

Surface Retreats Used among Four Genera of Terrestrial Salamanders in the Great Smoky Mountains National Park

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ABSTRACT.—Surface retreats (rocks, logs, and bark piles) provide important surface microhabitat for plethodontid salamanders; inconsistencies exist, however, among studies of retreat use by salamanders in natural habitats. I determined the relationships among 14 taxa (12 species, 2 hybrids) of plethodontid salamanders and retreat area and type as well as patterns of occurrence when multiple salamanders were found under the same retreat. Plethodontid salamanders in the Great Smoky Mountains National Park used both woody retreats (logs and bark piles) and larger retreats more often than expected. Additionally, the presence, number, area, and mass of salamanders were associated positively with retreat area; however, the variation explained by retreat area was low. Elevation was the best predictor of the relationship between salamanders and retreat area; low and mid elevations had a more positive relationship between salamanders and retreat area. When multiple salamanders were found under the same retreat, species pairings were no different from expected based on the species present at each site, and paired salamanders were more similar in size than expected. This study revealed patterns of retreat use for terrestrial plethodontid salamanders and makes suggestions for future studies to clarify the relationships between salamanders and retreats.

Warm, dry conditions limit the surface activity of plethodontid salamanders (Spotila, 1972) because, being lungless, these salamanders require cool, moist conditions to exchange gases across their skin without desiccating (Petranka, 1998). During surface activity, retreats (e.g., rocks, logs, and piles of loose bark) provide cool and moist microhabitats (Spight, 1967; Keen, 1984; Mathis, 1990). These microhabitats are important to salamanders because they allow efficient capture of prey (Fraser, 1976; Jaeger, 1980; Feder and Landos, 1984) and offer protection from predation (Krzyzysik, 1979) and desiccation (Mathis, 1990; Grover, 2000). Territorial salamanders often defend retreats (Jaeger et al., 1982) and show site fidelity to retreats (Mathis, 1990; Marvin, 2001). Body size is a major influence on the spatial distribution of individuals: larger salamanders displace smaller salamanders (Fraser, 1976; Keen, 1982; Roudebush and Taylor, 1987; Houck, 1988; Mathis, 1990; but see Jaeger et al., 1982). When a resident salamander is removed, a new and often smaller salamander will colonize the open territory (Mathis, 1990); limited resources, therefore, will reduce salamander cohabitation. Thus, surface retreats are a necessary component of the niche space of plethodontid salamanders, which are key components of forest ecosystem function (Burton and Likens, 1975; Davic and Welsh, 2004).

Multiple studies have documented relationships between salamanders and their use of different retreats; the results, however, are inconclusive among studies, and we have only a partial understanding of these relationships. Some studies found no relationship between salamander size and the size of surface retreats (Gabor, 1995; Faragher and Jaeger, 1997), whereas others described a positive association between salamander size and retreat size (Mathis, 1990; Grover, 2006; Richmond and Trombulak, 2009) or a seasonal difference in the salamander size–retreat size relationship (Moore et al., 2001). Plethodontid salamanders have shown biases for rocks (Hom, 1988; Grover, 2000), logs (Grover, 2000), or no biases (Moore et al., 2001; Richmond and Trombulak, 2009). Inconsistencies may be explained, in part, by the different ecological roles among taxa. For example, *Desmognathus fuscus* and *Desmognathus*

monticola, within stream habitats, used rocks more frequently than they used logs (Hom, 1988; Grover, 2000), whereas *Plethodon cinereus*, in terrestrial habitats, used retreats underneath logs more often (Grover, 2000). Even when comparing surface retreat use within one species (*P. cinereus*), however, the use of retreats is not consistent; also, similar proportions under rocks and logs have been found (Moore et al., 2001; Richmond and Trombulak, 2009).

A better understanding of the discriminate use of retreats should enable ecologists and land managers to evaluate forest floor quality more precisely. Therefore, I studied the use of surface retreats for 13 different taxa of terrestrial plethodontid salamanders. The goals of this study were to 1) evaluate species size-specific use of surface retreats, 2) determine whether salamanders show bias toward larger retreats, and 3) determine whether plethodontid salamanders show biases with respect to type of retreats.

