

Burrow Availability and Desiccation Risk of Mole Salamanders (*Ambystoma talpoideum*) in Harvested versus Unharvested Forest Stands

BETSI B. ROTHERMEL¹ AND THOMAS M. LUHRING

Savannah River Ecology Laboratory, University of Georgia, Drawer E, Aiken, South Carolina 29802, USA

ABSTRACT.—Clearcutting and other forest management practices that remove canopy and disturb ground cover may exacerbate the risk of desiccation, particularly for newly metamorphosed amphibians. We examined dehydration rates of juvenile Mole Salamanders (*Ambystoma talpoideum*) in relation to burrow availability in four experimental forest management treatments. Juvenile salamanders ($N = 41$) were confined to small enclosures in four treatments representing a range of habitat disturbance: clearcut with coarse woody debris (CWD) removed; clearcut with CWD retained; thinning; and an unharvested control of second-growth, mature loblolly pine. Half of the salamanders in each habitat treatment were provided with artificial burrows. Water loss over 72 h was significantly higher in the clearcut with CWD retained than in the other three treatments. Most water loss occurred during the first two nights, when salamanders may have been most active. Only 40% of salamanders without burrows survived in the clearcuts, versus 90% in the thinned stand and 100% in the control. Ninety percent of the salamanders with access to a burrow survived in the clearcuts versus 100% in the thinning and control. We found no correlation between soil moisture and water loss and attribute higher desiccation rates in the clearcuts to high temperatures ($> 44^{\circ}\text{C}$). Although habitat changes resulting from thinning did not lead to increased desiccation, complete canopy removal greatly increased risk of mortality caused by desiccation. Our results also demonstrate that this risk is strongly mediated by the availability of burrows.

Forest management practices that result in extensive loss of canopy cover and disturbance to ground cover have been associated with reductions in relative abundance of salamanders and other amphibians (deMaynadier and Hunter, 1995). Raymond and Hardy (1991), for example, observed a decline in numbers of Mole Salamanders (*Ambystoma talpoideum*) returning to a breeding pond from the side of the pond adjacent to a recent clearcut. Similarly, Cromer et al. (2002) found fewer Mole and Marbled (*Ambystoma opacum*) Salamanders in gaps resulting from selective logging than in unharvested areas. A proposed mechanism for population declines of some species following logging is an increased risk of desiccation. Amphibians are particularly vulnerable to desiccation because they have a higher ratio of wet surface exposed to the air than any other vertebrate (Spight, 1968). The small size and elongated body shape of many salamanders exacerbates this risk via an increase in their surface-to-volume ratio.

Compared to the more extensive literature on plethodontids (e.g., Heatwole and Lim, 1961; Spotila, 1972; Wisely and Golightly, 2003), there is relatively little information on the factors influencing dehydration rates in ambystomatid salamanders. Despite the presumed importance of

desiccation risk in dictating amphibian responses to habitat alteration, few studies have measured dehydration rates or time to desiccation in habitats varying in degree of disturbance. Rothermel and Semlitsch (2002) found that juvenile Spotted (*Ambystoma maculatum*) and Small-Mouthed (*Ambystoma texanum*) Salamanders experienced greater evaporative water loss in fields than in forests over a 24-h period. Although they require wetlands for breeding, ambystomatids are completely terrestrial as juveniles and as adults during the nonbreeding season. The mean maximum migration distance for ambystomatids, calculated from values reported in the literature for seven species, is 253 m (Semlitsch and Bodie, 2003). This makes them vulnerable to clearcutting and other disturbances affecting the upland habitat surrounding wetlands (Faccio, 2003; Semlitsch and Bodie, 2003).

We compared desiccation rates of juvenile *A. talpoideum* among four experimental habitat treatments representing a range of disturbances associated with forest management activities. The treatments, a clearcut with coarse woody debris (CWD) removed, a clearcut with CWD retained, a partial harvest (thinning), and an unharvested control of second growth, mature loblolly pine (*Pinus taeda*), were applied to four 3.8-ha quadrants adjacent to a seasonal wetland. We predicted that the rates of desiccation for the salamanders would increase with the level of disturbance,

¹ Corresponding Author. E-mail: rothermel@srel.edu

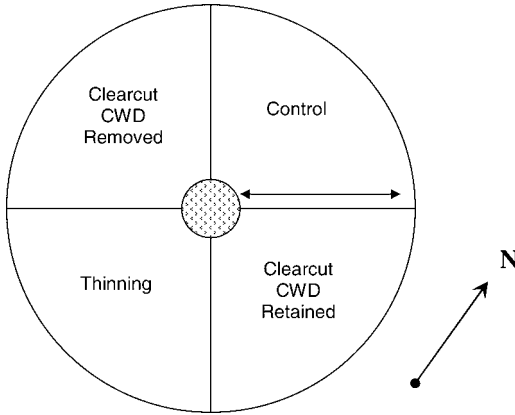


FIG. 1. Diagram showing the arrangement of the four 3.8-ha habitat treatments centered on Bay 1000. CWD = coarse woody debris.

such that salamanders in the clearcuts would experience the highest desiccation rates, followed by the thinning treatment.

