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PREDICTING VARIATION IN MICROHABITAT UTILIZATION OF TERRESTRIAL SALAMANDERS

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ABSTRACT: Understanding patterns of microhabitat use among terrestrial salamanders is important for predicting their responses to natural and anthropogenic disturbances. The dependence of terrestrial salamanders on cutaneous respiration limits their spatial distribution to moist, humid areas. Although many studies have shown negative effects of canopy removal on terrestrial salamander abundance, some have shown potential ameliorating effects of retaining coarse woody debris (CWD) as moist refugia (critical resources in the landscape). Because cover objects like CWD retain moisture longer than fine debris, terrestrial salamanders are often more locally abundant in areas of dense cover. Temporally variable environmental conditions could affect microhabitat quality and influence the fine-scale spatial distributions of salamanders. Spatial and temporal variability in microhabitat use greatly influence individual detectability, which is always a challenge for terrestrial salamanders. We conducted repeated area-constrained surveys to examine variation in salamander microhabitat use of terrestrial salamanders in relation to season, year, and weather conditions. We found that time since rain (TSR) was the best predictor of relative salamander microhabitat use, but the strength of this relationship varied among years. In addition, TSR was also the best predictor of salamander surface activity. We captured most salamanders within leaf litter, but the proportion of leaf litter captures varied with TSR. Our results illustrate the importance of accounting for variable detectability when sampling for terrestrial salamanders. Disturbances which affect leaf litter depth and decomposition rates could influence the availability and quality of microhabitats and potentially increase competition among individuals for natural cover objects.

Key words: Coarse woody debris; Detectability; Interannual variation; Leaf litter; *Plethodon serratus;* Southern Red-backed Salamander

UNDERSTANDING patterns of woodland salamander microhabitat use is important for predicting their response to natural and anthropogenic disturbances such as land use and climate change. Although many studies have shown negative effects of anthropogenic disturbances on woodland salamanders, such as timber harvest and tree canopy removal, (Petranka et al., 1993; Ash and Bruce, 1994; Ash, 1997; Herbeck and Larsen, 1999; Hocking et al., 2013), some research has shown the potential ameliorating effects of retaining coarse woody debris (CWD), which functions as moist refugia (Moseley et al., 2004; Patrick et al., 2006; Rittenhouse et al., 2008; Kluber et al., 2009). At fine spatial scales, woodland salamanders occupy spatially and temporally variable microhabitats such as leaf litter, rocks, and downed wood. This variability in microhabitat availability and use greatly influences individual detectability, which is notoriously low for woodland salamanders (Bailey et al., 2004) and thereby affects our ability to discern changes in habitat use and abundance.

Lungless salamanders require moisture to sustain cutaneous respiration (Gatz et al., 1975); thus, their ranges are limited to moist, humid areas (Spotila, 1972; Feder, 1983).

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Because cover objects like CWD retain moisture longer than does fine debris (e.g., leaf litter, fine woody debris), woodland salamanders are often more abundant and surface active in areas of higher CWD density (Mathis, 1990; Petranka et al., 1994; DeMaynadier and Hunter, 1995; Grover, 1998; McKenny et al., 2006). They are also more active under moist conditions (Heatwole, 1962; Jaeger, 1980; Grover, 1998). Heatwole (1962) showed that terrestrial salamanders move to areas of higher humidity, especially after desiccation. This often means moving under cover objects as the forest floor dries after rain events (Heatwole, 1962; Fraser, 1976; Jaeger, 1980).

Moisture and cover availability might also influence the foraging success of terrestrial salamanders. The volume of prey ingested by salamanders is negatively correlated with the time since the last heavy rainfall (Jaeger, 1972). Salamander foraging success is dependent on cover availability (Fraser, 1976; Jaeger, 1980), and the mass of salamanders is positively related to cover density (Grover, 1998).

We sought to elucidate the patterns of microhabitat use of woodland salamanders in relation to variation across seasons, years, and weather patterns. We predicted that salamanders would utilize cover objects during periods of low rainfall and high temperature, when they offer an important refuge. We sampled for Southern Red-backed Salamanders (*Plethodon serratus*) in seasons of high surface activity and tested how salamander activity varied in relation to habitat and weather conditions.

