Response of a Reptile Guild to Forest Harvesting

BRIAN D. TODD* AND KIMBERLY M. ANDREWS

Savannah River Ecology Laboratory, University of Georgia, Drawer E, Aiken, SC 29802, U.S.A.

Abstract: *Despite the growing concern over reptile population declines, the effects of modern industrial silviculture on reptiles have been understudied, particularly for diminutive and often overlooked species such as small-bodied snakes. We created 4 replicated forest-management landscapes to determine the response of small snakes to forest harvesting in the Coastal Plain of the southeastern United States. We divided the replicated landscapes into 4 treatments that represented a range of disturbed habitats: clearcut with coarse woody debris removed; clearcut with coarse woody debris retained; thinned pine stand; and control (unharvested second-growth planted pines). Canopy cover and ground litter were significantly reduced in clearcuts, intermediate in thinned forests, and highest in unharvested controls. Bare soil, maximum air temperatures, and understory vegetation all increased with increasing habitat disturbance. Concomitantly, we observed significantly reduced relative abundance of all 6 study species (scarletsnake [*Cemophora coccinea*], ring-neck snake [*Diadophis punctatus*], scarlet kingsnake [*Lampropeltis triangulum*], red-bellied snake [*Storeria occipitomaculata*], southeastern crowned snake [*Tantilla coronata*], and smooth earthsnake [*Virginia valeriae*]) in clearcuts compared with unharvested or thinned pine stands. In contrast, the greatest relative snake abundance occurred in thinned forest stands. Our results demonstrate that at least one form of forest harvesting is compatible with maintaining snake populations. Our results also highlight the importance of open-canopy structure and ground litter to small snakes in southeastern forests and the negative consequences of forest clearcutting for small snakes.*

Keywords: clearcutting, forest management, forest thinning, logging, logging effects, reptile, snake, *Tantilla coronata*, *Virginia valeriae*

Respuesta de un Gremio de Reptiles a la Cosecha de Bosques

Resumen: *No obstante el incremento de la preocupación sobre las declinaciones de poblaciones de reptiles, los efectos de la silvicultura moderna sobre los reptiles han sido poco estudiados, particularmente sobre especies diminutas y a menudo ignoradas como las serpientes pequeñas. Creamos 4 paisajes de gestión forestal replicados para determinar la respuesta de serpientes pequeñas a la cosecha de bosques en la Llanura Costera del sureste de Estados Unidos. Dividimos los paisajes replicados en 4 tratamientos que representaron un rango de hábitats perturbados: corte de clareo con la remoción de residuos leñosos, corte de clareo con retención de residuos leñosos, bosque de pinos con tala de reducción y control (pinos no cosechados). La cobertura del dosel y la hojarasca fueron significativamente bajos en los sitios clareados, intermedios en los bosques reducidos y mayores en los controles no cosechados. El suelo desnudo, la temperatura máxima del aire y la vegetación del sotobosque incrementaron con el incremento de la perturbación del hábitat. Concomitantemente, observamos una reducción significativa de la abundancia de las 6 especies estudiadas (*Cemophora coccinea, Diadophis punctatus, Lampropeltis triangulum, Storeria occipitomaculata, Tantilla coronata *y* Virginia valeriae*) en los sitios clareados en comparación con los sitios no cosechados. En contraste, la mayor abundancia de serpientes ocurrió en los bosques con tala de reducción. Nuestros resultados demuestran que por lo menos una forma de cosecha forestal es compatible con el mantenimiento de las poblaciones de serpientes. Nuestros resultados también destacan la importancia de la estructura de dosel abierto y la hojarasca para las serpientes pequeñas en los bosque del sureste y las consecuencias negativas del corte de clareo para las serpientes pequeñas.*

*email btodd@uga.edu
Paper submitted May 12, 2007; revised manuscript accepted October 22, 2007.

Conservation Biology, Volume 22, No. 3, 753–761

DOI: 10.1111/j.1523-1739.2008.00916.x

Palabras Clave: corte de clareo, efectos de la tala, gestión forestal, reptil, serpiente, tala, tala de reducción, *Tantilla coronata*, *Virginia valeriae*

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 & 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). Subsequently, many floral and faunal species associated with longleaf pine ecosystems have declined, leading to the designation of several species as endangered (Means & 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). In addition, 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 (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 & 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 & 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 & Hunter 1995; Todd & Rothermel 2006). Few 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. Some researchers have proposed that forest clearcutting may benefit reptiles by creating early-successional habitats (e.g., Campbell & 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 very abundant (Fitch 1975; Willson & 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 because of 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 relative abundances of small snakes would be greater in thinned canopy stands than in unharvested controls for 2 reasons. First, the most common species of small snake 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 small-snake abundance.

