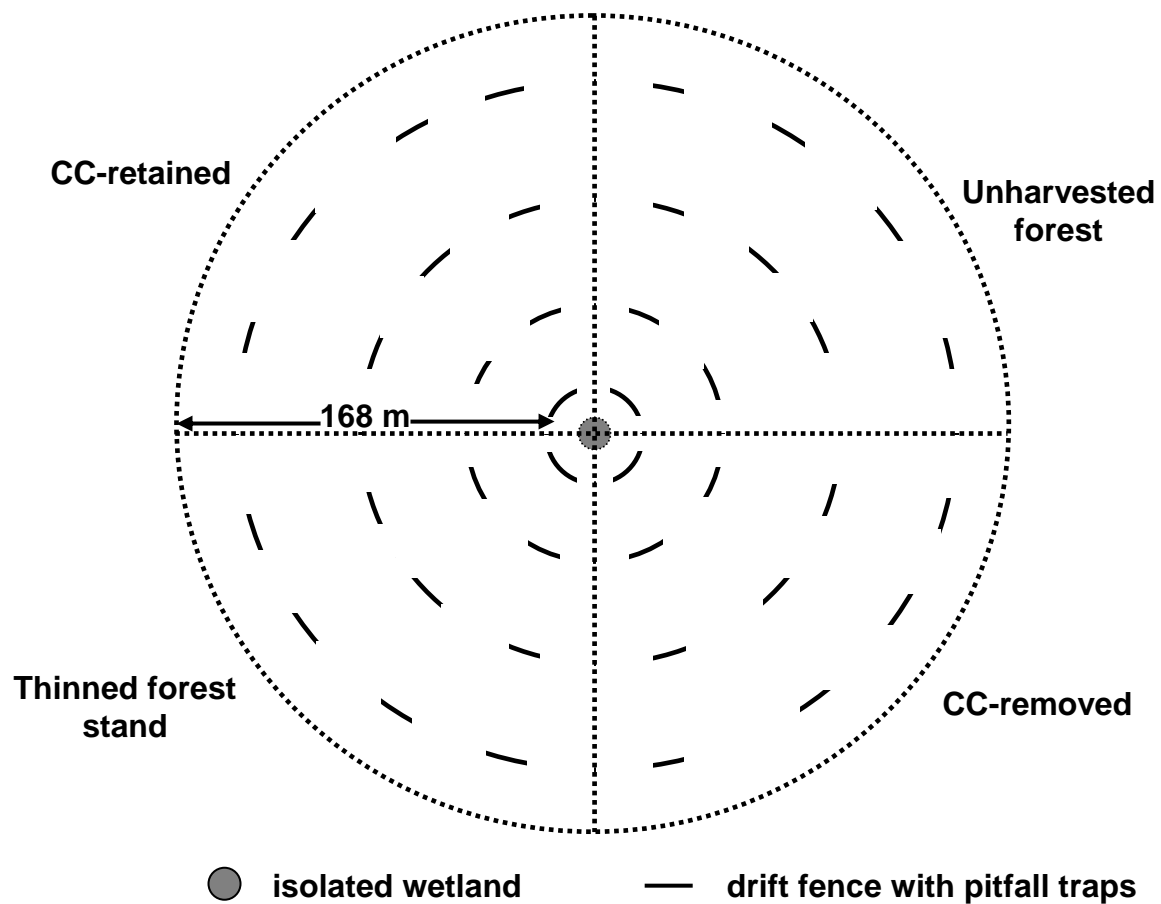
Figure 2.1 Diagram of 1 of 4 replicated sites showing the spatial arrangement of 4 randomly assigned forest management treatments and drift fences used to capture snakes in each quadrant. Figure is not to scale. CC-retained: clearcut with coarse woody debris retained; CC-removed: clearcut with coarse woody debris removed.
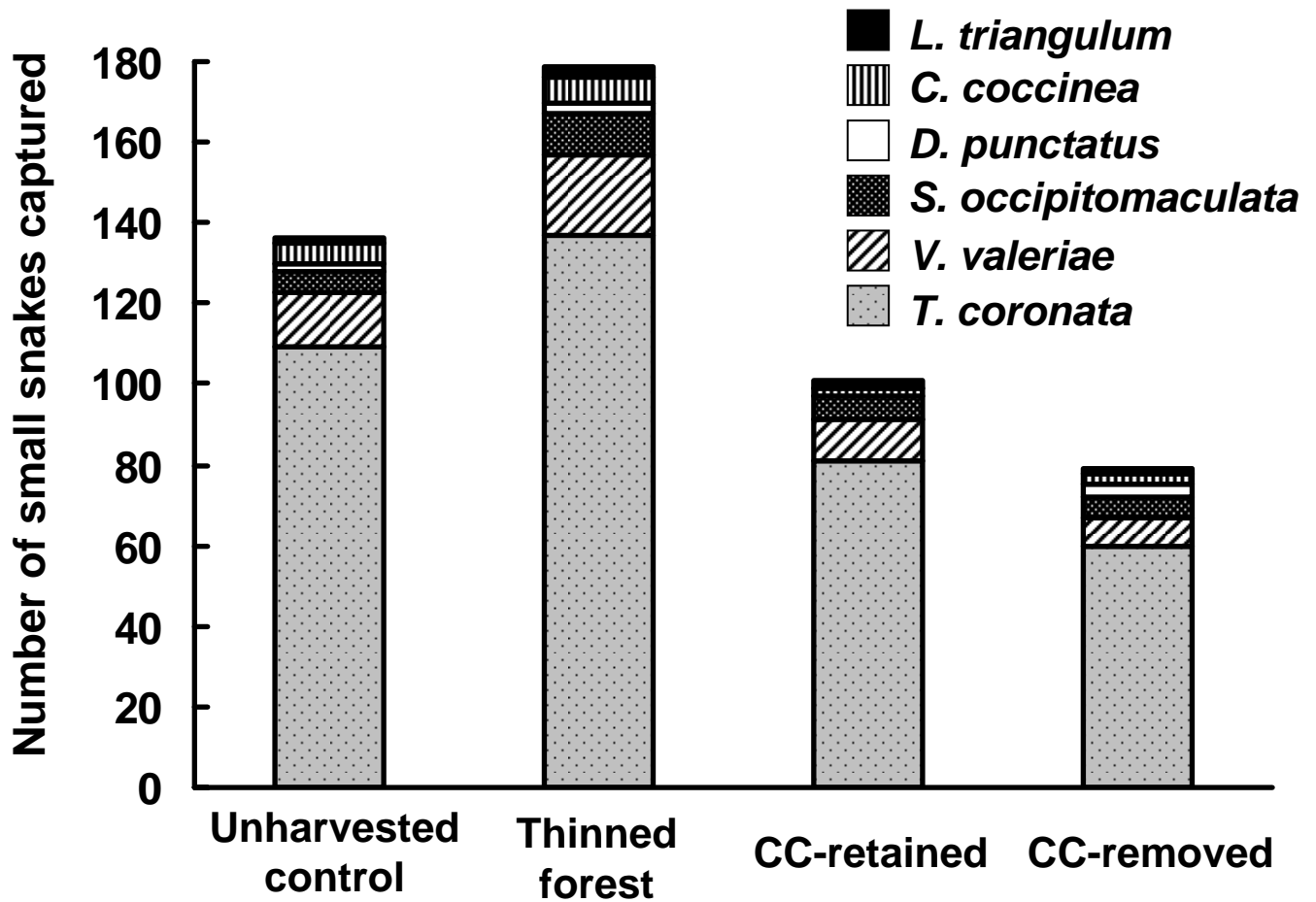
Figure 2.2 Total captures of the 6 small snake species over 3 years in the 4 treatments: unharvested control, thinned forest, CC-retained (clearcut with coarse woody debris retained), and CC-removed (clearcut with coarse woody debris removed).
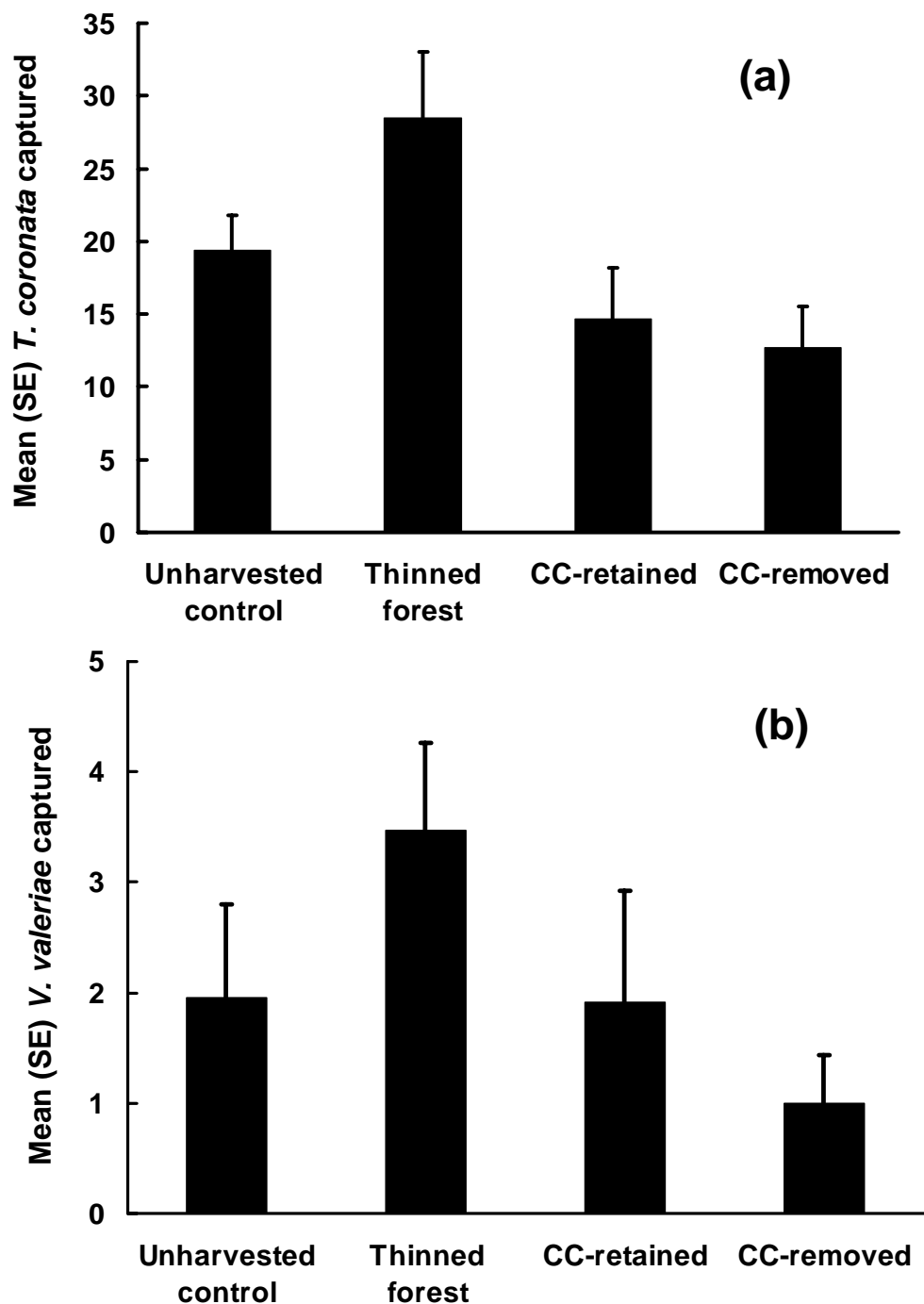
Figure 2.3 Mean number of (a) southeastern crowned snakes (*Tantilla coronata*) and (b) smooth earth snakes (*Virginia valeriae*) captured from 10 May – 31 July each year in the 4 treatments: unharvested control, thinned forest, CC-retained (clearcut with coarse woody debris retained), and CC-removed (clearcut with coarse woody debris removed).
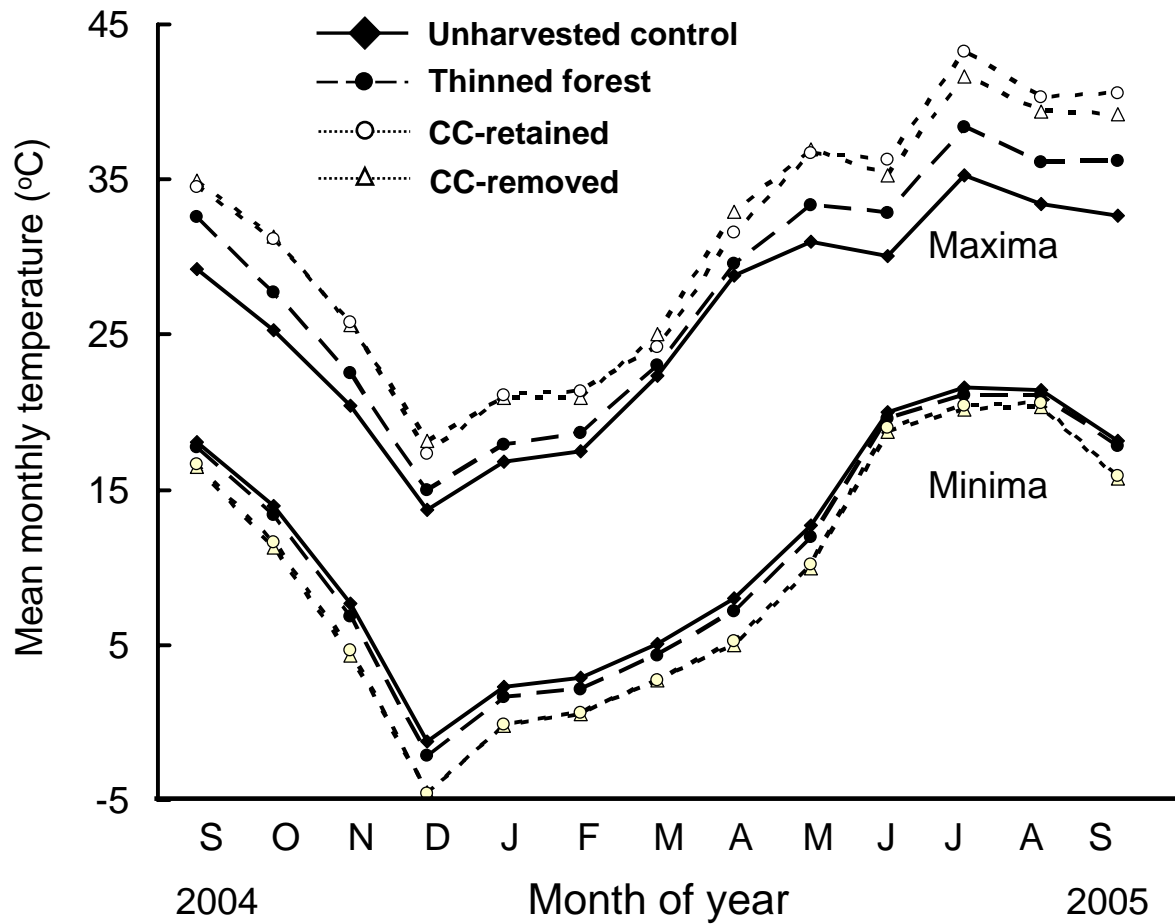
Figure 2.4 Monthly mean maximum and minimum near-ground air temperatures in the 4 treatments: unharvested control, thinned forest, CC-retained (clearcut with coarse woody debris retained), and CC-removed (clearcut with coarse woody debris removed).