MATERIALS AND METHODS

Study Sites and Species.—I sampled 40 sites in the Great Smoky and Balsam Mountain ranges within the Great Smoky Mountains National Park (Fig. 1; Appendix 1). These sites covered an area of 1,136 km² and elevations from 488 to 1,972 m. I chose these sites from a database of historic species presence (1960–2001) cataloged by the U.S. National Museum of Natural History (USNM) with the intention of covering a large geographic and elevational range (Fig. 1). I surveyed 14 taxa within the family Plethodontidae, including 12 species and 2 hybrids (*Plethodon jordani* × *teyahalee* and *Plethodon jordani* × *metcalfi*) from 4 different genera: *Plethodon*, *Desmognathus*, *Eurycea*, and *Gyrinophilus* (Appendix 2). Although I did not determine hybridization, I followed the species nomenclature established by the USNM database. I sampled adults and juveniles equally, except for *Desmognathus imitator*, *Desmognathus ocoee*, *Desmognathus santeetlah*, *Eurycea wilderae*, and *Gyrinophilus porphyriticus*, because I did not sample aquatic habitats. For all analyses, I combined *D. ocoee* and *D. imitator* (hereafter, *D. ocoee* + *imitator*) because of the difficulty to distinguish these species (Dodd, 2004).

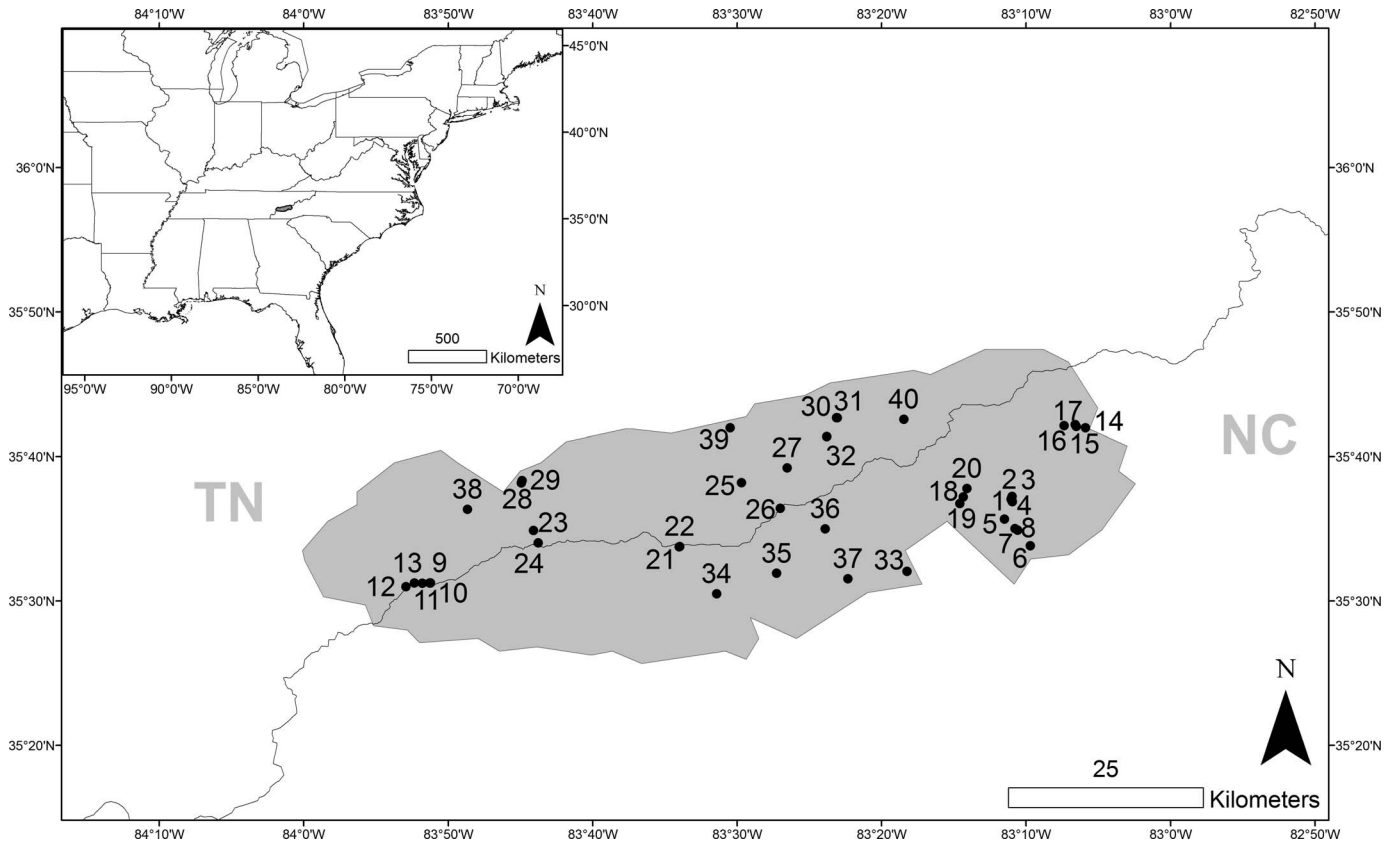


FIG. 1. Location of Great Smoky Mountains National Park within the eastern United States (inset map) and the study sites within the national park. Numbers correspond to the site numbers in Appendix 1.

Field Sampling.—During March, May through July, and November of 2009, field teams consisting of 1–3 researchers sampled two distinct 3×50 m diurnal plots at each site during either the morning or evening before dusk. Sites were sampled twice (site 29 was sampled 4 times), and new plots were constructed during each visit. All retreats that were feasible to turn and could realistically give shelter to a salamander were searched. Also, salamanders were caught on the surface, especially during wet weather. Upon capture, salamanders were placed in a new plastic bag to facilitate measuring accuracy, processed immediately by measuring the tip of snout to the posterior margin of the vent (SVL), and weighed with a spring scale. Retreats, both with and without salamanders, were classified and