We also tested the degree to which burrow availability mitigates the risk of desiccation by providing half the salamanders in each habitat treatment with a burrow. During the terrestrial phases of their life cycle, ambystomatid salamanders are largely fossorial, occupying small home ranges centered on small mammal burrows or other underground refugia (Douglas and Monroe, 1981; Semlitsch, 1981; Madison, 1997; Faccio, 2003). Such refuges provide protection from predators, desiccation, and freezing, and their density may influence terrestrial density of salamanders (Regosin et al., 2003). *Ambystoma talpoideum* are capable of burrowing in loose soil but often rely on existing crevices or burrows made by roots and other animals (Semlitsch, 1983). Thus, the compaction of soil by heavy machinery during logging could not only destroy existing burrows but could make it more difficult for salamanders to create new ones. At the same time, the additional cover provided by logging debris might compensate for the loss of burrows, at least over the short term (Moseley et al., 2004).

MATERIALS AND METHODS

The study site was an area being used for LEAP (Land-use Effects on Amphibian Populations), a multiregional, collaborative study of how land-use practices that degrade and fragment forest habitat affect the migratory success and demographics of pond-breeding amphibians. The study area was a pine-dominated woodland within a 170-m radius of a Carolina bay wetland (Bay 1000) on the Savannah River Site in Barnwell County, South Carolina. The study area was divided into four equal quadrants

delineated by two perpendicular transects that intersect at the center of the wetland (Fig. 1). One 3.8-ha quadrant served as a control, whereas each of the others was subjected to one of the three forest management treatments in March, 2004, four months prior to the start of the experiment. Treatments were assigned to each quadrant randomly, with the constraint that the clearcuts could not occur in adjacent quadrants.

The overstory in the control stand consisted of 27-year-old loblolly pine (*Pinus taeda*) with a dense understory of sweetgum (*Liquidambar styraciflua*), wax myrtle (*Morella cerifera*), and holly (*Ilex opaca*) and extensive ground cover dominated by Carolina jessamine (*Gelsemium sempervirens*), poison ivy (*Toxicodendron radicans*), grape (*Vitis* sp.), and grasses. In the thinning stand, the overstory of 51-year-old loblolly pine was uniformly thinned to achieve a 25% reduction in canopy cover relative to the control (67% vs. 89%, respectively). The thinned stand had a sparser understory and less extensive ground cover than the control, both before and after logging.

The clearcut areas were not subjected to site preparation practices or replanted. In the clearcut with CWD removed (CC-removed), logs were skidded to areas off the plot, where they were piled and delimbed. In the clearcut with CWD retained (CC-retained), logs were delimbed, piled, and loaded within the plot. After logging was completed, the woody debris in the CC-retained was spread more evenly across the plot using a bulldozer. By the time our experiment was conducted in July 2004, the regenerating vegetation in the clearcuts comprised a diverse mix of resprouting hardwoods, shrubs, vines, grasses, and herbaceous plants, all generally less than 1 m tall. Approximately 20% of the area of the CC-retained was bare ground, followed by 11% in the CC-removed, 4% in the thinning, and 0% in the control. Litter depth averaged 3.1 cm in the CC-retained, 3.2 cm in the CC-removed, 2.6 cm in the thinning, and 5.0 cm in the control. Although the CC-retained contained higher amounts of woody debris > 10 cm in diameter than the CC-removed (B. B. Rothermel and J. W. Gibbons, unpubl. data), the small size of the salamander enclosures (0.025 m²) only permitted inclusion of fine woody debris (i.e., smaller sticks and bark) and litter, which consisted predominantly of pine needles. Hence, salamanders in the CC-retained could not benefit directly from the greater volume of CWD in this treatment.

Enclosures for the salamanders were constructed by attaching a cylindrical sleeve of gray fiberglass screening to the rim of a 24-cm section of 18-cm diameter polyvinyl chloride (PVC) pipe. To create the sleeve, we rolled a piece of screening

(55 cm high \times 66 cm wide) into a cylinder and sewed the side seam closed with 14-lb. monofilament fishing line. We then used caulk to attach the sleeves to one end of each open-ended section of PVC. Twelve enclosures were placed 1.1 m apart in a 3×4 grid in the center of each quadrant. The PVC was buried so the top of the pipe was level with the ground and only the screen was above ground. When the salamanders were added, the enclosure was closed from the top by rolling the screen down, folding in the corners, and securing with binder clips. Burrows were constructed in half of the enclosures by driving a section of 2.2-cm diameter metal conduit 10 cm into the ground at an approximately 30° angle.