CHAPTER 3

ASSESSING QUALITY OF CLEARCUT HABITATS FOR AMPHIBIANS: EFFECTS ON

ABUNDANCES VERSUS VITAL RATES IN THE SOUTHERN TOAD (*BUFO*

TERRESTRIS)[2]

INTRODUCTION

Habitat alteration is a major factor in the global decline of amphibians (Collins and Storfer 2003; Stuart et al. 2004). Timber harvesting is one form of habitat alteration that may decrease the suitability of the terrestrial environment for amphibians. Clearcutting and other intensive forest management practices create a mosaic of fragmented habitats, with potentially negative consequences for amphibian populations. The increased air and soil temperatures and reduced ground litter in early-successional habitats (Russell et al. 2004) may reduce survival and migratory success of amphibians (deMaynadier and Hunter 1999). Clearcuts may also become barriers to movement if amphibians avoid entering them in favor of forested habitats (Rothermel and Semlitsch 2002; Chan-McLeod 2003; Rothermel 2004). Because up to 82% of amphibian species are forest-dependent (Stuart et al. 2004), forest management practices have the potential to affect a large proportion of amphibians and contribute to ongoing population declines.

Recognition of population declines and concerns over the potentially negative effects of timber harvesting have generated much interest in the response of amphibians to forest alteration. DeMaynadier and Hunter (1995) reviewed the literature regarding the effects of clearcutting on amphibians and found that, in general, both abundance and richness are reduced following harvest. However, these patterns are often dependent on forest type, elevation, and species assemblage, and several studies contradict this negative trend. A number of studies in the southeastern U.S., for example, have documented greater amphibian abundances in clearcuts compared to unharvested reference sites (Pais et al. 1988; Phelps and Lancia 1995; Clawson et al. 1997; Ryan et al. 2002). While at least one author has warned that species abundances are not a direct measure of habitat quality (Van Horne 1983), many studies continue to focus on changes in abundance as the sole metric for habitat comparisons.

Relying on abundances to compare the quality of habitats is problematic for several reasons. First, populations do not always respond immediately to habitat change, but often exhibit time lags (Brooks et al. 1999). Therefore, abundances of some species may not decrease initially despite the habitat being of poorer quality. Second, if a poor-quality habitat patch with high animal mortality is sustained by immigration from other patches, abundances will provide the misleading appearance that there is no effect of habitat alteration. Third, determining the effects of habitat alteration on abundances does not indicate which processes are responsible for observed changes. Determining whether altered habitats affect species by influencing migration or by causing changes in survival or reproduction is important in formulating subsequent conservation strategies. Last, comparative abundance surveys, especially for amphibians and reptiles, often rely on the number of animal captures as a proxy for animal abundance in different habitats. Captures from any sampling method (i.e., pitfall traps) are a product of both population abundances and detection probabilities, which are partly a function of the behavior of the animals and their activity levels. If behavior or movement rates vary among habitats with differing levels of alteration, then resulting abundance estimates are likely to be biased (Bailey et al. 2004b). For these reasons, determining changes in vital rates (birth, immigration, death, or emigration) following habitat alteration provides the only direct measure of habitat quality (Van Horne 1983; Armstrong 2005).

We studied the effects of forest clearcutting on the southern toad (*Bufo terrestris*) using two approaches simultaneously. First, we conducted a comparative abundance survey using drift fences with pitfall traps to compare abundances of southern toads in recent clearcuts with abundances in adjacent unharvested pine (*Pinus* spp.) forests. Second, we performed an experimental study using field enclosures to determine the effects of clearcutting on the survival

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and growth of juvenile southern toads. The juxtaposition of these two approaches allowed us to evaluate the quality of forest clearcuts for a common amphibian species by comparing both an indirect and direct measure of habitat quality. Consequently, our results illuminate a larger problem in interpreting the effects of forest management on amphibians and demonstrate why more research should focus on changes in vital rates of amphibian populations following habitat alteration.

METHODS

Study species

Southern toads (*B. terrestris*) are habitat generalists that are often encountered in highly fragmented landscapes, including suburban areas and golf courses (Scott et al. 2003). As anurans, they generally are able to tolerate higher temperatures and desiccation risks than many amphibian species, especially in comparison to salamanders (Stebbins and Cohen 1995; Zug 2001). They are also capable of storing and reabsorbing large quantities of water in their bladders (Thorson and Svihla 1943; Hillyard 1999). These factors may predict a tolerance to warmer temperatures found in altered landscapes. For these reasons, the response of southern toads in our studies can be viewed as a conservative metric for examining the effects of forest clearcutting on amphibians.

Abundance survey

We selected four forested sites on the U.S. Department of Energy's Savannah River Site in Barnwell County, South Carolina, as part of the LEAP (Land-use Effects on Amphibian Populations) study, a multi-regional, collaborative investigation of the effects of land-use practices on migratory success and demographics of pond-breeding amphibians. These sites are second-growth forests comprised predominantly of loblolly pine (*Pinus taeda*) in the Upper

Coastal Plain of the southeastern U.S. Each study site was a circular area 350 m in diameter centered on an isolated, seasonal wetland. Each wetland was located at least 200 m from paved roads, powerline rights-of-way, and other open areas. We divided each study site into four 4-ha quadrants delineated by two perpendicular transects that intersected at the center of the wetland (Fig. 3.1). Each quadrant was randomly assigned one of four treatments: 1) an unharvested control (> 30 years old); 2) a partially harvested stand, in which the canopy was thinned to approximately 85% of that in the control; 3) a clearcut with coarse woody debris retained (CC-retained); and 4) a clearcut with coarse woody debris removed (CC-removed). The last treatment represents the most extreme level of alteration and produces a habitat typical of even-aged forest management in the southeastern U.S. Logging was completed at the sites in March 2004.

In April 2004, we installed nine 15-m sections of drift fence in each quadrant at all four sites. We placed six 8-L pitfall traps (30 cm in diameter and 25 cm high) paired on opposite sides of each section of drift fence, yielding a total of 54 pitfall traps within each quadrant. Pitfall traps contained 1-3 cm of standing water and floating sponges in the bottom. We constructed the drift fences of aluminum flashing buried 15 cm into the ground and standing 45 cm tall. We distributed the drift fences evenly throughout each quadrant to maximize the likelihood of capturing animals in the treatments (Fig. 3.1). We checked the drift fences daily from 1 June - 28 July 2004 and recorded all amphibian captures, including juvenile southern toads. Animals were released on capture and were not marked, yielding raw counts. This period of drift fence monitoring coincided with the period during which juvenile southern toads leave their natal ponds to establish terrestrial home ranges, where they abide until they become reproductive adults. For the purposes of this study, we only analyzed captures from the control and CC-

removed treatments to permit a direct comparison of abundance data to the enclosure study conducted in these two habitats.

Field enclosure study

We measured growth and survival of juvenile southern toads in terrestrial enclosures in the control and CC-removed treatments. Although enclosures confine the animals, they eliminate the possibility that other processes, such as immigration and emigration, affect perceived abundance within the experimental populations and ensure that the growth and survival of the toads is a reflection of time spent in a single habitat. We constructed two enclosures in each treatment (control and CC-removed) at two of the four sites for a total of four control enclosures and four CC-removed enclosures. We constructed enclosures of aluminum flashing buried 25 cm deep, standing 65 cm tall and measuring 4 m x 4 m. Similarly constructed enclosures of larger sizes have been used in studies of terrestrial density-dependence in ambystomatid salamanders (Pechmann 1995). We systematically placed the enclosures within the interior of the treatments at least 50 m from the edges of the quadrant (Fig. 3.1). We minimized disturbance to the soil and ground cover within the enclosures to maintain an environment suitably representative of the overall treatment.

We collected 240 recently metamorphosed southern toads as they emigrated from a wetland located near our study sites. We maintained all toads indoors in ventilated containers at 23° C on paper towels wet with aged well-water for less than one week prior to release into experimental enclosures. We randomly assigned groups of 30 toads to each of the eight enclosures. Our experimental density of 1.8 toads per m^2 is lower than natural densities encountered along pond margins during the post-metamorphic period (Beck and Congdon 1999). We individually marked each animal by toe-clipping and recorded snout-vent length (SVL) and

fully hydrated mass prior to release into the enclosures on 10 July 2004. After one month, we censused the animals for three consecutive days, recording the SVL and mass of each animal in the field upon capture with an Ohaus $^{\circledR}$ Scout Pro battery-powered balance. We released all animals back into the enclosures immediately following data collection. We repeated this process again two months after the initial release.

To census the toads, we hand-captured them in the enclosures between 06:00 and 08:00 each morning during the three-day sampling periods. Consecutive days of censusing during a sampling period combined with individual marking of toads enabled the capture histories to be analyzed in a robust-design mark-recapture format using program MARK (Pollock 1982; White and Burnham 1999). No animals were captured on the third day of censusing that had not been previously captured in one of the two earlier days, resulting in high probabilities of successfully capturing surviving toads during the census periods. Subsequent population estimates derived from program MARK for each census period differed only slightly (i.e., by one or two animals) from the minimum number known alive during the census period (MNKA; Krebs 1966). Because program MARK does not currently allow fit-testing for robust design recapture models (Bailey et al. 2004a), we opted to use the typically more conservative MNKA at each interval for the comparison of survival rates. Although not shown here, tests of our hypotheses based on model-derived population estimates resulted in the same conclusions.

Statistical Analyses

To test whether clearcutting affected the number of juvenile southern toads captured at drift fences, we performed an analysis of variance (ANOVA) on the total captures at all nine drift fences within a treatment, using site as a blocking factor. To test the effect of treatment on survival of penned toads over two months, we performed a multivariate repeated measures

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analysis of variance (MANOVA; Von Ende 2001) using the MNKA at each of the three intervals and we accounted for the nestedness of the enclosures within two sites in our analysis. To test the effect of treatment on body size over two months, we performed a repeated measures MANOVA using the mean SVL from each enclosure at each of the three intervals, again accounting for the nestedness of the enclosures within two sites.

We tested the hypothesis that larger animals had greater survival by pooling all toads in clearcut enclosures and forested enclosures separately and conducting logistic regressions to test for an effect of initial SVL on survival to the first month. We repeated this procedure to test for an effect of initial SVL on survival to the second month. We also used non-parametric bootstrap resampling (Lunneborg 2000) to test whether animals that perished in the second month of the enclosure study, regardless of treatment, represented a non-random sample of all penned toads with respect to their growth rate in the first month. Most toads that were recaptured in the enclosures and weighed in the field appeared to lose body mass because initial release weights were recorded in the laboratory when toads were fully hydrated. Thus, change in body mass was a reflection of both growth and hydration state at the time of capture, whereas SVL was more likely a reflection of growth alone. Therefore, we performed two resampling analyses, one using change in SVL and one using change in body mass.

All statistical assumptions were examined prior to analyses and no transformations were needed. All statistical analyses were performed using SAS$^{®}$ version 9 (SAS Institute Inc. 2000) and significance was evaluated at the $\alpha = 0.05$ level.

RESULTS

A total of 357 juvenile southern toads were captured in the four clearcut quadrants and 307 toads were captured in the four forested quadrants from 1 June - 28 July 2004. Juvenile toads

were captured at drift fences in clearcuts more frequently than in unharvested forests at three of the four sites (Fig. 3.2). However, neither treatment nor site had a significant effect on the number of captures (treatment: $F_{1,3} = 0.18$, $p = 0.70$; site: $F_{3,3} = 2.76$, $p = 0.21$).

In contrast, we found significant effects of treatment and time on the number of toads surviving over two months in the experimental enclosures (Table 3.1; Fig. 3.3). There were no effects of site, time-by-site, or time-by-treatment interactions on survival (Table 3.1).The average survival of toads in clearcut enclosures after two months was 17% ± 5% whereas the average survival in forested enclosures was 61% ± 3%. Individual contrasts revealed that treatment significantly affected survival of toads in the second month (Table 3.2).

The mean SVL of juvenile toads in both forested and clearcut enclosures increased over two months as the animals grew (Table 3.3). However, there was a significant treatment effect as the mean SVL of toads in forested enclosures increased significantly more than that of toads in clearcut enclosures (Table 3.3; Fig. 3.4), a response that was consistent through time (Table 3.4). Toads that survived in clearcut pens averaged 27.9 ± 0.1 mm SVL whereas toads that survived in forested pens averaged 30.3 ± 0.8 mm SVL. The results of the logistic regressions suggest that initial body size was not an important predictor of survival to any month in either clearcuts or forests (Table 3.5).

Results of non-parametric bootstrap resampling suggest that growth rate, as measured by change in SVL in the first month, did not correlate to greater survival in the second month (Table 3.6). However, with respect to body mass, there was a strong indication that the toads that perished in the second month were a non-random subset of all penned toads. Those that perished lost more mass in the first month, on average, than did similarly-sized samples drawn at random from the total pool of animals (Table 3.6).

Effects of clearcutting on toad abundance

Clearcutting typically has a negative effect on amphibian abundances and richness (Petranka et al. 1994; Ash 1997; Grialou et al. 2000; Knapp et al. 2003; Karraker and Welsh 2006). Indeed, several studies have suggested that forest cover is a critical factor that determines the distribution and density of many species (Porej et al. 2004; Herrmann et al. 2005). However, the response of amphibians to clearcutting varies considerably among species and physiographic regions (deMaynadier and Hunter, 1995; Russell et al., 2004). The results of our study agree with others that show little effect of clearcutting on anuran abundances, and in some cases, increases in anuran abundances (e.g., Pais et al. 1988; Phelps and Lancia 1995; Clawson et al. 1997; Ryan et al. 2002). A critical and untested assumption in some of these studies, and one that is true of the abundance survey in this study, is that capture probabilities and detection do not vary with treatment. Ideally, the application of mark-recapture techniques to analyze captures of individually-marked animals can reduce possible bias resulting from such assumptions and can clarify the inferences made about the effects of habitat type on amphibian populations based on abundance measures.

