Estimation of Core Terrestrial Habitat for Stream-Breeding Salamanders and Delineation of Riparian Buffers for Protection of Biodiversity

JOHN A. CRAWFORD* AND RAYMOND D. SEMLITSCH

University of Missouri, Division of Biological Sciences, 105 Tucker Hall, Columbia, MO 65211-7400, U.S.A.

Abstract: *Many species of wildlife depend on riparian habitats for various life-history functions (e.g., breeding, foraging, overwintering). Although this unique habitat is critical for many species, delineations of riparian zones and buffers for various taxa are lacking. Typically when buffer zones are determined to mitigate edge effects, they are based on criteria that protect aquatic resources alone and do not consider impacts to wildlife and other terrestrial resources. Using two different survey methods (area-constrained daytime searches and nighttime visual encounter searches), we estimated core terrestrial habitat and buffer widths for stream-breeding salamanders in southern Appalachian streams from May to August 2004. A core terrestrial habitat of 27.0 m encompassed 95% of the salamander assemblage (four species of stream plethodontids), and an additional 50 m (to buffer edge effects) yielded a total buffer of 77.0 m. When each species of the assemblage was analyzed separately, the maximum core terrestrial habitat needed for the Blue Ridge two-lined salamander (*Eurycea wilderae*), a dominant member and the farthest-ranging species from the stream, was 42.6 m. Thus, we recommend an overall buffer width of 92.6 m in southern Appalachian streams. To protect stream amphibians and other wildlife dependent on riparian areas, land managers and policy makers must consider conserving more than aquatic resources alone. Developing core terrestrial habitat estimates and buffer zone widths for wildlife populations is a critical first step in the conservation of many semiaquatic organisms and protecting biodiversity.*

Keywords: amphibian conservation, buffers, core habitat, *Desmognathus*, *Eurycea*, stream salamander

Estimación del Hábitat Terrestre Núcleo para Salamandras que se Reproducen en Arroyos y Definición de Áreas de Amortiguamiento Ribereñas para la Protección de Biodiversidad

Resumen: *Muchas especies de vida silvestre dependen de hábitats ribereños para varias funciones de su historia de vida (e.g., reproducción, forrajeo, hibernación). Aunque este hábitat exclusivo es crítico para muchas especies, la definición de zonas y amortiguamientos ribereños para varios taxa no existe. Típicamente, la determinación de zonas de amortiguamiento para mitigar efectos de borde se basa en criterios que solo protegen recursos acuáticos y no considera los impactos a la vida silvestre y otros recursos terrestres. Mediante dos métodos diferentes de muestreo (búsquedas diurnas en áreas constreñidas y búsquedas nocturnas de encuentros visuales), estimamos el hábitat terrestre núcleo y amplitudes de amortiguamiento para salamandras que se reproducen en arroyos en el sur de los Apalaches entre mayo y agosto de 2004. Un hábitat terrestre núcleo de 27.0 m englobó 95% del ensamble de salamandras (cuatro especies de pletodóntidos de arroyo), y 50 m adicionales (para amortiguar efectos de borde) produjo un amortiguamiento total de 77.0 m. Cuando cada especie del ensamble fue analizada por separado, el máximo hábitat terrestre núcleo requerido para* Eurycea wilderae*, un miembro dominante y la especie que más se aleja del arroyo, fue de 42.6 m. Por lo tanto, recomendamos un amortiguamiento total de 92.5 en arroyos de los Apalaches. Para proteger anfibios de arroyo*

**email jac7vc@mizzou.edu*

Paper submitted October 6, 2005; revised manuscript accepted May 11, 2006.

DOI: 10.1111/j.1523-1739.2006.00556.x

y otras especies dependientes de áreas ribereñas, los gestores y tomadores de decisiones deben considerar la conservación de no solo los recursos acuáticos. El desarrollo de estimaciones de hábitat terrestre núcleo y amplitudes de zonas de amortiguamiento para poblaciones de vida silvestre es un primer paso crítico para la conservación de muchos organismos semi acuáticos y para la protección de la biodiversidad.

