

The Distribution of a Stream-breeding Salamander, *Desmognathus ocoee*, in Terrestrial Habitat Suggests the Ecological Importance of Low-order Streams

Grant M. Connette¹, Michael S. Osbourn², and William E. Peterman³

Small headwater streams are a common feature of many forested landscapes, and their integrity is considered critical to the maintenance of water quality and biodiversity within broader drainage networks. Although riparian buffer zones are often established to limit disturbance to stream ecosystems from human land use, various buffer zone management strategies may provide effective protection to certain aquatic or semi-aquatic species while only encompassing a portion of core habitat for other species. Thus, an improved understanding of species distributions within riparian forests can be useful for predicting the overall effectiveness of various forest management practices. In this study, we conducted area-constrained surveys for salamanders at 16 plots within terrestrial habitat. We then employed an information-theoretic (AIC) approach to model selection to quantify the distribution of aquatic-breeding Ocoee Salamanders, *Desmognathus ocoee*, within terrestrial habitat as a function of stream length, width, and/or proximity within the surrounding landscape. Based on a mechanistic model for salamander counts, we estimated that 95% of Ocoee Salamanders are distributed within 79 m of their stream of origin and that relative abundance should decline exponentially with distance into terrestrial habitat. However, a simple model describing salamander counts as an exponential decay with distance from the nearest stream received the strongest support overall, suggesting that this may represent a good predictive model for the distribution of *D. ocoee* in terrestrial habitat. Due to the prevalence of headwater streams and seeps which do not appear on topographic maps, protecting 95% of core terrestrial habitat around all stream features would require protecting 59.3% of our study landscape. Models describing the spatial distributions of semi-aquatic organisms within terrestrial habitat can be useful for providing spatially explicit density estimates for species conservation or management efforts.

ALL flowing waters are part of an intricately connected, hierarchical, dendritic network. The upper-most reaches of these networks, where water first begins to coalesce and flow over land, are called headwater streams and can account for 60–80% of the total length of a drainage network (Leopold et al., 1964; Benda et al., 2005). Headwater streams contribute substantially to both the physical and biological processes of stream networks, and their integrity is considered critical to the health of the river network as a whole (Vannote et al., 1980; Ward, 1989; Meyer and Wallace, 2001; Gomi et al., 2002; Lowe and Likens, 2005). Further, headwater streams often harbor high biodiversity and unique community assemblages (Meyer et al., 2007; Clarke et al., 2008), which are ecologically linked to downstream ecosystems through the movement of organisms (Pringle, 1997, 2001).

Despite their ubiquity across the landscape, headwater streams are rarely delineated on topographic maps or spatial data layers used to guide management activities (Hansen, 2001; Meyer and Wallace, 2001; Lowe and Likens, 2005). Although riparian buffer zones are often established to protect biodiversity and preserve the water quality and geomorphology of stream systems, the level of protection afforded to small, fishless headwaters varies with land ownership and is generally more permissive than for permanent, fish-bearing streams (Adams, 2007; Olson et al., 2007). Riparian buffers around headwater streams are critical for stabilizing air and water temperatures, maintenance of soil moisture, and retention of nutrients and sediments (Brosofske et al., 1997; Swank et al., 2001; Wilkerson et al., 2006; Anderson et al., 2007). However, the width of riparian forest protected around a headwater stream may serve

different functions for different species. For instance, minimal riparian buffers may fully protect aquatic species, but such a buffer may only encompass a portion of core habitat for semi-aquatic species (Crawford and Semlitsch, 2007; Peterman et al., 2011). This is important to consider when developing forest management guidelines since semi-aquatic amphibians, especially stream salamanders, often represent the dominant vertebrate taxa in low-order, headwater streams (Hairston, 1987; Davic and Welsh, 2004; Milanovich et al., 2015).

In many parts of the United States, semi-aquatic salamanders can contribute considerably to terrestrial vertebrate biomass (Davic, 1983; Peterman et al., 2008). As the dominant vertebrate predator in many riparian habitats, semi-aquatic salamanders are likely integral to the trophic dynamics of riparian-aquatic food webs (Hairston, 1987; Davic and Welsh, 2004; Keitzer and Goforth, 2013). These salamanders vary in their use of terrestrial habitat away from headwater streams, with larger species tending to remain close to streams and smaller species often occurring more than 100 meters into the forest (Hairston, 1949; Organ, 1961; Petranka and Smith, 2005; Crawford and Semlitsch, 2007; Bruce, 2011). The effects of riparian buffer width on semi-aquatic salamanders are varied. In most studies, the abundance of semi-aquatic species decreases as riparian buffer width narrows (Peterman and Semlitsch, 2009; Peterman et al., 2011; Olson and Burton, 2014; Olson et al., 2014). However, because salamanders are relatively long-lived (>5 yrs; Castanet et al., 1996; Bruce et al., 2002), the effects of riparian habitat loss may not be immediately apparent (Olson and Rugger, 2007; Peterman et al., 2011). Longer-term assessments of species responses have shown that

¹ Conservation Ecology Center/Myanmar Program, Smithsonian Conservation Biology Institute, 1500 Remount Road, Front Royal, Virginia 22630; Email: grmcco@gmail.com. Send reprint requests to this address.

² Department of Biology, 171b Rankin Science West, 572 Rivers Street, Appalachian State University, Boone, North Carolina 28608; Email: osbournms@appstate.edu.