Effects of clearcutting on survival and body size

The reduced survival and body size of southern toads in clearcuts indicates that clearcuts are poor-quality habitats for these amphibians. Juvenile toads experienced higher mortality in clearcuts and those that did survive were smaller in size than their forest-dwelling cohorts after two months. Increased juvenile mortality can reduce population sizes by eliminating future reproductive animals (Vonesh and De la Cruz 2002). Additionally, smaller body size in juvenile amphibians results in a delayed onset of maturity (e.g., Smith 1987; Semlitsch et al. 1988;

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Berven 1990; Scott 1990, 1994), which reduces the number of reproductive animals available in the breeding adult population. The results of the logistic regressions on body size suggest that changes in the mean size of toads in enclosures were products of growth and not a reflection of differential survival based on body size.

Because southern toads have a greater tolerance to the conditions found in clearcuts than do many other amphibians (Thorson and Svihla 1943), other amphibians are likely to suffer even greater physiological responses to clearcutting. However, the results from studies of other species have been mixed. Chazal and Niewiarowki (1998) found no effects of clearcutting on body mass, clutch size, lipid storage, or the number of recaptured mole salamanders (*Ambystoma talpoideum*) maintained in 100 m^2 field enclosures when compared to salamanders from forested enclosures. In contrast, Rothermel and Luhring (2005), using very small (0.33 m^2) enclosures, found that mortality of *A. talpoideum* could occur quite rapidly in recent clearcuts, particularly if salamanders did not have access to burrows. In the 16 m^2 enclosures used in our study, we found that mortality of juvenile southern toads in clearcuts increased significantly after the first month. Apart from species differences, there are at least two other explanations for the variation in results among these enclosure-based studies. First, as field enclosures increase in size, relocating highly fossorial amphibians can become difficult, and relying on pitfall traps to recapture animals for survival comparisons (as in Chazal and Niewiarowki 1998) may begin to approximate comparisons of capture data from drift fence studies. Second, and more plausibly, larger field enclosures may incorporate more habitat complexity, allowing amphibians to find suitable refugia in otherwise hostile environments. Thus, while altered habitats are generally of poorer quality due to desiccating conditions and other factors, the ability to find and use suitable microhabitats in a larger landscape may mitigate some of the negative impacts associated with

forest removal. Studies that specifically examine habitat selection and use by amphibians can greatly improve our understanding of amphibian responses to forest alteration.

Clearcuts used in forest management at the Savannah River Site typically range from 2 to 30 ha (Krementz and Christie 2000). Due to the small size of clearcuts used in our study (< 4 ha) and the ability of adult southern toads to move long distances overnight (up to 300 m; Graeter 2005), clearcuts in our study may have been easily traversed by juvenile southern toads. When juvenile toads spend short amounts of time in clearcuts, their probability of surviving is likely comparable to that of toads in forests. In contrast, sizeable clearcuts that require lengthy passages (>30 days based on the current study) to escape could result in increased animal mortality due to the greater amount of time spent in poor-quality habitat. For amphibians that are less vagile or have high site fidelity (e.g., *Ensatina exchscholtzii* and *Plethodon elongatus*; Karraker and Welsh 2006), clearcuts may represent significant barriers that trap populations and contribute to local declines.

Our field enclosure study provides critical insight into the processes that can reduce amphibian abundance following habitat alteration not revealed by drift fence or monitoring studies. Canopy removal during forest clearcutting causes an increase in daytime temperatures that can accelerate desiccation or exceed lethal limits, leading to rapid mortality (e.g., Rothermel and Luhring 2005). Although many juvenile southern toads in our study lost body weight in the first month relative to their fully hydrated initial mass, we found that individuals that lost the most mass in the first month were significantly less likely to survive to the second month. Therefore, dehydration probably influenced toad mortality in clearcuts. Other possible reasons for reduced survival in clearcuts include an increase in predation, inadequate prey populations, or a reduction in time spent foraging as animals acted to minimize water loss in recent clearcuts.

However, enclosures probably excluded many non-avian predators (e.g., colubrid snakes), possibly reducing predation on toads. Additional manipulative studies are needed to identify the specific causes of decreased amphibian survival following clearcutting.

CONSERVATION IMPLICATIONS

Although estimates of vital rates provide the only direct measures of the effect of habitat alteration on amphibians and other wildlife (Armstrong 2005), many studies continue to focus on changes in abundance and richness as indicators of habitat quality. The results of our study suggest that differences in abundance should not be used as the sole metric of habitat quality and that a more thorough experimental approach incorporating estimation of vital rates may be required to understand the implications of habitat alteration.

Vital rates are directly affected by habitat change, often without the inherent time lags that occur with population sizes (Brooks et al. 1999). Therefore, they may be particularly useful in the early identification of problems arising from habitat alteration. Also, examining vital rates can identify which demographic processes are responsible for changes in local populations (i.e., survival, reproduction, or migration), providing planners with explicit targets for conservation management. In our study, field enclosures proved to be an effective tool for studying juvenile survival and growth in isolation from other demographic processes.

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Table 3.1 Results of the repeated-measures analysis of variance of the effects of habitat treatment, site, and time on the number of surviving southern toads in enclosures over two months.

	df	MS	F	p
Between-subject				
Site	1	66.667	3.92	0.119
Treatment	2	124.333	7.31	0.044
Error	4	17		
	df	Wilks' λ	F	p
Within-subject				
Time	2,3	0.0025	80.87	0.003
Time x Site	2,3	0.5008	1.49	0.354
Time x Treatment	4,6	0.0837	3.68	0.076

Table 3.2 Results of individual contrasts from a repeated-measures analysis of variance testing the effects of treatment and site on the number of surviving toads in enclosures at each interval.

Source	df	MS	F	p
First month interval				
Mean	1	578.0	28.54	0.006
Site	1	72.0	3.56	0.132
Treatment	2	24.5	1.21	0.388
Error	4	20.3		
Second month interval				
Mean	1	882.0	51.88	0.002
Site	1	8.0	0.47	0.530
Treatment	2	121.0	7.12	0.048
Error	4	17.0		

Table 3.3 Results of the repeated-measures analysis of variance of the effects of habitat treatment, site, and time on the mean snout-vent length of southern toads in enclosures over two months.

	df	MS	F	p
Between-subject				
Site	1	0.118	0.25	0.642
Treatment	2	6.125	13.09	0.018
Error	4	0.467		

	df	Wilks' λ	F	p
Within-subject				
Time	2,3	0.0631	22.25	0.016
Time x Site	2,3	0.7975	0.38	0.712
Time x Treatment	4,6	1.667	2.97	0.439

Table 3.4 Results of individual contrasts from a repeated-measures analysis of variance testing the effects of treatment and site on mean snout-vent length of toads in enclosures.

Source	df	MS	F	p
First month interval				
Mean	1	22.883	28.54	0.002
Site	1	0.008	3.56	0.898
Treatment	2	1.349	1.21	0.146
Error	4	0.417		
Second month interval				
Mean	1	4.720	5.08	0.087
Site	1	0.544	0.59	0.487
Treatment	2	2.037	2.19	0.228
Error	4	0.929		

Table 3.5 Results of the logistic regressions testing for effect of initial body size on survival among toads in enclosures.

	χ^2	p
Clearcut pens		
survival to first month	0.03	0.86
survival to second month	0.01	0.94
Forested pens		
survival to first month	1.15	0.29
survival to second month	0.02	0.76

Table 3.6 Mean change in snout-vent length and body mass during the first month of toads that perished in the second month (n = 84). Confidence intervals were derived from 1,000 bootstrap resampled subsets (of size n = 84) drawn from the entire pool of toads that survived the first month.

	Mean change	90% CI
SVL (cm)	1.4	1.21 – 1.85
Mass (g)	-0.189	-0.185 – -0.068
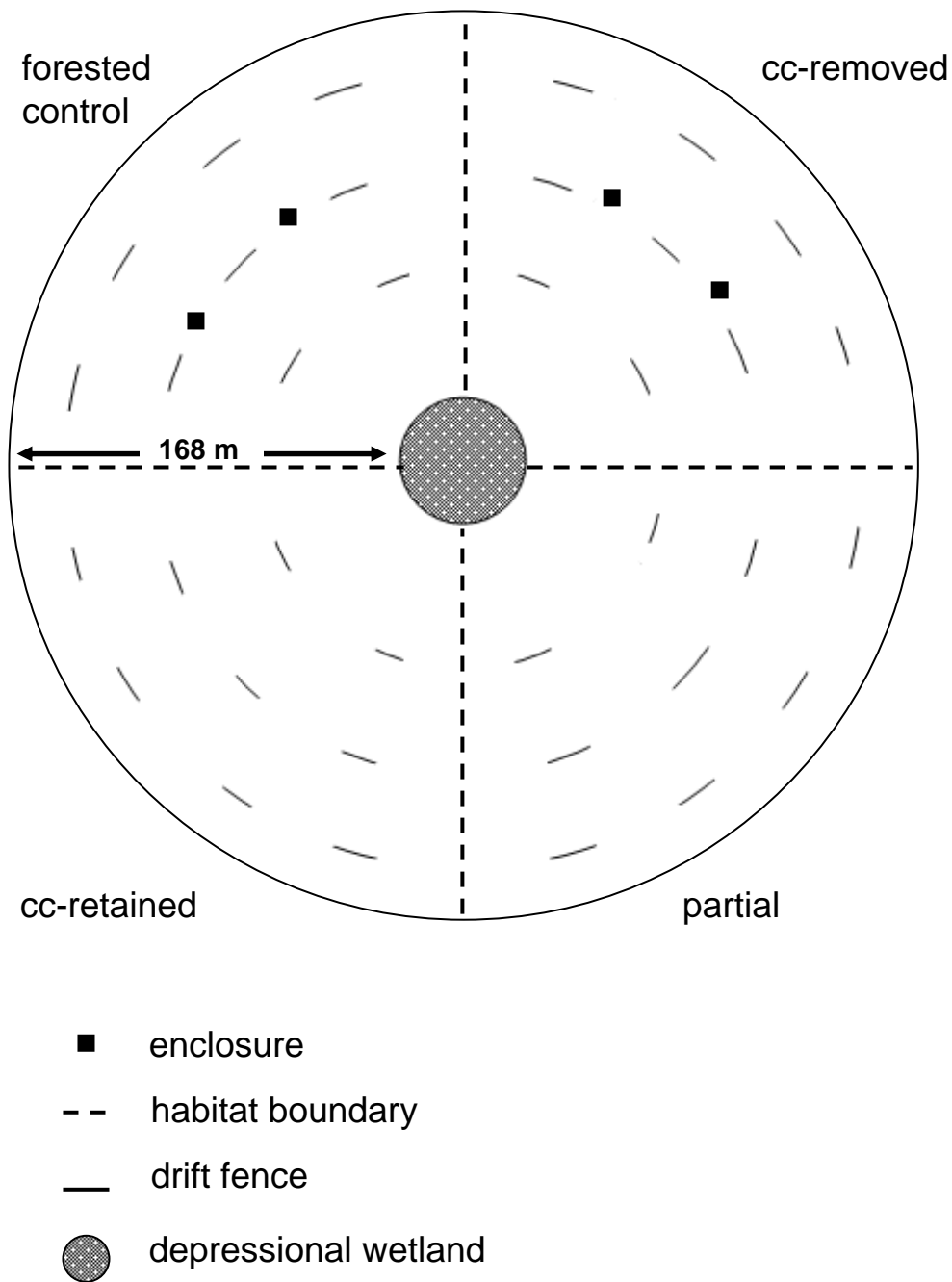
Figure 3.1 Diagram showing the arrangement of drift fences and enclosures at each site. See text for description of the four treatments. Note that drift fences, wetland, and enclosures are not pictured to scale.
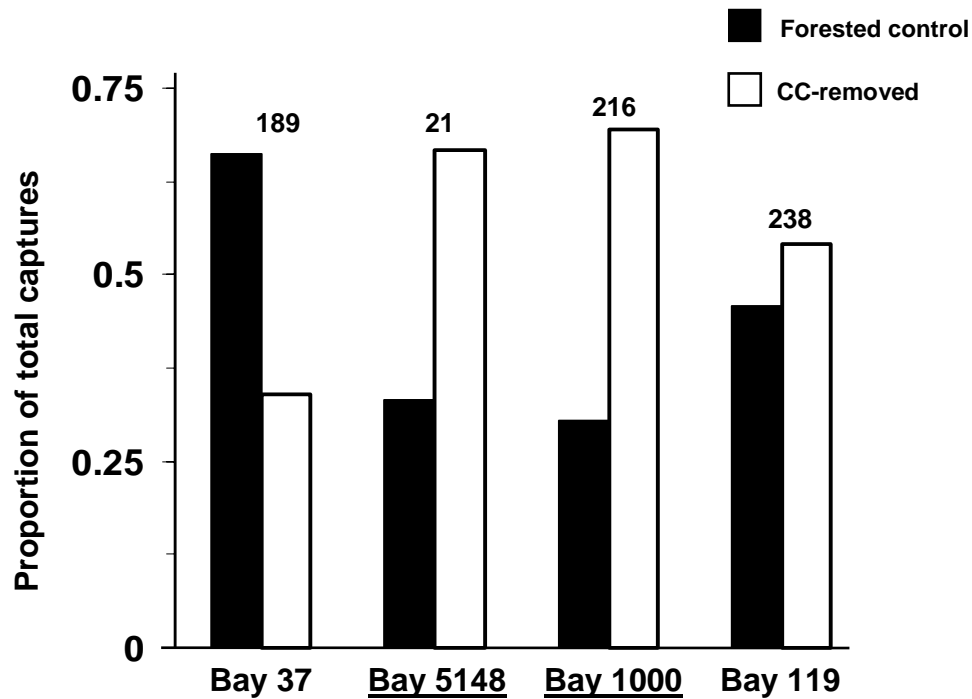
Figure 3.2 Proportion of juvenile southern toads captured in forested controls versus CC-removed habitats at each study site using drift fences and pitfall traps. Our field enclosures were located at Bay 5148 and Bay 1000. The total number of captures of juvenile southern toads at each site is given above the bars.
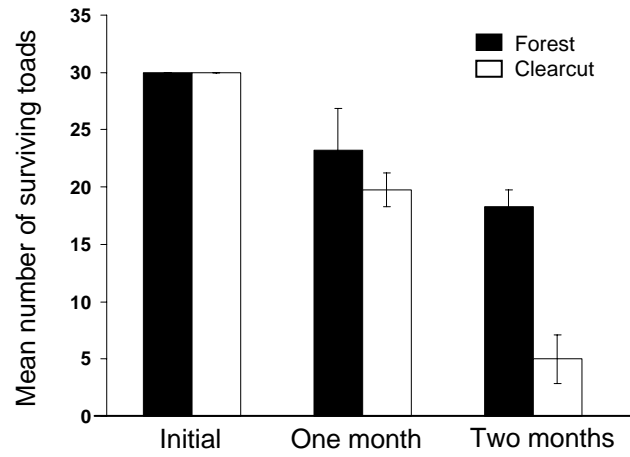
Figure 3.3 Mean (SE) number of surviving toads in each treatment (n = 4 enclosures per treatment).
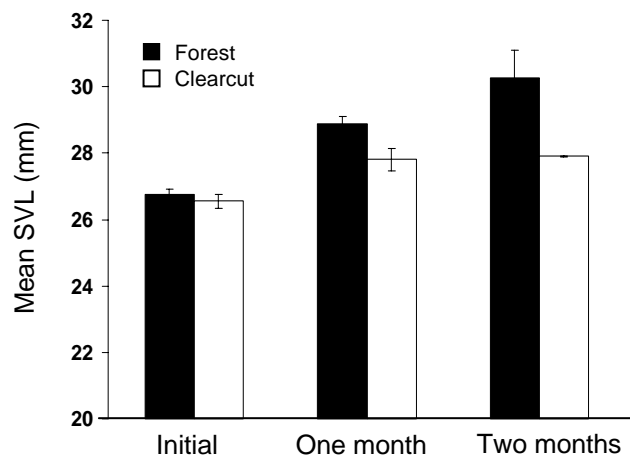
Figure 3.4 Mean (SE) snout-vent length of surviving toads in each treatment (n = 4 enclosures per treatment).

