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Assessing quality of clearcut habitats for amphibians: Effects on abundances versus vital rates in the southern toad (*Bufo terrestris*)

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ARTICLE INFO

Article history:

Received 24 January 2006

Received in revised form

30 May 2006

Accepted 5 June 2006

Available online 26 July 2006

Keywords:

Amphibians

Demographic rates

Forest management

Population monitoring

Survival

ABSTRACT

Forest clearcutting is a form of habitat alteration that drastically alters the landscape and may contribute to declines in amphibian populations. Indeed, many studies have documented decreases in amphibian abundances and species richness in clearcuts. The development of effective conservation strategies to reduce the effects of timber harvesting has been hindered by lack of knowledge of the mechanisms underlying these changes in abundance. To better understand the potentially negative consequences of forest clearcutting, we used field enclosures in forested and clearcut habitats to examine changes in the survival and growth of juvenile southern toads (*Bufo terrestris*) over a two-month period. We also conducted a comparative monitoring study using drift fences and pitfall traps in forests and clearcuts to determine the effect of clearcutting on the abundance of juvenile southern toads. We found no significant effect of habitat on the number of juvenile southern toads captured in forests or clearcuts. In contrast, the average survival of toads in clearcut enclosures was significantly reduced compared to that of toads in forested enclosures ($17 \pm 5\%$ versus $61 \pm 3\%$). Toads surviving in clearcuts were also significantly smaller than those surviving in forested enclosures (27.9 ± 0.1 mm versus 30.3 ± 0.8 mm SVL). Our results highlight the difficulty in interpreting abundance patterns as a sole metric for habitat comparison. Because there is much interest in studying the effects of habitat alteration on amphibian populations, we recommend that future studies place more emphasis on determining changes in vital rates of populations following habitat alteration.

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1. Introduction

Habitat alteration is a major factor in the global decline of amphibians (Collins and Storfer, 2003; Stuart et al., 2004). Timber harvesting is one form of habitat alteration that may decrease the suitability of the terrestrial environment for amphibians. Clearcutting and other intensive forest management practices create a mosaic of fragmented habitats, with potentially negative consequences for amphibian populations. The increased air and soil temperatures and reduced

ground litter in early-successional habitats (Russell et al., 2004) may reduce survival and migratory success of amphibians (deMaynadier and Hunter, 1999). Clearcuts may also become barriers to movement if amphibians avoid entering them in favor of forested habitats (Rothermel and Semlitsch, 2002; Chan-McLeod, 2003; Rothermel, 2004). Because up to 82% of amphibian species are forest-dependent (Stuart et al., 2004), forest management practices have the potential to affect a large proportion of amphibians and contribute to ongoing population declines.

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0006-3207/\$ - see front matter Published by Elsevier Ltd.

doi:10.1016/j.biocon.2006.06.003

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

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

We studied the effects of forest clearcutting on the southern toad (*Bufo terrestris*) using two approaches simultaneously. First, we conducted a comparative abundance survey using drift fences with pitfall traps to compare abundances of southern toads in recent clearcuts with abundances in adjacent unharvested pine (*Pinus* spp.) forests. Second, we performed an experimental study using field enclosures to determine the effects of clearcutting on the survival and growth of juvenile southern toads. The juxtaposition of these two approaches allowed us to evaluate the quality of forest clearcuts for a common amphibian species by comparing both an indirect and direct measure of habitat quality. Consequently, our results illuminate a larger problem in interpreting the effects of forest management on amphibians and demonstrate why more research should focus on changes in

vital rates of amphibian populations following habitat alteration.

2. Materials and methods

2.1. Study species

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

2.2. Abundance survey

We selected four forested sites on the US Department of Energy's Savannah River Site in Barnwell County, South Carolina, as part of the LEAP (Land-use Effects on Amphibian Populations) study, a multi-regional, collaborative investigation of the effects of land-use practices on migratory success and demographics of pond-breeding amphibians. These sites are second-growth forests comprised predominantly of loblolly pine (*Pinus taeda*) in the Upper Coastal Plain of the southeastern US. Each study site was a circular area 350 m in diameter centered on an isolated, seasonal wetland. Each wetland was located at least 200 m from paved roads, power-line right-of-ways, and other open areas. We divided each study site into four 4-ha quadrants delineated by two perpendicular transects that intersected at the center of the wetland (Fig. 1). Each quadrant was randomly assigned one of four treatments: (1) an unharvested control (>30 years old); (2) a partially harvested stand, in which the canopy was thinned to approximately 85% of that in the control; (3) a clearcut with coarse woody debris retained (CC-retained); and (4) a clearcut with coarse woody debris removed (CC-removed). The last treatment represents the most extreme level of alteration and produces a habitat typical of even-aged forest management in the southeastern US. Logging was completed at the sites in March 2004.