Although *A. talpoideum* occur at Bay 1000, the wetland hydroperiod is too short to support larval development and recruitment of this species. Thus, we collected recently metamorphosed juveniles between 8 and 22 June from Ellenton Bay, located 24 km away but also on the Savannah River Site in Barnwell County, South Carolina. We were able to obtain only 41 postmetamorphic *A. talpoideum*, rather than the 48 envisioned in our original study design. We kept the salamanders in plastic trays lined with moist paper towels and stored in a room at 25°C and 50% relative humidity with a 12:12 light:dark cycle until the start of the experiment. The salamanders were fed crickets ad libitum until two days before the experiment to obtain a fully hydrated mass without prey items present in the digestive tract.

Salamanders were transferred to individual, numbered containers containing 1 cm of well water at 1700 h on 7 July 2004, the day the experiment was initiated. Prior to transporting salamanders to the field site, we measured their SVL and mass to the nearest 0.01 g using a Scout II electronic balance (Ohaus Corporation, Florham Park, NJ). Salamanders were then randomly assigned to enclosures, transported to the field site, and added to the enclosures between 1845 and 2130 h. Except for periodic removal for determination of mass, each salamander was confined to its enclosure for 72 h. During this time, we returned every 12 h to obtain salamander mass and measure environmental conditions. Decrease in mass over the 72 h was attributed to water loss and used as a measure of desiccation rate.

Upon checking the enclosures every morning (from 0830–1100 h) or evening (from 1930–2200 h), we noted whether salamanders with burrows were in or out of their burrows. We also noted the location of the salamanders without burrows as either exposed or under litter, as well as their relative position in the enclosure. Each *A. talpoideum* was removed from its enclosure, its mass determined, and immediately returned to the en-

closure. Because most burrows were damaged in the process of removing salamanders, all burrows were reconstructed prior to returning the salamander.

At each determination of mass, we measured soil moisture of the top 8 cm of soil inside each enclosure with a TH2O portable soil moisture meter (Dynamax Inc, Houston, TX). We used a sling psychrometer to measure relative humidity in each habitat at the time of addition of salamanders and every 12 h thereafter. We also measured air temperature at 30-min intervals using a Hobo H8 logger (Onset Computer Co., Bourne, MA) mounted 0.5 m above the ground in the middle of each enclosure grid.

We examined the effects of habitat treatment, burrow availability, and their interaction on water loss at 12 h, when all salamanders were still alive, using analysis of variance (ANOVA). We examined changes in water loss over the entire 72-h experiment using repeated-measures ANOVA (Scheiner and Gurevitch, 2001), which included only salamanders for which there was a complete set of measurements (i.e., individuals that survived the entire experiment). We used similar analyses to test for effects of habitat, burrow availability, and time on soil moisture. We used PROC GLM in SAS (SAS Institute, Cary, NC), basing F -ratios on Type III sums of squares because of the slightly unequal sample sizes among treatment groups and assessing significance based on $\alpha = 0.05$. To further explore how rates of water loss varied over time, we ran univariate ANOVAs for each successive 12-h time interval, applying a Bonferroni-corrected $\alpha = 0.0083$ to account for the multiple contrasts (PROFILE option in SAS; Scheiner and Gurevitch, 2001). We also calculated Pearson correlation coefficients between soil moisture and salamander water loss for each 12-h interval.

RESULTS

The initial mass of salamanders ranged from 4.9–8.5 g (Table 1), but mean mass did not differ significantly among treatments according to ANOVA (Habitat: $F_{3,33} = 1.20$, $P = 0.3239$; Burrow: $F_{1,33} = 0.92$, $P = 0.3446$). During the first 12 h, water loss (defined as proportional mass loss relative to initial, fully hydrated mass) varied significantly among habitat treatments ($F_{3,33} = 3.06$, $P = 0.0415$, $N = 41$). Salamanders in the CC-retained experienced significantly higher water loss than salamanders in the other three habitats (Scheffé's Test, $P < 0.05$). Salamanders without a burrow lost significantly more water than salamanders provided with a burrow during the first 12 h ($F_{1,33} = 8.78$, $P = 0.0056$). This effect was consistent across habitats; thus, there was no significant habitat \times burrow interaction ($F_{3,33} = 0.95$, $P = 0.4269$).

TABLE 1. Mean (SD) initial mass and snout-vent length (SVL) of juvenile Mole Salamanders (*Ambystoma talpoideum*) added to 0.025-m² enclosures in each habitat treatment. Half of the salamanders in each habitat were provided with artificial burrows ("Burrow"), and half did not have access to a burrow ("No Burrow").