CHAPTER 4

EFFECTS OF FOREST HARVESTING ON SURVIVAL OF MARBLED SALAMANDERS,

AMBYSTOMA OPACUM [3]

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[3] Todd, B.D. To be submitted to *Ecological Applications*.

Habitat loss is a major factor in the global decline of amphibians (Alford and Richards 1999; Stuart et al. 2004). Unlike nearly all other terrestrial vertebrates, many amphibians are biphasic and require both aquatic and terrestrial habitats in which to complete their life histories. This aspect of their ecology makes them doubly responsive to habitat loss or alteration and may account for their unparalleled imperilment among vertebrates (Stuart et al. 2004). Historically, most studies of amphibians have focused on aspects of their aquatic ecology but there is growing recognition of the importance of terrestrial habitat to their life histories and population persistence (Semlitsch 1998, 2000).

In the southeastern United States, as in many regions of the world, forest harvesting is an important economic activity that shapes the terrestrial environment. Nearly 82% of amphibians are at least partially forest-dependent during parts of their lives (Stuart et al. 2004), making the potential scope of forestry impacts large. Past studies have generally found a trend of decreased amphibian abundance and richness in harvested forests, particularly in clearcuts (reviewed in deMaynadier and Hunter 1995), although no significant differences are observed in some cases (e.g., Ryan et al. 2002). Ultimately, many mechanisms may underlie observed changes in abundance and richness, including increased mortality in harvested forests, evacuation of harvested forests by amphibians, or changes in amphibian behavior that leads to avoidance of harvested habitats or retreat underground (Semlitsch et al. 2008). Understanding the degree to which these mechanisms contribute to amphibian declines is an important first step to mitigating the impacts of forest harvesting on amphibian populations.

Ambystomatid salamanders are a family of salamanders broadly distributed across much of North America (Lannoo 2005). Several ambystomatid salamanders are protected in the United

States by federal or state regulations or are designated as species of concern due to recent and severe population declines (Lannoo 2005). Like many pond- or wetland-breeding amphibians, ambystomatid salamanders reproduce in aquatic habitats but reside for most of their lives in adjacent uplands (Semlitsch 1998). Ambystomatid salamanders are highly fossorial and often dwell beneath leaf litter or seek permanent refuge in small mammal burrows or other subterranean openings (Lannoo 2005). Because of their reliance on ground litter and soil structure on the forest floor, forest harvesting activities have the potential to disturb their habitat and possibly affect their survival. Forest harvesting, especially clearcutting, degrades ground litter, eliminates immediate litter inputs, increases soil temperatures, increases evaporative water potential (Chen et al. 1999; Zheng et al. 2000), and may compact soil and destroy burrows. Such changes may degrade important terrestrial habitat for ambystomatid salamanders and further reduce populations.

The primary goal of our study was to determine the effects of forest harvesting on the survival of marbled salamanders (*Ambystoma opacum*). We obtained estimates of survival of both juvenile and adult marbled salamanders using field enclosures in forest habitats harvested at varying intensities. In particular, we were interested in comparing survival of marbled salamanders among unharvested forests, partially thinned forests, and clearcuts with two levels of coarse woody debris (CWD). In a similar study, survival and growth of mole salamanders (*Ambystoma talpoideum*) did not differ significantly between unharvested forests and recent clearcuts (Chazal and Niewiarowski 1998). Marbled salamanders do not burrow as proficiently as mole salamanders and may be less able to retreat from poor surface conditions by escaping to subterranean refuges (Semlitsch 1983). Therefore, we predicted that marbled salamanders would exhibit decreased survival in recently clearcut forests compared with unharvested controls. We

also predicted that partial forest thinning would produce survival rates intermediate to those of salamanders in clearcuts and unharvested forests. Finally, we predicted that survival over 1-yr periods would be lower for juvenile marbled salamanders than adults because of their small body size and correspondingly greater potential lose body water.

METHODS

Experimental arrays

We selected 4 forested sites on the SRS for study (see also Rothermel and Luhring 2005; Todd and Rothermel 2006). These sites were second-growth, managed-pine forests of loblolly pine (*Pinus taeda*) with a few interspersed hardwoods (oaks [*Quercus* spp.], red maple [*Acer rubrum*], hickories [*Carya* spp.], dogwood [*Cornus florida*], and sweetgum [*Liquidambar styraciflua*]). Where present, understory consisted of sweetgum (*Liquidambar styraciflua*), wax myrtle (*Morella cerifera*), and holly (*Ilex opaca*), with ground cover dominated by Carolina jessamine (*Gelsemium sempervirens*) and grasses.

We centered each of the 4 circular experimental sites on isolated, seasonal wetlands that hold water during winter and early spring. The experimental sites extended outward from the wetland boundaries for 168 m. We divided each circular site into 4, 4-ha quadrants delineated by 2 perpendicular transects that intersected at the center of the wetland (Fig. 4.1). Each quadrant was assigned randomly to 1 of 4 treatments: (1) unharvested control (> 30 years old); (2) partially thinned stand in which the canopy was thinned to approximately 85% of that in the control (thinned forest); (3) clearcut with coarse woody debris retained (CC-retained); and (4) clearcut with coarse woody debris removed (CC-removed). The 2 forested plots were opposite each other (Fig. 4.1). Logging commenced in February 2004 and was completed at the sites in

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April 2004. We did not perform any additional site preparation such as replanting, harrowing, burning, or the application of herbicides.

Enclosure study

After logging was completed, we constructed two sets of enclosures in each treatment at each site. We constructed enclosures of aluminum flashing buried 25 cm deep, standing 65 cm tall and measuring 12 m x 4 m (Todd and Rothermel 2006). Enclosures were further partitioned into three adjoining 4 m x 4 m pens using aluminum flashing. Similar enclosures of greater area (Pechmann 1995; Chazal and Niewiarowski 1998) and smaller area (Rothermel and Semlitsch 2006) have been used successfully in previous studies of the terrestrial ecology of ambystomatid salamanders. We systematically placed the enclosures within the interior of the treatments at least 50 m from the edges of the quadrant (Fig. 4.1). We minimized disturbance to the soil and litter cover within the enclosures to maintain an environment suitably representative of the overall treatment. We buried 6 cylindrical pitfall traps (20 cm tall x 15 cm dia.) along the insides of each 4m x 4m enclosure and left them closed when not in use.

In May 2005 we collected 960 recently metamorphosed marbled salamanders as they emigrated from a wetland located near our study sites. We maintained juvenile salamanders indoors in ventilated containers at 15 $^{\circ}$C on paper towels moistened with aged well-water for less than one week prior to release. All animals were individually marked using an equal number of toe-clips and we recorded snout-vent length (SVL) of each animal to the nearest mm and mass to the nearest mg using an Ohaus$^{\circledR}$ field scale. We randomly assigned groups of 30 juvenile salamanders to enclosures so that 2 non-adjoining 4 x 4 m enclosures in each treatment at each site contained juvenile salamanders (for a total of 32 enclosures containing juvenile salamanders at a density of 1.8 salamanders/m^2). We released animals into enclosures at night following rain

in May 2005. We opened pitfall traps and captured animals in enclosures for 3-6 day periods during rainfall in June and August. Animals were identified, measured, and released under moist cover in the interior of the enclosure the following morning. From late November to December we sampled the enclosures continuously with open pitfall traps for 25 continuous days and we removed all animals from the enclosures upon capture. We also searched leaf litter and cover objects by hand to recover any uncaptured salamanders that we could find.

In January 2006 we collected 144 post-reproductive adult salamanders as they emigrated from a wetland located near our study sites. We maintained adult salamanders indoors in ventilated containers at 10 $^{\circ}$C on paper towels moistened with aged well-water for less than one week prior to release. All animals were individually marked using an equal number of toe-clips and we recorded snout-vent length (SVL) of each animal to the nearest mm and mass to the nearest mg. We randomly assigned groups of 16 adult salamanders to 4 x 4 m enclosures in an unharvested control, a partially harvested stand, and a clearcut with no retained CWD at three sites (for a total of 9 enclosures containing adult salamanders at a density of 1 salamander/m^2). We released animals into enclosures at night following rain in January 2006. We opened pitfall traps and captured animals in enclosures for 3-6 day periods during rainfall in April, May, and July. Animals were identified, measured, and released under moist cover in the interior of the enclosure the following morning. In November we sampled the enclosures continuously with open pitfall traps for 20 days and we removed all animals from the enclosures upon capture. We also searched leaf litter and cover objects by hand to recover any uncaptured salamanders that we could find.

Habitat characterization

In May 2005, we characterized habitat conditions inside enclosures used for juvenile salamanders. We visually estimated the proportion of bare soil, leaf litter, understory vegetation and CWD covering the ground to the nearest 5%. We used a spherical densitometer to calculate the proportion of canopy cover over enclosures and we used a ruler to measure litter depth to the nearest mm at four equidistant points inside each enclosure. In January 2006 we repeated all measurements for the separate enclosures that were used for adult salamanders.

Data analysis

We calculated the minimum number of salamanders known alive (MKNA) during each census to compare salamander survival among the forest harvest treatments. By identifying each animal upon capture, we were able to determine if animals captured in later censuses had been missed in previous censuses so that past censuses could be retroactively adjusted accordingly (Rothermel and Semlitsch 2006). To determine whether the minimum number of salamanders known alive at each interval was affected by treatment, we use multivariate analyses of variance (MANOVA) with the MKNA at initial release and each subsequent census as a repeated measure. We performed MANOVA separately for juveniles and adults.

We used logistic regression to determine whether initial body size or relative mass of salamanders affected the likelihood of recapture during the course of the study, irrespective of treatment or enclosure. Relative mass was calculated as $[(mass/SVL^3) \times 10,000]$ and regressions were run separately for juveniles and adults to determine the effects of body size (SVL) and relative mass separately. Animals that were never recaptured were scored as a '0' and animals that were recaptured again at least once were scored as '1'.

We constructed multiple regression models using a stepwise model selection procedure in the SAS® statistical package (SAS Institute Inc. 2000) to determine which environmental characteristics at each enclosure most contributed to observed survival to first census. We used litter depth, canopy cover, and the proportion of bare soil, leaf litter, and CWD cover as independent variables and the MNKA at first census as our dependent variable in regressions that were performed separately for juveniles and adults. We set $\alpha=0.15$ for inclusion of independent factors into the regression models. We arcsine square-root transformed all proportional data including canopy density.

RESULTS

Treatment effects on survival

The number of juvenile marbled salamanders that were known to be alive in the field enclosures declined rapidly during the first two months of the study and then leveled off (Fig. 4.2a). Survival of juvenile marbled salamanders through completion of the study was significantly affected by treatment ($F_{3,25}=3.1$, $P=0.04$). Generally, survival of juvenile marbled salamanders was greatest in the unharvested forest controls compared with the other three treatments (Fig. 4.2b). There was also a significant decrease in the number of juveniles known to be alive in the enclosures over time ($F_{3,75}=525.7$, $P<0.001$) but there was no significant time-by-treatment interaction ($F_{9,75}=1.5$, $P=0.20$). Seven percent of the salamanders initially released into enclosures in unharvested forests were recaptured alive in December at the conclusion of the study. In contrast, less than 1% of salamanders were recaptured from enclosures in clearcuts with CWD retained and no surviving salamanders were recaptured from enclosures in clearcuts with no CWD retained or in partially thinned forests (Fig. 4.2a).

The number of adult marbled salamanders that were known to be alive in the field enclosures did not decline as precipitously in the first several months as had the number of juveniles (Fig. 4.2b). However, the number of adults known alive did decrease more in the first several months than throughout the rest of the study. Survival of adult marbled salamanders was significantly affected by treatment ($F_{2,4}$=9.3, P=0.03). Survival of adults appeared greater in both unharvested forest controls and partially thinned forests compared with clearcuts with no CWD retained (Fig. 4.2b). There was a significant decrease in the number of adults known to be alive over time ($F_{4,16}$=21.4, P<0.001) but there was no significant time-by-treatment interaction ($F_{8,16}$=0.96, P=0.49). At the conclusion of the study, 19% of adult salamanders initially released into enclosures in unharvested forest controls were recaptured alive. Similarly, 23% of the salamanders initially released into enclosures in partially harvested forests were recaptured at the conclusion of the study. In contrast, no salamanders were recaptured in clearcut enclosures during the last two sampling periods, including the removal sampling conducted at the conclusion of the study.

Effects of initial body size on survival

Juvenile marbled salamanders that were recaptured alive in field enclosures at some point during the study were initially longer at release than were juveniles that were not recaptured, irrespective of treatment (χ^2= 4.7, P=0.03). The significant difference in body size was only 0.62 mm but apparently led to a greater likelihood of recapture among juveniles (Fig. 4.3). Similarly, juveniles that were heavier for a given length were more likely to be recaptured than were juveniles of less mass, irrespective of treatment (χ^2= 4.8, P=0.03). Among adults, there was no significant difference between animals that were recaptured versus those not seen again for length (χ^2= 0.05, P=0.83) or relative body mass (χ^2= 2.3, P=0.13).

Correlates of habitat and survival

The model selection procedure found that percentage of ground covered by both litter cover and CWD were positively correlated with the number of juvenile marbled salamanders surviving until the first census (overall model: $F_{2,31} = 25.96$, P <0.001, adj-$R^2 = 0.64$). For adult salamanders, no model correlating environmental characteristics with survival to first census was found to fit the data significantly ($F_{1,8} = 3.85$, P = 0.09) but the top model found that survival of adult salamanders was positively correlated with litter depth in the enclosures.

