

Communications

Ecological Applications, 18(2), 2008, pp. 283–289
© 2008 by the Ecological Society of America

EFFECTS OF TIMBER HARVESTING ON POND-BREEDING AMPHIBIAN PERSISTENCE: TESTING THE EVACUATION HYPOTHESIS

RAYMOND D. SEMLITSCH,¹ CHRISTOPHER A. CONNER, DANIEL J. HOCKING, TRACY A. G. RITTENHOUSE,
AND ELIZABETH B. HARPER

Division of Biological Sciences, 105 Tucker Hall, University of Missouri, Columbia, Missouri 65211-7400 USA

Abstract. Numerous studies have documented the decline of amphibians following timber harvest. However, direct evidence concerning the mechanisms of population decline is lacking and hinders attempts to develop conservation or recovery plans and solutions for forest species. We summarized the mechanisms by which abundance of amphibians may initially decline following timber harvest into three testable hypotheses: (1) mortality, (2) retreat, and (3) evacuation. Here, we tested the evacuation hypothesis within a large-scale, replicated experiment. We used drift fences with pitfall traps to capture pond-breeding amphibians moving out of experimental clearcut quadrants and into control quadrants at four replicate arrays located within the Daniel Boone Conservation Area on the upper Ozark Plateau in Warren County, Missouri, USA. During the preharvest year of 2004, only 51.6% of the 312 individuals captured were moving out of pre-clearcut quadrants, and movement did not differ from random. In contrast, during both postharvest years of 2005 and 2006, the number of captures along the quadrant edge increased, and a higher proportion of individuals (59.9% and 56.6%, respectively, by year) were moving out of clearcut quadrants than entering. Salamanders moved out of clearcuts in large percentages (*Ambystoma annulatum*, 78.2% in 2005, 78.2% in 2006; *A. maculatum*, 64.0% in 2005, 57.1% in 2006). Frogs and toads also moved out of clearcut quadrants, but in lower percentages (*Bufo americanus*, 59.6% in 2005, 53.3% in 2006; *Rana clamitans*, 52.7% in 2006). Salamanders moved out of clearcuts with low-wood treatments more than out of clearcuts with high-wood treatments. Movement of salamanders out of clearcuts was independent of sex. Estimated movement out of clearcuts represented between 8.7% and 35.0% of the total breeding adults captured for two species of salamanders. Although we recognize that some portion of the amphibian population may retreat underground for short periods and others may not survive the effects of timber harvest, these data are the first direct evidence showing that individuals are capable of leaving clearcuts and shifting habitat use.

Key words: *Ambystoma spp.*; anuran; clearcut; evacuation hypothesis; forest management; frogs; mortality; salamanders.

INTRODUCTION

In many parts of the world, the loss of habitat associated with the extraction of natural resources, such as timber, is a major threat to animal populations. Despite a general agreement among biologists about the negative effects of timber harvest on amphibian abundance (e.g., Bury 1983, Noss 1989, Petranka et al. 1994, de Maynadier and Hunter 1995, Grialou et al. 2000, Knapp et al. 2003), there are scant data and even

some conflicting views concerning the mechanisms of population decline, especially among lungless woodland salamanders (e.g., Ash and Bruce 1994, Ash 1997, Petranka 1999). A summary of mechanisms across studies indicates three general hypotheses: (1) mortality hypothesis, which assumes that abundance in clearcuts declines due to mortality from lack of food or refuge from desiccation and an inability to evacuate; (2) retreat hypothesis, which assumes that individuals remain in the clearcuts but move to more suitable underground habitat where individuals survive for limited periods on minimal resources and energy stores, perhaps reduce activity, and re-emerge as vegetative recovery proceeds; and (3) evacuation hypothesis, which assumes that

Manuscript received 24 May 2007; revised 21 August 2007; accepted 24 September 2007. Corresponding Editor: R. A. Relyea.