Habitat treatment	N	Mean (SD) initial mass (g)		Mean (SD) SVL (mm)	
		Burrow	No burrow	Burrow	No burrow
Control	11	5.93 (0.45)	5.89 (0.49)	55.8 (1.2)	56.4 (1.7)
Thinning	10	6.67 (1.07)	6.13 (0.49)	57.8 (3.9)	56.2 (2.6)
Clearcut CWD retained	10	5.92 (0.45)	6.82 (0.72)	56.2 (1.1)	57.4 (2.6)
Clearcut CWD removed	10	6.15 (0.81)	6.69 (1.01)	57.0 (3.2)	58.4 (2.4)

The repeated-measures ANOVA was based only on animals that survived the experiment ($N = 32$). Over the entire three-day period, water loss changed significantly with time and varied according to habitat and burrow availability (Table 2, Fig. 2). Individual contrasts revealed significant time effects during only the first two nights (0–12 h: $F_{1,24} = 55.88$, $P < 0.0001$; 24–36 h: $F_{1,24} = 11.84$, $P = 0.0021$). Despite the significant effects of habitat and burrow availability in the multivariate ANOVA, neither of these factors significantly affected water loss within any individual time interval when judged against the adjusted α (all $P > 0.02$).

When available, burrows were heavily used as refuges; we found salamanders outside their burrow on only two occasions (1.6% of the relocations). Salamanders supplied with burrows in the control and thinning areas experienced no mortality over the 72-h period, whereas one salamander with a burrow died in the CC-removed after 72 h, and one salamander with a burrow died in the CC-retained after 60 h (Fig. 3).

Salamanders without burrows fared worse in overall survival, with the exception of the control, in which there were no mortalities (Fig. 3). One salamander without a burrow died in the

thinning, whereas three salamanders without burrows died in each of the clearcuts. Although the salamander in the thinning area died after 24 h, it was alive at 12 h after losing 27.5% of its mass. The two surviving *A. talpoideum* without burrows in the CC-removed were located next to a large clump of resprouting sweetgum that shaded their enclosures. They sustained maximum losses of 21.1% and 10.4% of their initial body mass during the 72-h period. Although mean water loss in the clearcuts appeared to level off and even decline after 48 h (Fig. 2), we consider this an artifact of the increasing mortality over time (Fig. 3), which resulted in the

TABLE 2. Results of the repeated-measures analysis of variance of the effects of habitat treatment, burrow availability, and their interaction on water loss of juvenile *Ambystoma talpoideum* over 72 h ($N = 32$).

	df	MS	F	P
Between-subject				
Habitat	3	0.0317	2.96	0.0524
Burrow	1	0.0683	6.38	0.0186
Habitat \times Burrow	3	0.0030	0.28	0.8391
Error	24	0.0107		
	df	Wilks' λ	F	P
Within-subject				
Time	6, 19	0.1402	19.43	< 0.0001
Time \times Habitat	18, 54	0.2345	2.02	0.0244
Time \times Burrow	6, 19	0.4254	4.28	0.0068
Time \times Habitat \times Burrow	18, 54	0.2587	1.85	0.0427

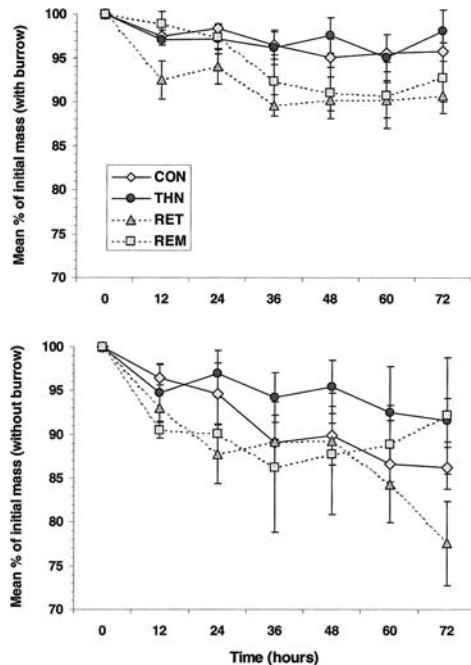


FIG. 2. Mean water loss (percent of initial mass \pm SE) for surviving juvenile *Ambystoma talpoideum* with burrows (top) and without burrows (bottom) in four habitat treatments over 72 h. Error bars are standard errors; CON = control, THN = thinning, RET = clearcut with coarse woody debris retained, REM = clearcut with coarse woody debris removed.