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 & 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 (*P. elliottii*) and loblolly (*P. taeda*) pine (Kilgo & Blake 2005). By 2001 nearly all the SRS was forested and 72% of the forest stands were more than 30 years old (Kilgo & 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 & Luhring 2005; Todd & Rothermel 2006). These sites were second-growth, managed-pine forests of loblolly pine. 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 four 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. 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.

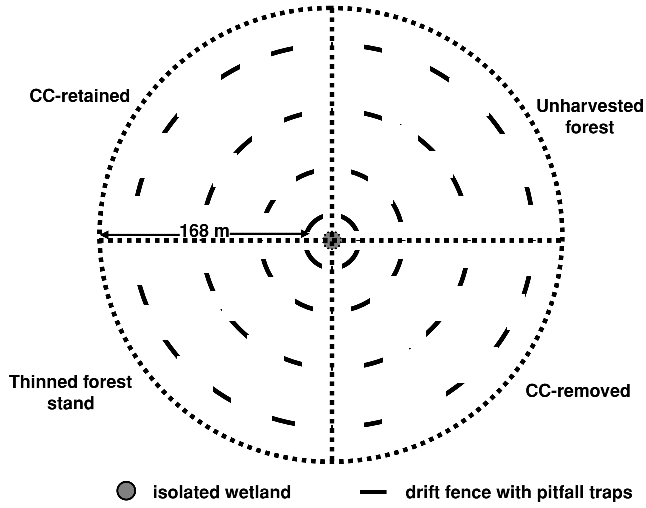

Figure 1. Diagram of 1 of 4 replicated sites showing the spatial arrangement of 4 randomly assigned forest management treatments and drift fences used to capture snakes in each quadrant (CC-retained, clearcut with coarse woody debris retained; CC-removed, clearcut with coarse woody debris removed). Figure is not to scale.

In April 2004 we installed nine 15-m sections and one 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 nine 15-m sections were located in the surrounding xeric uplands 50, 100, and 150 m from the wetland (Fig. 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 twelve 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 & 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. In addition, sampling effort was concentrated during periods of the year when small-bodied snakes are most active (April–November; Semlitsch et al. 1981; Gibbons & Semlitsch 1987), excluding August.

We recorded capture date and location of all snakes. We measured snout-to-vent length (SVL) and tail length to the nearest millimeter 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 snake abundances. Instead we relied on replication and randomization of treatments to allow comparisons of treatment effects on snake abundance.

In July 2004 we established permanent habitat-sampling points at all nine 15-m drift fences in each quadrant. We positioned the permanent sampling points 15 m toward the wetland from each drift fence and 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, and 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 & Hazard 1978). We calculated the mean CWD volume along transects for each quadrant and mean log densities per hectare for each quadrant, and used means from each quadrant to make statistical comparisons among habitats.

Statistical Analyses

We excluded from analyses captures from the 6 pitfall traps along the inside of each 45-m drift fence closest to the wetland. We limited our analyses to only small-bodied snake species because (1) large snakes have greater home ranges and probably were 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: scarletsnakes (*Cemophora coccinea*), ring-neck snakes (*Diadophis punctatus*), scarlet kingsnakes (*Lampropeltis triangulum*), red-bellied snakes (*Storeria occipitomaculata*), southeastern crowned snakes (*T. coronata*), and smooth earthsnakes (*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 (MANOVAs) 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. Count data were normalized with square-root transformations (Zar 1998). We pooled captures of *T. coronata* across years, separated data on males from nongravid females, and used analyses of covariance (ANCOVA) to determine whether size-specific body mass was affected by treatment. We used 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. Log-transformed lengths were used as covariates and log-transformed counts of clutch size as response variables. We excluded all recaptures from statistical analyses and examined all data prior to analyses to ensure that analytical assumptions were met (Zar 1998).

We compared mean litter depth, canopy density and coverage of bare soil, litter, and understory vegetation 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. Finally, we used a canonical correlation analysis to determine which habitat characteristics most affected small-snake abundance.