¹ E-mail: SemlitschR@missouri.edu

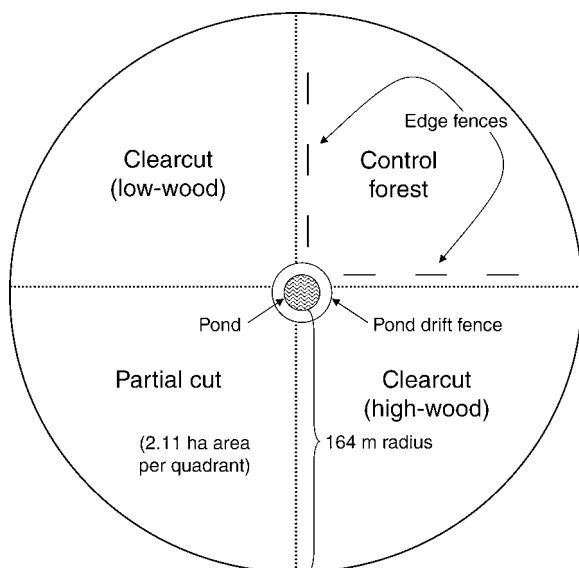


FIG. 1. A schematic diagram of the experimental forest treatments, central breeding pond, and edge fences used to sample amphibians.

individuals leave clearcuts in response to increasing temperature, reduced moisture and food, and select more suitable habitat nearby.

We currently have some direct support for the mortality hypothesis for several pond-breeding amphibians. Experimental studies have shown that when amphibians are confined to enclosures in clearcuts they exhibit higher desiccation rates and lower survival than those confined to closed canopy forest (Rothermel and Semlitsch 2006, Todd and Rothermel 2006; E. B. Harper and R. D. Semlitsch, *unpublished manuscript*; T. A. G. Rittenhouse, E. B. Harper, L. R. Rehard, and R. D. Semlitsch, *unpublished manuscript*). However, enclosure studies cannot determine if amphibians would choose to remain in these unsuitable habitats or would evacuate clearcuts to reduce the risk of desiccation and mortality. Distinguishing among mechanisms of decline is important because in the case of mortality, individuals are permanently lost and the population declines. Yet, if the retreat or evacuation hypotheses are important, individuals may only be temporarily absent from the habitat as reflected by low abundance, but could return, and the population may not decline permanently. Thus, distinguishing among the mechanisms of decline is required to affect solutions for reversing declines and the recovery of amphibian populations, especially those already threatened or endangered. Amphibians are the most threatened vertebrate taxa globally, with one-third, or 1896 species, currently threatened with extinction (Stuart et al. 2004).

We acknowledge that the three hypotheses are likely not mutually exclusive. Declines in abundance of amphibians may be due to a combination of factors, depending on habitat alteration type, time to habitat

recovery, and species of concern. Here, we present a large-scale, replicated experiment designed to monitor the movement of pond-breeding amphibians out of clearcuts to test the evacuation hypothesis. We use the term “evacuation” because it is not known whether individuals are dispersing to new populations, dispersing and subsequently suffering mortality, or emigrating and will eventually return. Providing a rigorous test of the evacuation hypothesis at this time is crucial to direct current mechanistic studies of population declines to help understand how alternative timber extraction practices or the scale of management might ameliorate detrimental effects on amphibian populations and to balance resource extraction with the urgent need for conservation of biodiversity.

METHODS

Our experiment was conducted as a part of the National Science Foundation (NSF) Collaborative Project “Land-use Effects on Amphibian Populations” (LEAP) underway at the University of Missouri to test amphibian responses to forest management treatments. Four replicate arrays were located within the Daniel Boone Conservation Area (1424.5 ha) on the upper Ozark Plateau in Warren County, Missouri, USA. The arrays were spaced 0.38–1.35 km apart and situated in mature (80–100 years old), second-growth oak (*Quercus* spp.) and hickory (*Carya* spp.) overstory, with varying amounts of sugar maple (*Acer saccharum*) in the understory. Each array was centered on a natural breeding pond and selected from ~40 ponds in the conservation area to meet our criteria of being >300 m apart and similar in size (high water area 160–330 m²). These ponds were originally built for other wildlife (e.g., turkey and deer), are between 27 and 47 years old, and have naturally colonized breeding populations of up to 16 species of amphibians (D. J. Hocking, T. A. G. Rittenhouse, B. Rothermel, J. Johnson, C. A. Conner, E. B. Harper, and R. D. Semlitsch, *unpublished manuscript*).