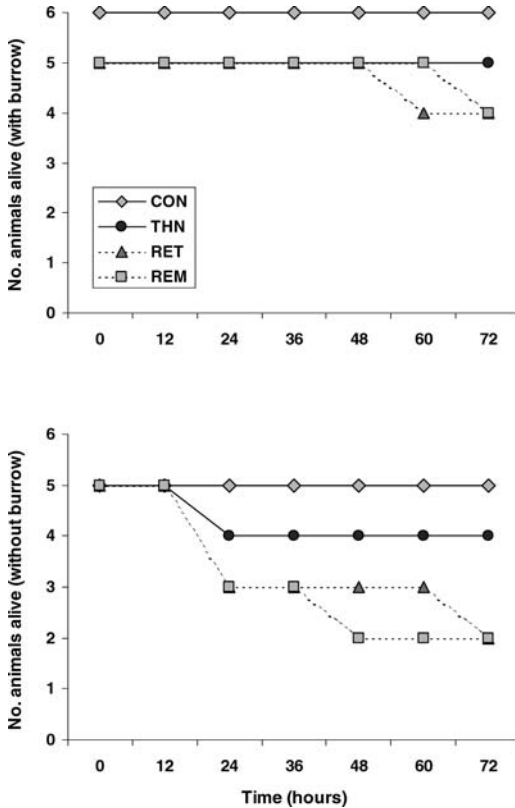


FIG. 3. Survivorship for juvenile *Ambystoma talpoideum* in enclosures with burrows (top) and without burrows (bottom) in four habitat treatments over 72 h. CON = control, THN = thinning, RET = clearcut with coarse woody debris retained, REM = clearcut with coarse woody debris removed.

censoring of individuals experiencing the most severe water loss.

The two surviving *A. talpoideum* without burrows in the CC-retained lost a maximum of 27.3% and 17.6% of their initial body mass during the 72-h period. We could not locate one salamander in the CC-retained at the final 72-h check. The salamander had access to a burrow and had maintained a fairly steady body mass throughout the experiment. We assumed it had escaped and was still alive, although no measurements could be collected for that individual at the 72-h mark. The four deceased animals in the CC-retained were covered with Fire Ants (*Solenopsis invicta*) when found. The deaths of three of these animals were probably the result of extreme desiccation. The fourth animal, however, seemed well hydrated and was found outside its burrow, suggesting that Fire Ants were the cause of death.

Initial soil moisture varied significantly among habitat treatments ($F_{3,33} = 33.34, P < 0.0001$) but

TABLE 3. Results of the repeated-measures analysis of variance of the effects of habitat treatment, burrow availability, and their interaction on soil moisture over 72 h ($N = 32$).

	df	MS	F	P
Between-subject				
Habitat	3	941.1380	32.83	< 0.0001
Burrow	1	217.3279	7.58	0.0111
Habitat × Burrow	3	119.9293	4.18	0.0162
Error	24	28.6674		
	df	Wilks' λ	F	P
Within-subject				
Time	6, 19	0.2501	9.50	< 0.0001
Time × Habitat	18, 54	0.3807	1.23	0.2746
Time × Burrow	6, 19	0.8191	0.70	0.6535
Time × Habitat × Burrow	18, 54	0.4180	1.09	0.3880

not according to burrow availability ($F_{1,33} = 1.68, P = 0.2035$), and there was no significant interaction ($F_{3,33} = 2.06, P = 0.1250$). At the start of the experiment, soils in the CC-removed were significantly moister than in the other three habitats (Scheffe's Test, $P < 0.05$). Because no measurable precipitation fell during the experiment, the soils gradually dried, resulting in a significant effect of time in the repeated-measures ANOVA (Table 3). Soil moisture over the entire three-day period varied significantly among habitats, remaining consistently higher in the CC-removed (Table 3; Fig. 4). Soils in enclosures with burrows tended to be slightly drier. There were no significant correlations between soil moisture and water loss in any time periods ($P > 0.05$).

The control had the lowest 72-h average temperature as well as the highest average relative humidity of all the habitat treatments (Table 4). Mean daily maximum temperatures in the clearcuts exceeded those in the control by 2.0°C and the thinning area by 7.1°C. The CC-removed had the lowest average relative humidity, although mean humidity varied by less than 4% among habitats (Table 4).

DISCUSSION

Canopy removal and other habitat changes resulting from clearcutting greatly increased the risk of mortality because of desiccation for juvenile *A. talpoideum* in our study. Juvenile *A. talpoideum* in the clearcut treatments suffered 60% mortality in the absence of a burrow. Proximity to shade-providing shrubs may have facilitated survival of remaining salamanders in the clearcuts. The only mortality not in a clearcut was a juvenile without a burrow in the thinning treatment. Thus, salamanders in the recently thinned

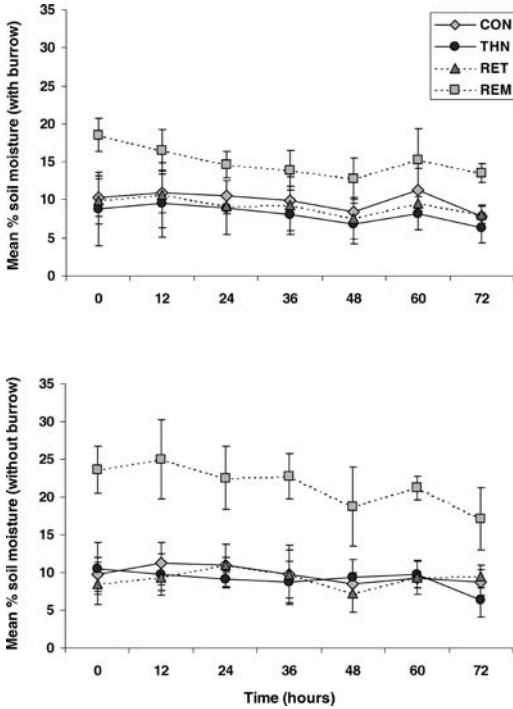


FIG. 4. Mean soil moisture over 72 h in each habitat treatment in enclosures with burrows (top) and without burrows (bottom). Error bars are standard deviations; CON = control, THN = thinning, RET = clearcut with coarse woody debris retained, REM = clearcut with coarse woody debris removed.

