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Coarse woody debris and pine litter manipulation effects on movement and microhabitat use of *Ambystoma talpoideum* in a *Pinus taeda* stand

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Abstract

We examined effects of coarse woody debris (CWD) and pine litter (PL) manipulations on movement and microhabitat use by mole salamanders (*Ambystoma talpoideum*) in the upper Coastal Plain of South Carolina. Individuals were tracked within field enclosures using harmonic radar detection from 3 December 2002 to 1 August 2003. Enclosure study one (ES1) consisted of three treatments: (1) high CWD/high PL; (2) low CWD/low PL; (3) high CWD/low PL. Enclosure study two (ES2) consisted of two treatment types: complete PL removal and unmanipulated control. Activity of *A. talpoideum* within ES1 high CWD/low PL, low CWD/high PL and high CWD/high PL treatments did not differ. Individuals subject to ES2 PL removal treatments moved during more nights than individuals in control treatments. During night surveys ES2 PL removal treatments moved on a greater percentage of nights, and were active for longer periods of time, than individuals in control treatments. *A. talpoideum* exposed to low PL treatments may have utilized CWD as a means of compensating for inadequate microclimate conditions provided by reduced pine litter depth. Our results suggest that reduction of CWD and pine litter has little effect on *A. talpoideum* activity levels. Conversely, complete pine litter removal prompts individual salamanders to move more frequently and for longer periods, thereby potentially being subjected to increased desiccation and predation risk. Within managed pine forests in the southeastern United States, forest management practices that minimize pine litter and CWD removal can help to maintain suitable habitat for amphibian groups such as ambystomatid salamanders.

Keywords: Ambystomidae; *Ambystoma talpoideum*; Coarse woody debris; Pine litter; Plantation silviculture

1. Introduction

Alteration and destruction of forest habitat has been cited as a major factor in the decline of many amphibian populations (Blaustein and Wake, 1990, 1995; Wyman, 1990). Conversion of natural forests to intensively managed plantations is increasing to meet burgeoning demand for wood fiber products. In the southeastern United States, these intensively managed plantations typically contain a less diverse and abundant amphibian assemblage as those in less disturbed unmanaged pine or hardwood stands (Bennett et al., 1980; Grant et al., 1994; Hanlin et al., 2000). Reduction of microhabitat features through use of intensive harvesting and subsequent plantation reestablishment methods are believed to be a major factor leading to the

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decrease of amphibian populations within these stands (Enge and Marion, 1986).

Pine plantations account for 15% of timberland in the southeastern United States, occurring predominately in the Coastal Plain and Piedmont physiographic regions. These stands are generally much younger than natural pine stands, with 81% less than 23 years old (Conner and Hartsell, 2002). Because plantations are managed on short rotation lengths, disturbance occurs more frequently than in unmanaged pine stands. Plantations generally are subject to clearcut harvesting followed by intensive site preparation such as stump removal, roller chopping and mechanical bedding (Hunter, 1990; Smith et al., 1997). Even-aged harvest methods and subsequent site preparation compact soil, reduce litter depth and cover, displace mineral soil and reduce volume of coarse woody debris (CWD) (Harmon et al., 1986; Reisinger et al., 1988; deMaynadier and Hunter, 1995), leading to the development of more homogenous and structurally simplified forest stands. Reduction of these microhabitat features diminishes on-site moisture, a critical component for amphibians which require moist skin to respire (Duellman and Trueb, 1994), and reduces favorable cover sites used to escape extreme temperature and dry surface conditions (Russell et al., 2002). While response of amphibian species to forest management in the southeastern Coastal Plain region has been documented, little information exists on the underlying causal mechanisms, especially for members of the family Ambystomatidae.

Existing information indicates that establishment of pine plantations has an adverse affect on *Ambystoma* populations. Means et al. (1996) found that a breeding population of flatwoods salamanders (*Ambystoma cingulatum*) drastically declined after their terrestrial habitat, a natural longleaf pine (*Pinus palustris*)–wiregrass (*Aristida* spp.) forest in Florida, had been converted into an intensively managed slash pine (*Pinus elliottii*) plantation. Raymond and Hardy (1991) documented a reduction in survival of adult mole salamanders (*Ambystoma talpoideum*) at a Louisiana pond that migrated from an adjacent portion of forest that had been clearcut. Management practices that produce sites with increased climatic variation and inadequate microhabitat may result in reduced survival of individuals within altered forest stands. However, effects of microhabitat alterations on *Ambystoma* species are not well understood because of their highly fossorial behavior.