We included mean litter depth; canopy density; coverage of bare soil, litter, and understory vegetation; 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, and performed all statistical analyses with SAS (version 9; SAS Institute 2000).

Results

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). 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).

Treatment significantly affected the number of *T. coronata* captured (MANOVA: $F_{3,9} = 4.18$; $p = 0.041$; Fig. 3a), and there was a marginal interaction of treatment with time for this species (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. Size-specific body mass of *T. coronata* did not vary among treatments for males (ANCOVA: $F_{3,87} = 0.61$; $p = 0.612$) or nongravid females (ANCOVA: $F_{3,48} = 1.58$; $p = 0.208$). Similarly, clutch size of gravid females did not vary among treatments (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. 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.

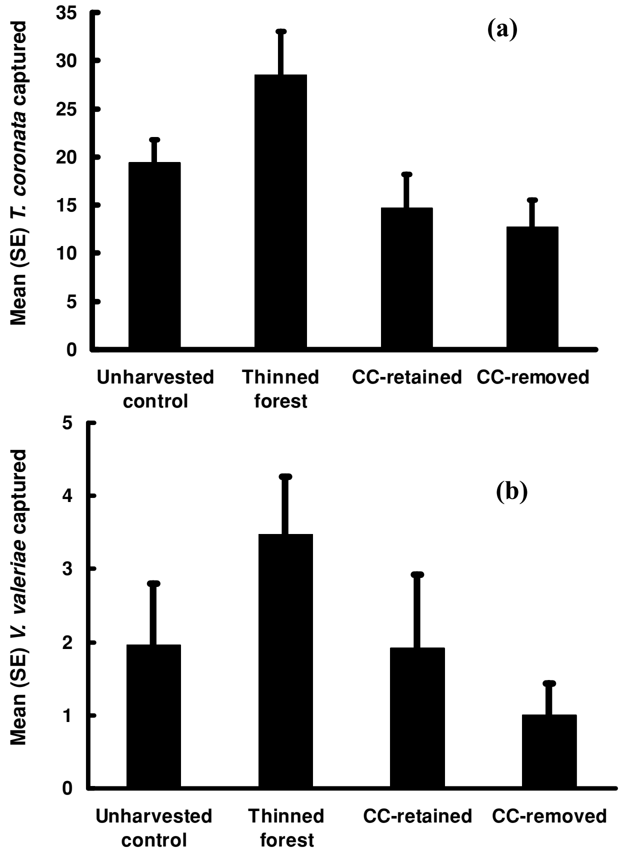

*Figure 3. Mean number of (a) southeastern crowned snakes (*Tantilla coronata*) and (b) smooth earth snakes (*Virginia valeriae*) captured from 10 May to 31 July each year in the 4 treatments: unharvested control, thinned forest, clearcut with coarse woody debris retained (CC-retained), and clearcut with coarse woody debris removed (CC-removed).*

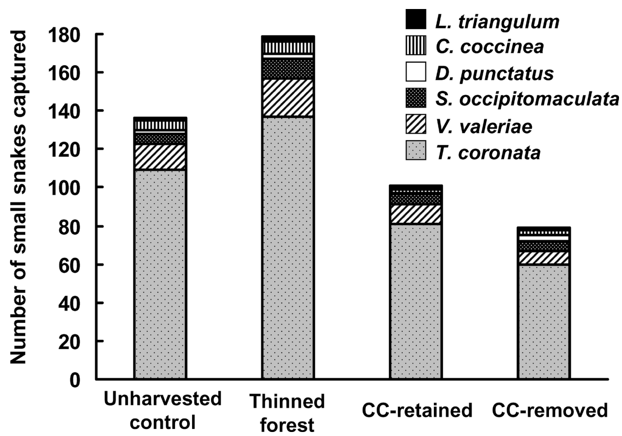

Figure 2. Total captures of the 6 species of small snakes over 3 years in the 4 treatments: unharvested control, thinned forest, clearcut with coarse woody debris retained (CC-retained), and clearcut with coarse woody debris removed (CC-removed).

Table 1. Mean (SE) habitat characteristics of the 4 treatments: unharvested control, thinned forest, clearcut with coarse woody debris retained (CC-retained), and clearcut with coarse woody debris removed (CC-removed).