stand experienced only a slightly elevated risk of desiccation compared to the unharvested control. We caution that our scope of inference is limited because we did not incorporate replication at the stand level or over time. Our experiment was conducted in July, which is within the migratory period for this species. Juvenile *A. talpoideum* may metamorphose and leave wetlands any time between May and September (Gibbons and Semlitsch 1991), depending on annual and site-specific variation in environmental conditions.

As demonstrated for other amphibians (e.g., *Bufo marinus*; Seebacher and Alford, 2002), the presence of suitable shelters greatly mitigated

water loss. In clearcut treatments, the mean maximum dehydration rate in a 12-h period for salamanders with burrows was 80.9 mg/g, 36% less than for salamanders without burrows (125.6 mg/g). Having access to a burrow prevented salamanders from reaching lethal levels of desiccation in at least 19 of 21 (~90%) cases. The death of one salamander with a burrow was likely caused by predation by Fire Ants, which invaded several enclosures in the CC-retained treatment. Increased risk of Fire Ant predation may be another consequence of habitat disturbance for salamanders inhabiting forests of the southeastern United States. The importance of burrows suggests that, for ambystomatids, the time required for habitat quality to be restored following logging depends in part on how compacted the soil is (thus whether salamanders can dig their own burrows), as well as how quickly burrows are reestablished via small mammal activity.

Although ambystomatids lose water at slower rates than plethodontids (Spight, 1968), our results show they are still subject to high rates of desiccation in unsuitable habitats. Six *A. talpoideum* survived after losing more than 20% of their initial body mass. Three salamanders survived after losing more than 27% of their initial body mass. The most water loss tolerated by an *A. talpoideum* in a 12-h period was 28.9%. In laboratory studies, Heatwole and Lim (1961) found that *Plethodon cinereus* can also survive a maximum water loss of 28.9%. Pough and Wilson (1970) determined the average lethal limits for juvenile *A. maculatum* to be 36% of their original body weight (range 23–45%).

The small size of our enclosures prevented us from testing whether retention of CWD mitigates the risk of desiccation. Salamanders in the CC-retained experienced higher dehydration rates than those in the CC-removed. Salamanders in the CC-removed may have benefited from the higher soil moisture in that treatment, although we found no significant correlations between soil moisture and water loss. Although recently harvested sites often have higher soil moisture (e.g., Ash, 1997; Chazal and Niewiarowski, 1998) due to reduced evapotranspiration following tree

TABLE 4. Mean (SD) air temperature and relative humidity in the four habitat treatments over the 72 h of the experiment. CWD = coarse woody debris.

Habitat treatment	Temperature (°C)			Mean relative humidity (%)
	72-h average	Mean daily maximum	Mean daily minimum	
Control	27.7 (6.0)	42.6 (4.0)	21.2 (0.4)	77.6 (7.8)
Thinning	28.1 (5.4)	37.5 (2.0)	21.3 (0.7)	76.4 (11.3)
Clearcut CWD retained	29.9 (9.1)	44.6 (2.3)	19.8 (1.0)	75.4 (7.8)
Clearcut CWD removed	30.3 (8.8)	44.6 (1.0)	20.2 (0.7)	74.3 (7.7)

removal (Williams 1998), this does not account for the difference between our two clearcuts, which may have differed slightly in soil type or compaction caused by skidding.

Dehydration rates of amphibians are determined by the interaction of many factors, including temperature. Dehydration rate increases as temperature increases if relative humidity is held constant (Moore and Sievert, 2001). The high daytime temperatures in the clearcut treatments (Table 4) presumably resulted in greater desiccation, which in turn made animals more susceptible to heat stress. Desiccation lowers an individual's critical thermal maximum, creating a synergistic interaction between temperature and dehydration that poses an additional threat to amphibians in harsh environments (Pough and Wilson, 1970).