Although ambystomatid salamanders primarily utilize underground retreat sites, surface cover conditions can have a significant influence on microclimate within burrows by buffering against temperature and moisture extremes in the soil (Williams and Gray, 1974; Geiger et al., 1995). The objectives of our study were to determine how alterations in pine litter depth and CWD volume affect movement, activity levels, and microhabitat use of *A. talpoideum*. Because individuals of this species are too small for radiotransmitters and because of difficulty in obtaining permits to use radioisotope tagging, a new tracking technique called harmonic radar detection (HRD) was employed to track movement of individuals within an enclosed area.

2. Study site and methods

2.1. Site description

Our study was conducted in a 50-year-old loblolly pine (*Pinus taeda*) stand on the US Department of Energy's Savannah River Site (SRS), a 78,000 ha National Environmental Research Park in Aiken, Barnwell and Allendale Counties, South Carolina (33°0–25′N, 81°25–50′W). The SRS is located on the upper Coastal Plain physiographic region in an area known as the Sandhills. Historically, the longleaf pine–wiregrass community dominated upland areas of the SRS before being cleared for agriculture in the early 1800s. Upon acquisition of the land comprising the SRS by the Atomic Energy Agency in 1951, the US Forest Service planted abandoned agricultural fields in loblolly and slash pine. Stands were established on these sites primarily by hand planting. Our study stand was located on a well-drained Sandhill at an elevation of 100 m. Soils were of the Blanton–Lakeland association. Understory vegetation was sparse, consisting mostly of poison oak (*Toxicodendron radicans*), black cherry (*Prunus serotina*), muscadine (*Vitis rotundifolia*) and broomsedge (*Andropogon virginicus*). Our study stand was last prescribed burned in 1993 (D. Shea, USFS Savannah River Site, pers. commun.). Mean annual temperature is 18 °C and mean annual precipitation is 122.5 cm.

2.2. Treatments and experimental design

Our first enclosure study (ES1) consisted of three replicate sets of three enclosure treatments of high CWD/high pine litter (PL), low CWD/low PL and high CWD/low PL. We added three pieces of similarly sized, slightly decayed CWD with mostly shed bark to the center of each enclosure. High CWD treatments had a volume of $91{,}730 \pm 6736\ cm^3$, whereas those with low CWD treatments had a volume of $25{,}061 \pm 3190\ cm^3$. We removed the L, F1, and F2 layers of the A-horizon (Millar, 1974) within each treatment enclosure and replaced it with pine litter collected from the pine stand. Pine litter in high and low PL enclosures had a mean depth of 2.98 ± 1.02 and 0.78 ± 0.43 cm, respectively. Because of soil disturbance caused by removal of pine litter, we created 16 burrows at 64 cm intervals with a 0.64 cm diameter lead pipe. We randomly assigned treatments for one set of enclosures; we then assigned treatment types in remaining enclosures depending upon which treatment had been assigned to enclosures in the first set. This was to ensure that center enclosures, which share walls with adjoining enclosures, received each of the three treatment types in order to eliminate any possible bias associated with having two common walls with adjoining enclosures as opposed to one shared by outside enclosures.

We constructed enclosures for ES1 of 0.635 cm plastic hardware cloth to prevent salamanders from escaping while permitting prey items, primarily insects, to move freely through enclosures. We buried hardware cloth to a depth of 30 cm with an above ground height of 30 cm. We attached polyvinyl chloride (PVC) pipe to the top of fences as well as 12.7 cm above the ground to create a barrier to salamanders attempting to climb out. We then attached a 12.7 cm piece of hardware cloth to the bottom of each side of enclosures to reduce hole size. Each enclosure was $4.57\ m \times 4.57\ m$, with a total area of $20.88\ m^2$. We oriented all enclosures with each side facing one of the cardinal directions. We completed enclosures and treatments for ES1 on 25 July 2002.