³ School of Environment and Natural Resources, The Ohio State University, 210 Kottman Hall, 2021 Coffey Road, Columbus, Ohio 43210-1085; Email: Peterman.73@osu.edu.

Submitted: 1 December 2014. Accepted: 3 September 2015. Associate Editor: M. E. Gifford.

© 2016 by the American Society of Ichthyologists and Herpetologists DOI: 10.1643/OT-14-215 Published online: 21 March 2016

species are likely to persist with limited riparian protection while terrestrial habitat use and abundance are reduced (Peterman et al., 2011; Olson et al., 2014).

The growing literature detailing species-specific and assemblage responses to riparian forest loss and alteration clearly demonstrates the importance of these habitats to the ecology and life history of amphibians generally, and semi-aquatic salamanders specifically. Mechanistic and in-depth assessments of how individuals are spatially distributed throughout riparian forests can also be used to inform management activities, and several studies have sought to define the core terrestrial habitat of species by considering density as a function of linear distance from streams (e.g., Vesely and McComb, 2002; Petranka and Smith, 2005; Crawford and Semlitsch, 2007). In our study, we assess how the abundance of a semi-aquatic salamander, *Desmognathus ocoee*, is affected by stream size, stream length, and stream proximity. *Desmognathus ocoee* is a member of the widely distributed *D. ochrophaeus* complex and is found in the southwestern Blue Ridge and Piedmont physiographic region as well as the Appalachian Plateau of northeastern Alabama (Lannoo, 2005). The relatively short larval period of *D. ocoee* (7–10 months, depending upon elevation) has allowed this species to exploit a variety of wetted habitats, including seepages, springs, wet rock faces, and small streams (Lannoo, 2005). Despite this dependence upon water for reproduction, *D. ocoee* are the most terrestrial of the stream-breeding desmognathine salamanders (Petranka, 1998), and their abundance and distribution away from streams tends to increase with elevation (Hairston, 1987; Ford et al., 2002). Because of their extensive use of terrestrial riparian habitats adjacent to headwater streams and other wetted features on the landscape, *D. ocoee* are an ideal species to mechanistically assess how individuals are distributed throughout riparian forest and to enumerate in greater detail the importance of small, unmapped aquatic features on the landscape. Our objectives in this study were to (1) illustrate a framework for quantifying the terrestrial distributions of semi-aquatic species; (2) assess abundance of *D. ocoee* in relation to (i) distance from aquatic habitat, (ii) type of aquatic habitat, (iii) total amount of aquatic habitat; and (3) make management recommendations for headwater habitats that account for the distribution of semi-aquatic salamanders throughout riparian forests.

MATERIALS AND METHODS

In 2009, we established 16 terrestrial survey plots (25×25 m) in the vicinity of Perry Gap on the Nantahala National Forest, North Carolina, U.S.A. (approx. 35.1028°N , 83.6457°W). These survey plots were located in and around four forest stands which had timber harvested according to a two-aged regeneration harvest method between 2011 and 2013. We performed nighttime area-constrained searches of each plot during the summers of 2009 (1–2 surveys/plot), 2010 (3 surveys/plot), 2011 (3–4 surveys/plot), 2012 (2–3 surveys/plot), 2013 (3 surveys/plot), and 2014 (3 surveys/plot). Within years, each plot was visited at approximately one-month intervals. All surveys were performed between 2130 and 0545 hr EST and typically lasted 1–2 hours per plot, depending primarily on the number of salamanders captured. During these exhaustive area-constrained searches, we attempted to hand capture all salamanders encountered but did not disturb natural cover objects. Upon capture, we marked each salamander's unique capture location with a

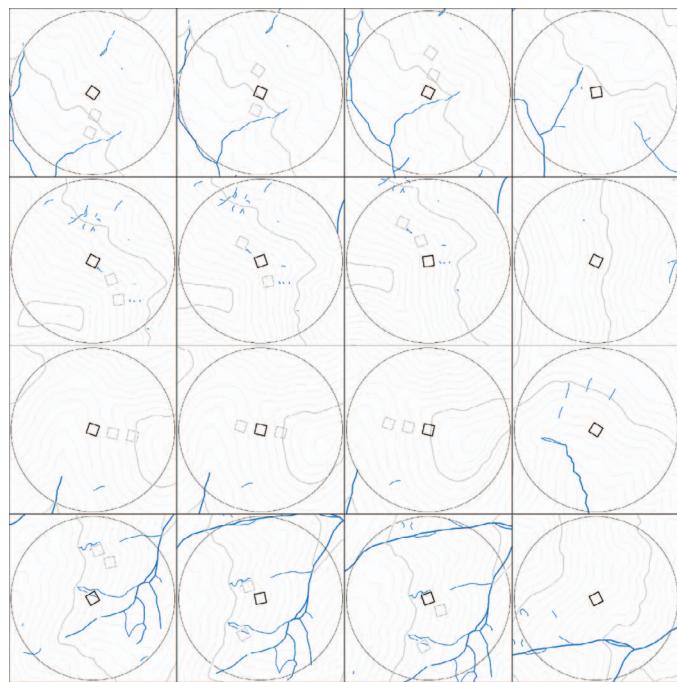


Fig. 1. Stream and seep locations relative to terrestrial survey plots. Small squares show survey plot locations. Each panel is focused on the survey plot shown in bold and depicts the circular area of 200 m radius that was intensively searched for stream features.

numbered survey flag. All unmarked salamanders were individually marked with Visual Implant Elastomer (Northwest Marine Technology, Shaw Island, WA) and returned to within 5 m of their unique capture location, almost always 1–3 nights after capture.