Palabras Clave: amortiguamientos, conservación de anfibios, *Desmognathus*, *Eurycea,* hábitat núcleo, salamandra de arroyo

Introduction

Concern over amphibian declines has increased dramatically over the past decade (e.g., Blaustein et al. 1994; Pechmann & Wilbur 1994; Houlahan et al. 2000). Stuart et al. (2004) indicated that amphibians are far more threatened than either birds or mammals. Although many factors have been implicated in this decline (e.g., disease, introduction of exotic species, chemical pollution, global climate change), habitat loss and degradation are generally accepted as the major factor responsible for most declines (e.g., Lips 1998; Wake 1998; Carey et al. 1999; Semlitsch 2000). Furthermore, many amphibians require both aquatic and terrestrial habitats to complete their life cycle and therefore are especially susceptible to the loss and degradation of either habitat (Semlitsch 2000).

To combat habitat loss and degradation in stream ecosystems (in addition to providing wildlife corridors and protecting essential habitat required for completing the life cycles of riparian species), riparian buffer strips adjacent to streams have been used in managed forests for more than 2 decades (Vesely & McComb 2002). Buffer strips protect water quality from activities such as agriculture and silviculture, which cause siltation and increased water temperatures (Lowrance et al. 1984; Jones et al. 1999; Vesely & McComb 2002). Nevertheless, riparian buffer strips not only are critical to the protection of aquatic resources, they can play a role in the conservation of biodiversity. A number of studies have documented the importance of terrestrial habitat adjacent to streams and wetlands for semiaquatic species, including amphibians (e.g., deMaynadier & Hunter 1995; Semlitsch 1998; Vesely & McComb 2002).

Salamander communities make up an important ecological component of many forested ecosystems and often exceed the combined biomass of other terrestrial vertebrates (Burton & Likens 1975; Hairston 1987; Petranka & Murray 2001). Some of these salamanders (e.g., *Desmognathus, Eurycea, Gyrinophilus, Pseudotriton*) are associated with streams and creeks. The four focal species of this study differ markedly in larval periods (*Desmognathus monticola*, 10 months; *D. ocoee*, 9 months; *D. quadramaculatus*, up to 4 years; *Eurycea wilderae*, up to 2 years), but all depend on aquatic habitats for reproduction and larval development (Petranka 1998). However, terrestrial habitats are used for foraging and potentially for overwintering (e.g., Barbour et al. 1969; Ashton & Ashton 1978). The three species of *Desmognathus* in this study spatially segregate themselves in the terrestrial habitat, most likely because of competition and predation (Hairston 1949; Organ 1961). The largest of the three species, the black-bellied salamander (*D. quadramaculatus*), occurs closest to the stream. The next largest species, the seal salamander (*D. monticola*), is slightly more terrestrial, and the Ocoee salamander (*D. ocoee*) is the most terrestrial of the three *Desmognathus* species and occurs the farthest from the stream edge. The Blue Ridge two-lined salamander (*E. wilderae*) occurs the farthest from the stream edge in the salamander assemblage (J.A.Crawford, personal observation).

Although terrestrial buffer distances have been established for the protection of aquatic resources, little information exists for the explicit protection of semiaquatic species that require terrestrial habitat adjacent to streams. In the Pacific Northwest (U.S.A.), a few studies have addressed this need (Corn & Bury 1989; McComb et al. 1993; Gomez & Anthony 1996; Vesely & McComb 2002). Of these studies, Vesely and McComb (2002) report that buffer strips of 20 m contain approximately 80% of detectable torrent salamanders (*Rhyacotriton* spp.), Pacific giant salamanders (*Dicamptodon tenebrosus*), and Dunn's salamanders (*Plethodon dunni*) along the first- through third-order streams they surveyed. Nevertheless, the data are still relatively limited for stream salamanders in other areas of the United States.