Characteristic	*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)

Effects on Forest Habitat

In general, litter depth and 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 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 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 1). Understory vegetation increased significantly in clearcuts and thinned stands compared with unharvested controls ($F_{3,9} = 7.51$, $p = 0.008$; Table 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 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. 4). The trend was reversed for monthly minimum air temperatures: overnight minima were reduced in clearcuts, intermediate in thinned forests, and warmest in unharvested forests ($F_{3,9} = 74.8$, $p < 0.0001$; Fig. 4).

Correlates of Habitat and Abundance of Small Snakes

Canonical correlation analysis revealed that only 1 of the 2 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 & Christman 1982; Greenberg et al. 1994), our results revealed 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. In addition, forest clearcutting affects the understory and can change the availability and distribution of ground cover, simultaneously eliminating the

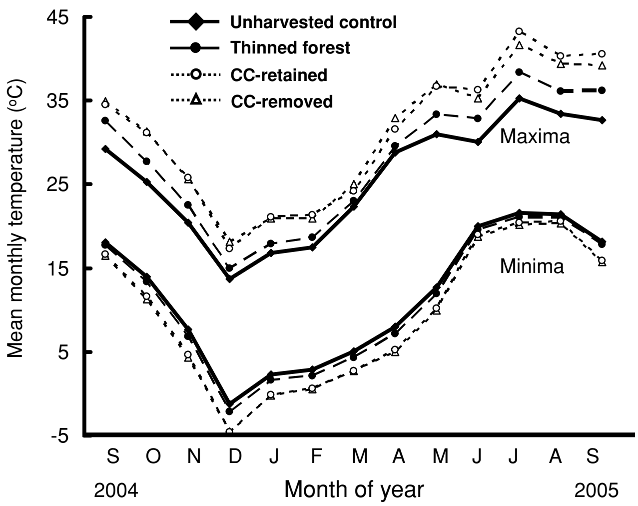

Figure 4. Monthly mean maximum and minimum near-ground air temperatures in the 4 treatments: unharvested control, thinned forest, clearcut with coarse woody debris retained (CC-retained), and clearcut with coarse woody debris removed (CC-removed).

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 & 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). Nevertheless, 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 the number of small snakes captured. This was further evidenced by the decreased abundance of small snakes in clearcuts that 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 species of small snake, *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 & 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 species of small snakes 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 the relative abundance of small snakes was greatest, the amount of forest floor covered by CWD was not a significant contributor to the abundance of small snakes 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 relative 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 species of small snakes (*Carphophis amoenus*, *D. punctatus*, and *S. occipitomaculata*) were 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. In addition, 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 & Luhring 2005). A partially thinned forest likely provides an acceptable trade-off 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 in a few key ways. 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 species of small snakes (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. In addition, 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 planted pine forests that are under different management regimes.

The difference we observed in the relative abundance of small snakes among forest treatments can occur through several mechanisms, including changes in survival and fecundity, mortality incurred during harvesting, 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 & Semlitsch 1992). Nevertheless, we found no evidence of treatment effects on body condition or clutch size in *T. coronata*. In addition, no small snakes were ever recaptured in a habitat other than that of their initial capture. Small-bodied snakes have small home ranges (approximately 250 m^2 for *C. amoenus*, Barbour et al. 1969) and movement distances are short. 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 °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 relative abundances of small snakes. 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 & Means 2000; *Heterodon simus*, Tuberville et al. 2000; *L. 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 affect 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. In addition, the effects of clearcutting on snakes may be greater in practice than demonstrated in our study because of 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 & 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.

Acknowledgments

We thank R. D. Semlitsch and L. Smith for reviewing earlier versions of the manuscript. We thank G. Graeter, A. Green, J. Greene, C. Jennison, M. Langley, T. Luhring, B. Metts, B. Morris, J. Nestor, J. Norman, B. Rothermel, S. Rothermel, L. Wilkinson, J. Willson, C. Winne, and U.S. Forest Service–Savannah River for assisting the study. Animals were collected under South Carolina Department of Natural Resources Scientific Collection permits (07-2004, G-05-03, G-06-04) and all procedures were conducted in accordance with The University of Georgia's animal care and use guidelines. This research was conducted as part of the Land-use Effects on Amphibian Populations (LEAP) study funded by the National Science Foundation (Award DEB- 0242874). Additional support and manuscript preparation were aided by the Environmental Remediation Sciences Division of the Office of Biological and Environmental Research, U.S. Department of Energy through Financial Assistance Award DE-FC09-96SR18546 to the University of Georgia Research Foundation.