measured. For rocks and logs, area was measured as the greatest length \times the greatest width of the portion that was in contact with the ground. For bark piles, area was measured as the greatest length \times the greatest width of the total pile. All surface retreats were replaced, and all salamanders were returned to their original point of capture.

Habitat Variables.—To determine the influence of two large-scale habitat covariates, elevation and aspect, I used the raster package (Hijmans, 2014) in R version 3.1.0 (R Core Team, 2014) to download 0.5 arc-minute (i.e., 1 km^2) resolution elevation data (Hijmans et al., 2005); aspect (in degrees) was subsequently derived from elevation and converted into northness. I chose elevation and aspect because elevation is highly correlated with both annual temperature ($r = -0.998$; $t_{5554} = -1,092.133$; $P < 0.001$) and precipitation ($r = 0.952$; $t_{5554} = 230.652$; $P < 0.001$) and because southern facing slopes receive more direct sunlight than northern facing slopes. Finally, I binned elevation and aspect into three quantiles. Elevation was binned into low (560–1,148 m),

mid (1,149–1,430 m), and high (1,431–1,857 m), whereas aspect was binned into south (-0.974 – -0.179), mid (-0.180 – 0.783), and north (0.784 – 1.000).

Analyses.—I investigated the relationship between the area of surface retreats and size (SVL and mass), number and presence of salamanders, and whether those relationships varied with elevation or aspect. For SVL and mass (log-transformed), I used a linear model. I investigated the relationship between retreat area and counts of salamanders using a Poisson generalized linear model. I used a logistic regression to determine the relationship between retreat area and the presence of salamanders, a binary response. For each of the response variables, I fit three models based on different predictors: 1) retreat area, 2) elevation and retreat area, and 3) aspect and retreat area. I selected the best model based on the lowest Akaike's information criterion (AIC; Burnham and Anderson, 2002). I used type II sum of squares (Langsrud, 2003), F -tests (SVL and mass), and likelihood ratio tests (number and presence) to evaluate top models (car package; Fox and Weisberg, 2011).