Typically when buffer zones are defined, they are based on criteria that protect the aquatic resources alone and do not consider impacts to semiaquatic species and other terrestrial resources (Semlitsch & Bodie 1998; Semlitsch & Jensen 2001). For example, in Oregon (U.S.A.), the minimum buffer strip required to protect water resources is 6.1 m, although a minimum buffer of 20 m is needed to protect certain salamander species (Vesely & McComb 2002). We defined core terrestrial habitat as the spatial delineation of 95% of the population that encompasses terrestrial foraging, breeding, and overwintering habitats rather than buffers, following Semlitsch and Jensen (2001). Although not all available habitat contained within these core areas is suitable at any one time, critical habitat patches (e.g., logs, piles of leaf litter, rocks) are contained within them. Determining core terrestrial habitats for stream-breeding salamanders is the critical first step in formulating conservation plans and addressing larger-scale issues such as connectivity among populations.

We sought to develop biologically based management criteria to protect stream salamanders. Specifically, we defined the core terrestrial habitat used by an assemblage of four species of stream salamanders to provide recommendations on appropriate stream buffer widths. We also devised a direct test of whether day versus night sampling yields the best estimate of core terrestrial habitat for these salamanders.

Methods

To define core terrestrial habitat use by an assemblage of stream salamanders, we sampled riparian forests adjacent to 14 headwater streams (streams were the unit of replication) in the southern Appalachian Mountains, Nantahala National Forest, Macon County, North Carolina (U.S.A.). All sites were located between 718 and 1248 m elevations, had not been subject to logging for at least 80 years, and were located at least 1 km apart (Table 1). To ensure maximum capture success and detection of rare species (Hyde & Simons 2001), we used two different sampling methods. Sites were sampled six times each (three day transects, three night transects) from May to August of 2004.

Table 1. Habitat characteristics of stream sites used in the Nantahala National Forest, North Carolina (U.S.A.).

Locality (UTM)	*Stream order*	*Canopy (%)*	*Slope (°)*	*Forest type*
17S 0301518 3881167	headwater	91.2	15.5	pine
17S 0304637 3879204	headwater	87.6	15.5	mixed deciduous
17S 0304364 3879082	headwater	90.3	13.5	mixed deciduous
17S 0302750 3876075	headwater	88.5	17.5	pine
17S 0301733 3876558	headwater	90.2	21.7	mixed deciduous
17S 0298076 3878383	headwater	90.2	12.1	mixed deciduous
17S 0297721 3878097	headwater	91.6	24.2	mixed deciduous
17S 0296901 3878721	headwater	90.4	17.5	mixed deciduous
17S 0295741 3876678	headwater	88.0	30.0	mixed deciduous
17S 0295829 3876035	headwater	89.2	13.5	pine
17S 0297122 3885702	headwater	93.2	19.3	mixed deciduous
17S 0296072 3886657	headwater	88.4	14.6	pine
17S 0297839 3885471	headwater	90.3	19.3	mixed deciduous
17S 0301596 3879760	headwater	91.8	14.5	mixed deciduous

During day transects, we monitored one paired transect that was separated by 1 m (to increase sample sizes of salamanders; data for each plot were combined) and extended perpendicular from the stream bank into the adjacent forest. Monitoring stations were established at 1, 3, 7, 10, 15, 25, 50, and 100 m from the stream bank, based on the home range sizes and potential distances traveled by the target species of stream-breeding salamanders. At each stream we checked daytime transects by conducting area-constrained searches (2.25 m^2) of leaf litter and coarse woody debris at each monitoring station for an average of 10 minutes. We used a visual encounter search (VES) during the three night transects to capture surface-active salamanders. Two researchers walked a straight line that was perpendicular from the stream edge (defined as the edge of the streambed) out to 100 m and recorded distance from the stream edge for each salamander encountered. While walking the perpendicular transect, each researcher searched 2.5 m to the right and left of the transect line. We identified all salamanders (day and night transects) to species, weighed and measured for snout-vent length and total length, and determined sex. We released all salamanders at the site of capture. We determined age class (adult/juvenile) by comparing measured snout-vent lengths of each individual to published size classes for each species (Petranka 1998).