Literature Cited

Aldridge, R. D., and R. D. Semlitsch. 1992. Female reproductive biology of the southeastern crowned snake (*Tantilla coronata*). Amphibia-Reptilia **13:**209–218.

Barbour, R. W., M. J. Harvey, and J. W. Hardin. 1969. Home range, movements, and activity of the Eastern worm snake, *Carphophis amoenus amoenus*. Ecology **50:**470–476.

Brattstrom, B. H. 1965. Body temperatures of reptiles. American Midland Naturalist **73:**376–422.

Campbell, K. R., and T. S. Campbell. 2001. The accumulation and effects of environmental contaminants on snakes: a review. Environmental Monitoring and Assessment **70:**253–301.

Campbell, H. W., and S. P. Christman. 1982. The herpetological components of Florida sandhill and sand pine scrub associations. Pages 163–171 in N. J. Scott Jr., editor. Herpetological communities. Research report 13. U.S. Fish and Wildlife Service, Washington, D.C.

Chen, J., S. C. Saunders, T. R. Crow, R. J. Naiman, K. D. Brosofske, G. D. Mroz, B. L. Brookshire, and J. F. Franklin. 1999. Microclimate in forest ecosystem and landscape ecology. BioScience **49:**288–297.

deMaynadier, P. G., and M. L. Hunter Jr. 1995. The relationship between forest management and amphibian ecology: a review of North American literature. Environmental Reviews **3:**230–261.

Enge, K. M., and W. R. Marion. 1986. Effects of clearcutting and site preparation on herpetofauna of a North Florida flatwoods. Forest Ecology and Management **14:**177–192.

Fitch, H. S. 1975. A demographic study of the ringneck snake (*Diadophis punctatus*) in Kansas. University of Kansas Museum of Natural History Miscellaneous Publications **62:**1–53.

Gardner, T. A., J. Barlow, and C. A. Peres. 2007. Paradox, presumption and pitfalls in conservation biology: the importance of habitat change for amphibians and reptiles. Biological Conservation **138:**166–179.

Gibbons, J. W., and R. D. Semlitsch. 1982. Terrestrial drift fences with pitfall traps: an effective technique for quantitative sampling of animal populations. Brimleyana **1982:**1–16.

Gibbons, J. W., and R. D. Semlitsch. 1987. Activity patterns. Pages 396–421 in R. A. Seigel, J. T. Collins, and S. S. Novak, editors. Snakes: ecology and evolutionary biology, MacMillan, New York.

Gibbons, J. W., et al. 2000. The global decline of reptiles, déjà vu amphibians. BioScience **50:**653–666.

Godley, J. S. 1980. Foraging ecology of the striped swamp snake, *Regina alleni*, in southern Florida. Ecological Monographs **50:**411–436.

Greenberg, C. H. 2001. Response of reptile and amphibian communities to canopy gaps created by wind disturbance in the southern Appalachians. Forest Ecology and Management **148:**135–144.

Greenberg, C. H., D. G. Neary, and L. D. Harris. 1994. Effect of high-intensity wildfire and silvicultural treatments on reptile communities in sand-pine scrub. Conservation Biology **8:**1047–1057.

Hammond, H. 1883. South Carolina: resources and population, institutions and industries. State Board of Agriculture of South Carolina, Charleston.

Hanula, J. L., K. E. Franzreb, and W. D. Pepper. 2000. Longleaf pine characteristics associated with arthropods available for red-cockaded woodpeckers. Journal of Wildlife Management **64:**60–70.

Hunter, M. L., Jr. 1990. Wildlife, forests, and forestry. Prentice Hall, Englewood Cliffs, New Jersey.

Kilgo, J. C., and J. I. Blake. 2005. Ecology and management of a forested landscape: fifty years on the Savannah River Site. Island Press, Washington, D.C.

Martin, W. H., and D. B. Means. 2000. Distribution and habitat relationships of the eastern diamondback rattlesnake (*Crotalus adamanteus*). Herpetological Natural History **7:**9–34.

Means, D. B. 2005. Pine silviculture. Pages 139–145 in M. Lannoo, editor. Amphibian declines. University of California Press, Berkeley, California.

Means, D. B., and G. O. Grow. 1985. The endangered longleaf pine community. ENFO (Florida Conservation Foundation) **85:**1–12.