DISCUSSION

Our results demonstrate the degree to which forest loss can negatively affect survival of marbled salamanders. For example, survival of juveniles in both partially harvested forests and clearcuts was dramatically reduced compared with unharvested controls. Interestingly, a few juveniles did survive in clearcuts in which CWD was retained, whereas no juveniles were recaptured in partially harvested forests at the conclusion of the study, possibly because CWD levels were low to nonexistent in treatments in which it was not intentionally retained (see Todd and Andrews 2008). These results also correspond with our multiple regression models which found that CWD was positively correlated with the number of juvenile marbled salamanders captured at first census. Salamanders are often found to be highly associated with CWD, especially plethodontids with direct development (reviewed in deMaynadier and Hunter 1995). This has led some to suggest that the retention of CWD during forest harvesting may mitigate harvesting affects on small amphibians by providing important refuge to desiccation-prone salamanders and frogs (deMaynadier and Hunter 1995; Chazal and Niewiarowski 1998). Although marbled salamanders did appear to benefit from the retention of CWD in forest clearcuts, mortality in clearcuts at the end of the study was nevertheless nearly absolute.

Consequently, CWD may be beneficial to salamanders inasmuch as it may help sustain them long enough to evacuate clearcuts during nights favorable to overland movement, but it may not help sustain salamanders in clearcuts indefinitely (Semlitsch et al. 2008).

For adult marbled salamanders, survival was only significantly diminished in clearcuts compared with unharvested forests. In fact, mortality of adult salamanders in clearcuts which had no CWD retained was complete. In contrast, adult survival in partially thinned stands was comparable with that in unharvested forests, suggesting that intermediate levels of forest disturbance may not diminish the suitability of terrestrial habitat for adults. We were unable to test whether retention of CWD in clearcuts was beneficial to adult marbled salamanders because too few adult salamanders were captured for use in our study. Adult survival was generally much greater than juveniles in all treatments, particularly in partially thinned stands. Adults tend to be much larger than juveniles, a factor that may improve their survival because rates of evaporative body water loss decrease with increasing surface area to volume ratio (Spight 1968; Spotila 1972).

Survival of juveniles to their first winter in forest enclosures was approximately 7%. This estimate lies within the range of survival estimates generated from other studies of recently metamorphosed marbled salamanders living in unharvested forest habitat. For example, survival to first reproduction in marbled salamanders was estimated at 4-9% in similar forest enclosures (Pechmann 1995) and 3-15% based on return rates of free-ranging marbled salamanders (Scott 1994). Likewise, our finding that the likelihood of recapture in experimental enclosures was correlated with initial post-metamorphic body size and relative mass is also consistent with previous studies. Salamanders that metamorphose at larger body size and relative mass better endure food shortages (Scott 1994), have greater lipid stores (Scott 1994), and in turn often have

greater survival (Scott 1994; Rothermel and Semlitsch 2006; Scott et al. 2007). In studies using field enclosures, body size may be particularly important to survival of juveniles because habitat choice is restricted and conspecifics may compete for suitable refugia (Regosin et al. 2004), or for food resources at a time when terrestrial growth is usually most rapid. In fact, the availability of burrows has been shown to be an important factor for short-term survival of ambystomatid salamanders, especially in forest clearcuts (Rothermel and Luhring 2005). For adults, such effects of body size may be less apparent, particularly if they are better able to dig burrows or otherwise create their own retreats (Semlitsch 1983).

The reductions in salamander survival that we observed in enclosures in harvested forests is likely attributed to several factors. Notably, mechanical forest harvesting can disturb soil and eliminate or reduce ground litter (Todd and Andrews 2008), microclimatic factors that are vital to ground-dwelling amphibians. Also, loss of canopy cover increases air and soil temperatures (Todd and Andrews 2008) which may exceed lethal limits or facilitate body water loss in amphibians that remain in harvested forests (Todd et al. 2008). The combination of these factors has been shown to lead to mortality of ambystomatid salamanders that can occur in a little as 24 h when salamanders find themselves in harvested forests without suitable burrows (Rothermel and Luhring 2005).

Most previous studies of the effects of forest harvesting on amphibian populations have focused on comparisons of relative abundance or species richness among habitats. The results of our study demonstrate one potential mechanism that may act singly or in concert with other factors to explain observed declines from forest harvesting. In studies in which the relative abundance of salamanders decreases after forest clearcutting, mortality may play a large role in those declines. Even so, we recognize that other factors may also affect amphibian populations in

harvested forests. For example, it is still unknown how much mortality occurs during actual harvesting activities or during mechanized post-harvest site preparation and replanting (Russell et al. 2004). Nonetheless, because terrestrial habitat is vital to the long-term persistence of pond-breeding salamanders (Semlitsch 2000), our study indicates that land managers should be concerned about habitat changes that diminish survival of forest-dwelling amphibians. It is nevertheless encouraging to note that partial forest thinning appears compatible with the survival of adult salamanders and that CWD may be a valuable tool to aid short-term survival of forest amphibians in altered habitats.

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control

cc-removed

168 m

cc-retained

partial

■■■■ enclosure   – – habitat boundary

depressional wetland
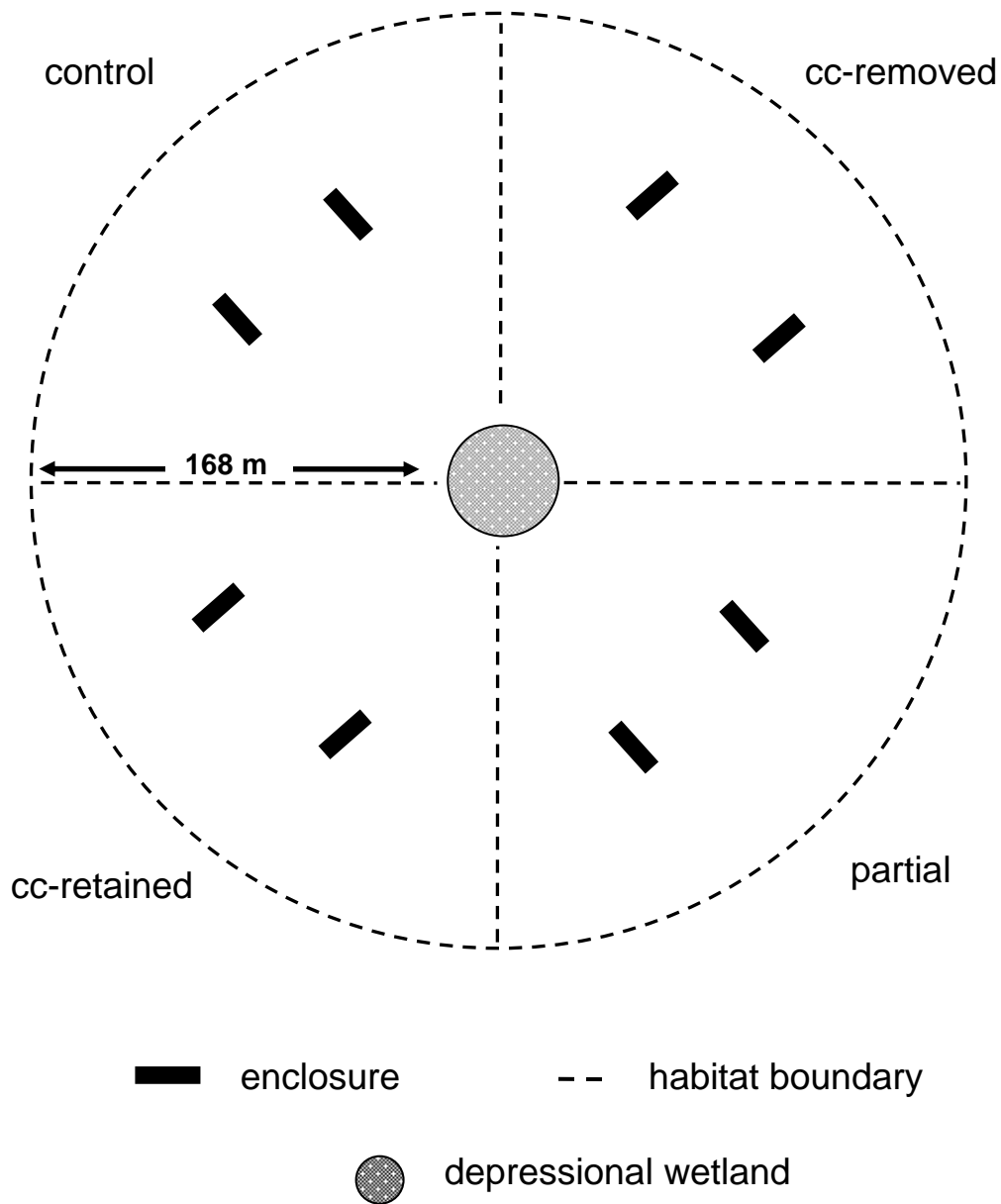
Figure 4.1 Diagram of 1 of 4 replicate experimental arrays showing the arrangement of enclosures and treatments at each site. See text for description of the four treatments. Note that figure is not necessarily to scale.
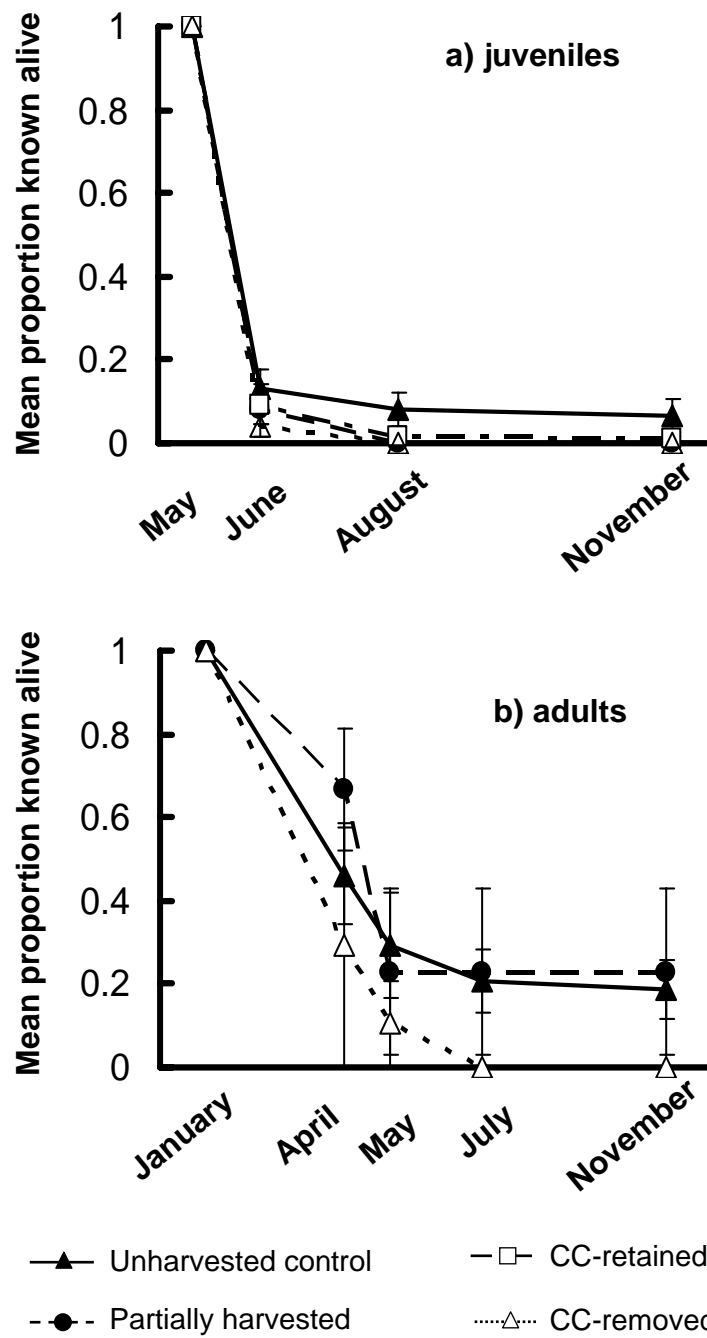
Figure 4.2 The mean proportion (SE) of marbled salamanders known alive at each census for (a) juveniles and (b) adults.
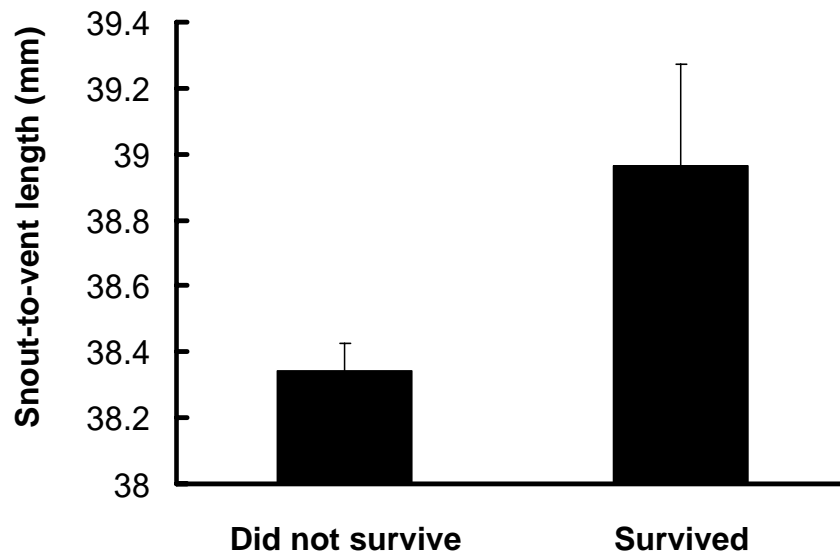
Figure 4.3 The mean (SE) snout-to-vent length of juvenile marbled salamanders that were either recaptured at least once or not seen again in field enclosures, irrespective of treatment.

CHAPTER 5

INTERSPECIFIC EFFECTS OF UPLAND FOREST HARVESTING ON AMPHIBIAN

MIGRATIONS: IMPLICATIONS FOR HABITAT AND POPULATION CONNECTIVITY [4]

INTRODUCTION

Species declines highlight an ongoing loss of global biodiversity and portend a looming extinction crisis (Lawton and May 1995; Vitousek et al. 1997). In fact, current global extinction rates of species are estimated to be many times greater than the background rate revealed from the fossil record (Wilson 1999; McCallum 2007). Perhaps most representative of these declines are the amphibians, 33% of which are classified as threatened, a proportion greater than that of all other terrestrial vertebrates (Stuart et al. 2004). Despite being the greatest cause of amphibian imperilment, habitat loss and fragmentation continue largely unabated and compete for recognition of their often insidious effects on amphibian populations (Alford and Richards 1999; Stuart et al. 2004). Unlike nearly all other terrestrial vertebrates, many amphibians are biphasic and require both aquatic and terrestrial habitat elements for their life histories. Whereas the importance of aquatic habitat for amphibians has historically been recognized, there is growing awareness of the critical value of terrestrial habitat to amphibians (Semlitsch 1998; Semlitsch and Bodie 2003).