In this study, we used relative count data from these area-constrained surveys to examine the extent of terrestrial habitat use by the Ocoee Salamander, *Desmognathus ocoee*. Specifically, we used catch-per-unit-effort (CPUE) as our response variable in all analyses, which was calculated by dividing the cumulative number of salamander captures at each plot by the total number of surveys conducted before timber harvest treatments were applied. Thus, CPUE represents the average count through time for each study plot. Counts were averaged from all surveys in control plots ($n = 4$), while only captures from pre-harvest surveys were used to derive CPUE for treatment plots ($n = 12$). Because these salamanders make migratory movements to aquatic habitat for reproduction, obtaining unbiased abundance estimates from mark-recapture models would require accounting for this potential transience behavior (e.g., Clavel et al., 2008; Conn et al., 2011). Further, such estimates can be sensitive to correct specification of the transience process (Conn et al., 2011). Lack of population closure among surveys also precluded the use of repeated count analyses that account for imperfect detection of individuals (e.g., Royle, 2004). Our analyses are then predicated on the assumption that abundance, rather than detection probability, varies in relation to stream locations on the surrounding landscape.

To identify stream locations relative to our survey plots, we exhaustively searched a minimum radius of 200 m around the center of each plot during 2013 and 2014 (Fig. 1). All streams were mapped using a handheld GPS unit (Garmin GPSMAP 60CSx), and specific stream reaches were broadly categorized according to their mean width (recorded in 0.5 m intervals) as either a 1) Seep (generally 0.5–1 m wide), 2)

Table 1. Proposed models describing abundance of *Desmognathus ocoee* in terrestrial survey plots.

| Model type | Model name | Covariate(s) |
|------------|------------------------|--|
| Linear | 50 m Buffer | Total stream length within 50 m |
| Linear | 100 m Buffer | Total stream length within 100 m |
| Linear | 200 m Buffer | Total stream length within 200 m |
| Linear | Distance to stream (A) | Distance to the nearest stream feature |
| Non-linear | Distance to stream (B) | Distance to the nearest stream feature |
| Composite | Seeps < Stream | Distance and size of each 1 m stream section |
| Composite | Seeps = Stream | Distance of each 1 m stream section |
| Composite | Seeps > Stream | Distance and inverse-size of each 1 m stream section |

Small Stream (1–2 m wide), or 3) Large Stream (>2 m wide). A small number of broad wet rock faces ($n = 12$) and areas near springs with very shallow, slow-moving water ($n = 8$) were also categorized as seeps in spite of their greater width. Mapped streams were later converted into a 1 m resolution raster layer in ArcGIS 10.1 (ESRI, Redlands, CA) with each pixel assigned a value of 0 (no seep or stream), 0.5 (seep), 1 (small stream), or 2 (large stream), representing the minimum width for each stream classification.

Data analysis.—We fit models to describe counts (CPUE) of *D. ocoee* as a function of stream locations in the surrounding landscape (Table 1). First, we fit simple linear regression models with exact distance to nearest stream or total stream length within 50 m, 100 m, or 200 m of the plot center as covariates (Table 1—“Linear Models”). We also considered a single *post hoc* model which included exact distance to nearest stream (m) as a predictor of CPUE according to a non-linear exponential decay model (Table 1—“Non-linear Model”):

$$\hat{Y}_i = ae^{-bx_i}$$

In this model, \hat{Y}_i represents the predicted CPUE at each survey plot, i , and x_i indicates the distance from the center of a given survey plot to the nearest stream feature on the landscape. The parameters a and b control the starting value and rate of exponential decay and are estimated from the data.

Finally, we developed models with all streams within 200 meters potentially contributing to the observed counts of salamanders (Table 1—“Composite Models”), with each 1 m length of stream being weighted by both its size (stream width in m) and its exact distance from the center of a given survey plot.

$$\hat{Y}_i = \sum_{j=1}^n v_j ae^{-bx_j}$$

Here, \hat{Y}_i represents the predicted CPUE at each survey plot, i , where the observed counts are assumed to be the sum of the contributions from each 1 m stream section, j , within a 200 m radius. The expected number of salamanders contributed

by each 1 m stream section is weighted by a value, v_j which corresponds to stream size in meters ($v_j = 0.5$ [seep], 1 [small stream], or 2 [large stream]). The distance from each stream section to the center of each survey plot, x_{ij} , also influences the predicted CPUE according to an exponential decay function. Again, the parameters a and b control the starting value and rate of the exponential decay and are estimated from the data. We also consider two modifications of this basic model by using alternative weightings of streams according to their size. In the first case, all streams are assigned equal importance irrespective of their size ($v_j = 1$ for all 1 m stream sections). Alternatively, small streams are assumed to contribute more salamanders to survey plots by using the inverse of their width to weight their contributions to salamander counts ($v_j = 2$ [seep], 1 [small stream], or 0.5 [large stream]).