Our second enclosure study (ES2) consisted of nine pairs of two enclosure treatments, total pine litter removal and unmanipulated controls. We constructed enclosures from aluminum flashing buried 15 cm below ground with 15 cm above ground. We bent tops of enclosure walls to create a lip to prevent climbing salamanders from escaping. Each enclosure measured $3\ m \times 3\ m$. We randomly assigned treatments to each enclosure pair. For PL removal treatments, we removed all pine litter to expose mineral soil while control enclosures were left undisturbed. Pine litter in control enclosures had a mean depth of 4.04 (± 1.23) cm. We completed enclosures and treatments on 15 February 2002.

We collected individual *A. talpoideum* during breeding migrations at nearby Carolina Bay wetlands (Sharitz and Gibbons, 1982) from November 2002 until cessation of emigration from wetlands in April 2003. We used only females for ES1 because they stay at breeding sites for shorter periods than males and therefore spend more time in terrestrial environments (Semlitsch, 1981). In ES2, we used both male and female *A. talpoideum* captured emigrating from wetlands. We kept captured individuals in $20\ cm \times 15\ cm \times 5\ cm$ containers with moist paper towels at 21 °C and natural L:D periods. We did not keep individuals in captivity longer than 21 days. We constructed harmonic radar tags from Zener-telefunken BAT85S schottky-barrier diodes with two 11 mm antennae (total length: 25.9 mm) and a total weight of 0.1 g. We subcutaneously implanted one into each salamander. HRD consists of a hand held transceiver and a diode tag. The transceiver emits a 1.7 W continuous microwave frequency of 917 MHz. When the microwaves strike a diode attached to an animal they are reflected at double the frequency (1834 MHz), which is detected by the receiver. We recorded snout-vent-length (SVL, cm), total length (cm), sex and weight (g) of individuals. We allowed individuals to recover for 7–10 days post-implantation and following a random assignment to treatment, we released animals at night into 10.2 cm deep artificially constructed burrows (initial burrow). If a tagged salamander in an enclosure died, escaped, or lost its tag, and was not subsequently recovered, we replaced that individual. If individuals expelled tags and were recovered, we implanted new tags and released them back into enclosures. Because adult *A. talpoideum* are not easily found once breeding migrations have ended, we collected a group of individuals from a breeding wetland on 9 April 2003 ($n = 12$) and placed them in a $2\ m \times 2\ m$ enclosure in the study area for use in replacing lost, dead, or escaped individuals.

2.3. Sampling

We located individuals in ES1 using harmonic radar once during daylight (0800–1800 h) and once during night (2100–0200 h), 2–7 days a week from 3 December 2002 to 3 August 2003 ($n = 241$ days). We located individuals in ES2 during the same time periods from 15 February 2003 to 3 August 2003 ($n = 166$ days). We conducted intensive night surveys when heavy precipitation occurred and movement seemed likely. During night surveys we located individuals once every 60–90 min from sunset until sunrise. We collected daily temperature and rainfall at the study site during daily readings from a thermometer (°C) and rain gauge (cm) located 30 cm above ground level. We conducted night surveys on 26 February (ES1 only), 15 March (ES1 only), 8 April, 6 May (ES1 only), 18 May, 22 May, and 1 July 2003. We marked the location of each individual and time was recorded for each reading. We measured nearest point of locations (cm) using an *XY* coordinate with the southwest corner of enclosures serving as the origin. We then plotted coordinates and total distance moved (cm) was measured for each individual in QuickCAD 8.0.

2.4. Statistical analysis

We converted measured variables during each 24 h sampling period and analyzed them on a per day basis because some enclosures were occupied longer than others. We did not count individuals occupying enclosures for less than 14 days in final analysis. We compared number of activity areas and number of nights moved during 24 h sampling periods among treatments in ES1 using one-way analysis of variance (ANOVA) with individuals nested within treatments. We also compared movement rate, defined as distance moved (cm) per minute, and total minutes of activity during night surveys among treatments in ES1 using one-way ANOVA with individuals nested within treatments. We considered an activity area to be any point occupied by an individual for ≥ 1 day. We compared percent of nights an individual was active within enclosures during night surveys among treatments in ES1 using a one-way ANOVA. We compared percent of days in which individuals occupied pine litter and CWD among treatments using a one-way ANOVA. We used linear contrasts to compare high PL with low PL treatments and high CWD with low CWD treatments for all variables in ES1. For ES2, we compared number of activity areas and number of nights moved during 24 h sampling periods and movement rate and total minutes of activity during night surveys between treatments using one-way ANOVA with individuals nested within treatments. We compared percent of nights an individual was active within enclosures during night surveys between treatments in ES2 with a two-sample t-test. Effect of sex on number of activity areas and nights moved were compared using a two-sample t-test. All variables were tested for normality with Shapiro-wilk's test for normal distribution. Percentage data were arcsine transformed. Data that were not normally distributed and that could not be successfully transformed were ranked and analysis was performed on the ranks. All analyses were performed in SAS statistical analysis software (SAS Institute, 1997).