In April 2004, we installed nine 15-m sections of drift fence in each quadrant at all four sites. We placed six 8-L pitfall traps (30 cm in diameter and 25 cm high) paired on opposite sides of each section of drift fence, yielding a total of 54 pitfall traps within each quadrant. Pitfall traps contained 1–3 cm of standing water and floating sponges in the bottom. We constructed the drift fences of aluminum flashing buried 15 cm into the ground and standing 45 cm tall. We distributed the drift fences evenly throughout each quadrant to maximize the likelihood of capturing animals in the treatments (Fig. 1). We checked the drift fences daily from 1 June to 28 July 2004 and recorded all amphibian captures, including juvenile southern toads. Animals were released on capture and were

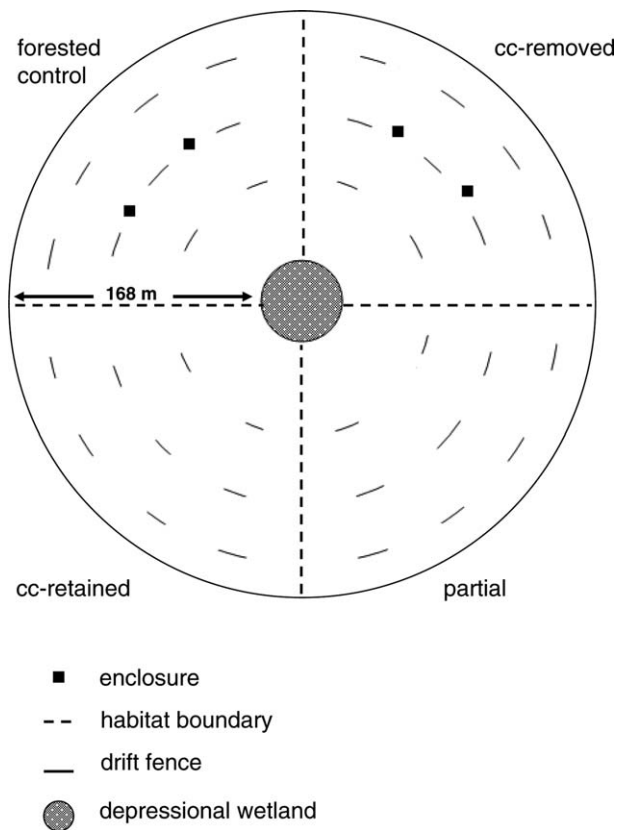


Fig. 1 – Diagram showing the arrangement of drift fences and enclosures at each site. See text for description of the four treatments. Note that drift fences, wetland, and enclosures are not pictured to scale.

not marked, yielding raw counts. This period of drift fence monitoring coincided with the period during which juvenile southern toads leave their natal ponds to establish terrestrial home ranges, where they abide until they become reproductive adults. For the purposes of this study, we only analyzed captures from the control and CC-removed treatments to permit a direct comparison of abundance data to the enclosure study conducted in these two habitats.

2.3. Field enclosure study

We measured growth and survival of juvenile southern toads in terrestrial enclosures in the control and CC-removed treatments. Although enclosures confine the animals, they eliminate the possibility that other processes, such as immigration and emigration, affect perceived abundance within the experimental populations and ensure that the growth and survival of the toads is a reflection of time spent in a single habitat. We constructed two enclosures in each treatment (control and CC-removed) at two of the four sites for a total of four control enclosures and four CC-removed enclosures. We constructed enclosures of aluminum flashing buried 25 cm deep, standing 65 cm tall and measuring 4 m × 4 m. Similarly constructed enclosures of larger sizes have been used in studies of terrestrial density-dependence in ambystomatid salamanders (Pechmann, 1995). We systematically placed the enclosures within the interior of the treat-

ments at least 50 m from the edges of the quadrant (Fig. 1). We minimized disturbance to the soil and ground cover within the enclosures to maintain an environment suitably representative of the overall treatment.