All models were fit by maximum-likelihood estimation using the “optim” function in program R (R Core Team, 2012) and assuming a normal error structure. We used Akaike’s Information Criterion, adjusted for small sample size (AIC_c), to rank the seven *a priori* models and single *post hoc* model described above (Table 1). This allowed us to identify the models best describing the distribution of *D. ocoee* relative to streams in the surrounding landscape. We calculated the ΔAIC_c value for each model, which indicates the difference between each model and the best-supported model in the candidate set. We also calculated Akaike weights, ω , which represent the probability that each model is the best among the candidate models (Burnham and Anderson, 2002). As a check of model assumptions, we conducted a Shapiro-Wilk test and found that the distributions of residuals from our top *a priori* model and our sole *post hoc* model were not significantly different from normal ($P > 0.05$). All data and R code for these analyses can be found on the University of Missouri’s MOspace Institutional Repository (<https://hdl.handle.net/10355/48113>).

RESULTS

From 2009–2014, we recorded a total of 1,520 captures of *D. ocoee* in all terrestrial survey plots. These captures included 1,371 unique individuals, of which 1,251 were never recaptured. The majority of the 120 recaptured individuals were identified as males ($n = 79$; 65.8%). Forty-four individuals were last recaptured in the same year that they were originally marked. Of the individuals recaptured over multiple years, 38 were last recaptured in the first year after marking, 15 in their second year, 14 in their third year, and nine in their fourth year (i.e., recaptures spanned five years). Five of the nine individuals with recaptures spanning five years were first captured at a likely age of at least four years (based on SVL > 40 mm; Bruce et al., 2002), indicating that certain individuals in our study populations reach at least eight years of age. Spatial location data of individuals within survey plots was recorded between 2009 and 2013. In total, 49 between-year movement distances were observed, with 81.6% of these displacements being less than 7.5 m (Fig. 2).

To assess the terrestrial distribution of *D. ocoee* under control conditions, we thinned our dataset to 968 captures by excluding captures occurring after timber harvest in treatment plots. Catch-per-unit-effort at each plot ranged from 0 (1 plot) to 29.56 individuals (mean ± 1 SD; 6.36 ± 8.43), and the center of each survey plot ranged from 6.4–141.1 m to the nearest stream or seep feature (mean ± 1 SD; 66.31 ± 46.62 m). All proposed models relating abun-

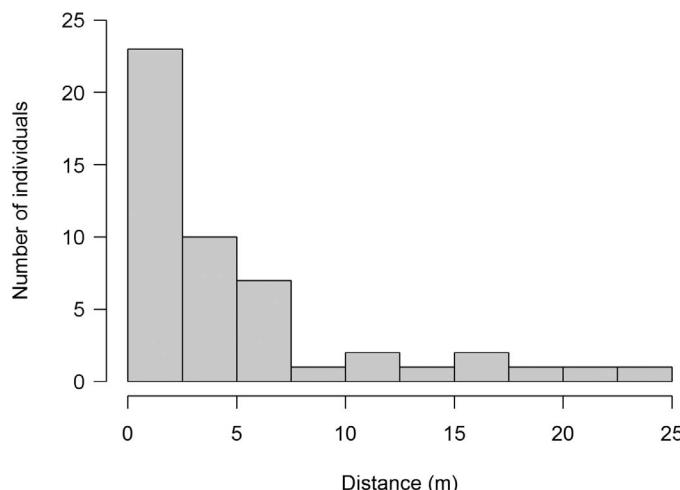


Fig. 2. Observed distances between sequential spatial locations of individual *D. ocoee* across years ($n = 49$). All observed locations were within 25×25 m survey plots, which imposes an upper limit on observable movement distances and should lead to some underrepresentation of large inter-year movements.

dance of *D. ocoee* to stream amount or proximity in the surrounding landscape were better supported than an intercept-only model (Table 2). In all models, predicted abundance of *D. ocoee* was positively related to total stream length or negatively associated with distance to stream features (Table 3). The best-supported *a priori* model was a “composite” model, which formalizes the biologically reasonable assumptions that 1) semi-aquatic salamanders in terrestrial habitat do not necessarily originate from the nearest stream and 2) two-dimensional dispersion of individuals into terrestrial habitat should result in nearer streams making a greater relative contribution to local abundance. The estimated exponential decay rate for this model was 0.04 (95% CI: 0.02–0.07), which led to the predictions that 80% of individuals of *D. ocoee* are found within 43 m of their breeding stream, 95% are found within 79 m, and 99% are found within 122 m (Fig. 3). Although there was some evidence for autocorrelation in CPUE among nearby sites, there was no such tendency after explicitly accounting for stream locations in the surrounding landscape (Fig. 4). The three most parsimonious *a priori* models differed only in their weightings of streams according to their width. This resulted in little resolution among models, with the best-supported *a priori* model assuming that seeps and small streams were

likely to support larger numbers of breeding individuals than large streams.

Although it seems unrealistic to assume that semi-aquatic salamanders in terrestrial habitat necessarily breed in the nearest stream, especially when multiple streams are of roughly equal proximity, our initial analysis confirmed our expectation that terrestrial abundance should more strongly depend on nearer streams than distant ones. This suggested that a non-linear model describing salamander counts as an exponential decay with distance from the nearest stream could represent a reasonable predictive model for abundance of *D. ocoee* in terrestrial habitat. The estimated exponential decay rate for this *post hoc* model was 0.07 (95% CI: 0.04–0.10). This model received the greatest support of all models we considered, with a difference in AIC_c of 1.21 separating the next model in our candidate set.