3. Results

There was a total of 618, 628, and 640 salamander nights in high CWD/low PL, low CWD/low PL, and high CWD/high PL, respectively. Number of activity areas and number of nights moved during daily locations for ES1 did not differ among treatments (Table 1). Percent use of pine litter and CWD were not different among treatments (Table 2). However, linear contrasts revealed that individuals in low CWD treatments utilized CWD to a greater extent than individuals in high CWD treatments ($F = 6.94$, $P = 0.0388$). Time active (min), movement rate and percent of nights active in ES1 during night surveys were not different among treatments (Table 1).

In ES2 there was a total of 835 and 987 salamander nights for PL removal and control treatments, respectively. Number of activity areas for ES2 did not differ between treatments (Table 3). However, individuals in PL removal treatments moved more frequently than control individuals during night surveys (Fig. 1). Individuals in PL removal enclosures also were active for longer periods and moved during a larger percentage of night surveys than control individuals (Table 3). Males and females did not differ in any other variables measured.

Table 1
Mean (±S.E.) number of activity areas and nights moved per day during daily locations, and mean (±S.E.) time active, movement rate, and nights active during night surveys for *A. talpoideum* in high CWD/low pine litter (PL) ($n = 618$ salamander days), low CWD/low PL ($n = 628$ salamander days), and high CWD/high PL ($n = 640$ salamander days) enclosures at the Savannah River Site, Aiken County, South Carolina, from 3 December 2002 to 1 August 2003

Variable	High CWD/low PL, mean ± S.E. (n)	Low CWD/low PL, mean ± S.E. (n)	High CWD/high PL, mean ± S.E. (n)	F (d.f.)	P
Daily locations					
Activity areas[a]	0.06 ± 0.03 (3)	0.04 ± 0.01 (3)	0.04 ± 0.01 (3)	0.29 (2.6)	0.7586
Nights moved[a]	0.06 ± 0.03 (3)	0.04 ± 0.01 (3)	0.02 ± 0.01 (3)	0.66 (2.6)	0.5491
Night surveys					
Time active (min)	445 ± 96.1 (3)	423 ± 82.3 (3)	261 ± 32.2 (2)	1.86 (2.5)	0.2485
Movement rate (cm/min)	2.65 ± 0.6 (3)	2.85 ± 0.6 (3)	2.07 ± 0.7 (2)	0.19 (2.5)	0.8345
Nights active (%)	42.86 ± 20.53 (3)	29.21 ± 7.7 (3)	18.89 ± 14.2 (2)	0.74 (2.5)	0.5146

[a] ANOVA performed on ranked data.

Table 2
Mean (±S.E.) percentage of days pine litter and coarse woody debris were used by *A. talpoideum* during daily locations in high CWD/low pine litter (PL) ($n = 618$ salamander days), low CWD/low PL ($n = 628$ salamander days), and high CWD/high PL ($n = 640$ salamander days) enclosures at the Savannah River Site, Aiken County, South Carolina, from 3 December 2002 to 1 August 2003

Variable	High CWD/low PL, mean ± S.E. (n)	Low CWD/low PL, mean ± S.E. (n)	High CWD/high PL, mean ± S.E. (n)	F (d.f.)	P
Pine litter use (%)	49.72 ± 16.96 (3)	45.46 ± 11.91 (3)	35.64 ± 21.03 (3)	0.18 (2.6)	0.8410
CWD use (%)	16.81 ± 12.75 (3)	37.62 ± 7.40 (3)	2.15 ± 2.15 (3)	4.17 (2.6)	0.0732

4. Discussion

Pine litter removal had a significant effect on movement and activity levels of *A. talpoideum*. Individuals within ES2 PL removal enclosures were active an average 91.7% of nights surveyed, 32% more than those within control enclosures, and moved 61.6% more than controls during the 166-day sampling period. Increased activity is likely due to absence of adequate microclimate conditions within removal enclosures. Litter acts as an insulating layer for soil, buffering against extreme surface temperatures and retaining moisture during dry periods (Williams and Gray, 1974; Geiger et al., 1995). Elimination of ground cover reduces availability of suitable temperature and moisture conditions for salamanders (Pough