Average distance salamanders were found from the stream was calculated across the 14 streams and was tested for normality with Wilk's Lambda (data in Table 2).

Table 2. Summary of occurrence distances[a] (m) from stream edge for an assemblage of stream salamanders in the southern Appalachian Mountains.

Species (transect type)[b]	*Adults*	*Juveniles*	*All age classes*
Stream day	10.0, 13.4 $n = 107$	6.3, 8.7 $n = 95$	8.4, 10.7 $n = 202$
Stream night	26.0, 29.6 $n = 280$	21.5, 25.5 $n = 211$	24.4, 27.0 $n = 491$
Desmognathus day	5.2, 7.5 $n = 74$	3.8, 5.8 $n = 79$	5.1, 7.4 $n = 153$
Desmognathus night	7.5, 9.2 $n = 130$	6.6, 8.0 $n = 104$	7.3, 8.5 $n = 234$
Eurycea day	17.9, 24.1 $n = 33$	18.5, 24.5 $n = 16$	18.4, 23.4 $n = 49$
Eurycea night	41.0, 44.1 $n = 150$	36.4, 43.2 $n = 107$	39.3, 42.6 $n = 257$

[a] *Distance encompassing 50% and 95% of the population, respectively.*
[b] *Stream denotes salamanders in the assemblage (*Desmognathus monticola, D. quadramaculatus, D. ocoee, *and* Eurycea wilderae*).* Desmognathus *denotes 3 species in the genus (*D. monticola, D. quadramaculatus, *and* D. ocoee*).* Eurycea *denotes 1 species in the genus (*Eurycea wilderae*).*

To find the distance from the stream edge that would encompass the majority of each species of salamander and the assemblage, an upper confidence interval was calculated.

Results

Four species of stream salamanders, the seal salamander, the Ocoee salamander, the black-bellied salamander, and the Blue Ridge two-lined salamander were encountered during 2004. Individuals were found an average of 8.4 m from the edge of their aquatic habitats during day transects and 24.4 m during night transects (Table 2). If we assumed the distances of salamanders from the edge of streams were normally distributed, then by definition the mean of salamanders of all species (8.4 m day, 24.4 m night) represents a distance that includes only 50% of the assemblage. Although the night transects had a normal distribution ($W = 0.939$, $p = 0.441$), the day transects had a non-normal distribution ($W = 0.820$, $p = 0.01$); this was due to the sampling of monitoring stations that were not equally distributed (1, 3, 7, 10, 15, 25, 50, and 100 m from the stream edge) and the fact that not all habitat could be sampled from stream edge out to 100 m. A distance of 27.0 m from the stream's edge encompassed 95% of the total salamander assemblage (adults and juveniles of all species) according to capture data from the night transects. The average distance adults were found from the stream was only slightly larger than the distance for juveniles (adults, 29.6 m; juveniles, 25.5 m) and marginally significant ($p = 0.086$, df = 26). The farthest-ranging species from streams in our assemblage (*E. wilderae*) yielded a 95% confidence interval of 42.6 m (Table 3).

To determine whether day or night sampling yielded the best estimate of salamander distribution from the stream, we made a direct comparison. Captures from the night transects were adjusted and a mean distance from the stream was calculated for direct testing with day transects. Only animals captured within 2.25-m^2 plots at each of the day sampling distances were used for the night-adjusted values. To equalize search intensity, time spent searching these plots was approximately equal to daytime sampling (10 minutes). Distribution estimates were significantly different between day and night transects ($p = 0.033$, df = 26). Day transects yielded a mean distance from the stream of 8.4 m (10.7 m encompassed 95% of the assemblage), whereas night transects had a mean distance from the stream of 12.6 m (15.8 m encompassed 95% of the assemblage).

The number of dusky (*Desmognathus*) salamanders decreased sharply with distance from the stream edge (Fig. 1). The number of brook (*Eurycea*) salamanders remained somewhat constant from the stream edge into the forest for 70–75 m (Fig. 1). The majority of dusky salamanders were found within 15 m of the stream's edge, whereas brook salamanders were found at very low numbers near the stream edge and did not increase in number until 15–20 m from the stream's edge (Fig. 1). Overall, the distribution of all salamanders from the edge of the streams showed a relatively smooth decline as distance from the stream increased.