The application of spatial ecology to the study of flora and fauna has a rich tradition (Andrewartha and Birch 1954; MacArthur and Wilson 1967) and remains essential to the study of many species, including amphibians. Biphasic amphibians are typically clustered in terrestrial habitat that surrounds reproductive ponds (Semlitsch 1998; Semlitsch and Bodie 2003; Rittenhouse and Semlitsch 2007), often leading to irregular distributions. The development of metapopulation theory (Hanski 1999), combined with patchy amphibian distributions, has led to a "ponds-as-patches" model that promotes terrestrial connectivity between ponds to preserve metapopulation dynamics (Alford and Richards 1999). Still, the application of metapopulation theory to the study and conservation of amphibian populations has been controversial and such

dynamics in amphibians may be more apparent than real (Marsh and Trenham 2001; Smith and Green 2005). In many cases, metapopulation conditions (Hanski 1999) are assumed but remain untested, and in other cases metapopulation conditions have not been met (Smith and Green 2005). Regardless of whether amphibians always conform to the conditions required for metapopulation dynamics, the connectivity of local populations to one another via suitable terrestrial habitat has repeatedly been shown to shape amphibian communities and local populations (e.g., Gamble et al. 2007; Werner et al. 2007). For these reasons, the conservation of upland terrestrial habitat remains essential.

Pond-breeding amphibians spend the majority of their lives in terrestrial habitat where they abide, forage, and over-winter when not breeding at ponds (Semlitsch 2008). Consequently, suitable terrestrial habitat is required for their survival (Semlitsch 1998; Semlitsch and Bodie 2003). Pond-breeding amphibians also undertake major overland breeding migrations between their terrestrial homes and their aquatic reproductive sites (Semlitsch 2008). Thus, habitat loss that fractures the continuity of terrestrial and aquatic environments might disrupt amphibian migrations or create barriers to post-metamorphic dispersal, a factor that has been shown to reduce species richness of biphasic amphibians (Becker et al. 2007). Lastly, loss of terrestrial habitat may increase isolation of local populations and affect community composition, gene flow, or species abundance (Hitchings and Beebee 1997; Gibbs 1998; Werner et al. 2007). As a result, it is important to understand what mechanisms underlie amphibian responses to terrestrial land use and habitat alteration.

Forest harvesting and conversion for other types of land use are pervasive forms of habitat loss that shape terrestrial environments. The loss of forest habitat is particularly relevant to amphibians because 82% of amphibian species are forest-dependent (Stuart et al. 2004). Past

studies have shown that clearcutting can reduce amphibian richness and abundance (deMaynadier and Hunter 1995) by reducing survival and growth (Todd and Rothermel 2006) or by causing amphibians to evacuate clearcuts (Raymond and Hardy 1991; Semlitsch et al. 2008). Although clearcuts are hallmarks of even-aged forest management, these modified landscapes are also representative of other forms of land use such as suburban development, power-line rights-of-way, and agriculture. Our goal in this study was to examine the effects of upland forest management on the migration of adult amphibians into and out of adjacent wetlands. We hypothesized that (1) the number of amphibians migrating through habitats would decrease as the intensity of forest harvesting in those habitats increased, (2) a smaller proportion of salamanders would migrate through clearcuts than would frogs due to differences in their movement abilities (e.g., Lemckert 2004; Cushman 2006), (3) a greater proportion of amphibians would emigrate through forested habitats than had immigrated through them, and (4) amphibians emigrating into clearcuts would be more likely to immediately retreat from clearcuts but less likely to return to wetlands to breed in successive years than those emigrating into forested habitat.

METHODS

Study site and experimental arrays

We selected 4 forested sites on the SRS for study (see also Rothermel and Luhring 2005; Todd and Rothermel 2006). These sites were second-growth, managed-pine forests of loblolly pine (*Pinus taeda*) with a few interspersed hardwoods (oaks [*Quercus* spp.], red maple [*Acer rubrum*], hickories [*Carya* spp.], dogwood [*Cornus florida*], and sweetgum [*Liquidambar styraciflua*]). Where present, understory consisted of sweetgum (*Liquidambar styraciflua*), wax

myrtle (*Morella cerifera*), and holly (*Ilex opaca*), with ground cover dominated by Carolina

jessamine (*Gelsemium sempervirens*) and grasses.

We centered each of the 4 circular experimental sites on isolated, seasonal wetlands that

hold water during winter and early spring. The circular sites extended outward from the wetland

boundaries for 168 m. We divided each circular site into 4, 4-ha quadrants delineated by 2

perpendicular transects that intersected at the center of the wetland (Fig. 1). Each quadrant was

assigned randomly to 1 of 4 treatments: (1) unharvested control (> 30 years old); (2) partially

thinned stand in which the canopy was thinned to approximately 85% of that in the control

(thinned forest); (3) clearcut with coarse woody debris retained (CC-retained); and (4) clearcut

with coarse woody debris removed (CC-removed). The 2 forested plots were opposite each other

(Fig. 5.1). The isolated wetlands in the interior of the experimental arrays were unharvested.

Logging started in February 2004 and was completed at the sites in April 2004. We did not

perform any additional site preparation such as replanting, harrowing, burning, or the application

of herbicides.

Data collection

We installed a 45 m section of drift fence along the wetland edge in each quadrant. Drift

fences were located centrally in the base of each pie-shaped wedge and stopped approximately

10m from quadrant edges on both sides (Fig. 5.1). We constructed the drift fences of aluminum

flashing buried 15 cm into the ground and standing 45 cm tall. We placed twelve 19-L pitfall

traps (28 cm in diameter and 35 cm high) paired on opposite sides of each section of drift fence

evenly spaced along the 45 m of drift fence. Pitfall traps contained 1–3 cm of standing water and

floating sponges in the bottom. We checked the drift fences daily from1 February 2004 to 31

July 2007 and recorded all amphibian captures. We marked animals only upon their first capture

emigrating from wetlands into terrestrial quadrants and we marked them to identify the year of their marking and the quadrant into which they were emigrating. All marked amphibians had one front toe clipped and one hind toe clipped. We did not clip inside front toes of anurans because they are used during reproduction. All animals were released on the opposite side of the drift fence where captured to continue their migrations after being identified and marked (if applicable). Although we captured many amphibian species, we only marked the following species which we examined in our analyses (migration periods are noted parenthetically), *Ambystoma opacum* (September to May), *A. talpoideum* (November to June), *Bufo terrestris* (February to July), *Pseudacris ornata* (November to April), *Rana catesbeiana* (February to July), *R. clamitans* (February to July), *R. sphenocephala* (February to July), and *Scaphiopus holbrookii* (February to July). Too few of each ranid species were captured so we analyzed ranids collectively as a genus. Because of the date at which logging was completed, only 3 years of migratory seasons were collected for *A. opacum, A. talpoideum*, and *P. ornata*, whereas all other species were sampled for 4 years.

Statistical analyses

We used repeated measures multivariate analyses of variance (MANOVA) to test whether the number of animals captured at drift fences was affected by treatment for each species. We used the total number of individuals captured from each quadrant in each migration season as a repeated measure in our MANOVA and we used treatment as our independent factor and experimental array as a blocking factor. We performed a separate MANOVA for each species and each migration direction (immigration or emigration). We only included adult animals in our analyses and we used total counts from each season irrespective of sex. In further analyses, we combined counts from the two clearcut treatments and from the two forested

treatments (control and partial thinning) and used MANOVA to test for differences in the number of animals migrating through forested quadrants versus quadrants that had been clearcut. We grouped salamanders together and frogs together and again performed the analyses described above to test for an effect of treatment (or forested habitat versus clearcut habitat) on the number of animals captured at drift fences separately in both salamanders and frogs. Lastly, we used MANOVA to test whether the proportion of amphibians migrating through the forest control (or the combined forest control and partially thinned treatments) was greater in salamanders than in frogs. We performed a separate MANOVA for each migration direction and we used taxonomic group (salamander or frog) as our independent factor with the proportion of animals captured at drift fences in the forest control (or combined forest control and partially thinned treatment) in migration seasons 2, 3, and 4 as repeated measures. We again used experimental array as a blocking factor.

We used MANOVA to test whether the proportion of animals emigrating into forest controls was greater than the proportion that had immigrated from forest controls for each species except ranids; no ranids were captured at one experimental array in one year eliminating the ability to calculate a proportion. We used migration direction as our independent factor, migration seasons as repeated measures, and experimental arrays as blocking factors. In additional analyses, we compared the proportion of animals emigrating into the two forested treatments (control and partial thinning) with the proportion that had emigrated from them and we also examined movements by taxonomic group (salamander or frog).

Using data from marked animals, we calculated the proportion of amphibians returning from a quadrant that they had emigrated into that season to determine whether they were more likely to retreat from the two clearcut quadrants than the two forested quadrants (control and

partial thinning). We calculated proportions across all migration seasons for each species excluding ranids, for frogs as a group, and for salamanders as a group and we performed analyses of variance (ANOVA) with experimental arrays as blocking factors; we did not use data from each season as repeated measures because too few animals were recaptured in each year. We also used data from marked animals to determine whether animals marked emigrating into forested quadrants (control and partial thinning) were more likely to return to the wetland to breed in any successive years than were animals marked emigrating into the two clearcut quadrants. We calculated proportions returning in successive years across all migration seasons for each species excluding ranids, for frogs as a group, and for salamanders as a group and we again performed analyses of variance (ANOVA) with experimental arrays as blocking factors. We square root transformed count data and arcsine-square root transformed proportions for all analyses.

RESULTS

The number of amphibians migrating in and out of the wetlands through the four quadrants typically varied depending on species, year, and wetland replicate. In several cases, the number of amphibians migrating through the four quadrants was also significantly affected by the harvest treatments and whether a quadrant had been clearcut or remained partially forested (Fig. 2; Table 1). Generally there was no consistent difference in the number of amphibians immigrating through the quadrants when comparing all 4 treatments or when comparing both clearcuts with the 2 forested quadrants (control and partial thinning). Nevertheless, significant time-by-treatment interactions in *B. terrestris* and *P. oranata* revealed a tendency for those animals to immigrate through forested habitat later in the study; a significant time-by-treatment interaction in ranids revealed considerable variation in immigration preference throughout the

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study (Fig. 5.2; Table 5.1). *Ambystoma opacum*, *A. talpoideum*, salamanders as a group, and *S. holbrookii* were more likely to emigrate through forest controls or the forested and partially thinned quadrants rather than the clearcut quadrants (Fig. 5.2; Table 5.1). In contrast, significantly fewer *P. ornata* emigrated through forest controls than the other treatments (Fig. 5.2; Table 5.1). Time-by-treatment interactions for several groups revealed some variation in their emigration responses to the upland harvesting. In many cases, the clearcuts in which no CWD was retained often had the fewest amphibians migrating through them (Fig. 5.2; *A. opacum*, *A. talpoideum*, *S. holbrookii*). The partially harvested quadrants were second only to the unharvested controls in the number of amphibians moving through them for *A. opacum* and *A. talpoideum* and were otherwise not consistently second (Fig. 5.2). Individual between-subject contrasts were not available in MANOVA.

Overall, the proportion of amphibians immigrating through forest controls or both forested habitats combined was greater in salamanders than in frogs (Fig. 5.3; control only: $F_{1,3}=12.47$, P=0.04; combined forest and partially thinned: $F_{1,3}=10.45$, P=0.05). Likewise, the proportion of amphibians emigrating through forest controls or both forested habitats combined was significantly greater in salamanders than in frogs (Fig. 5.3; control only: $F_{1,3}=7.52$, P=0.07; combined forest and partially thinned: $F_{1,3}=56.8$, P<0.001). Time-by-treatment interactions were only significant or marginally significant for immigrating amphibians combined in both forest habitats ($F_{2,6}=4.46$, P=0.07) and emigrating amphibians combined in both forest habitats ($F_{2,6}=6.86$, P=0.03), apparently because the proportion of frogs migrating through forested habitat increased dramatically between the first and second year (Fig. 5.3).

The proportion of amphibians that emigrated away from wetlands through forest controls rather than the harvested treatments was marginally greater than the proportion that immigrated

into wetlands through the forest controls each season for *A. talpoideum* and for salamanders as a group (Table 5.2). Further, the proportion of amphibians that emigrated through the 2 forested quadrants (control and partial thinning) rather than the 2 clearcut quadrants was significantly greater than the proportion that immigrated through the 2 forested quadrants each season for *A. talpoideum*, salamanders as a group, *B. terrestris*, and frogs as a group (Table 5.2).

There was a trend for salamanders as a group, frogs as a group, and *B. terrestris* to be more likely to retreat from a clearcut after emigrating into it than the forested quadrants, although the trend was not significant at the $\alpha = 0.05$ level (Table 5.3). There was no significant difference in the proportion of amphibians returning to the wetland in successive years that had been marked and released emigrating into the 2 forested quadrants compared with the 2 clearcut quadrants at each experimental array for any species or group (Table 5.3). Very few animals ever immigrated in successive years through quadrants which they had not emigrated through so statistical tests on likelihood of animals to switch were not performed.

DISCUSSION

Our results demonstrate the diversity of amphibian responses to forest harvesting and also the degree to which forest harvesting can affect the connectivity of both terrestrial-aquatic habitats and local populations. For example, we found that the number of amphibians immigrating to wetlands in our study was not consistently affected by upland forest harvesting but that a few species, and salamanders in particular, had greater numbers emigrating through forested habitats or unharvested controls rather than clearcuts. Salamanders typically have lower tolerances to water loss (Thorson and Svihla 1953) and greater surface area to volume ratios than frogs. Consequently, frogs often move lengthier individual distances and have larger terrestrial core activity zones than salamanders as a result (Rittenhouse and Semlitsch 2007; Graeter et al.

2008). This variation in movement ability between frogs and salamanders is one possible reason why salamanders were more sensitive to the clearcut treatments and were more likely to migrate through forested habitats than were frogs in our study. Also, frogs typically live at much greater distances from wetlands than do salamanders (Rittenhouse and Semlitsch 2007). Thus, frogs may have immigrated to our central wetlands from beyond our experimental arrays without necessarily having had to survive in adjacent clearcuts during the non-breeding season.