Materials and Methods

Study Site

We conducted our study at the US Forest Service Sinkin Experimental Forest within the Mark Twain National Forest, Dent County, Missouri, USA. The site is located in the Ozark Plateau and consists of mature (80–100 yr old), fully stocked, oak-dominated stands (primarily white, black, scarlet, and post oak, *Quercus* spp.); other species include hickory (*Carya* spp.), maple (*Acer* spp.), dogwood (*Cornus florida*), shortleaf pine (*Pinus echi-nata*), blackgum (*Nyssa sylvatica*), and sassafras (*Sassafras albidum*) (Kabrick et al., 2014). We conducted surveys for terrestrial salamanders on 20 experimental units that were each 5 ha in size and separated by ≥10 m, and which were oriented on a slope encompassing a mesic-to-xeric moisture gradient. There is little variation in forest cover among sites—they are all within a mature, oak–hickory forest in the same landscape.

Field Methods

We surveyed two 9-m^2 plots within each unit, yielding 40 survey plots. Plots were selected at the top (dry) and bottom (moist) of the slope to encompass the moisture gradient within each unit. We surveyed each of the 40 plots 3–5 times in each spring and autumn 2010–2012; surveys were separated by an average (±1 SD) of 7 ± 3.7 d. We conducted diurnal, area-constrained searches by hand-raking through leaf litter and turning over natural cover objects. Each round of sampling lasted until each plot was surveyed once (2–4 d per round); the search order of plots was randomly determined. We recorded the life-history stage and snout–vent length (SVL, ±1 mm) of each salamander captured (juveniles were categorized as any individual ≤31 mm SVL; Herbeck and Semlitsch, 2000). We also recorded the capture location of each individual (e.g., leaf litter, rock, and woody cover object [WCO] ≥3 cm in diameter), the total number of rocks (≥5 cm in size) and WCOs encountered in each plot, the soil temperature using a Raytek Mini Temp noncontact thermometer gun (a mean of 3 measurements), and leaf litter depth (±0.5 cm; a mean of 3 points in each plot). Individuals were returned to their point of capture upon survey completion. Daily rainfall and temperature data were obtained from the Sinkin Experimental Forest weather station.

Statistical Analysis

We used multinomial logistic regression to assess the effects of (1) season (spring versus autumn), (2) year, and (3) time since rainfall (TSR) ≥0.25 cm (in days) on the probability of salamanders using various microhabitats. We fitted seven a priori models (3 single variable [season, year, TSR], 4 multiple variable

TABLE 1.—Effect sizes of environmental variables on *Plethodon serratus* counts per plot (salamander surface activity) within the Mark Twain National Forest, Missouri, from 2010–2012. Significant parameters (95% CI not overlapping zero) are indicated in bold. WCO = woody cover objects; TSR = time since rain.

Parameter	Estimate	Robust SE[a]	LL[b]	UL[b]
(Intercept)	**0.963**	**0.173**	**0.624**	**1.301**
Soil temperature[c]	–0.010	0.006	–0.022	0.002
Litter depth[c]	0.044	0.035	–0.025	0.113
No. rocks[c]	**0.008**	**0.002**	**0.004**	**0.012**
No. WCOs[c]	**0.052**	**0.008**	**0.037**	**0.066**
TSR (days)[c]	**–0.575**	**0.047**	**–0.666**	**–0.483**
Season	–0.052	0.058	–0.166	0.063
Year	**–0.303**	**0.040**	**–0.381**	**–0.226**

[a] Robust SE obtained via sandwich covariance matrix estimator.
[b] The LL and UL are 95% confidence limits.
[c] Parameter standardized using z-score method prior to analysis.

[combinations of season, year, TSR]) using the multinom function in the nnet package (Venables and Ripley, 2002) of program R (R Core Development Team, 2013) and compared these models using Akaike Information Criterion (AIC). Using the top-ranking model, we calculated the predicted probabilities of finding an active salamander within each microhabitat type. We also tested for additive effects of life-history stage (juvenile versus adult) and SVL in post hoc modeling. We assessed model fit using a likelihood ratio test.

We analyzed the effects of seven environmental variables on salamander surface activity (counts per plot) using a Poisson generalized linear model (Table 1). We scaled all covariates using a z-score procedure prior to analysis to promote model convergence, fitted models using the glm function in R, and performed a likelihood ratio test to assess goodness-of-fit. We accounted for overdispersion in the Poisson distribution by calculating robust standard errors and 95% confidence intervals via the sandwich package in R (Zeileis, 2006).