Four forestry treatments were applied at each array and consisted of a clearcut with high levels of coarse down wood (high-wood), a clearcut with less coarse down wood (low-wood), a partial-canopy removal, and a control forest (Fig. 1). The two clearcut treatments were designed to test the potential for retaining more wood to mitigate negative effects of clear-cutting on amphibians. Coarse down wood has the potential to benefit amphibians by providing moisture-retaining refugia (e.g., Herbeck and Larsen 1999). In the clearcuts, all marketable timber >25 cm diameter at breast height (dbh) was removed for sale. The clearcuts with the high wood had the remaining trees (<25 cm dbh) felled and left on the ground. In the clearcuts with low wood, the remaining trees (<25 cm dbh) were girdled and left standing to reduce the down wood on the ground. The partial-cut treatment was thinned by girdling or felling poor quality trees and undesirable species (primarily

Acer saccharum) to a basal area of 13.8 m²/ha that was ~60% of the stocking level. This type of partial-cut treatment is a common part of timber stand improvement in central Missouri. However, we did not address movement patterns in or out of the partial harvest quadrants in this study.

To delineate the treatments around each pond, a circular area with a radius of 164 m from a pond was divided into four equal quadrants (~2.11 ha each). A radius of 164 m was used because it is proposed to encompass 95% of the core terrestrial habitat needed by breeding populations of six species of salamanders in the area (Semlitsch 1998). The control treatment was randomly assigned to one quadrant, the two clearcut treatments were randomly assigned to the two quadrants adjacent to the control, and the partial treatment was fixed in the quadrant opposite the control (Fig. 1). All experimental forest treatments were harvested between March 2004 and January 2005.

We completely encircled the central breeding ponds at the four arrays with a drift fence and pitfall traps during October–December 2003. This drift fence enabled us to census the breeding population of each species each year. The drift fence was constructed of aluminum flashing buried ~30 cm into the ground and extending 60 cm above ground (Gibbons and Semlitsch 1982). Pitfall traps consisted of plastic plant pots (23 cm diameter, 24 cm deep) buried such that the top is flush with the ground and against the fence. Traps were paired along each side of the fence every 3.0 m. A wooden board was held 4 cm above each trap to reduce predation and a moist sponge was placed in the bottom of each trap to reduce desiccation.

To test whether amphibians were moving out of clearcut quadrants into controls after harvesting, we installed six additional drift fences (each 15.4 m long) between control and clearcut quadrants at each array (hereafter called “edge fences”; Fig. 1) to capture individuals moving laterally in the terrestrial habitat (i.e., perpendicular to expected migrations to and from the breeding pond). We placed drift fences 1–2 m within the control treatment quadrant parallel to clearcut edges on each side of the control (total of 46.2 m or 28.2% of the total length of each side; Fig. 1). Throughout each year (2004, 2005, 2006; February–November), pitfall traps at pond and edge fences were checked every 1–3 days, depending on amphibian activity and rainfall. At all arrays we recorded date, species, sex, age class, and direction of movement for all individuals captured in our traps and released them on the opposite side of the fence, the presumed direction of travel.

We used total number of adults captured exiting the complete pond fences to approximate breeding population sizes of select species and to assess what portion of the total captures might be leaving clearcuts. To assess movement out of clearcuts, we first tested captures using pre-harvest data from edge fences in 2004 against the random expected ratio of 50% in and 50% out of the

clearcut quadrants. The spring and early-summer migration period of 2004 had above average rainfall (49.7 cm) compared to the 20-year mean (44.3 cm) and was reflected in high captures of breeding adults in drift fences at all ponds. Thus, we considered the 2004 edge data to be robust and reflect the typical “control” condition for lateral movement between experimental quadrants prior to timber harvest. Under these conditions, our data showed subtle biases in capture probabilities in one direction at edge fences that was due to variation in landscape features (i.e., slope) that channel movements consistently from year to year (based on decades of drift fence studies; R. D. Semlitsch, *personal observation*), but have no relationship to our randomly assigned forest treatments. Even when we tested post-harvest data each year using the random expected ratio of 50:50, the overall amphibian and salamander movement was still significantly biased out of clearcuts. However, we used the preharvest data from edge fences in 2004 to more accurately establish expected values (proportion of total captures) for all amphibians moving laterally in and out of clearcut quadrants. We totaled amphibian captures at edge fences during post-harvest years (2005 and 2006) in and out of clearcuts for each array to test against expected captures determined from observed 2004 ratios. Total amphibian captures (primarily four species) at edge fences for each year were then tested using log-likelihood *G* tests (Zar 1974). Dependence of drift fences along edges or within arrays, and high variance in captures precluded using variance analysis. Additional *G* tests were conducted separately for anurans and salamanders, postharvest years, coarse woody debris (CWD) treatments, sex, and by individual species where sample sizes were adequate to address species differences in responses: adult *Ambystoma annulatum* (ringed salamander; see Plate 1), adult *Ambystoma maculatum* (spotted salamander), adult and juvenile *Bufo americanus* (American toad), and juvenile *Rana clamitans* (green frog).