DISCUSSION

Although riparian buffer zones are often designated to protect water resources and preserve habitat quality for aquatic species, they may also function as core habitat or dispersal corridors for both semi-aquatic and fully terrestrial species (Semlitsch and Bodie, 2003; Olson et al., 2007). Many aquatic-breeding amphibians are dependent on terrestrial habitat for part of their life cycle (Petraska, 1998), and optimization of forest management strategies for protection of these species can be aided by a basic understanding of their terrestrial distributions. In practice, however, species often vary in the extent to which they use terrestrial habitat (Vesely and McComb, 2002; Petraska and Smith, 2005; Crawford and Semlitsch, 2007; Rittenhouse and Semlitsch, 2007), and these differences in the relative use of aquatic versus terrestrial habitat may correspond with sensitivity to riparian zone disturbance (Surasinghe and Baldwin, 2015).

Many studies describing the terrestrial distributions of semi-aquatic species are based on relative count data and assume that the probability of detecting individuals does not vary with proximity to aquatic habitat. This may be an unrealistic assumption if higher moisture or dense riparian vegetation affect either animal activity patterns or survey effectiveness. In our study, we found that plot-specific recapture rates of marked individuals did not vary significantly with distance to the nearest stream (Binomial GLM, $P = 0.76$). This likely indicates that a similar proportion of the population was sampled regardless of proximity to aquatic habitat and that inferences made from average counts of salamanders should largely reflect the underlying distribution of individuals in terrestrial habitat.

Table 2. Ranking of models describing abundance of *Desmognathus ocoee* in terrestrial survey plots*.

| Model type | Model name | K | ΔAICc | Model likelihood | Weight |
|------------|------------------------|---|---------------------|------------------|--------|
| Non-linear | Distance to stream (B) | 3 | 0.00 | 1.00 | 0.44 |
| Composite | Seeps > Stream | 3 | 1.21 | 0.55 | 0.24 |
| Composite | Seeps = Stream | 3 | 1.63 | 0.44 | 0.20 |
| Composite | Seeps < Stream | 3 | 2.71 | 0.26 | 0.11 |
| Linear | 50 m Buffer | 3 | 9.41 | 0.01 | 0.00 |
| Linear | 100 m Buffer | 3 | 14.28 | 0.00 | 0.00 |
| Linear | 200 m Buffer | 3 | 15.06 | 0.00 | 0.00 |
| Linear | Distance to stream (A) | 3 | 16.13 | 0.00 | 0.00 |
| Linear | Intercept-only | 2 | 20.87 | 0.00 | 0.00 |

* K = number of parameters in a given model, ΔAICc = difference in AICc between each model and the best-supported model in the set, Model likelihood = $e^{-\Delta\text{AICc}/2}$, Weight = Akaike weight (ω) for each model

Table 3. Maximum-likelihood estimates for model parameters*.

| Non-linear models | a | 95% CI | b | 95% CI |
|------------------------|-----------|------------------|-----------|----------------|
| Distance to stream (B) | 232.06 | (146.99, 342.81) | 0.07 | (0.04, 0.10) |
| Seeps > Stream | 0.86 | (0.31, 1.62) | 0.04 | (0.02, 0.07) |
| Seeps = Stream | 1.71 | (0.66, 3.32) | 0.04 | (0.02, 0.08) |
| Seeps < Stream | 4.01 | (1.66, 7.64) | 0.05 | (0.03, 0.09) |
| Linear models | β_0 | 95% CI | β_1 | 95% CI |
| 50 m buffer | 13.60 | (−1.99, 29.19) | 0.60 | (0.34, 0.86) |
| 100 m buffer | 7.13 | (−14.00, 28.26) | 0.17 | (0.07, 0.27) |
| 200 m buffer | 2.17 | (−21.91, 26.26) | 0.05 | (0.02, 0.07) |
| Distance to stream (A) | 69.06 | (39.48, 98.68) | −0.56 | (−0.93, −0.19) |
| Intercept-only | 31.80 | (10.54, 53.07) | — | — |

* Model names correspond to those given in Table 1 and Table 2

To characterize terrestrial habitat use of semi-aquatic amphibians, researchers have often sampled continuously away from streams in order to relate observed densities to distance from particular stream features (e.g., Vesely and McComb, 2002; Petranka and Smith, 2005; Crawford and Semlitsch, 2007). In our study, we collected count data from scattered survey areas and compared models representing relative abundance of *D. ocoee* as a function of stream length, width, and/or proximity within the surrounding 200 m landscape. As a generality, there was little support for simple linear regression models with counts predicted by (i) distance to nearest stream, (ii) stream length within 50 m, (iii) stream length within 100 m, or (iv) stream length within 200 m. We found considerably stronger support for several mechanistic models which potentially allow all streams within 200 m to contribute to salamander counts according to their size and proximity. Although these models assume that semi-aquatic salamanders in terrestrial habitat do not necessarily originate from the nearest stream, the estimated exponential relationship between distance to stream and abundance suggests that the closest stream should contribute the greatest number of individuals to adjacent terrestrial habitat. Finally, we considered a *post hoc* model representing relative abundance as a simple exponential decay with distance from the nearest stream feature and found that this model was slightly better supported than any of our *a priori* models. Thus, when distance to the nearest stream feature is known but all

aquatic habitat has not been georeferenced, a model representing counts of *D. ocoee* as a negative exponential function of distance to stream would likely provide useful predictions of relative terrestrial densities.