We collected 240 recently metamorphosed southern toads as they emigrated from a wetland located near our study sites. We maintained all toads indoors in ventilated containers at 23 °C on paper towels wet with aged well-water for less than one week prior to release into experimental enclosures. We randomly assigned groups of 30 toads to each of the eight enclosures. Our experimental density of 1.8 toads per m² is lower than natural densities encountered along pond margins during the post-metamorphic period (Beck and Congdon, 1999). We individually marked each animal by toe-clipping and recorded snout-vent length (SVL) and fully hydrated mass prior to release into the enclosures on 10 July 2004. After one month, we censused the animals for three consecutive days, recording the SVL and mass of each animal in the field upon capture with an Ohaus® Scout Pro battery-powered balance. We released all animals back into the enclosures immediately following data collection. We repeated this process again two months after the initial release.

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

2.4. Statistical analyses

To test whether clearcutting affected the number of juvenile southern toads captured at drift fences, we performed an analysis of variance (ANOVA) on the total captures at all nine drift fences within a treatment, using site as a blocking factor. To test the effect of treatment on survival of penned toads over two months, we performed a multivariate repeated measures analysis of variance (MANOVA; Von Ende, 2001) using the MNKA at each of the three intervals and we accounted for the nestedness of the enclosures within two sites in our analysis. To test the effect of treatment on body size over two months, we performed a repeated measures MANOVA using the mean SVL from each enclosure at each of the three intervals, again accounting for the nestedness of the enclosures within two sites.

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

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

3. Results

A total of 357 juvenile southern toads were captured in the four CC-removed quadrants and 307 toads were captured in the four forested control quadrants from 1 June to 28 July 2004. Juvenile toads were captured at drift fences in CC-removed clearcuts more frequently than in unharvested forests at three of the four sites (Fig. 2). However, neither treatment nor site had a significant effect on the number of captures (treatment: $F_{1,3} = 0.18$, $p = 0.70$; site: $F_{3,3} = 2.76$, $p = 0.21$).

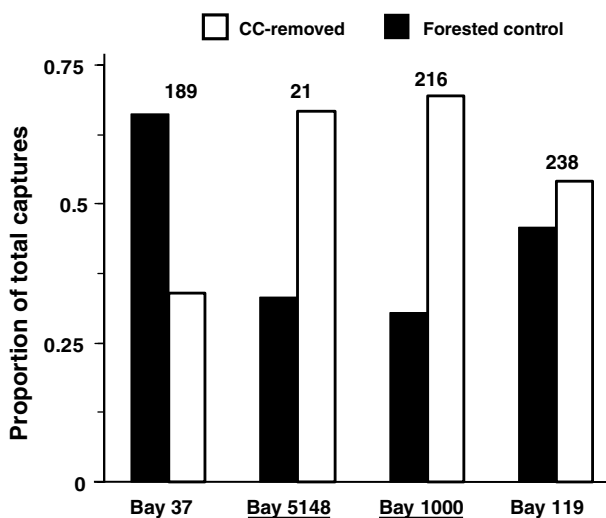


Fig. 2 – Proportion of juvenile southern toads captured in forested controls versus CC-removed habitats at each study site using drift fences and pitfall traps. Our field enclosures were located at Bay 5148 and Bay 1000. The total number of captures of juvenile southern toads at each site is given above the bars.

In contrast, we found significant effects of treatment and time on the number of toads surviving over two months in the experimental enclosures (Table 1; Fig. 3). There were no effects of site, time-by-site, or time-by-treatment interactions on survival (Table 1). The average survival of toads in clearcut enclosures after two months was $17 \pm 5\%$ whereas the average survival in forested enclosures was $61 \pm 3\%$. Individual contrasts revealed that treatment significantly affected survival of toads in the second month (Table 2).

The mean SVL of juvenile toads in both forested and clearcut enclosures increased over two months as the animals grew (Table 3). However, there was a significant treatment effect as the mean SVL of toads in forested enclosures increased significantly more than that of toads in clearcut enclosures (Table 3; Fig. 4), a response that was consistent through time (Table 4). Toads that survived in clearcut pens averaged 27.9 ± 0.1 mm SVL whereas toads that survived in forested pens averaged 30.3 ± 0.8 mm SVL. The results of the logistic regressions suggest that initial body size was not an important predictor of survival to any month in either clearcuts or forests (Table 5).