Mushinsky, H. R. 1985. Fire and the Florida sandhill herpetofaunal community: with special attention to responses of *Cnemidophorus sexlineatus*. Herpetologica **41:**333–342.

Noel, J. M., W. J. Platt, and E. B. Moser. 1998. Structural characteristics of old- and second-growth stands of longleaf pine (*Pinus palustris*) in the Gulf Coastal Region of the U.S.A. Conservation Biology **12:**533–548.

Noss, R. F. 1988. The longleaf pine landscape of the Southeast: almost gone and almost forgotten. Endangered Species Update **5:**1–8.

Noss, R. F. 1989. Longleaf pine and wiregrass: keystone components of an endangered ecosystem. Natural Areas Journal **9:**211–213.

Perison, D., J. Phelps, C. Pavel, and R. Kellison. 1997. The effects of timber harvest in a South Carolina blackwater bottomland. Forest Ecology and Management **90:**171–185.

Pickford, S. G., and J. W. Hazard. 1978. Simulation studies on line intersect sampling of forest residue. Forest Science **24:**469–483.

Prestemon, J. P., and R. C. Abt. 2002. Timber products supply and demand. Pages 299–325 in D. N. Wear and J. G. Greis, editors. Southern forest resource assessment. General technical report SRS- 53. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, North Carolina.

Rothermel, B. B., and T. M. Luhring. 2005. Burrow availability and desiccation risk of mole salamanders (*Ambystoma talpoideum*) in harvested versus unharvested forest stands. Journal of Herpetology **39:**619–626.

Russell, K. R., H. H. Hanlin, T. B. Wigley, and D. C. J. Guynn. 2002. Responses of isolated wetland herpetofauna to upland forest management. Journal of Wildlife Management **66:**603–617.

Russell, K. R., T. B. Wigley, W. M. Baughman, H. H. Hanlin, and W. M. Ford. 2004. Responses of southeastern amphibians and reptiles to forest management: a review. Pages 319–334 in H. M. Rauscher and K. Johnsen, editors. Southern forest science: past, present, and future. Southern Research Station, Asheville, North Carolina.

Semlitsch, R. D., K. L. Brown, and J. P. Caldwell. 1981. Habitat utilization, seasonal activity, and population size structure of the southeastern crowned snake, *Tantilla coronata*. Herpetologica **37:**40–46.

Siry, J. P. 2002. Chapter 14: intensive timber management practices. Pages 327–340 in D. N. Wear and J. G. Greis, editors. Southern forest resource assessment. General technical report SRS- 53. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, North Carolina.

Todd, B. D., and B. B. Rothermel. 2006. Assessing quality of clearcut habitats for amphibians: effects on abundances versus vital rates in the southern toad *(Bufo terrestris)*. Biological Conservation **133:**178–185.

Todd, B. D., C. T. Winne, J. D. Willson, and J. W. Gibbons. 2008. Getting the drift: examining the effects of timing, trap type, and taxon on herpetofaunal drift fence surveys. American Midland Naturalist **158**(2):292-305.

Tuberville, T. D., J. R. Bodie, J. B. Jensen, L. LaClaire, and J. W. Gibbons. 2000. Apparent decline of the southern hog-nosed snake, (*Heterodon simus*). Journal of the Elisha Mitchell Scientific Society **116:**19–40.

Willson, J. D., and M. E. Dorcas. 2004. Aspects of the ecology of small fossorial snakes in the western Piedmont of North Carolina. Southeastern Naturalist **3:**1–12.

Winne, C. T., J. D. Willson, K. M. Andrews, and R. N. Reed. 2006. Efficacy of marking snakes with disposable medical cautery units. Herpetological Review **37:**52–54.

Winne, C. T., J. D. Willson, B. D. Todd, K. M. Andrews, and J. W. Gibbons. 2007. Enigmatic decline of a protected population of eastern kingsnakes, *Lampropeltis getula*, in South Carolina. Copeia **2007:**507–519.

Zar, J. J. 1998. Biostatistical analysis. 4th edition. Prentice-Hall, Englewood Cliffs, New Jersey.

Zheng, D., J. Chen, B. Song, M. Xu, P. Sneed, and R. Jansen. 2000. Effects of silvicultural treatments on summer forest microclimate in southeastern Missouri Ozarks. Climate Research **15:**45–59.