Our results provided clear support for models that described density of *D. ocoee* as an exponential decay function with increasing distance from aquatic habitat. However, the rate at which abundance decreases will likely vary both among species and intra-specifically among sites. Previous research by Crawford and Semlitsch (2007) found that 42.6 m of riparian forest would encompass 95% of terrestrial habitat for two semi-aquatic salamanders in the southern Appalachian Mountains, but suggested that 92.6 m should be protected to buffer against edge effects. A separate study of streamside habitat use by semiaquatic Appalachian salamanders proposed that a minimum of 30–35 m of terrestrial habitat should be protected as core habitat (Petranka and Smith, 2005), though the distribution of individuals beyond this threshold could not be inferred due to the sampling protocol. According to our top *a priori* model, a distance of 79 m from a single stream feature would be expected to encompass 95% of all individuals of *D. ocoee*. Although Crawford and Semlitsch (2007) reported that 95% of *D. ocoee* were captured within 9.7 m of streams during

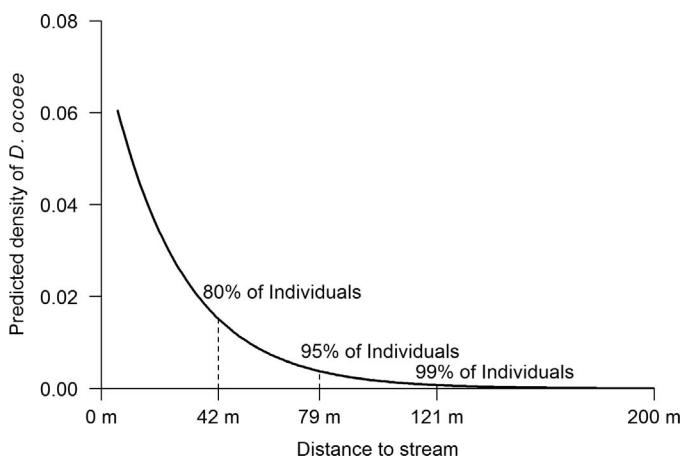


Fig. 3. Predicted relative density of *D. ocoee* in relation to distance from stream. The y-axis represents the proportion of individuals expected at a given distance, such that the area under the curve equals one.

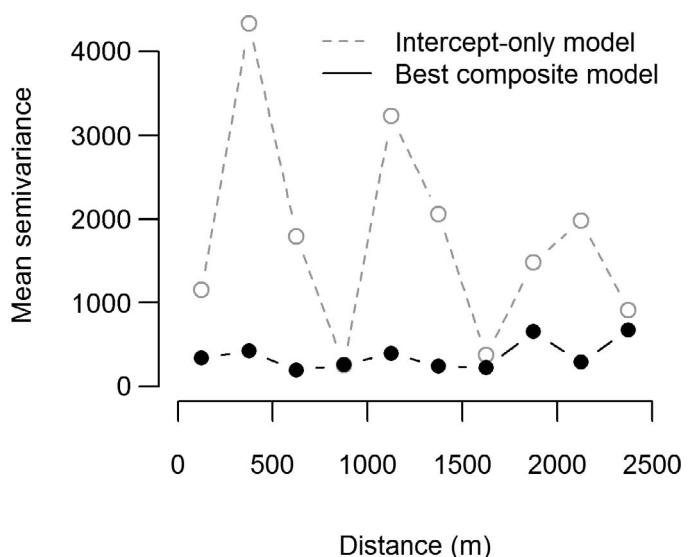


Fig. 4. Empirical semivariogram illustrating autocorrelation of residuals among sites, grouped by 250 m inter-site distance classes. Higher semivariance represents a greater autocorrelation among residuals.

night sampling, their sites tended to be at lower elevation, and terrestrial habitat use of several semi-aquatic salamanders has been shown to increase with elevation (Hairston, 1987; Ford et al., 2002; Petranka and Smith, 2005). Our model-based estimates were also consistent with the fact that the only survey plot with no captures of *D. ocoee* was located at a distance of 137 m from a single wet rock face which represented the nearest aquatic habitat. Small numbers of *D. ocoee* were captured at two other sites of comparable distance from aquatic habitat (132 and 141 m), demonstrating that individuals of this species can occur at large distances from aquatic habitat.

Despite their prevalence across many landscapes, headwater streams are often missing from topographic maps or spatial hydrography data layers (Hansen, 2001; Meyer and Wallace, 2001; Lowe and Likens, 2005). Although headwater streams have been defined as streams with drainage basins <100 ha (e.g., Clarke et al., 2008), Connette and Semlitsch (2013) reported that a minimum drainage area of just 0.75 ha seemed to best correspond with known stream locations on a southern Appalachian landscape. In our study, we georeferenced 4,517 m of aquatic habitat within 200 m of our survey plots and found that only 817 m (18.1%) of this stream length was represented in the 1:24,000-scale National Hydrography Dataset. Although these unmapped headwaters were often small or intermittent, our salamander count data provided weak evidence that the smallest seeps and streams were a greater source of *D. ocoee* in terrestrial habitat than larger streams. This is in concurrence with our personal observation that shallow, rocky streams with slow-moving water tend to have higher in-stream abundances of *D. ocoee* than larger, channelized streams with fast-flowing water. Furthermore, there was relatively little variation across sites in terms of distance to nearest streams according to the National Hydrography Dataset, while counts of *D. ocoee* varied considerably among survey plots and in close correspondence with the locations of previously unmapped stream features. Although our inference may be limited by the analysis of count data from just 16 survey plots, future studies may provide further evidence for the disproportionate influence of the smallest headwaters on the terrestrial abundance of semi-aquatic salamanders.