RESULTS

We searched 1080 9-m^2 plots during 27 sampling rounds from 9 April 2010 to 26 October 2012 and captured 2309 *P. serratus*. Sampling was conducted from April to May (spring) and September to October (autumn), which corresponded with periods of greatest salamander surface activity (Herbeck and Semlitsch, 2000). We captured 1018 individuals in 2010 (10 rounds), 856 in 2011 (10 rounds), and 435 in 2012 (7 rounds). Across all years, 72.1% of captured salamanders were in leaf litter; the remaining salamanders were under WCO (13.4%), rocks (13.9%), or other locations (0.6%; Fig. 1).

Of the seven a priori multinomial regression models, the best prediction of salamander microhabitat use probability contained TSR, year, and an interaction between TSR and year. The day following a rain event, the most-likely capture location in each year was leaf litter (Fig. 2). As TSR increased, the probability of capturing a salamander within the leaf litter decreased while the probability of capture under a cover object increased. The lowest initial probability of being captured in leaf litter was in 2012; that year also had the lowest precipitation total (82.5 cm) during the approximate salamander active season (1 April–31 October; for comparison, 2010 = 94.6 cm, 2011 = 115.6 cm). In each year, the predicted probability of capturing a salamander in leaf litter was greater than under a cover object (WCO or rock) for a period of at least 7 d following rainfall (Fig. 2). We incorporated additive effects of life-history stage (juvenile versus adult) and SVL into the top three models (ΔAIC < 15) in a post hoc analysis. The model consisting of life stage, season, TSR, year, and the TSR × year interaction outranked the previous top model (ΔAIC = 24.3); however, it was not more likely than the same model with season excluded (ΔAIC = 0.3). A chi-squared (χ^2) likelihood ratio test of the top model versus an intercept-only model suggested adequate model fit ($P < 0.001$).
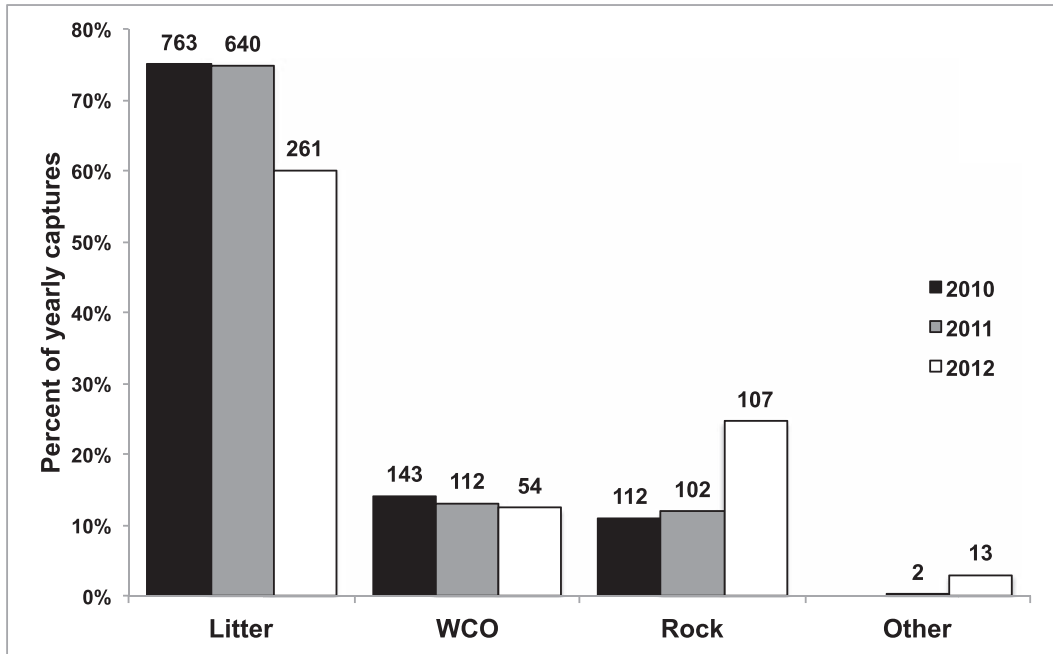
FIG. 1.—Percent of *Plethodon serratus* captures within the Mark Twain National Forest, Missouri, from 2010–2012, in each of four microhabitat types (WCO = woody cover objects ≥3 cm in size). Numbers of captures are indicated above each bar.