Results of non-parametric bootstrap resampling suggest that growth rate, as measured by change in SVL in the first month, did not correlate to greater survival in the second

Table 1 – Results of the repeated-measures analysis of variance of the effects of habitat treatment, site, and time on the number of surviving southern toads in enclosures over two months

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

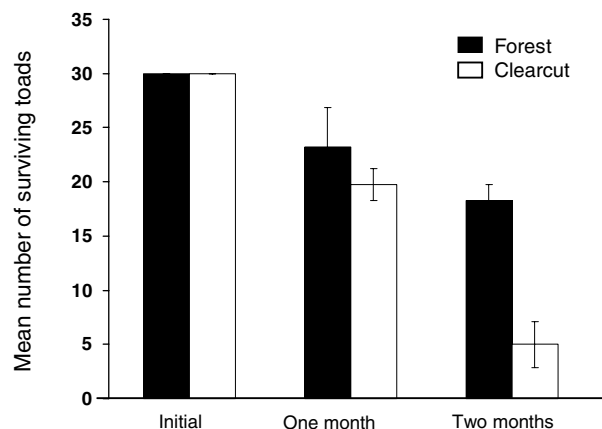


Fig. 3 – Mean number of surviving toads (± 1 SE) in each treatment ($n = 4$ enclosures per treatment).

Table 2 – Results of individual contrasts from a repeated-measures analysis of variance testing the effects of treatment and site on the number of surviving toads in enclosures at each interval

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

Table 3 – Results of the repeated-measures analysis of variance of the effects of habitat treatment, site, and time on the mean snout-vent length of southern toads in enclosures over two months

	df	MS	F	p
Between-subject				
Site	1	0.118	0.25	0.642
Treatment	2	6.125	13.09	0.018
Error	4	0.467		
	df	Wilks' λ	F	p
Within-subject				
Time	2,3	0.0631	22.25	0.016
Time \times site	2,3	0.7975	0.38	0.712
Time \times treatment	4,6	1.667	2.97	0.439

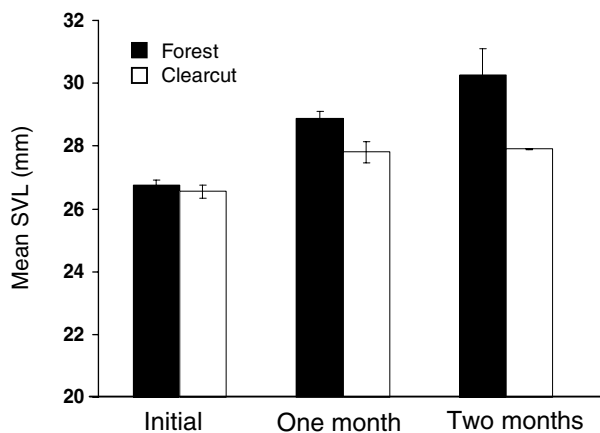


Fig. 4 – Mean snout-vent length of surviving toads (± 1 SE) in each treatment ($n = 4$ enclosures per treatment).

month (Table 6). However, with respect to body mass, there was a strong indication that the toads that perished in the second month were a non-random subset of all penned toads. Toads that perished in the second month lost more mass in the first month, on average, than did toads randomly drawn from the total pool of animals that survived the first month (Table 6).

Table 4 – Results of individual contrasts from a repeated-measures analysis of variance testing the effects of treatment and site on mean snout-vent length of toads in enclosures

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

Table 5 – Results of the logistic regressions testing for effect of initial body size on survival among toads in enclosures

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

Table 6 – Mean change in snout-vent length and body mass during the first month of toads that perished in the second month ($n = 84$)

	Mean change	90% CI
SVL (cm)	1.4	1.21 to 1.85
Mass (g)	-0.189	-0.185 to -0.068

Confidence intervals were derived from 1000 bootstrap resampled subsets (of size $n = 84$) drawn from the entire pool of toads that survived the first month.