RESULTS

A total of 1661 individuals representing primarily four species of amphibians were captured in edge fences during the three years of our study (Table 1). During the preharvest year of 2004, only 51.6% of the 312 individuals captured were moving out of clearcut quadrants, and movement did not differ from that expected at random. Salamanders were captured more frequently than anurans, and salamanders moved into clearcut quadrants (*Ambystoma annulatum* 62%, *A. maculatum* 52.1%) and anurans moved out of clearcut quadrants prior to cutting (*Bufo americanus* 67.6%, *Rana clamitans* 64.9%; Table 1). However, only the combined total of anurans and *B. americanus* alone differed from random movement (Table 1).

In contrast, during both postharvest years of 2005 and 2006, more individuals ($n = 736$ and $n = 613$,

TABLE 1. Total amphibian captures from four replicate study arrays at the Daniel Boone Conservation Area, Missouri, USA.

Taxon	2004 (preharvest)		2005 (1 yr postharvest)		2006 (2 yr postharvest)	
	In:out	P^\dagger	In:out	P^\ddagger	In:out	P^\ddagger
Total amphibians	151:161	0.571	295:441	<0.001	266:347	0.013
Salamanders	124:112	0.435	107:243	<0.001	90:151	<0.001
<i>Ambystoma annulatum</i>	31:19	0.090	39:140	<0.001	17:61	<0.001
<i>Ambystoma maculatum</i>	75:69	0.617	40:71	<0.001	51:68	0.044
Anurans	27:49	0.012	188:198	<0.001	176:196	<0.001
<i>Bufo americanus</i>	12:25	0.033	38:56	0.010	43:49	0.003
<i>Rana clamitans</i>	13:24	0.071	148:138	<0.001	130:145	<0.001

Note: Cumulative numbers of individuals moving into and out of clear-cut quadrants are shown for each species or group of amphibians for each year of the study.

† P values generated from a χ^2 ratio using an expected ratio of 1:1, in:out.

‡ P values generated from an adjusted χ^2 ratio using observed amphibian movements in and out of clearcuts for each array tested against expected captures determined from observed 2004 ratios.

respectively) were captured at edge fences, and a higher percentage of individuals (59.9% and 56.6%, respectively) were moving out of clearcut quadrants. When we analyzed the capture data by species, salamanders were now moving out of clearcuts in highly significant percentages (*A. annulatum*, 78.2% in 2005, 78.2% in 2006; *A. maculatum*, 64.0% in 2005, 57.1% in 2006; Table 1). Anurans were also moving out of clearcut quadrants (*B. americanus*, 59.6% in 2005, 53.3% in 2006; *Rana clamitans*, 52.7% in 2006; Table 1), but not in as high percentages as salamanders. In only one case, *Rana clamitans* were moving into clearcuts in higher percentages (51.7% in 2005; Table 1).

We also detected a significant year effect ($\chi^2 = 11.2$, $P = 0.0008$), with more individuals and higher percentages moving out of clearcuts in 2005 ($n = 736$, 59.9%) than in 2006 ($n = 613$, 56.6%) for all species, but especially for salamanders (Table 1). When we tested the two species of salamanders that were most abundant, combining 2005 and 2006 data, a higher portion of individuals moved out of low-wood treatments and a lower portion moved out of high-wood treatments than would be expected at random ($\chi^2 = 61.0$, $P < 0.0001$). The percentage of individuals moving out of clearcuts was independent of sex ($\chi^2 = 2.11$, $P = 0.146$). When we used the total number of captured breeding adults to approximate minimum population size for the two primary species of salamanders and to estimate what percentage of individuals were leaving the two clearcut quadrants, we found that between 10.6% and 35.0% of *A. annulatum* and 8.7% and 30.0% of *A. maculatum* were leaving clearcuts each year (Table 2).