Table 3. Summary of occurrence distances (m) from stream edge for individual species of stream salamanders in the southern Appalachian Mountains.*

Species (transect type)	*Adults*	*Juveniles*	*All age classes*
D. monticola day	4.6, 6.7	3.1, 5.6	3.8, 5.4
	$n = 22$	$n = 20$	$n = 42$
D. monticola night	6.8, 8.6	5.1, 7.7	6.6, 8.8
	$n = 64$	$n = 30$	$n = 94$
D. ocoee day	5.6, 8.6	4.4, 7.2	5.5, 8.3
	$n = 48$	$n = 59$	$n = 107$
D. ocoee night	10.4, 13.8	7.3, 9.5	8.2, 9.7
	$n = 43$	$n = 74$	$n = 117$
D. quadramaculatus day	2.0, 4.5	NA	2.0, 4.5
	$n = 4$	$n = 0$	$n = 4$
D. quadramaculatus night	3.2, 4.7	NA	3.2, 4.7
	$n = 23$	$n = 0$	$n = 23$
E. wilderae day	17.9, 24.1	18.5, 24.5	18.4, 23.4
	$n = 33$	$n = 16$	$n = 49$
E. wilderae night	41.0, 44.1	36.4, 43.2	39.3, 42.6
	$n = 150$	$n = 107$	$n = 257$

**Distance encompassing 50% and 95% of the population, respectively; NA, not available.*

Discussion

Salamanders generally comprise the greatest biomass of any vertebrates in forested ecosystems (Burtons & Likens

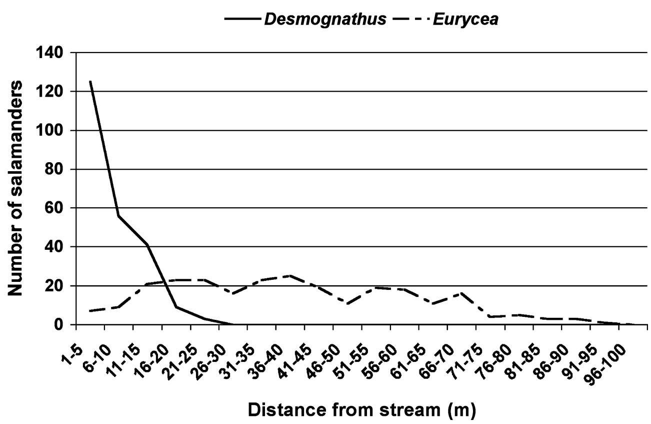

*Figure 1. Distribution of dusky (*Desmognathus*) and brook (*Eurycea*) salamanders from edges of headwater streams in the Nantahala National Forest, North Carolina (U.S.A.), based on nighttime visual encounter searches.*

1975; Petranka & Murray 2001) and thus are of vital importance to the ecosystem as a whole because they consume invertebrates and serve as prey for other vertebrates. Many stream-dwelling salamanders are highly philopatric and long-lived, and typically exist in relatively stable populations (Welsh Jr. & Ollivier 1998). These traits make them reliable indicators of potential biotic diversity in stream and riparian ecosystems, and their relative abundance can be a critical indicator of stream and riparian ecosystem health (Welsh Jr. & Ollivier 1998). Determining and maintaining the terrestrial habitat that salamanders require is critical to maintaining existing populations and potentially ecosystem function. With accurate estimates of core terrestrial habitat, policy makers and land managers will be better equipped to make management decisions pertaining to stream salamanders and potentially other species that rely on riparian habitats (e.g., reptiles, birds, mammals).