I used a one-way analysis of variance (ANOVA) to determine whether the mean of log-transformed retreat area varied among genera and species. To account for the differences in body size among species (see Appendix 2), I used an ANOVA to determine whether the mean ratio of retreat area to salamander SVL (log transformed) varied among species and genera. Significant post hoc relationships were analyzed using Tukey's Honest Significant Differences. Additionally, I used an ANOVA to determine whether the average log-transformed SVL of salamanders differed among different numbers of salamanders underneath a single retreat. To determine whether salamanders

TABLE 1. AIC values for the response of SVL, mass, number, and presence of salamanders. Linear models were used for SVL and mass; generalized linear model with Poisson errors was used for the number of salamanders; and logistic regression was used for the presence of salamanders. All models included both main effects as well as interaction term. The top model, with lowest AIC, for each response is shown in bold.

	SVL		Mass		Number of salamanders		Presence of salamanders	
	df	AIC	df	AIC	df	AIC	df	AIC
Elevation × Retreat area	7	347.9	7	1,473.4	6	4,563.3	6	3,484.6
Aspect × Retreat area	7	351.8	7	1,477.7	6	4,612.1	6	3,527.4
Retreat area	3	356.7	3	1,479.8	2	4,639.1	2	3,527.4

used larger or smaller retreats than what were available, I compared the mean retreat area for Plethodontidae, *Plethodon*, and *Desmognathus* to the mean of each of 10,000 bootstrapped iterations, sampling the same number of retreats for family (577 retreats) or genus (*Plethodon* = 419 retreats; *Desmognathus* = 138 retreats). I included only retreats that were at least as large as the smallest retreat used by each group.

To determine whether salamanders used retreats of a given type and area at different frequencies from the actual frequencies of retreats at a site, I compared observed and expected frequencies of the types of retreats with a chi-squared test. I analyzed these data for the family Plethodontidae and the genera *Plethodon* and *Desmognathus*; I did not analyze *Eurycea* ($N = 17$) or *Gyrinophilus* ($N = 3$) separately because of small sample sizes. Expected frequencies, Plethodontidae ($N = 4,904$), *Plethodon* ($N = 4,819$), and *Desmognathus* ($N = 2,760$), were based on the total number of retreats searched at sites where each group was found.

For those surface retreats under which multiple salamanders were found, I tested whether these species pairings were the result of chance or whether intra- or interspecific pairings were more common. When salamanders were found in groups of 3–5 underneath a retreat, I counted each unique pairing (e.g., groups of three salamanders resulted in three pairings). I randomly selected species pairings based on the frequency of each species at each site. I included only sites where multiple salamanders were found underneath a single retreat to limit any biases (e.g., if a study site had smaller retreats). I analyzed these data at both the species and genus levels with two types of pairings, paired with itself (e.g., species-level: *P. jordani* with *P. jordani*; genus-level: *Plethodon* with *Plethodon*) or paired with a different species/genus. I analyzed the difference between observed and random pairings for each species and genus as well as for all species and genera combined with a chi-squared test. I applied a Bonferroni correction to reduce the likelihood of a type I error (four comparisons; $\alpha = 0.0125$). Additionally, I compared the mean difference in SVL between all paired salamanders and the distribution of average differences in SVL when any two salamanders were selected at random from sites where I found multiple salamanders under one retreat. I

compared the actual mean SVL difference to each of 10,000 bootstrapped iterations of the same number of randomly paired salamanders ($N = 94$). All statistical analyses were performed using program R version 3.1.0 (R Core Team, 2014).