Because salamanders migrate at night, when temperature and humidity levels are relatively favorable, an interesting question becomes what cues they use to select habitat. Juvenile Spotted Salamanders (*A. maculatum*) have been shown to select wet substrates over dry ones in laboratory choice tests (Rittenhouse et al., 2004). If salamanders use substrate moisture as a cue indicating habitat suitability, then they may travel into clearcut areas at night and experience high rates of desiccation and mortality the following day. However, *A. talpoideum* tend to migrate only during or immediately after rainfall, when differences in soil moisture are probably minimal (Semlitsch, 1981, 1985). Rittenhouse et al. (2004) found that, moisture levels being equal, juvenile *A. maculatum* discriminated against soil from old fields, spending more time on soil from forested sites. They concluded that ambystomatids must rely heavily on olfactory cues but probably use a variety of information when selecting habitat under natural conditions. Juvenile *A. maculatum* oriented toward forest over old-field habitat in choice tests conducted on habitat edges (Rothermel and Semlitsch, 2002), but the tendency of juvenile *A. talpoideum* to enter clearcut areas and the cues dictating their migratory behavior have not been studied.

If emigrating juveniles fail to avoid recently harvested areas, then their probability of survival hinges on their rate of travel, physiological tolerances, and availability of refuges. Semlitsch (1981) found that newly metamorphosed *A. talpoideum* traveled through undisturbed habitat at a median speed of 3.9 m/h. At this rate, it would have taken a constantly moving juvenile over 57 h to emigrate through our 3.8-ha clearcuts (Fig. 1). Because ambystomatids move only at night, and only when it is raining or the leaf litter is wet (Semlitsch, 1981), the trip would require at least seven days. This trip could be shortened if juvenile ambystomatids exhibit com-

pensatory behavior by traveling faster in unfavorable habitats, as demonstrated in a plethodontid salamander (Rosenberg et al., 1998). However, access to suitable refuges would clearly remain a critical factor determining their migratory success.

Despite high temperatures during the day, patterns of water loss we observed suggest that most water loss occurred during the first two nights. We believe differences in activity level over time may explain this result and highlight the importance of behavior in determining susceptibility to environmental stressors. Salamanders were probably active during the first two nights in the enclosures, incurring high rates of evaporative water loss. During the day and as dehydration became more severe, they probably increased burrow use, if that was an option, or adopted water-conserving behaviors, such as remaining inactive, seeking shade, and positioning themselves to reduce the amount of exposed surface area (Semlitsch, 1983; Rohr and Madison, 2003). Moseley et al. (2004) found that *A. talpoideum* were capable of exploiting different microhabitats depending on what was available. Despite having access to burrows, salamanders in their study exhibited increased surface activity in the absence of pine litter, implying that severe conditions stimulated salamanders to move in search of better habitat. Likewise, if the salamanders in our study had not been confined, they might have been able to find suitable microhabitats (e.g., under logs, in clumps of vegetation) in clearcut areas even if many burrows were destroyed during logging. However, salamanders subjected to dehydrating conditions for long periods would incur high costs in terms of reduced growth (Petranka, 1994) and potentially increased risks of predation (Rohr and Madison, 2003). Although comparing physiological tolerances with environmental parameters may be the first step toward predicting the sensitivity of amphibians to habitat alteration, a complete picture can only be gained by incorporating how animals respond behaviorally to elevated risks of desiccation and predation in disturbed habitats.

Acknowledgments.—We thank J. Segar, R. Williams, D. Imm, R. Crais, and D. Wilson of the Savannah River unit of the USDA Forest Service for facilitating the LEAP study by overseeing timber harvesting and providing other critical assistance. We are also grateful to B. Metts, B. Boone, B. Todd, C. Winne, K. Andrews, L. Steadman, and others at SREL for their help in the lab and the field. The thoughtful comments of J. W. Gibbons, S. B. Castleberry, J. D. Willson, and two anonymous reviewers greatly improved the manuscript. Salamanders were captured under scientific research permit 56-2003 from

the South Carolina Department of Natural Resources, and experiments were conducted under University of Georgia IACUC approval A2003-10167. Funding for this research was provided by the National Science Foundation (Awards DEB-0242874 and DBI-0139572) and the Savannah River Ecology Laboratory under Financial Assistance Award DE-FC09-96SR18-546 between the University of Georgia and the U.S. Department of Energy.