During the past 10–15 years, increased attention has focused on defining and delineating riparian areas. In Texas, Rudolph and Dickson (1990) captured more amphibians in wide buffers (50–95 m) versus narrow buffers (0–25 m) along intermittent streams that passed through even-aged pine plantations. They recommend 30-m buffers for amphibians. deMaynadier and Hunter (1995) recommend buffers of 10–25 m along streams surrounded by a wider management zone where partial harvesting of trees could occur. Vesely and McComb (2002) found that 47 m buffers along first-, second-, and third-order streams were necessary to support amphibian assemblages similar to those in unlogged forests in Oregon. Although many of these studies provide buffer recommendations, they actually provide core terrestrial habitat estimates and do not include a true buffer from the edge effects caused by surrounding land use.

We used two sampling methods (day transects vs. night transects) to determine the most appropriate way to yield core terrestrial habitat estimates for stream-breeding salamanders. We defined core terrestrial habitat as the spatial delineation of 95% of the population that encompasses terrestrial foraging, breeding, and overwintering habitats, which was determined by the 95% confidence interval. The day transects yielded a core terrestrial habitat estimate of 10.7 m, whereas the adjusted night transects yielded a significantly different core terrestrial habitat estimate of 15.8 m. This comparison and distinction is important because most plethodontid monitoring techniques employ only daytime searches. In our study the daytime searches lead to inadequate estimation of the amount of habitat salamanders require. The overall night transects yielded a core habitat estimate of 27.0 m, which was more than double the estimate based on day transects.

Because of the importance of core terrestrial habitat to population persistence, a buffer is necessary to reduce potential edge effects that can penetrate great distances into forested habitats (Murcia 1995; deMaynadier & Hunter 1995). Therefore, to fully protect the salamander assemblage, we recommend applying a stream buffer of 50 m. Although edge effects can extend farther than 50 m (e.g., Murcia 1995; Haskell 2000), the amount of edge needed to protect core terrestrial habitat for salamanders is poorly resolved for southern Appalachian forests, so we view 50 m as conservative. This recommendation is supported by Marsh and Beckman (2004), who found edge effects for red-backed salamanders (*Plethodon cinereus*) that range from 20 m to 80 m (80 m in a dry year). Similarly, 20-m edge effects were found for red-backed salamanders in New Hampshire (deGraaf & Yamasaki 2002). Thus, 50 m should adequately protect the core terrestrial habitat of this salamander assemblage, especially under all but dry conditions or on more exposed south-facing slopes.

The two different genera we encountered had drastically different core terrestrial habitat requirements. Although the difference in core terrestrial habitat usage between adults and juveniles within each genus was minimal, the difference between dusky salamanders and brook salamanders was large (8.5 m for dusky vs. 42.6 m for brook). Current U.S. Forest Service (USFS) guidelines for southern Appalachian streams require an ~9-m (30 feet) buffer for headwater through second-order streams and an ~30-m (100 feet) buffer for streams third-order and above. The USFS buffer regulations would not be adequate to protect brook salamanders in smaller streams and would provide dusky salamanders with little protection from edge effects.

Both of these genera are in the family Plethodontidae, which is a lungless family of salamanders (Petranka 1998). This means these salamanders are even more dependent on moist habitats for respiration than other families of amphibians. In instances where there is only a 9-m buffer along the stream, brook salamanders would be forced into an "ecological decision" between two adverse environments. The majority of dusky salamanders resided within 15 m of the stream's edge, whereas brook salamanders occurred primarily 15–20 m from the edge (Fig. 1). This is most likely due to predation and competition pressures exerted by the larger dusky salamanders on the brook salamanders. Both black-bellied salamanders and seal salamanders prey on juvenile and adult two-lined salamanders (Beachy 1993; Crawford, personal observation). Thus, the brook salamanders might choose to remain in less-suitable habitat (e.g., drier, no leaf litter), risking desiccation and potential death, or they might choose to move closer to the stream and face higher risks of predation and greater rates of competition from dusky salamanders. Both these scenarios would likely lead to increased mortality and a decline in population numbers (e.g., Hairston 1987; Jaeger et al. 1998). It also assumes that all 9 m of the buffer will be equally suitable habitat, which is unrealistic because edge effects would extend completely through this small area.