RESULTS

I captured and measured 624 salamanders among 4 genera, 11 species, and 2 hybrids (Appendix 2); 577 (92%) salamanders were beneath retreats, whereas 47 (8%) were found on the surface. For salamanders underneath retreats, 87% ($N = 503$) were under logs, 10% ($N = 56$) under rocks, and 3% ($N = 18$) were under bark piles. Elevation was the top model for SVL, mass, number, and presence of salamanders (Table 1). Larger salamander SVL was associated with higher elevations and larger retreats, but the relationship between SVL and retreat area was consistent among elevations (Table 2; Fig. 2A,B). Salamanders with more mass were associated with higher elevations and larger retreats at low and mid elevations; however, at the highest elevations, salamander mass was constant across retreat area (Table 2; Fig. 2C,D,E); however, the variance explained by both of these relationships (SVL: $r^2 = 0.03$; Mass: $r^2 = 0.03$) were low. A greater number of salamanders was associated with higher elevations and larger retreats; however, at high elevations, the relationship between the number of salamanders and retreat area was less positive (Table 2; Fig. 2F,G,H). Finally, salamanders were more likely found at higher elevations and under larger objects; however, the relationship between salamander presence and retreat area was consistent among elevations (Table 2; Fig. 2I,J).

Log-transformed retreat area did not vary among genera ($F_{3,573} = 2.316$; $P = 0.075$); however, the area of retreats varied among species ($F_{12,564} = 4.016$; $P < 0.001$), although the mean retreat area was similar for 9/13 (69%) species (Table 3). Similarly, the ratio of retreat area to salamander SVL did not vary among genera ($F_{3,573} = 1.212$; $P = 0.305$) but did vary among species ($F_{12,564} = 2.219$; $P = 0.010$); yet, post hoc analysis revealed that no species pairs differed significantly.

Salamanders in the genera *Desmognathus* ($\chi^2 = 6.797$; $df = 2$; $P = 0.033$) and *Plethodon* ($\chi^2 = 43.923$; $df = 2$; $P < 0.001$) used

TABLE 2. Summary statistics for the top models for SVL, mass, number, and presence of salamanders. Linear models were used for SVL and mass; generalized linear model with Poisson errors was used for the number of salamanders; and logistic regression was used for the presence of salamanders. Terms in bold indicate significant relationships between the response and explanatory variable(s).

Response	Explanatory variable	df	F	P	Response	Explanatory variable	df	χ^2	P
SVL	Elevation	2,571	6.681	< 0.001	Number	Elevation	2	65.158	< 0.001
	Retreat area	1,571	5.724	< 0.001		Retreat area	1	69.813	< 0.001
	Elevation × Retreat area	2,571	2.840	0.059		Elevation × Retreat area	2	28.040	< 0.001
Mass	Elevation	2,571	7.183	< 0.001	Presence	Elevation	2	37.189	< 0.001
	Retreat area	1,571	7.223	< 0.001		Retreat area	1	36.040	< 0.001
	Elevation × Retreat area	2,571	3.127	0.045		Elevation × Retreat area	2	0.875	0.646