Table 3
Mean (±S.E.) number of activity areas and nights moved per day during daily locations, and mean (±S.E.) time active, movement rate, and nights active during night surveys for *A. talpoideum* in pine litter removal ($n = 835$ salamander days) and control ($n = 987$ salamander days) enclosures at the Savannah River Site, Aiken County, South Carolina, from 15 February 2003 to 1 August 2003

Variable	Pine litter removal, mean ± S.E. (n)	Control, mean ± S.E. (n)	F (d.f.)	P
Daily locations				
Activity areas	0.06 ± 0.01 (9)	0.05 ± 0.01 (9)	0.01 (1.16)	0.9171
Nights moved[a]	0.06 ± 0.01 (9)	0.03 ± 0.01 (9)	5.21 (1.16)	0.0365
Night surveys				
Time active (min)	463 ± 32.83 (7)	272 ± 56.05 (6)	13.21 (1.11)	0.0039
Movement rate (cm/min)	2.45 ± 0.14 (7)	2.54 ± 0.25 (6)	0.14 (1.11)	0.7110

[a] ANOVA performed on ranked data.

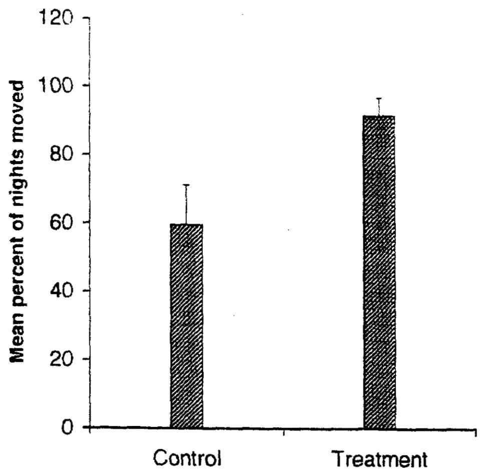

Fig. 1. Percent of nights in which *A. talpoideum* in pine litter removal ($n = 835$ salamander days) and control ($n = 987$ salamander days) treatment enclosures were active on the forest floor during night surveys conducted on 8 April, 18 May, 22 May, and 1 July 2003. Treatments were compared by ranks with a two-sample t-test (t-value $= -2.42$, $P = 0.0341$).

et al., 1987). Reduction of forest floor litter depth also has been found to reduce abundance of arthropod prey (Seastedt and Crossley, 1981; Shure and Phillips, 1991; Siira-Pietikainen et al., 2003). Initial burrows within PL removal treatments were not insulated from fluctuations in ambient climatic conditions, prompting individuals to attempt relocation more frequently during rainy nights. Exposure of the soil surface to rain further decreased available microhabitats by eroding burrow entrances, forcing individuals to maintain occupancy in suboptimal initial burrows. Reductions in microhabitat and arthropod density may have been responsible for the increased surface activity of individuals in PL removal enclosures. In contrast, *A. talpoideum* within control treatments were exposed to more suitable microenvironments, enabling them to spend less time on the surface where they were at risk of being consumed by predators.

During our study, snakes consumed two individuals. The first was depredated on 12 May 2003 by a southern hognose snake (*Heterodon simus*) and another on 1 August 2003 by an eastern garter snake (*Thamnophis sirtalis*). While neither depredation occurred in ES2 removal enclosures (both depredations occurred within plots of ES1), they illustrate the predation risk encountered during surface activity and while occupying burrows with an exposed entrance. Increased surface activity time also may subject individuals to desiccation (Semlitsch, 1983a). One individual in an ES2 removal plot was found exposed on the surface alive during daylight hours, and two were found dead more than 30 days after being put into enclosures from what appeared to be desiccation. Although PL removal treatments were mostly devoid of suitable habitat, *A. talpoideum* were able to exploit several microhabitats including plant root systems and shallow patches of pine litter that collected in small depressions.