Variation in the surface activity (counts per plot) of *P. serratus* was most strongly related to TSR and year (Table 1). Rock and WCO abundances were also significant predictors of surface activity (Table 1). Surface activity decreased steadily as TSR increased (Fig. 3); this corresponded with the decline in the proportion of salamanders captured within the leaf litter (Fig. 4). A χ^2 likelihood ratio test comparing the full model to an intercept-only
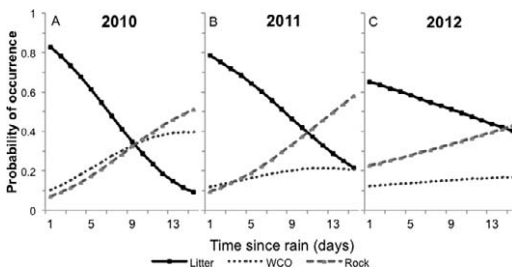

FIG. 2.—Predicted probabilities of *Plethodon serratus* occurrence within the Mark Twain National Forest, Missouri, from 2010–2012, in each of three microhabitat types (leaf litter, woody cover objects [WCO], rocks) relative to time since last rainfall.

model indicated adequate goodness-of-fit ($P < 0.001$).

DISCUSSION

We observed a clear shift in salamander microhabitat use from leaf litter to surface cover objects and subterranean areas as TSR increased. Our observation that *P. serratus* decreased surface activity as the forest floor dried is consistent with previous studies of woodland salamanders (Heatwole, 1962; Grover, 1998). However, our finding contrasts with what Jaeger (1980) observed in *Plethodon cinereus* (Eastern Red-backed Salamander), a close relative of *P. serratus*. Whereas Jaeger (1980) observed a shift in microhabitat use in drier conditions, from leaf litter to cover objects, his measure of surface activity did not change as a function of recent rainfall. Because surface activity decreased as TSR increased in our study system, it appears that the concurrent decline in proportion of leaf litter captures is partially caused by salamanders retreating underground into burrows rather than shifting to surface cover objects.
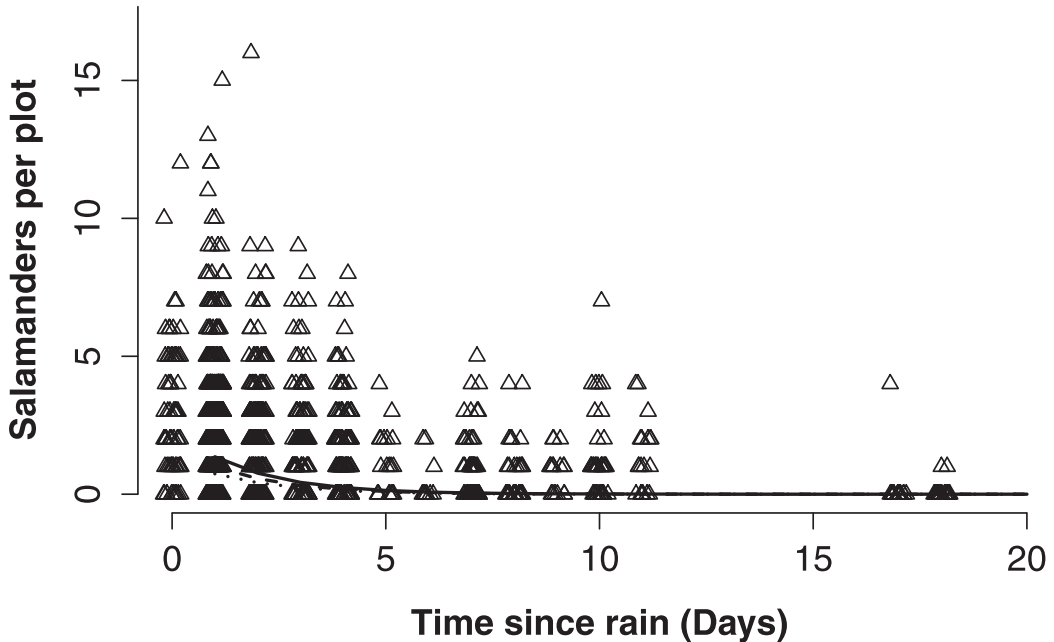
Fig. 3.—Relationship between *Plethodon serratus* surface activity and recent rainfall across three years in the Mark Twain National Forest, Missouri. Lines indicate predicted relationships for each year (solid = 2010, dashed = 2011, dotted = 2012).