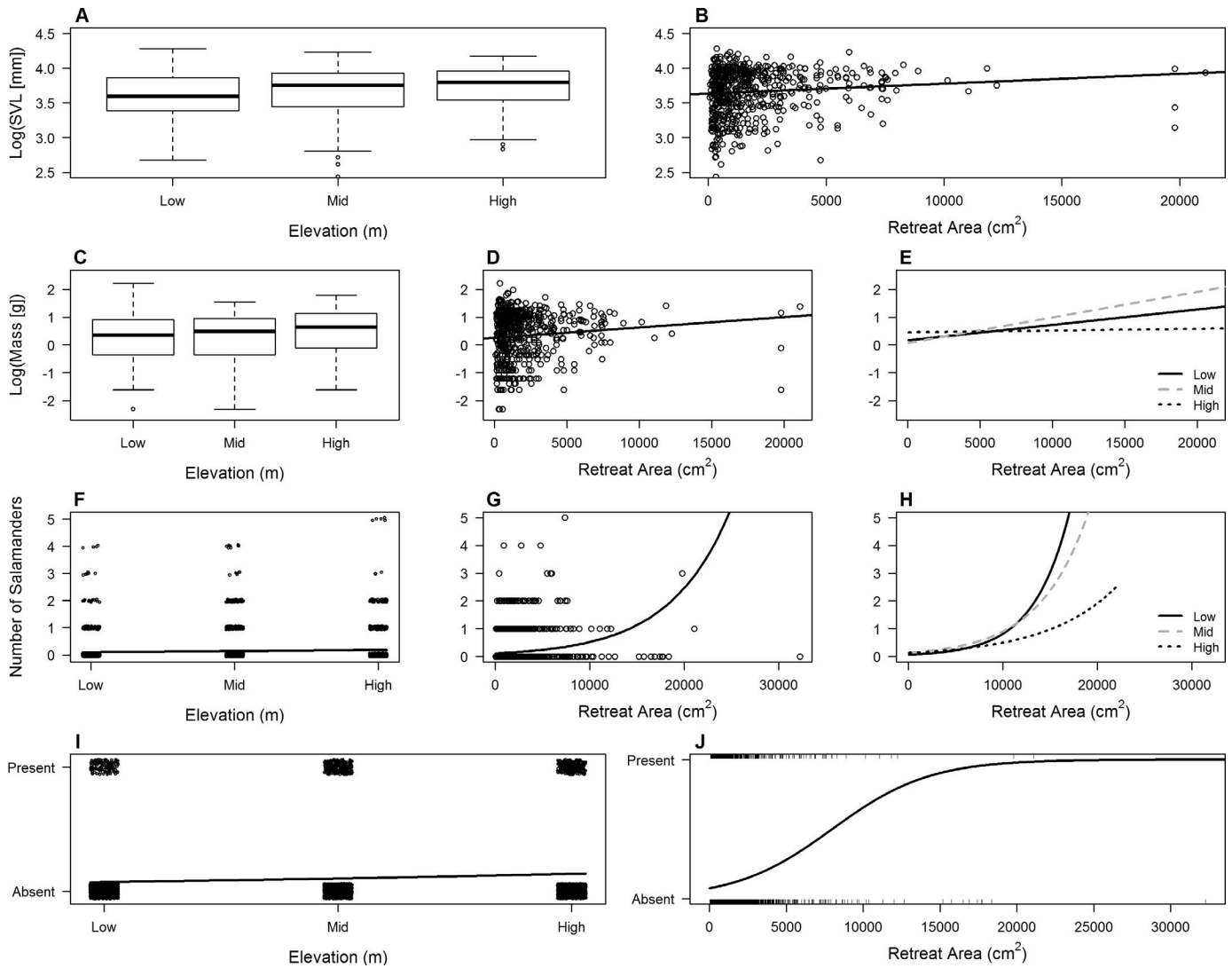


FIG. 2. Relationship between the log-transformed SVL and (A) elevation and (B) retreat area; log-transformed mass and (C) elevation, (D) retreat area, and (E) elevation and retreat area; number of salamanders and (F) elevation, (G) retreat area, and (H) elevation and retreat area; presence of salamanders and (I) elevation and (J) retreat area. Lines in panels B, D, and E represent linear model fit; lines in panels F, G, and H represent the fit from the generalized linear Poisson model; lines in panels I and J represent the fit from the logistic regression.

TABLE 3. Size (mean, range; in cm²) of surface retreats for each taxa with proportion of total captures of each retreat site shown in parentheses. Each individual letter following each taxon denotes similarities in retreat size. Dashes (–) denote no data.