Management implications.—Within our study area, *D. ocoee* appears to be widely distributed in terrestrial habitat, and the small inter-year movement distances of most recaptured individuals (Fig. 2) suggest that at least some individuals maintain stable, multi-year home ranges in terrestrial habitat. After georeferencing all aquatic habitat within 200 m of our survey plots, we calculated that 59.3% of this area falls within the observed 95% core terrestrial habitat for *D. ocoee* (79 m). Protecting 95% core habitat and an additional buffer of 50 m around all stream features (e.g., Crawford and Semlitsch, 2007) would require restricting management activities across 78.5% of this landscape. In practice, however, most small headwaters receive much less protection under current riparian management guidelines (Crawford and Semlitsch, 2007; Olson et al., 2007). For semi-aquatic species with nearly continuous distributions in terrestrial habitat, focusing forest management strategies on protection of high-density areas may be a practical, and possibly more effective, alternative to substantial expansion of riparian buffer zones. In these cases, models describing the distributions of semi-aquatic organisms within terrestrial habitat can be useful for providing spatially explicit density estimates for

species of conservation or management interest. Furthermore, such an approach may allow management decisions to be informed by the extent to which various riparian management strategies maintain sufficiently large source populations for future recolonization of harvested areas.

ACKNOWLEDGMENTS

We thank A. Connette, K. LaJeunesse Connette, K. Corbett, K. Dipple, J. Lewis, M. Mackey, W. Overton, K. Pursel, and S. Schlick for assisting with fieldwork. Funding for this research was provided by the Highlands Biological Foundation, a Graduate Student Research Grant from the Chicago Herpetological Society, and a Grant-in-Aid of Research from Sigma Xi. GMC was supported by a University of Missouri Life Sciences Fellowship. In addition, this publication was developed under a STAR Research Assistance Agreement No. FP917444 awarded by the U.S. Environmental Protection Agency. It has not been formally reviewed by EPA. The views expressed in this document are solely those of the authors, and EPA does not endorse any products or commercial services mentioned in this publication. Research was conducted under a North Carolina Wildlife Resources Commission collection permit (10-SC00405), U.S. Forest Service special use permit (TUS649001, TUS649002), and approved IACUC protocols through the University of Missouri (6144, 7403) and the Highlands Biological Station.

LITERATURE CITED

- Adams, P. W. 2007. Policy and management for headwater streams in the Pacific Northwest: synthesis and reflection. *Forest Science* 53:104–118.
- Anderson, P. D., D. J. Larson, and S. S. Chan. 2007. Riparian buffer and density management influences on microclimate of young headwater forests of western Oregon. *Forest Science* 53:254–269.
- Benda, L., M. A. Hassan, M. Church, and C. L. May. 2005. Geomorphology of steepland headwaters: the transition from hillslopes to channels. *JAWRA Journal of the American Water Resources Association* 41:835–851.
- Brososke, K. D., J. Chen, R. J. Naiman, and J. F. Franklin. 1997. Harvesting effects on microclimate gradients from small streams to uplands in Western Washington. *Ecological Applications* 7:1188–1200.
- Bruce, R. C. 2011. Community assembly in the salamander genus *Desmognathus*. *Herpetological Monographs* 25:1–24.
- Bruce, R. C., J. Castanet, and H. Francillon-Vieillot. 2002. Skeletochronological analysis of variation in age structure, body size, and life history in three species of desmognathine salamanders. *Herpetologica* 58:181–193.
- Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Second edition. Springer-Verlag, New York.
- Castanet, J., H. Francillon-Vieillot, and R. C. Bruce. 1996. Age estimation in desmognathine salamanders assessed by skeletochronology. *Herpetologica* 52:160–171.
- Clarke, A., R. MacNally, N. Bond, and P. S. Lake. 2008. Macroinvertebrate diversity in headwater streams: a review. *Freshwater Biology* 53:1707–1721.
- Clavel, J., A. Robert, V. Devictor, and R. Julliard. 2008. Abundance estimation with a transient model under the robust design. *Journal of Wildlife Management* 72:1203–1210.