Despite the fact that salamanders were more sensitive than frogs to upland forest harvesting, greater proportions of both salamanders and frogs were captured emigrating through unharvested controls and forested habitats than had immigrated through them. This pattern could indicate that although amphibians may immigrate to wetlands from within, or beyond, clearcuts, they prefer migrating through forested habitat when given a choice. Other studies have demonstrated that amphibians do typically prefer to migrate through forested habitat when it is available and that adults will avoid clearcuts and open grasslands (Chan-McLeod 2003; Rittenhouse and Semlitsch 2006). Also, the 4-ha clearcuts in our study were at the small end of clearcuts used in most Coastal Plain forestry (2 – 30 ha; Krementz and Christie 2000) and may have been easily traversed in one night. If our clearcuts had been larger, it likely would have taken longer for salamanders and frogs to traverse them with correspondingly greater reductions in the number of amphibians successfully immigrating through them. We also present evidence that salamanders, frogs, and *B. terrestris* emigrating into clearcuts were more likely to retreat to the wetland shortly after release compared with those emigrating into forested habitat, providing an additional indication that they avoided migrating through clearcuts.

An alternative explanation for the greater proportion of amphibians emigrating through forest habitat than immigrating is that survival of clearcut-immigrating amphibians may have

been lower in the wetlands than was survival of forest-immigrating amphibians. In other words, more animals that immigrated through clearcuts may have died at the wetland and therefore have been unable to return to the terrestrial environment. We sought to determine whether survival of animals was affected by migration routes using marked animals but we found no evidence that animals marked emigrating through clearcuts were less likely to survive and return to the wetland in successive years. However, we caution that this does not necessarily mean that animals were unaffected after moving through clearcuts. In fact, forest-dependent spotted salamanders (*A. maculatum*) have been shown to exhibit elevated stress when migrating through open habitats (Homan et al. 2003), a physiological response that may affect survival. Clearcut-immigrating amphibians may also have been in poorer condition because they lived in clearcut habitats during the non-breeding season, a factor that may have diminished their survival further when breeding at the wetland.

Our finding that the number of salamanders immigrating to wetlands was unaffected by upland forest harvesting was unexpected. Pond-breeding amphibians, and salamanders in particular, generally migrate linearly between their terrestrial homes and reproductive wetlands, follow routes perpendicular to the wetland shore, and are often philopatric to one wetland (Semlitsch 2008). Further, it is estimated that 95% of ambystomatid salamanders abide in upland terrestrial habitat within 165 m of wetlands (Semlitsch 1998), a distance that we intentionally encompassed in our experimental arrays. Young clearcuts are known to reduce survival of some amphibians (Todd and Rothermel 2006) and can lead to rapid water loss and mortality of ambystomatids (Rothermel and Luhring 2005; Todd et al. 2008). We therefore expected that post-logging mortality of ambystomatid salamanders would increase in clearcuts and would result in fewer captures of immigrating animals at clearcut drift fences compared with forest

controls. We believe that a closer look at the immigration patterns of *A. opacum* does reveal their

tendency to immigrate through forest habitats compared with clearcuts, a result that likely would

have been significant had *A. opacum* been present at all 4 wetlands instead of just 2. In contrast,

immigration in *A. talpoideum* was not consistently greater in forest habitat. Interestingly, *A*

talpoideum is known to be a better burrower than *A. opacum* (Semiltsch 1983). One study

demonstrated that young clearcuts did not reduce survival of *A. talpoideum*, albeit during the fall

and winter months (Chazal and Niewiarowski 1998), possibly explaining the difference in the

observed responses between the species. Of all the amphibian species studied, salamanders were

the only species with the consistently fewest number of animals migrating through clearcuts with

no CWD, suggesting that CWD may play some role in mitigating clearcutting impacts to the

landscape. Semlitsch et al. (2008) found reduced evacuation of salamanders from clearcut sites

with high CWD. Partially harvested quadrants frequently had more salamanders emigrating

through them than did either clearcut quadrant, indicating that partial harvesting may have less

impact on salamander populations and movement than does clearcutting.

When forest area is cleared, either for land development or for timber harvest as part of a

management program, the resulting landscapes can be inhospitable for amphibians. Loss of

forest canopy increases both air and soil temperatures and reduces ground litter (Todd and

Andrews in press), factors important to desiccation-prone animals that dwell on the forest floor

(deMaynadier and Hunter 1995). Consequently, such changes may reduce survival (Todd and

Rothermel 2006), promote evacuation (Semlitsch et al. 2008), or lead to behavioral avoidance of

cleared habitats by some amphibians (e.g., Chan-McLeod 2003). When clearcuts alter amphibian

migrations as indicated in our study, they can disrupt terrestrial-aquatic habitat continuity and

reduce the connectivity of pond-encircling populations. Such mechanisms likely underlie the

observed changes in community composition and gene flow that result from decreasing forest cover (Richter-Boix et al. 2007; Werner et al. 2007; Zellmer et al. 2007). Disruption of habitat continuity and population connectivity because of forest loss is also implicated in large-scale declines in species richness and abundance, particularly among biphasic amphibians (Gibbs 1998; Herrmann et al. 2005; Becker et al. 2007), and may especially affect those amphibians that rely on metapopulation dynamics to persist. Nevertheless, our study demonstrates that there is interspecific variation in the degree to which amphibians respond to forest loss, with less mobile or more sensitive species like salamanders being more greatly affected by forest clearing than others. Variation in responses may also be driven by climatic, regional, or physiographic differences that are beyond the scope of our study.

ACKNOWLEDGMENTS

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Table 5.1 Results of MANOVA testing effects of upland harvesting on the number of amphibians migrating through quadrants. "All treatments" includes tests among all 4 harvesting treatments and "Forested/Clearcut" represents comparisons between counts from combined clearcut treatments and combined controls and partially harvested treatments. "n,d" represents the numerator and denominator degrees of freedom respectively.

| | Immigrating | | | | | | Emigrating | | | | | |
| | All treatments | | | Forested/Clearcut | | | All treatments | | | Forested/Clearcut | | |
Group or Species	n,d	F	P	n,d	F	P	n,d	F	P	n,d	F	P
Salamanders												
treatment	3,9	0.92	0.47	1,3	4.78	0.12	3,9	**7.89**	**<0.01**	1,3	**56.2**	**<0.01**
time x treatment	6,18	0.81	0.58	2,6	3.42	0.10	6,18	1.21	0.34	2,6	2.5	0.16
Ambystoma opacum												
treatment	3,3	1.4	0.39	1,1	1.78	0.41	3,3	2.31	0.25	1,1	**97.5**	**0.06**
time x treatment	6,6	1.07	0.47	2,2	1.25	0.44	6,6	1.5	0.31	2,2	2.28	0.31
Ambystoma talpoideum												
treatment	3,9	0.51	0.69	1,3	4.93	0.11	3,9	**7.68**	**<0.01**	1,3	**22.9**	**0.02**
time x treatment	6,18	0.88	0.53	2,6	1.54	0.29	6,18	0.75	0.62	2,6	0.89	0.46
Frogs												
treatment	3,9	0.41	0.75	1,3	1.19	0.35	3,9	0.71	0.57	1,3	2.81	0.19
time x treatment	9,27	1.13	0.37	3,9	**3.56**	**0.06**	9,27	**2.37**	**0.04**	3,9	**20.6**	**<0.001**
Bufo terrestris												
treatment	3,9	1.94	0.19	1,3	2.46	0.22	3,9	0.14	0.93	1,3	0.31	0.61
time x treatment	9,27	**4.59**	**<0.001**	3,9	**31**	**<0.001**	9,27	**2.6**	**0.03**	3,9	**6.3**	**0.01**
Pseudacris ornata												
treatment	3,6	2.43	0.16	1,2	3.02	0.22	3,6	**4.04**	**0.07**	1,2	0.66	0.5
time x treatment	6,12	1.88	0.17	2,4	**12.7**	**0.02**	6,12	0.34	0.91	2,4	0.79	0.51
Rana spp.												
treatment	3,9	0.71	0.57	1,3	0.7	0.46	3,9	1.94	0.19	1,3	1.01	0.39
time x treatment	9,27	**2.66**	**0.02**	3,9	1.07	0.41	9,27	0.39	0.93	3,9	0.26	0.85
Scaphiopus holbrookii												
treatment	3,9	0.25	0.86	1,3	0.03	0.88	3,9	1.3	0.33	1,3	**19.4**	**0.02**
time x treatment	9,27	0.89	0.55	3,9	0.67	0.59	9,27	1.53	0.19	3,9	**5.66**	**0.02**

Table 5.2 Results of MANOVA testing whether greater proportions of amphibians emigrated through forest controls or both forested habitats than the proportion immigrating through them. "Both forested habitats" represents comparisons of proportions in which forest controls and partially thinned quadrants were combined. "n,d" represents the numerator and denominator degrees of freedom respectively.

Group or Species	Forest control			Both forested habitats		
	n,d	F	P	n,d	F	P
Salamanders						
treatment	1,3	**7.16**	**0.07**	1,3	**13.6**	**0.03**
time x treatment	3,9	0.06	0.95	2,6	0.78	0.50
Ambystoma opacum						
treatment	1,1	5.65	0.25	1,1	0.66	0.57
time x treatment	2,2	**116**	**0.01**	2,2	0.54	0.65
Ambystoma talpoideum						
treatment	1,3	**9.2**	**0.06**	1,3	**52.4**	**<0.01**
time x treatment	3,9	0.1	0.9	2,6	1.13	0.38
Frogs						
treatment	1,3	0.28	0.63	1,3	**23.1**	**0.02**
time x treatment	3,9	0.27	0.85	3,9	**3.31**	**0.07**
Bufo terrestris						
treatment	1,3	1.38	0.33	1,3	**62.3**	**<0.01**
time x treatment	3,9	1.89	0.2	3,9	**5.33**	**0.02**
Pseudacris ornata						
treatment	1,2	2.99	0.23	1,2	0.02	0.91
time x treatment	2,4	3.35	0.14	2,4	1.08	0.42
Scaphiopus holbrookii						
treatment	1,3	0.13	0.75	1,3	3.56	0.16
time x treatment	3,9	0.05	0.98	3,9	0.7	0.58

Table 5.3 Results of ANOVA comparing the proportion of amphibians retreating from clearcuts with the proportion retreating from combined forested habitats or the proportion of amphibians returning in successive years after emigrating through clearcuts or combined forested habitats. "n,d" represents the numerator and denominator degrees of freedom respectively.

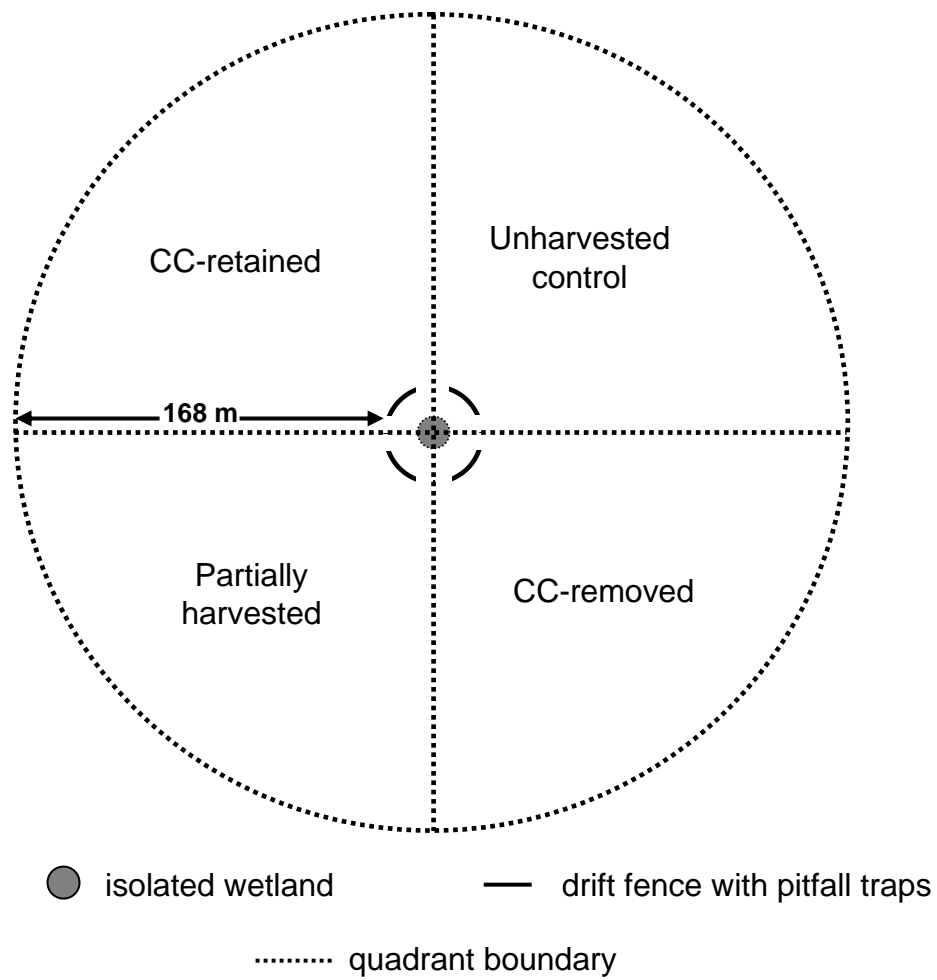| Group or Species	Retreating from clearcuts			Returning in successive years		
	n,d	F	P	n,d	F	P
Salamanders	1,3	**5.62**	**0.09**	1,3	4.26	0.13
Ambystoma opacum	1,1	8.37	0.21	1,1	1.13	0.48
Ambystoma talpoideum	1,3	4.93	0.11	1,3	1.69	0.29
Frogs	1,3	**8.9**	**0.06**	1,3	0.22	0.67
Bufo terrestris	1,3	**6.24**	**0.09**	1,3	0.0	0.95
Pseudacris ornata	1,3	0.0	0.98	1,3	2.98	0.18
Scaphiopus holbrookii	1,3	0.04	0.85	1,3	0.0	0.97