4. Discussion

4.1. Effects of clearcutting on toad abundances

Clearcutting typically has a negative effect on amphibian abundances and richness (Petranka et al., 1994; Ash, 1997; Grialou et al., 2000; Knapp et al., 2003; Karraker and Welsh, 2006). Indeed, several studies have suggested that forest cover is a critical factor that determines the distribution and density of many species (Porej et al., 2004; Herrmann et al., 2005). However, the response of amphibians to clearcutting varies considerably among species and physiographic regions (deMaynadier and Hunter, 1995; Russell et al., 2004). The results of our study agree with others that show little effect of clearcutting on anuran abundances, and in some cases, increases in anuran abundances (e.g., Pais et al., 1988; Phelps and Lancia, 1995;

Clawson et al., 1997; Ryan et al., 2002). A critical and untested assumption in some of these studies, and one that is true of the abundance survey in this study, is that capture probabilities and detection do not vary with treatment. Ideally, the application of mark-recapture techniques to analyze captures of individually marked animals can reduce possible bias resulting from such assumptions and can clarify the inferences made about the effects of habitat type on amphibian populations based on abundance measures.

4.2. Effects of clearcutting on survival and body size

The reduced survival and body size of southern toads in clearcuts indicates that clearcuts are poor-quality habitats for these amphibians. Juvenile toads experienced higher mortality in clearcuts, and those that did survive were smaller in size than their forest-dwelling cohorts after two months. Increased juvenile mortality can reduce population sizes by eliminating future reproductive animals (Vonesh and De la Cruz, 2002). Additionally, smaller body size in juvenile amphibians results in a delayed onset of maturity (e.g., Smith, 1987; Semlitsch et al., 1988; Berven, 1990; Scott, 1990, 1994), which reduces the number of reproductive animals available in the breeding adult population. The results of the logistic regressions on body size suggest that changes in the mean size of toads in enclosures were products of growth and not a reflection of differential survival based on body size.

Because southern toads have a greater tolerance to the conditions found in clearcuts than do many other amphibians (Thorson and Svihla, 1943), other amphibians are likely to suffer even greater physiological responses to clearcutting. However, the results from studies of other species have been mixed. Chazal and Niewiarowski (1998) found no effects of clearcutting on body mass, clutch size, lipid storage, or the number of recaptured mole salamanders (*Ambystoma talpoideum*) maintained in 100 m² field enclosures when compared to salamanders from forested enclosures. In contrast, Rothermel and Luhring (2005), using very small (0.33 m²) enclosures, found that mortality of *A. talpoideum* could occur quite rapidly in recent clearcuts, particularly if salamanders did not have access to burrows. In the 16 m² enclosures used in our study, we found that mortality of juvenile southern toads in clearcuts increased significantly after the first month. Apart from species differences, there are at least two other explanations for the variation in results among these enclosure-based studies. First, as field enclosures increase in size, relocating highly fossorial amphibians can become difficult, and relying on pitfall traps to recapture animals for survival comparisons (as in Chazal and Niewiarowski, 1998) may begin to approximate comparisons of capture data from drift fence studies. Second, and more plausibly, larger field enclosures may incorporate more habitat complexity, allowing amphibians to find suitable refugia in otherwise hostile environments. Thus, while altered habitats are generally of poorer quality due to desiccating conditions and other factors, the ability to find and use suitable microhabitats in a larger landscape may mitigate some of the negative impacts associated with forest removal. Studies that specifically examine habitat selection and use by amphibians can greatly improve our understanding of amphibian responses to forest alteration.

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

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

5. Conservation implications

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

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

Acknowledgments

We thank J.W. Gibbons, P.H. Niewiarowski, R.D. Semlitsch, C.T. Winne and one anonymous reviewer for assistance with final review of this manuscript. G.J. Graeter, B.S. Metts, E. Harper and S. Blomquist also provided helpful comments on earlier drafts. We also thank M. Langley, T. Luhring, J. Nestor, J. Cospers, K. Todd, and S. Rothermel for their assistance constructing enclosures and checking drift fences. A. Green, E. Brown, and K. Sanborn also provided valuable assistance in the field. Animals used in this study were collected under South Carolina Department of Natural Resources Scientific Collection permit (07-2004) and all procedures were conducted in accordance with The University of Georgia's animal care and use guidelines. This research was conducted as part of the collaborative Land-use Effects on Amphibian Populations study funded by the National Science Foundation (Award DEB-0242874). Additional support and manuscript preparation were aided by the Environmental Remediation Sciences Division of the Office of Biological and Environmental Research, US Department of Energy through Financial Assistance Award No. DE-FC09-96SR18546 to the University of Georgia Research Foundation.

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