DISCUSSION

We report experimental evidence to support the hypothesis that evacuation plays a role in the initial decline in abundance of pond-breeding amphibians in terrestrial habitats following clearcut timber harvest at our sites in Missouri. We found that salamanders responded strongly by leaving clearcuts, but anurans demonstrated a weak or reverse response, that move-

ment out of clearcuts was greater during the first postharvest year than the second year, and that the presence of a higher amount of coarse down wood reduces evacuation. Although we recognize that some amphibians may retreat underground for short periods and others may die as a result of the clearcut harvest, especially small juveniles (e.g., Rothermel and Semlitsch 2006, Todd and Rothermel 2006), our data are the first experimental evidence showing that individuals of some species actually leave altered habitats and move into more suitable habitat.

We suggest that the high temperatures associated with removal of the overstory canopy (Geiger 1971, Keenan and Kimmins 1993, Chen et al. 1999) contribute to a net

TABLE 2. Total captures of breeding adults of two species of salamanders (*Ambystoma annulatum* and *A. maculatum*) totaled over four ponds for each year.

Species	Breeding year		
	2004	2005	2006
<i>A. annulatum</i>	4072	4200	2941
Number in clearcuts †	1784	1827	1474
Net number leaving ‡		101	44
Adjusted min. percentage leaving §		19.6	10.6
Adjusted max. percentage leaving $^ $		35.0	18.9
<i>A. maculatum</i>	2722	1695	2492
Number in clearcuts †	1416	848	1246
Net number leaving ‡		31	17
Adjusted min. percentage leaving §		16.8	8.7
Adjusted max. percentage leaving $^ $		30.0	15.6

Note: In postharvest years, the captures in clearcuts, net number of individuals captured leaving clearcuts, and the adjusted minimum and maximum percentage leaving clearcuts are shown.

† Based on total captures exiting ponds into the two clearcut quadrants at each pond.

‡ Based on captured individuals moving in and out of clearcuts presented in Table 1.

§ Adjusted to account for lateral movements and potential captures at drift fences encompassing 28.2% of each edge only between control and clearcut quadrants.

$^||$ Adjusted to account for lateral movements and potential captures at drift fences encompassing 15.8% of all possible clearcut edges along forest habitat.



PLATE 1. The ringed salamander (*Ambystoma annulatum*) is an endemic species of the Ozark Plateau, Warren County, Missouri, USA. Individuals of this species inhabit oak–hickory forests and breed in fishless ponds in autumn. Photo credit: D. J. Hocking.

movement of amphibians out of clearcut habitats and into nearby forested control habitats. For example, E. B. Harper and R. D. Semlitsch (*unpublished manuscript*) have shown that survival of juvenile woodfrogs and toads in terrestrial pens in the same experimental forest arrays is most closely negatively associated with maximum substrate temperature. Substrate temperatures under the leaf litter during the hottest months of the year reached high levels in clearcut quadrants (mean maximum = $46.3^{\circ} + 1.58^{\circ}\text{C}$ [mean + SE] in low down wood and $47.2^{\circ} + 1.49^{\circ}\text{C}$ high down wood) relative to control quadrants ($33.87^{\circ} + 0.76^{\circ}\text{C}$; E. B. Harper and R. D. Semlitsch, *unpublished manuscript*; Table 2) and likely exceeded the maximum critical limits for any amphibians (maximum recorded amphibian body temperatures 36° – 41°C ; Hutchison and Dupre 1992). Because the presence of high amounts of down wood reduced the proportion of salamanders leaving clearcuts at our sites in Missouri, we argue that down wood enhanced moisture and moderated temperature levels in slash piles following clearcutting and improved amphibian habitat as suggested in other studies (e.g., Herbeck and Larsen 1999). In support, T. A. G. Rittenhouse, E. B. Harper, L. R. Rehard, and R. D. Semlitsch (*unpublished manuscript*) showed that piles of slash left after clearcut harvest ameliorated the effects of water loss and reduced desiccation mortality relative to open areas on clearcuts in three species of frogs in Missouri.