LITERATURE CITED

- ASH, A. N. 1997. Disappearance and return of plethodontid salamanders to clearcut plots in the southern Blue Ridge Mountains. *Conservation Biology* 11:983-989.
- CHAZAL, A. C., AND P. H. NIEWIAROWSKI. 1998. Responses of mole salamanders to clearcutting: using field experiments in forest management. *Ecological Applications* 8:1133-1143.
- CROMER, R. B., J. D. LANHAM, AND H. H. HANLIN. 2002. Herpetofaunal response to gap and skidder-rut wetland creation in a southern bottomland hardwood forest. *Forest Science* 48:407-413.
- DEMAYNADIER, P. G., AND M. L. HUNTER JR. 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. *Environmental Reviews* 3:230-261.
- DOUGLAS, M. E., AND B. L. MONROE JR. 1981. A comparative study of topographical orientation in *Ambystoma* (Amphibia: Caudata). *Copeia* 1981:460-463.
- FACCIO, S. D. 2003. Postbreeding emigration and habitat use by Jefferson and spotted salamanders in Vermont. *Journal of Herpetology* 37:479-489.
- GIBBONS, J. W., AND R. D. SEMLITSCH. 1991. Guide to the Reptiles and Amphibians of the Savannah River Site. Univ. of Georgia Press, Athens.
- HEATWOLE, H., AND K. LIM. 1961. Relation of substrate moisture to absorption and loss of water by the salamander, *Plethodon cinereus*. *Ecology* 42: 814-819.
- MADISON, D. M. 1997. The emigration of radio-implanted Spotted Salamanders, *Ambystoma maculatum*. *Journal of Herpetology* 31:542-551.
- MOORE, C. M., AND L. M. SIEVERT. 2001. Temperature-mediated characteristics of the Dusky Salamander (*Desmognathus fuscus*) of southern Appalachia. *Journal of Thermal Biology* 26:547-554.
- MOSELEY, K. R., S. B. CASTLEBERRY, AND W. M. FORD. 2004. Coarse woody debris and pine litter manipulation effects on movement and microhabitat use of *Ambystoma talpoideum* in a *Pinus taeda* stand. *Forest Ecology and Management* 191:387-396.
- PETRANKA, J. W. 1994. Response to impact of timber harvesting on salamanders. *Conservation Biology* 8:302-304.
- POUGH, F. H., AND R. E. WILSON. 1970. Natural daily temperature stress, dehydration, and acclimation in juvenile *Ambystoma maculatum* (Shaw) (Amphibia: Caudata). *Physiological Zoology* 43:194-205.
- RAYMOND, L. R., AND L. M. HARDY. 1991. Effects of a clearcut on a population of the Mole Salamander, *Ambystoma talpoideum*, in an adjacent unaltered forest. *Journal of Herpetology* 25:509-512.
- REGOSIN, J. V., B. S. WINDMILLER, AND J. M. REED. 2003. Influence of abundance of small-mammal burrows and conspecifics on the density and distribution of Spotted Salamanders (*Ambystoma maculatum*) in terrestrial habitats. *Canadian Journal of Zoology* 81:596-605.
- RITTENHOUSE, T. A. G., M. C. DOYLE, C. R. MANK, B. B. ROTHERMEL, AND R. D. SEMLITSCH. 2004. Substrate cues influence habitat selection by Spotted Salamanders. *Journal of Wildlife Management* 68: 1151-1158.
- ROHR, J. R., AND D. M. MADISON. 2003. Dryness increases predation risk in efts: support for an amphibian decline hypothesis. *Oecologia* 135: 657-664.
- ROSENBERG, D. K., B. R. NOON, J. W. MEGAHAN, AND E. C. MESLOW. 1998. Compensatory behavior of *Ensatina eschscholtzii* in biological corridors: a field experiment. *Canadian Journal of Zoology* 76:117-133.
- ROTHERMEL, B. B., AND R. D. SEMLITSCH. 2002. An experimental investigation of landscape resistance of forest versus old-field habitats to emigrating juvenile amphibians. *Conservation Biology* 16:1324-1332.
- SCHEINER, S. M., AND J. GUREVITCH (eds). 2001. Design and Analysis of Ecological Experiments. 2nd ed. Oxford Univ. Press, New York.
- SEEBACHER, F., AND R. A. ALFORD. 2002. Shelter microhabitats determine body temperature and dehydration rates of a terrestrial amphibian (*Bufo marinus*). *Journal of Herpetology* 36:69-75.
- SEMLITSCH, R. D. 1981. Terrestrial activity and summer home range of the Mole Salamander (*Ambystoma talpoideum*). *Canadian Journal of Zoology* 59: 315-322.
- . 1983. Burrowing ability and behavior of salamanders of the genus *Ambystoma*. *Canadian Journal of Zoology* 61:616-620.
- . 1985. Analysis of climatic factors influencing migrations of the salamander *Ambystoma talpoideum*. *Copeia* 1985:477-489.
- SEMLITSCH, R. D., AND J. R. BODIE. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. *Conservation Biology* 17:1219-1228.
- SPIGHT, T. M. 1968. The water economy of salamanders: evaporative water loss. *Physiological Zoology* 41:195-203.
- SPOTILA, J. 1972. Role of temperature and water in the ecology of lungless salamanders. *Ecological Monographs* 42:95-125.
- WILLIAMS, T. M. 1998. Hydrology. In M. G. Messina and W. H. Conner (eds.), *Southern Forested Wetlands: Ecology and Management*, pp. 103-122. Lewis Publishers, Boca Raton, FL.
- WISELY, S. M., AND R. T. GOLIGHTLY. 2003. Behavioral and ecological adaptations to water economy in two plethodontid salamanders, *Ensatina eschscholtzii* and *Batrachoseps attenuatus*. *Journal of Herpetology* 37:659-665.

Accepted: 30 August 2005.