It is possible that this difference between the studies could be caused by species differences in moisture preference or the geographic differences in rainfall and rate of soil moisture decline. Mean annual precipitation at Jaeger's (1980) study area is 35 cm greater than ours (138 versus 103 cm); soils in the Missouri Ozarks are shallow, rocky, and dry rapidly.

There were minimal differences between life-history stages for predicted microhabitat

Fig. 4.—Effect of recent rainfall on *Plethodon serratus* use of leaf litter within the Mark Twain National Forest, Missouri, from 2010–2012.

location. Changes in predicted leaf litter captures did not differ between juveniles and adults; however, we predicted slightly more juveniles than adults would use WCO as TSR increased, but more adults than juveniles would use rocks. This effect is likely caused by juveniles' higher susceptibility to desiccation (compared to adults; Spotila, 1972) and the greater moisture-holding capacity of WCO versus rocks.

We have documented a difference in salamander surface activity among years. The reason for the drop in leaf litter capture proportion in 2012 is not clear. It is possible that the 2012 drought in Missouri (Nixon, 2013) caused soil and leaf litter moisture to be lower than average; however, rainfall amounts over longer time spans (1–3 mo prior to sampling) were not strongly predictive of surface activity. Interestingly, the within-year decline in leaf litter use as TSR elapsed was not as severe in 2012 as in the previous 2 yr (Fig. 2). We suspect that conditions were harsh in 2012 no matter how recently it had rained, even under cover objects that would normally provide suitable refuge. Thus, the
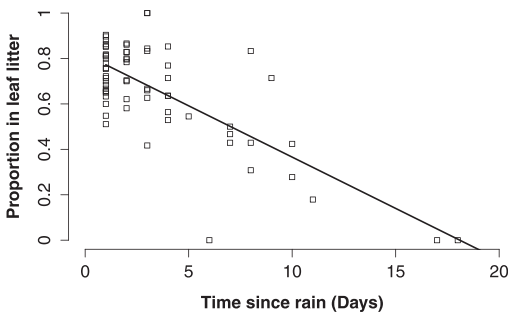
few salamanders that were surface active were more evenly distributed among the leaf litter and cover objects when surface active and foraging.

Our study focused on the salamanders' relative use of available microhabitats, but our results further support the prevalence of variable detectability within an amphibian species and the importance of accounting for changes in detectability when estimating woodland salamander abundance, occupancy, or density (Mazerolle et al., 2007). Even when moisture conditions were ostensibly similar (TSR = 1), the proportion of captures within the leaf litter varied from ≈50% to 90% (Fig. 4). This shows that, even if efforts are made to standardize sampling design, other factors that influence detectability must be acknowledged when estimating population density. Using area-constrained searches—rather than cover boards, natural cover searches, or pitfall traps—allows for a complete account of salamander microhabitat use (Marsh and Goicochea, 2003). This is especially important when distinguishing natural variation in microhabitat use from that caused by factors such as forest management or climate change.

In a companion study, we have developed a model that accounts for distinct components of detectability in light of variable salamander surface activity (i.e., availability for sampling/capture). We found that salamander availability probability varied widely among sites and surveys (range: 5–70%), but conditional capture probability (given salamander availability) was more stable (mean: 83%) because of our survey method. TSR was the strongest predictor of salamander availability, while cover object density best predicted conditional capture probability (personal observations).

There is considerable evidence that CWD can offset some of the negative effects of disturbances that reduce leaf litter availability (Moseley et al., 2004; Patrick et al., 2006; Rittenhouse et al., 2008; Kluber et al., 2009). It is clear that in our study system, however, terrestrial salamanders frequently occupy leaf litter microhabitat. Forest management practices (e.g., timber harvest, prescribed burns, etc.) that decrease leaf litter depth, increase decomposition rate, or alter soil or leaf litter moisture could substantially alter the distribution of microhabitats available to salamanders (Semlitsch et al., 2009). This could lead to decreased foraging opportunities and greater competition for remaining natural cover objects. Climate change could also alter patterns of microhabitat quality and utilization as salamanders cope with increased temperatures, more-variable rainfall, and potentially longer periods between rainfall events (IPCC, 2013). Ultimately, understanding patterns of microhabitat use will enable us to better assess changes in the abundance and behavior of organisms in relation to either natural or anthropogenic disturbance events.

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