We found that salamanders had a stronger evacuation response to clearcutting than anurans. Although speculative, we propose several likely reasons. Salamanders as a whole are more forest-associated than many anurans, especially our dominant frog species *R. clamitans*. Salamanders may be more sensitive to canopy removal, have a lower threshold to changes in temperature,

moisture or both, and are able to respond behaviorally by leaving clearcuts. We have previously shown that adult *A. maculatum* can detect grassland–forest edges during breeding migrations, reverse direction, and avoid entering unsuitable grassland habitats (Rittenhouse and Semlitsch 2006). In fact, part of the trend we observed for both salamanders between pre- and post-cut years (Table 1) indicates more total captures at edge fences, but somewhat lower numbers of individuals entering clearcuts (i.e., avoidance), which helped increase the proportion of individuals leaving clearcuts, especially for *A. maculatum* (Table 1). Second, salamanders may have survived in greater numbers both during and following timber harvest. Mole salamanders of the family Ambystomatidae use small-mammal burrows some distance underground as refugia (Madison 1997, Faccio 2003). They may have been able to retreat underground, protected from mechanical disturbance, and wait for suitable weather conditions to evacuate clearcuts. Further, the restriction of surface movement to the cool and wet months of early spring or late fall at our sites (D. J. Hocking, T. A. G. Rittenhouse, B. Rothermel, J. Johnson, C. A. Conner, E. B. Harper, and R. D. Semlitsch, *unpublished manuscript*) could have minimized exposure to dry and hot conditions experienced during summer in clearcuts and presumably reduced their risk of mortality. Other than toads, frogs may not burrow or use underground refuges such as rodent burrows as readily as salamanders. Post-breeding migrations of many anurans occur after salamanders (D. J. Hocking, T. A. G. Rittenhouse, B. Rothermel, J. Johnson, C. A. Conner, E. B. Harper, and R. D. Semlitsch, *unpublished manuscript*) when temperatures are higher and drier, possibly making evacuation risky and resulting in higher mortality than salamanders. Wood frogs (*R. sylvatica*)

are an exception among the anurans in our study; they are strongly forest associated and migrate very early in spring along with spotted salamanders. Thus, our two most abundant anurans (American toads and green frogs) may have been more susceptible to mortality from clear-cutting than the salamanders and, subsequently, this may explain their lower numbers, especially leaving. Third, the lack of any large net movement out of clearcuts by anurans may indicate that the primary species at our study site (adult *B. americanus* and juvenile *R. clamitans*) are habitat generalists and are able to utilize clearcut habitat as well as closed canopy habitat.

Variation in the response of these species has important implications for studies failing to consider such life history requirements while trying to develop effective conservation and management plans. For example, the weak evacuation response by *R. clamitans* to clearcutting is likely the opposite to what we would expect for wood frogs, which are infrequently captured in our arrays but have been found to be strongly forest associated and sensitive to the loss of forest canopy in other studies (*R. sylvatica*; Gibbs 1998, Skelly et al. 2002, Regosin et al. 2003). Thus, we caution that any management recommendation based on responses of one species of frog (*R. clamitans*) to clearcutting would have potentially devastating effects on efforts to protect another (*R. sylvatica*), even within the same family.

We also found that more amphibians moved out of clearcuts the first year following timber harvest (2005, $n = 736$) than in the second year (2006, $n = 613$). One possible explanation is that 2005 was drier (total precipitation = 34.9 cm) during February–June than in 2006 (38.6 cm) and below the 20-year average (44.3 cm; M. O. Hermann, *available online*).² Less rainfall at this time may have allowed the new clearcuts to dry more rapidly and to a greater extent, thereby creating a stronger cue to evacuate in 2005 than in 2006. Additionally, succession via the increasing density of herbaceous ground vegetation (e.g., blackberry thicket, grasses) and oak regeneration in our clearcuts occurred at a rapid rate in the first two years (*unpublished habitat data*). Effects of succession in the second year may have begun to ameliorate canopy removal by providing cover in the form of herbaceous vegetation and more suitable microhabitat needed to protect amphibians from heat and desiccation (Seebacher and Alford 2002). A desiccation experiment conducted at our sites in a variety of microhabitats using three species of anurans showed a significant year effect with greater water loss and mortality in 2005 than in 2006 (T. A. G. Rittenhouse, E. B. Harper, L. R. Rehard, and R. D. Semlitsch, *unpublished manuscript*). This experiment indicated that 2005 was a more environmentally stressful year than 2006, but still does not allow us to separate rainfall from succession effects. Finally, we cannot eliminate the possibility that the reduced number