Unlike conditions in ES2 PL removal treatments, ES1 enclosures containing pine litter and CWD appeared to have provided more suitable microhabitats for *A. talpoideum* to exploit. No differences were found among movement variables measured. Use of CWD compared to availability was greater for individuals in low PL treatments (Fig. 2). Individuals in low PL treatments were found under CWD 22.73% of days located, whereas those in high PL treatments occupied CWD only 2.15% of days located (Table 2). Increased pine litter depth in high PL treatments probably provided adequate moisture for individuals, reducing their need to utilize CWD as an alternative microhabitat. Inability of individuals in low PL treatments to find adequate moisture and temperature conditions under pine litter was probably mitigated through use of CWD.

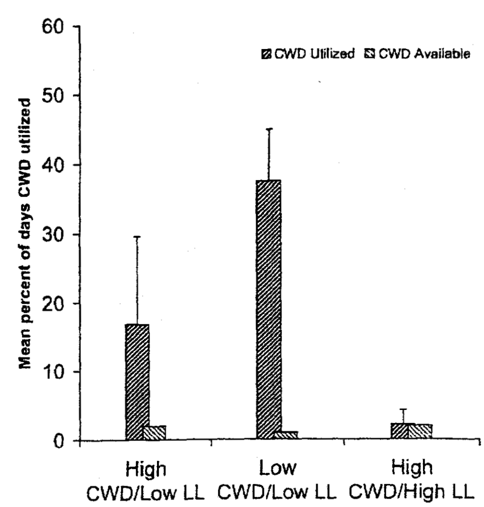

Fig. 2. Mean percent of days, with standard error, in which *A. talpoideum* were located under coarse woody debris within enclosures containing high CWD/low pine litter ($n = 618$ salamander days), low CWD/low PL ($n = 628$ salamander days), and high CWD/high PL ($n = 640$ salamander days) from 3 December 2002 to 1 August 2003.

Like pine litter, CWD buffers against extreme temperature fluctuations, retains moisture during dry periods (Boddy, 1983; Harmon et al., 1986) and contains abundant insect prey (Hanula, 1995). Coarse woody debris has been found to play an important role in the terrestrial ecology of plethodontid salamanders (Kleeberger and Werner, 1982; Aubrey et al., 1988; Bury and Corn, 1988; Dupuis et al., 1995; Maidens et al., 1998). However, CWD may be of less significance in the terrestrial ecology of ambystomatid salamanders, which prefer underground burrow systems (Williams, 1970; Semlitsch, 1983b; Douglas, 1981; Loredo et al., 1996; Madison, 1997; Madison and Farrand, 1998; Trenham, 2001) that are generally independent of CWD (Semlitsch, 1981). Locally, subterranean burrows created by small mammals such as moles (Talpidae) and *Peromyscus* spp., as well as preexisting cracks and crevices in the soil, can be exploited by *A. talpoideum* (Semlitsch, 1983a). However, if pine litter depth becomes inadequate in regulating burrow conditions from extreme climatic variation, individuals may seek refuge under CWD. At the Savannah River Site, Chazal and Niewiarowski (1998) compared juvenile *A. talpoideum* within enclosures in a 4-month-old clearcut to individuals maintained in an adjacent 40-year-old loblolly pine stand. Juveniles did not differ in abundance, body mass, snout-vent-length, clutch size, percent whole-body nonpolar storage lipid, or percent storage lipid of eggs after 5–6 months of exposure to enclosure conditions. Lack of difference between the two treatments was attributed partially to the large amounts of CWD in clearcut enclosures, which were believed to have ameliorated clearcut surface conditions by retaining on-site moisture.

In most natural situations where pine litter is sufficient, use of CWD by *A. talpoideum* probably is low. Following clearcutting and subsequent site preparation pine litter depth and cover is significantly reduced (Russell et al., 2002). During this stage, amount of residual CWD on-site may play a significant role in providing necessary microhabitat for *A. talpoideum*.