Figure 5.1 Diagram of 1 of 4 replicate experimental arrays showing arrangement of harvesting treatments and drift fences. Note that figure is not necessarily to scale.
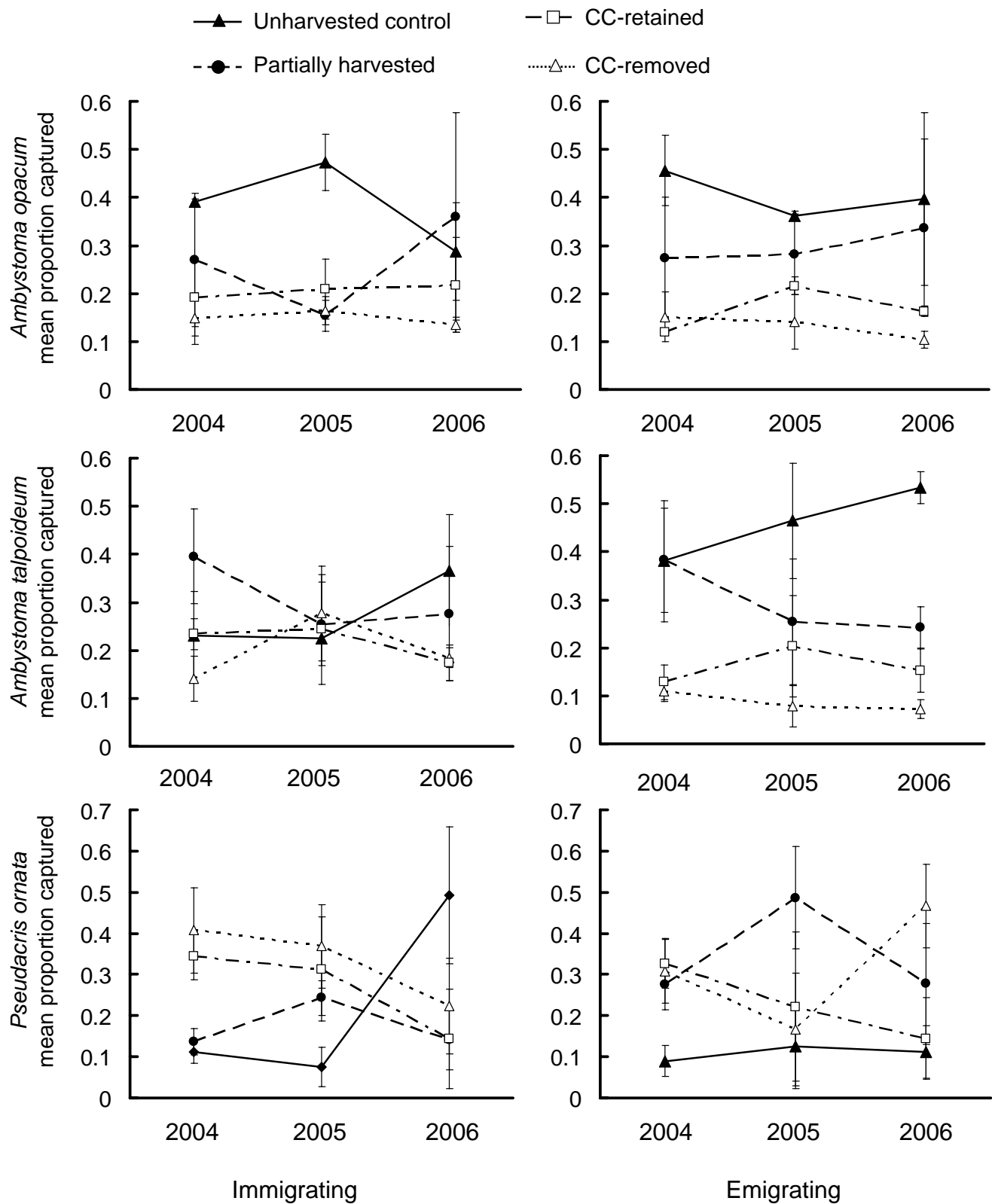
Figure 5.2 The mean (SE) proportion of amphibians captured migrating through forest quadrants during breeding seasons each year. Note that scales of y-axes differ for some figures.

Figure 5.2 (continued) The mean (SE) proportion of amphibians captured migrating through forest quadrants during breeding seasons each year. Note that scales of y-axes differ for some figures.
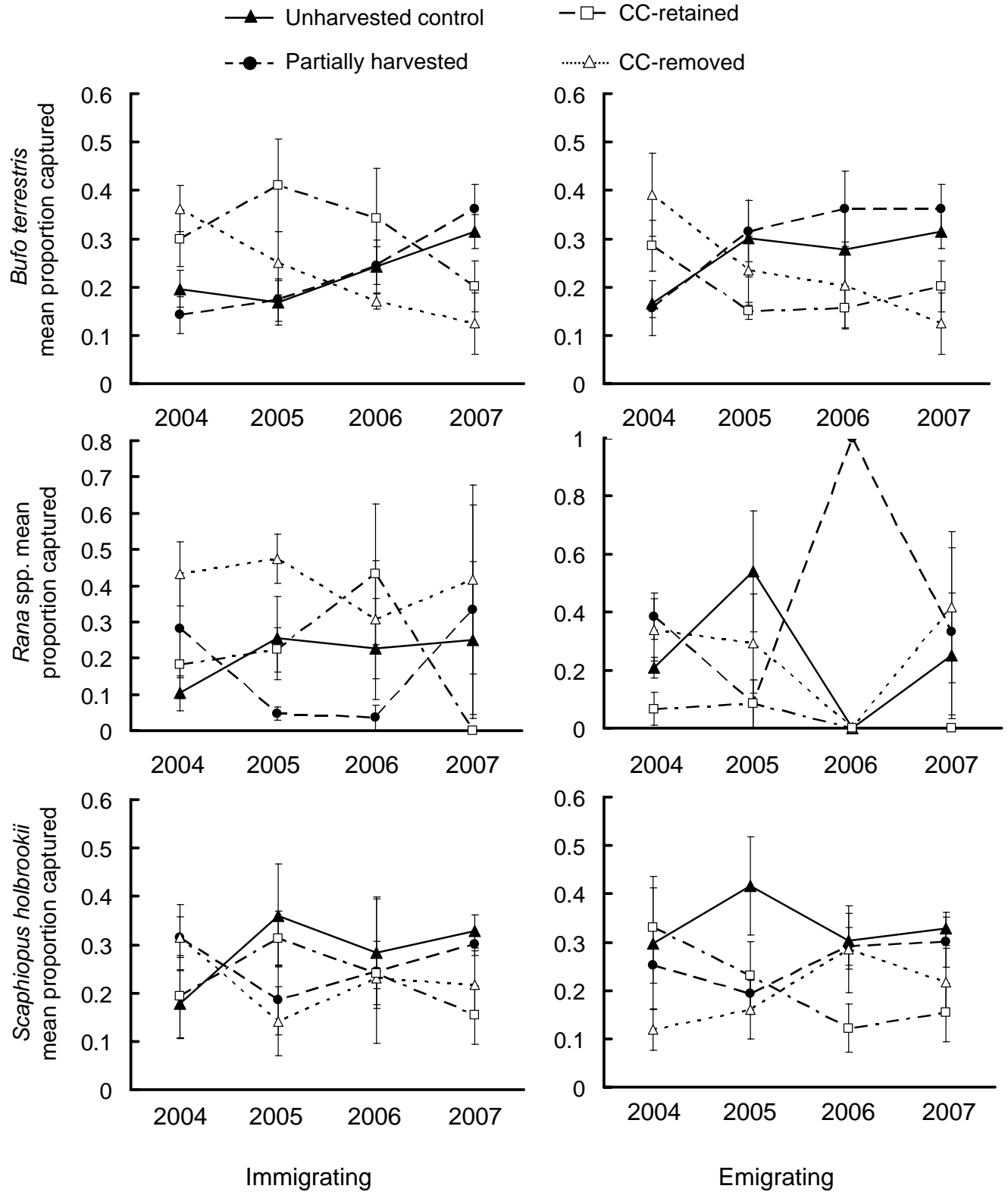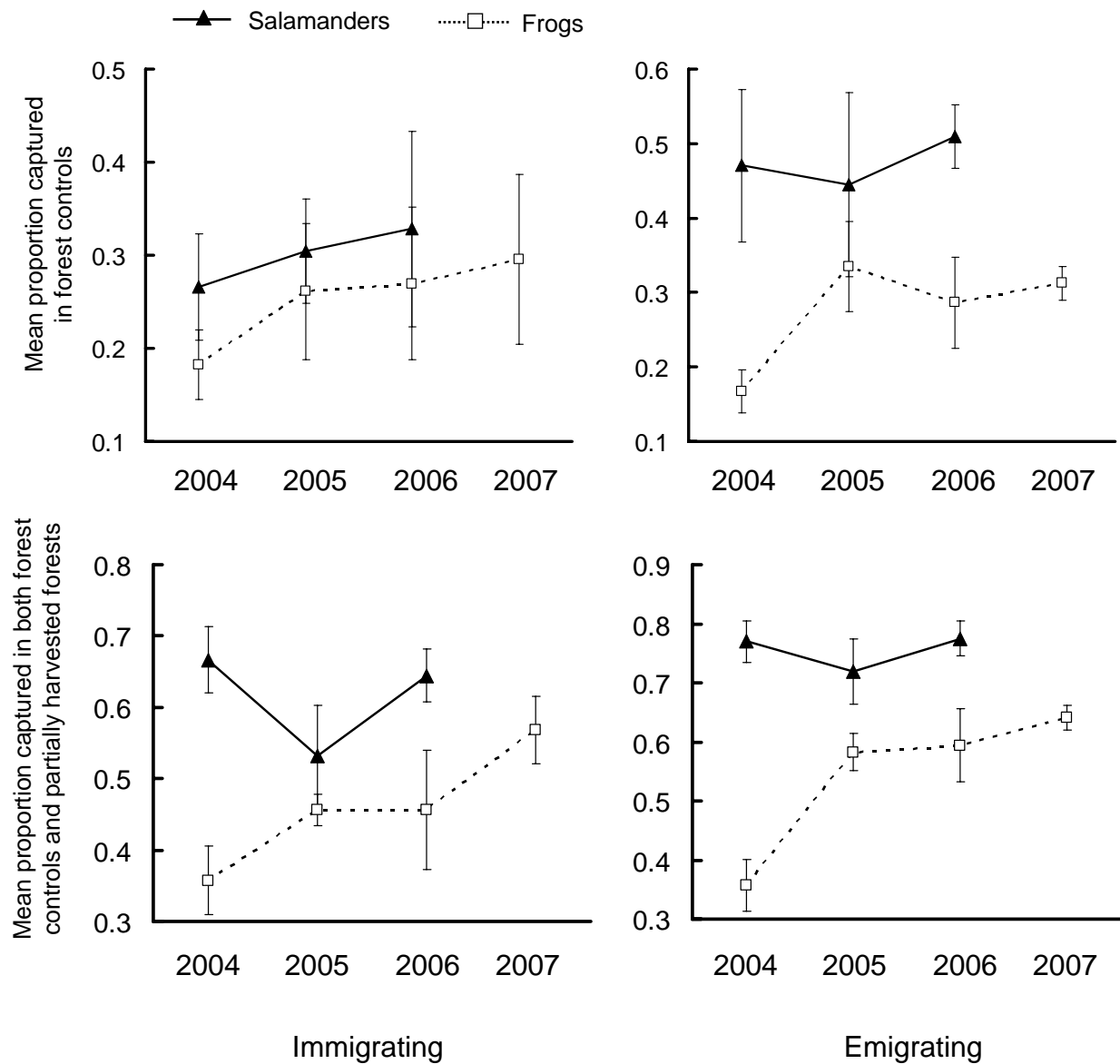
Figure 5.3 The mean proportion of salamanders or frogs (SE) captured migrating through forest controls or combined forest controls and partially harvested treatments during breeding seasons each year. Note that scales of y-axes differ for some figures.

CHAPTER 6

CONCLUSION

I had two major goals with my dissertation research. My first goal was to examine the effects of forest clearing on a seldom-studied group of reptiles to diversify our understanding of forestry impacts on reptiles. My second goal was to investigate possible mechanisms that contribute to patterns of amphibian declines that are reported after forests are clearcut. Although I conducted my studies in the context of forest management, the types of landscapes that we created are broadly representative of many forms of land-use. Forests are not cleared solely for timber extraction and logging operations. Forests are also clearcut for residential development, for conversion to agriculture, livestock operations, or for recreation (e.g., golf courses), and also to develop roadways or powerline rights-of-way. Thus, my studies may provide insight into the consequences that result from these forms of land-use as well. Moreover, because we did not perform any additional site preparation after the forests were harvested, it is likely that my results are a conservative estimate of the possible range of effects that result from forest clearing. For example, we did not use herbicides, roller-chopping, landscaping, ground-leveling, or industrial replanting of pine species, factors that are common in forestry and may also pertain to residential and recreational land development.

In chapter 2, I examined the effects of forest harvesting on the relative abundance of small snakes. Generally, the relative abundance of small snakes was lowest in clearcuts in which coarse woody debris (CWD) was removed, greater in clearcuts in which CWD was retained, intermediate in unharvested control forests, and greatest in partially thinned forests. These results

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indicate that not all reptiles respond positively to clearcutting but they do suggest that some degree of canopy reduction is beneficial to ectothermic reptiles so long as adequate floor structure and refugia are retained. These results also highlight the possible role of CWD in mitigating negative effects of forest clearcutting on these animals.

In chapter 3, I found that juvenile southern toads (*Bufo terrestris*), a presumably conservative metric, respond negatively to clearcuts. They had significantly reduced growth and survival in forest clearcuts compared with unharvested forest controls. Further, the abundance of juvenile southern toads did not differ significantly between clearcuts and forest controls, suggesting that the use of abundance as a metric of habitat suitability may be misleading and inappropriate compared with more specific information on effects on vital rates.

In chapter 4, I tested the effects of our four forest treatments on the survival of juvenile and adult marbled salamanders (*Ambystoma opacum*), a forest-associated salamander that is presumably more sensitive to forest loss than southern toads. In fact, I found that treatment significantly affected survival of both juvenile and adult marbled salamanders. Survival was highest in unharvested forest controls for both age classes. For adults, survival was not diminished by partial harvesting but mortality of juveniles in partially harvested forests was nearly absolute. For both age classes, mortality in clearcuts was nearly absolute except for juveniles, for which clearcuts with CWD had some animals survive to the end of the study.

In chapter 5, I examined the effects of forest harvesting on the migrations of adult amphibians in and out of wetlands centered in the middle of the experimentally harvested landscape. I found limited evidence of a treatment effect on the number of animals immigrating to wetlands through the upland habitats except in the open-canopy-breeding *Bufo terrestris* and *Rana* spp. which were captured in significantly greater numbers immigrating to wetlands through

clearcuts. However, I did identify a trend, albeit non-significant, for *Ambystoma opacum* to immigrate to wetlands through unharvested forest. I captured significantly greater numbers of salamanders (*A. opacum* and *A. talpoideum*) emigrating out of wetlands through unharvested or partially thinned forests than through clearcuts. Comparing salamanders with frogs, I found that a significantly greater proportion of salamanders used forested habitat for migrations rather than clearcuts. These results reflect the important differences that exist in the ecology and vagility of amphibian species. Further, they suggest that landscape-level effects of forest clearing, such as reductions in gene flow or local and metapopulation persistence, may be greater for pond-breeding salamanders than for pond-breeding frogs in the Coastal Plain region.