of amphibians moving out of clearcuts in the second year postharvest (2006) might also reflect a reduced number of remaining individuals. With each individual leaving or dying in clearcut quadrants, fewer remain. The evacuation in 2005 for even abundant species like salamanders, using the minimum estimate just along lateral edges of quadrants, can reduce abundance by large increments (Table 2). We assume that even abundant species could be reduced substantially, at minimum rates of evacuation of 8–10%, especially if evacuation continues for a number of years.

Our results in Missouri provide support for the evacuation hypothesis. Most amphibian studies reporting declines in abundance due to clear-cutting, especially on lungless woodland salamanders of the family Plethodontidae (e.g., Petranka et al. 1993, Ash 1997, Herbeck and Larsen 1999) have assumed mortality is the primary mechanism. We have shown that some species, especially mole salamanders, display a significant evacuation response and may reduce their short-term exposure and mortality on clearcuts by shifting to more suitable habitats. The novelty of our finding is that these individuals, if they survive, may eventually serve to recolonize the clearcut after succession produces suitable habitat. We are well aware, however, that our study focused on migratory species having greater vagility than the more sedentary plethodontids and that the size of our clearcuts and distance to suitable forest habitats was relatively short (~2.11-ha quadrants; 82-m mean dispersal distance from the center of our clearcuts). Woodland salamanders are known to have substantially reduced vagility, so our results may not be applicable (but see Marsh et al. 2004). It is also unknown whether individuals at our sites that move to adjacent forest habitats might displace resident populations, saturate the habitat, and subsequently reduce per capita resources to the extent that all individuals then suffer negative and long-term effects of density dependence on survival or other demographic parameters. Significant effects of density dependence in the terrestrial environment have only recently been revealed for two species of amphibians with strong effects on growth and survival (Harper and Semlitsch 2007). So, although we have documented a shift in habitat use that appears beneficial, long-term consequences are unknown.

Our results strengthen recommendations to manage and harvest timber in small plots to allow forest-dependent, pond-breeding amphibians to shift habitat to increase survival and increase the potential for subsequent recolonization after succession. Our results also show that evacuation of pond-breeding salamanders is reduced by the presence of high amounts of down wood and strengthens management recommendations to retain down wood on clearcuts, especially in the first few years, while plots are undergoing rapid succession. Further, our results indicate that species that are habitat generalists such as green frogs may not suffer strong effects from clear-cutting. More research is needed to

² (www.wunderground.com)

follow the fate of individuals shifting habitats, the succession of forests and subsequent changes in microclimate essential to amphibians, recolonization processes, and to determine the amount of time needed for species populations to recover to preharvest levels.

ACKNOWLEDGMENTS

We thank S. Altnether, T. Altnether, D. Patrick, L. Rehard, B. Scheffers, J. Sias, and E. Wengert for their help building fences and checking pitfall traps; J. Briggler and G. Raeker of the Missouri Department of Conservation and F. Thompson of the U.S. Forest Service for logistical support; and T. Little and S. Heinrich for technical support. A. Ash, J. W. Gibbons, J. Petranka, H. Welsh, and two anonymous reviewers provided useful comments on drafts of the manuscript. This research was supported by a collaborative grant from the National Science Foundation (DEB 0239943). Animals were sampled under University of Missouri Animal Care and Use Protocol 3368.