5. Conclusion

Availability of microhabitat is greatly influenced by silvicultural techniques used during harvesting and site preparation. Intensive mechanical treatments such as disking, harrowing and rollerchopping are frequently used in the southeastern Coastal Plain. The primary goal of these techniques is to reduce logging slash and competing vegetation, and expose mineral soil. Mechanical site preparation treatments likely produce the most harm by increasing bare ground cover, reducing forest floor depth, disturbing and compacting mineral soil, and eliminating much of the CWD left on-site following tree harvesting (Harmon et al., 1986; deMaynadier and Hunter, 1995; Russell et al., in press). Mechanical operations also mix organic material with mineral soil, accelerating decomposition (Salonius, 1983), and destroy underground burrows preferred by ambystomatid salamanders. Alteration of terrestrial habitat through intensive site preparation of a slash pine stand is believed to have been responsible for a 22 year decline in a breeding population of *A. cingulatum* within the disturbed stand (Means et al., 1996). Because *A. talpoideum* in our study were subject to pine litter and CWD manipulation within an intact 50-year-old slash pine stand, our results should be interpreted cautiously when applied to stand conditions produced by harvesting and site preparation. However, retaining some woody debris as refugia following site preparation (American Forest and Paper Association, 2002) may mitigate effects of inadequate pine litter depth and destruction of underground burrows.

Most CWD remaining after harvest and site preparation is generally lost through decay (Barber and Van Lear, 1984), prescribed fire and deficiency of new inputs by mid-rotation (Van Lear and Waldrop, 1994). However, loss of CWD at this period of stand development is probably not detrimental to ambystomatid salamanders, which favor use of underground burrows. Pine litter increases rapidly during the first 15-years following establishment of pine plantations due to the low decomposition rate of pine litter (Gholz et al., 1985). Once sufficient pine litter is available, *A. talpoideum* will become less dependent upon CWD for refugia. Increased pine litter facilitates recovery of soil structure (Switzer et al., 1979) and stabilizes microclimate in underground burrows. Therefore rapid recovery of pine litter depth ensures rapid restoration of preferred ambystomatid habitat.

Throughout the duration of stand development in much of the Southeast, land managers often employ practices that reduce forest floor material. Prescribed fire is frequently used to create wildlife habitat, reduce heavy fuel accumulation, expose mineral soil and control competing vegetation, insects and diseases (Hunter, 1990). Although prescribed burns reduce litter depth, they are generally not intense enough to remove all organic material on the forest floor. Organic matter in uneven-aged loblolly and shortleaf (*Pinus echinata*) pine stands in southeastern Arkansas was only 15% lower 1 year after a prescribed fire than in similar stands which had not been burned for 6-years or in unburned control stands (Cain et al., 1998). In the Atlantic Coastal Plain of Maryland, a 50-year-old stand dominated by loblolly pine and subject to eight prescribed burns in 13 years had a litter depth of 1.7 ± 0.8 cm, 46% deeper than litter depth in low PL enclosures of our study, whereas a similar unburned pine stand contained a depth of 4.9 ± 0.4 cm (McLeod and Gates, 1998). While prescribed fire reduces pine litter depth, remaining organic material should provide adequate buffering of the soil from climatic extremes and maintain integrity of underground burrows. However, reduction of pine litter through other removal practices, such as pine straw harvesting for horticultural and landscaping markets may have a negative impact on ambystomatid salamanders due to increased disturbance to the organic soil layer.

Demand for pine straw in natural landscaping is increasing (Morris et al., 1992). Harvesting of pine litter reduces litter depth and may increase soil bulk density (McLeod et al., 1979; Haywood et al., 1994); however, if removals are performed at 2–3 year intervals these effects should be negligible, leaving partially decomposed and fragmented needle litter intact. Although soil compaction may be a problem depending on techniques and equipment used, it is regarded as unlikely (Morris et al., 1992). Nonetheless, if removals are conducted too frequently, exposure of mineral soil may result (Morris et al., 1992), compelling resident *A. talpoideum*, or other ambystomatids, to move more frequently. Sustainable pine straw harvests should limit removal to 20% of pine litter (Duryea and Edwards, 2002), thereby leaving adequate litter depth and minimizing disturbance to underground burrows of *A. talpoideum*.

A. talpoideum are capable of exploiting a variety of refugia, responding to depletion of one microhabitat by utilizing another. Our study supports sustainable forestry initiative guidelines, which suggest leaving logging slash on-site following harvesting in order to provide refugia for salamander species (American Forest and Paper Association, 2002). Although our study demonstrated the ability of *A. talpoideum* to survive adverse conditions, immediate and long-term effects of frequent, mechanized habitat disturbance may have profound impacts on breeding populations of ambystomatid species. Quality of terrestrial habitat is important for maintaining viable amphibian populations (Semlitsch, 2000). Plantation forest management practices that minimize mechanical disturbance and retain adequate microhabitat throughout stand development will provide necessary habitat for resident fossorial salamander species.

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