We argue that our core terrestrial habitat estimate of 27.0 m for a stream salamander assemblage is conservative. Although this value is similar to the core habitat estimates of Petranka and Smith (2005), their estimates for some species were limited. They are limited because their terrestrial survey plots extended only 36–38 m from the stream, so animals occurring farther from the stream were not sampled. Our core terrestrial habitat value was calculated with all four stream species found in the assemblage; however, the estimate failed to fully protect one of the dominant species (*E. wilderae*). If the overall goal of core terrestrial habitats and buffer zones is to protect both diversity and abundance of an assemblage, we suggest calculating individual estimates for each species and using the greatest core terrestrial habitat estimate. This ensures protection of each species within the assemblage. On the basis of our results for *E. wilderae* alone, we recommend a core terrestrial habitat of 42.6 m and an overall buffer width of 92.6 m in southern Appalachian streams.

Although research on riparian habitats is increasing, a great deal of information is still lacking for many taxa requiring these habitats. We found that there are approximately 173 terrestrial vertebrates in the eastern United States alone that require riparian habitats for some life-history function (26 mammals, 27 birds, 50 reptiles, and 70 Amphibians; unpublished data). More information on core terrestrial habitats and buffer zone widths is needed to strike a balance between conservation and sustainable land use. Nevertheless, we have provided a reliable estimate of core terrestrial habitat required by southern Appalachian stream salamanders and an appropriate survey methodology that can be used in other regions to estimate core habitats. We hope that this research will provide land managers and policy makers with more information on which to delineate riparian buffer zones and will stimulate future work in these critical habitats.

Acknowledgments

We thank J. Faaborg, C. Gutmann, J. Johnson, B. Rothermel, M. Ryan, J. White, and three anonymous reviewers for insightful comments and criticisms on this manuscript. We especially thank R. Wyatt and the staff at the Highlands Biological Station, North Carolina, for use of the facilities and B. Cosentino and J. Alexander for invaluable field assistance. This research was partially supported by a GAANN fellowship from the U.S. Department of Education and the University of Missouri (JAC), a Highlands Biological Station fellowship (JAC), and a contractual agreement with the U.S. Forest Service Southern Research Station (JAC & RDS). This research was conducted under a U.S. Forest Service permit (authorization HIG6493) and under animal care protocols approved by the University of Missouri Animal Care and Use Committee (permit 3951).

Literature Cited

Ashton, R. E., and P. S. Ashton. 1978. Movements and winter behavior of *Eurycea bislineata* (Amphibia, Urodela, Plethodontidae). Journal of Herpetology **12:**295–298.

Barbour, R. W., J. W. Hardin, J. P. Schafer, and M. J. Harvey. 1969. Home range, movements, and activity of the dusky salamander, *Desmognathus fuscus*. Copeia **1969:**293–297.

Beachy, C. K. 1993. Guild structure in streamside salamander communities: a test for interactions among larval plethodontid salamanders. Journal of Herpetology **27:**465–468.

Blaustein, A. R., D. B. Wake, and W. P. Sousa. 1994. Amphibian declines: judging stability, persistence, and susceptibility of populations to local and global extinctions. Conservation Biology **8:**60–71.

Burton, T. M., and G. E. Likens. 1975. Salamander populations and biomass in the Hubbard Brook Experimental Forest, New Hampshire. Copeia **1975:**541–546.

Carey, C. L., N. Cohen, and L. Rollins-Smith. 1999. Amphibian declines: an immunological perspective. Developmental and Comparative Immunology **23:**459–472.

Corn, P. S., and R. B. Bury. 1989. Logging in western Oregon: response of headwater habitats and stream amphibians. Forest Ecology and Management **29:**39–57.

deGraaf, R. M., and M. Yamasaki. 2002. Effect of edge contrast on red-back salamander distribution in even-aged northern hardwoods. Forest Science **48:**351–363.

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.

Gomez, D. M., and R. G. Anthony. 1996. Amphibian and reptile abundance in riparian and upslope areas of five forest types in western Oregon. Northwest Science **70:**109–118.