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.
- Ash, A. N., and R. C. Bruce. 1994. Impacts of timber harvesting on salamanders. *Conservation Biology* 8:300–301.
- Bury, R. B. 1983. Differences in amphibian populations in logged and old-growth redwood forests. *Northwest Science* 57:167–178.
- 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.
- de Maynadier, 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.
- Faccio, S. 2003. Postbreeding emigration and habitat use by Jefferson and spotted salamanders in Vermont. *Journal of Herpetology* 37:479–489.
- Geiger, R. 1971. *The climate near the ground*. Harvard University Press, Cambridge, Massachusetts, USA.
- Gibbons, J. W., and R. D. Semlitsch. 1982. Terrestrial drift fences with pitfall traps: an effective technique for quantitative sampling of animal populations. *Brimleyana* 7:1–16.
- Gibbs, J. P. 1998. Amphibian movements in response to forest edges, roads, and streambeds in southern New England. *Journal of Wildlife Management* 62:584–589.
- Grialou, J. A., S. D. West, and R. N. Wilkins. 2000. The effects of forest clearcut harvesting and thinning on terrestrial salamanders. *Journal of Wildlife Management* 64:105–113.
- Harper, E. B., and R. D. Semlitsch. 2007. Density dependence in the terrestrial life history stage of two anurans. *Oecologia* 153:879–889.
- Herbeck, L. A., and D. R. Larsen. 1999. Plethodontid salamander response to silvicultural practices in Missouri Ozark forests. *Conservation Biology* 13:623–632.
- Hutchison, V. H., and K. Dupre. 1992. Thermoregulation. Pages 206–249 in M. E. Feder and W. W. Burggren, editors. *Environmental physiology of the amphibians*. University of Chicago Press, Chicago, Illinois, USA.
- Keenan, R. J., and J. P. Kimmins. 1993. The ecological effects of clear-cutting. *Environmental Review* 1:121–144.
- Knapp, S. M., C. A. Haas, D. N. Harpole, and R. L. Kirkpatrick. 2003. Initial effects of clearcutting and alternative silvicultural practices on terrestrial salamander abundance. *Conservation Biology* 17:752–762.
- Madison, D. M. 1997. The emigration of radio-implanted spotted salamanders, *Ambystoma maculatum*. *Journal of Herpetology* 31:542–552.
- Marsh, D. M., K. A. Thakur, K. C. Bulka, and L. B. Clarke. 2004. Dispersal and colonization through open fields by a terrestrial woodland salamander. *Ecology* 85:3396–3405.
- Noss, R. F. 1989. Longleaf pine and wiregrass: keystone components of an endangered ecosystem. *Natural Areas Journal* 9:211–213.
- Petranka, J. W. 1999. Recovery of salamanders after clearcutting in the southern Appalachians: a critique of Ash's estimates. *Conservation Biology* 13:203–205.
- Petranka, J. W., M. P. Brannon, M. E. Hopey, and C. K. Smith. 1994. Effects of timber harvesting on low elevation populations of southern Appalachian salamanders. *Forest Ecology and Management* 67:135–147.
- Petranka, J. W., M. E. Eldridge, and K. E. Haley. 1993. Effects of timber harvesting on southern Appalachian salamanders. *Conservation Biology* 7:363–370.
- Regosin, J. V., B. S. Windmiller, and J. M. Reed. 2003. Terrestrial habitat use and winter densities of the Wood Frog (*Rana sylvatica*). *Journal of Herpetology* 37:390–394.
- Rittenhouse, T. A. G., and R. D. Semlitsch. 2006. Grasslands as movement barriers for a forest-associated salamander: migration behavior of adult and juvenile salamanders at a distinct habitat edge. *Biological Conservation* 131:14–22.
- Rothermel, B. B., and R. D. Semlitsch. 2006. Consequences of forest fragmentation for juvenile survival in spotted (*Ambystoma maculatum*) and marbled (*A. opacum*) salamanders. *Canadian Journal of Zoology* 84:797–807.
- 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. 1998. Biological delineation of terrestrial buffer zones for pond breeding salamanders. *Conservation Biology* 12:1113–1119.
- Skelly, D. K., L. K. Freidenburg, and J. M. Kiesecker. 2002. Forest canopy and the performance of larval amphibians. *Ecology* 83:983–992.
- Stuart, S. N., J. S. Chanson, N. A. Cox, B. E. Young, A. S. L. Rodrigues, D. L. Fischman, and R. W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* 306:1783–1786.
- Todd, B., 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.
- Zar, J. J. 1974. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, New Jersey, USA.