- Conn, P. B., A. M. Gorgone, A. R. Jugovich, B. L. Byrd, and L. J. Hansen.** 2011. Accounting for transients when estimating abundance of bottlenose dolphins in Choctawhatchee Bay, Florida. *Journal of Wildlife Management* 75: 569–579.
- Connette, G. M., and R. D. Semlitsch.** 2013. Life history predicts salamander recovery rate from timber harvest in southern Appalachian forests. *Conservation Biology* 27: 1399–1409.
- Crawford, J. A., and R. D. Semlitsch.** 2007. Estimation of core terrestrial habitat for stream-breeding salamanders and delineation of riparian buffers for protection of biodiversity. *Conservation Biology* 21:152–158.
- Davic, R. D.** 1983. An investigation of salamander guild predation in a North Carolina stream: an experimental approach. Unpubl. Ph.D. diss., Kent State University, Kent, Ohio.
- Davic, R. D., and H. H. Welsh.** 2004. On the ecological roles of salamanders. *Annual Review of Ecology, Evolution, and Systematics* 35:405–434.
- Ford, W. M., M. A. Menzel, and R. H. Odom.** 2002. Elevation, aspect, and cove size effects on southern Appalachian salamanders. *Southeastern Naturalist* 1:315–324.
- Gomi, T., R. C. Sidle, and J. S. Richardson.** 2002. Understanding processes ad downstream linkages of headwater systems. *BioScience* 52:905–916.
- 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, U.K.
- Hansen, W. F.** 2001. Identifying stream types and management implications. *Forest Ecology and Management* 143: 39–46.
- Keitzer, C. S., and R. R. Goforth.** 2013. Salamander diversity alters stream macroinvertebrate community structure. *Freshwater Biology* 58:2114–2125.
- Lannoo, M. J. (Ed.).** 2005. *Amphibian Declines: The Conservation Status of United States Species*. University of California Press, Berkeley.
- Leopold, L. B., M. G. Wolman, and J. P. Miller.** 1964. *Fluvial Processes in Geomorphology*. W. H. Freeman, San Francisco.
- Lowe, W. H., and G. E. Likens.** 2005. Moving headwater streams to the head of the class. *BioScience* 55:196–197.
- Meyer, J. L., D. L. Strayer, J. B. Wallace, S. L. Eggert, G. S. Helfman, and N. E. Leonard.** 2007. The contribution of headwater streams to biodiversity in river networks. *JAWRA Journal of the American Water Resources Association* 43:86–103.
- Meyer, J. L., and J. B. Wallace.** 2001. Lost linkages and lotic ecology: rediscovering small streams, p. 295–317. In: *Ecology: Achievement and Challenge*. N. J. Huntly and S. Levin (eds.). Blackwell Science, Oxford, UK.
- Milanovich, J. R., J. C. Maerz, and A. D. Rosemond.** 2015. Stoichiometry and estimates of nutrient standing stocks of larval salamanders in Appalachian headwater streams. *Freshwater Biology* 60:1340–1353.
- Olson, D. H., P. D. Anderson, C. A. Frissell, H. H. Welsh, Jr., and D. F. Bradford.** 2007. Biodiversity management approaches for stream-riparian areas: perspectives for Pacific Northwest headwater forests, microclimates, and amphibians. *Forest Ecology and Management* 246:81–107.
- Olson, D. H., and J. I. Burton.** 2014. Near-term effects of repeated-thinning with riparian buffers on headwater stream vertebrates and habitats in Oregon, USA. *Forests* 5:2703–2729.
- Olson, D. H., J. B. Leirness, P. G. Cunningham, and E. Ashley Steel.** 2014. Riparian buffers and forest thinning: effects on headwater vertebrates 10 years after thinning. *Forest Ecology and Management* 321:81–93.
- Olson, D. H., and C. Rugger.** 2007. Preliminary study of the effects of headwater riparian reserves with upslope thinning on stream habitats and amphibians in western Oregon. *Forest Science* 53:331–342.
- 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.
- Peterman, W. E., J. A. Crawford, and R. D. Semlitsch.** 2008. Productivity and significance of headwater streams: population structure and biomass of the black-bellied salamander (*Desmognathus quadramaculatus*). *Freshwater Biology* 53:347–357.
- Peterman, W. E., J. A. Crawford, and R. D. Semlitsch.** 2011. Effects of even-aged timber harvest on stream salamanders: support for the evacuation hypothesis. *Forest Ecology and Management* 262:2344–2353.
- Peterman, W. E., and R. D. Semlitsch.** 2009. Efficacy of riparian buffers in mitigating local population declines and the effects of even-aged timber harvest on larval salamanders. *Forest Ecology and Management* 257:8–14.
- Petraska, J. W.** 1998. *Salamanders of the United States and Canada*. Smithsonian Institution Press, Washington, D.C.
- Petraska, 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.
- Pringle, C. M.** 1997. Exploring how disturbance is transmitted upstream: going against the flow. *Journal of the North American Benthological Society* 16:425–438.
- Pringle, C. M.** 2001. Hydrologic connectivity and the management of biological reserves: a global perspective. *Ecological Applications* 11:981–998.
- R Core Team.** 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.r-project.org>
- Rittenhouse, T. A. G., and R. D. Semlitsch.** 2007. Distribution of amphibians in terrestrial habitat surrounding wetlands. *Wetlands* 27:153–161.
- Royle, J. A.** 2004. N-Mixture models for estimating population size from spatially replicated counts. *Biometrics* 60: 108–115.
- Semlitsch, R. D., and J. R. Bodie.** 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. *Conservation Biology* 17:1219–1228.
- Surasinghe, T. D., and R. F. Baldwin.** 2015. Importance of riparian forest buffers in conservation of stream biodiversity: responses to land uses by stream-associated salamanders across two southeastern temperate ecoregions. *Journal of Herpetology* 49:83–94.
- Swank, W. T., J. M. Vose, and K. J. Elliott.** 2001. Long-term hydrologic and water quality responses following commercial clearcutting of mixed hardwoods on a southern Appalachian catchment. *Forest Ecology and Management* 143:163–178.

- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing.** 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:103–137.
- 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.
- Ward, J. V.** 1989. The four-dimensional nature of lotic systems. Journal of the North American Benthological Society 8:2–8.
- Wilkerson, E., J. M. Hagan, D. Siegel, and A. A. Whitman.** 2006. The effectiveness of different buffer widths for protecting headwater stream temperature in Maine. Forest Science 52:221–231.