Hairston, N. G. 1949. The local distribution and ecology of the plethodontid salamanders of the southern Appalachians. Ecological Monographs **19:**47–73.

Hairston, N. G. 1987. Community ecology and salamander guilds. Cambridge University Press, Cambridge, United Kingdom.

Haskell, D. G. 2000. Effects of forest roads on macroinvertebrate soil fauna of the Southern Appalachian Mountains. Conservation Biology **14:**57–63.

Houlahan, J. E., C. S. Findlay, B. R. Schmidt, A. H. Meyers, and S. L. Kuzmin. 2000. Quantitative evidence for global amphibian declines. Nature **404:**752–755.

Hyde, E. J., and T. R. Simons. 2001. Sampling plethodontid salamanders: sources of variability. Journal of Wildlife Management **65:**624–632.

Jaeger, R. G., C. R. Gabor, and H. M. Wilbur. 1998. An assemblage of salamanders in the Southern Appalachian Mountains: competitive and predatory behavior. Behaviour **135:**795–821.

Jones, E. B. D. III, G. S. Helfman, J. O. Harper, and P. V. Bolstad. 1999. Effects of riparian forest removal on fish assemblages in southern Appalachian streams. Conservation Biology **13:**1454–1465.

Lips, K. R. 1998. Decline of a tropical montane amphibian fauna. Conservation Biology **12:**106–117.

Lowrance, R., R. Todd, J. Fail Jr., O. Hendrickson Jr., R. Leonard, and L. Asmussen 1984. Riparian forests as nutrient filters in agricultural watersheds. BioScience **34:**374–377.

Marsh, D. M., and N. G. Beckman. 2004. Effects of forest roads on the abundance and activity of terrestrial salamanders. Ecological Applications **14:**1882–1891.

McComb, W. C., K. McGarigal, and R. G. Anthony. 1993. Small mammal and amphibian abundance in streamside and upslope habitats of mature Douglas-fir stands, western Oregon. Northwest Science **67:**7–15.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends in Ecology & Evolution **10:**58–62.

Organ, J. A. 1961. Studies of the local distribution, life history, and population dynamics of the salamander genus *Desmognathus* in Virginia. Ecological Monographs **31:**189–220.

Pechmann, J. H. K., and H. M. Wilbur. 1994. Putting declining amphibian populations in perspective: natural fluctuations and human impacts. Herpetologica **50:**65–84.

Petranka, J. W. 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington, D.C.

Petranka, J. W., and S. S. Murray. 2001. Effectiveness of removal sampling for determining salamander density and biomass: a case study in an Appalachian streamside community. Journal of Herpetology **35:**36–44.

Petranka, J. W., and C. K. Smith. 2005. A functional analysis of streamside habitat use by southern Appalachian salamanders: implications for riparian forest management. Forest Ecology and Management **210:**443–454.

Rudolph, D. C., and J. G. Dickson. 1990. Streamside zone width and amphibian and reptile abundance. Southwestern Naturalist **35:**472–476.

Semlitsch, R. D. 1998. Biological delineation of terrestrial buffer zones for pond-breeding salamanders. Conservation Biology **12:**1113–1119.

Semlitsch, R. D. 2000. Principles for management of aquatic breeding amphibians. Journal of Wildlife Management **64:**615–631.

Semlitsch, R. D., and J. R. Bodie. 1998. Are small, isolated wetlands expendable? Conservation Biology **12:**1129–1133.

Semlitsch, R. D., and J. B. Jensen. 2001. Core habitat, not buffer zone. National Wetlands Newsletter **23:**5–11.

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.

Vesely, D. G., and W. C. McComb. 2002. Salamander abundance and amphibian species richness in riparian buffer strips in the Oregon coast range. Forest Science **48:**291–297.

Wake, D. B. 1998. Action on amphibians. Trends in Ecology & Evolution **13:**379–380.

Welsh H. H. Jr., and L. M. Ollivier. 1998. Stream amphibians as indicators of ecosystem stress: a case study from California's redwoods. Ecological Applications **8:**1118–1132.