Genus	Species	Total Mean	Sample size (%)	Bark pile		Log		Rock	
				Mean (range)	Sample size (%)	Mean (range)	Sample size (%)	Mean (range)	Sample size (%)
<i>Desmognathus</i>	<i>ocoee + imitator</i> ^{AC}	1,949	3 (4)	5,557 (2,392–7,980)	71 (87)	1,902 (168–7,601)	7 (9)	870 (312–1,782)	
	<i>santeetlah</i> ^{AC}	732	–	–	2 (100)	732 (588–876)	–	–	
	<i>wrighti</i> ^C	1,382	2 (4)	1,515 (638–2,392)	45 (82)	1,548 (126–19,780)	8 (14)	419 (180–1,155)	
<i>Plethodon</i>	<i>glufinosus</i> ^{AC}	585	–	–	3 (100)	585 (190–1,190)	–	–	
	<i>jordani</i>	1,575	3 (3)	10,201 (4,738–21,080)	90 (86)	1,337 (117–6,510)	12 (11)	1,206 (264–3,570)	
	× <i>metcalfi</i> ^{BC}	–	–	–	–	–	–	–	
	<i>jordani</i>	2,630	3 (11)	5,078 (1,674–11,040)	25 (89)	2,337 (440–7,936)	–	–	
	× <i>teyahalee</i> ^{AB}	–	–	–	–	–	–	–	
	<i>jordani</i> ^A	2,393	7 (3)	4,870 (880–12,240)	192 (92)	2,374 (63–19,780)	10 (5)	1,012 (209–2,303)	
	<i>metcalfi</i> ^{AC}	2,222	–	–	28 (100)	2,222 (150–8,280)	–	–	
<i>serratus</i> ^{AC}	2,131	–	–	15 (94)	2,233 (288–6,900)	1 (6)	609		
<i>teyahalee</i> ^{AC}	1,419	–	–	7 (100)	1,419 (364–3,500)	–	–		
<i>ventralis</i> ^{AC}	842	–	–	7 (30)	1,101 (140–2,943)	16 (70)	729 (84–1,890)		
<i>Eurycea</i>	<i>wilderae</i> ^{AC}	1,545	–	–	15 (88)	1,707 (184–4,260)	2 (12)	329 (238–420)	
<i>Gyrinophilus</i>	<i>porphyriticus</i> ^{AC}	763	–	–	3 (100%)	763 (225–1,560)	–	–	

TABLE 4. The number and range and mean SVL of salamanders for the range of salamanders found under a single surface retreat. The standard deviation of SVL is shown in parentheses.

Salamanders per retreat	Number of salamanders (groups)	SVL range	Mean SVL (SD)
1	443	11.43–72.41	41.34 (12.07)
2	102 (61 pairs)	17.77–68.86	40.38 (11.81)
3	15 (5 groups)	23.00–68.90	39.37 (13.29)
4	12 (3 groups)	14.55–49.60	33.02 (9.93)
5	5 (1 group)	35.04–51.38	43.33 (6.00)

logs and bark piles more frequently and rocks less frequently than expected. Also, this pattern was consistent within the family Plethodontidae ($\chi^2 = 56.261$; $df = 2$; $P < 0.001$). Salamanders used larger retreats than expected; this pattern was consistent within the genera *Plethodon* (average retreat area = 2,068 cm²; $P < 0.001$) and *Desmognathus* (average retreat area = 1,705 cm²; $P < 0.001$) and family Plethodontidae (mean retreat area = 1,959 cm²; $P < 0.001$).

I found a range of 1–5 salamanders under a single retreat (Table 4). Average salamander size was similar regardless of the number underneath a single retreat ($F_{4,572} = 1.504$; $P = 0.199$; Table 4). When multiple salamanders were found under the same surface retreat, pairings were no different from randomly selected pairings based on the frequency of salamanders at each site. This pattern was consistent for species-level pairings ($\chi^2 = 12.551$; $df = 19$; $P = 0.843$), all species combined ($\chi^2 = 4.581$; $df = 1$; $P = 0.032$), and genus-level pairings ($\chi^2 = 6.572$; $df = 5$; $P = 0.242$), as well as all genera combined ($\chi^2 = 2.565$; $df = 1$; $P = 0.109$). The actual mean difference in SVL between paired salamanders (11.91 mm), however, was significantly less than expected based on random pairings (13.72 mm; $P = 0.039$).

DISCUSSION

Salamanders and Retreat Area.—This study examined the use of a wide range (63–21,080 cm²) of retreats among 14 plethodontid taxa. I found that size, number, and presence of plethodontid salamanders were positively associated with surface retreat area. Additionally, plethodontid salamanders, on average, used larger retreats than the available distribution; however, the use of different sized retreats, proportional to the salamander's SVL, did not differ among taxa. This similarity in retreat use is likely the result of the similar physiological requirements of these taxa (Petranka, 1998) and the type or quality of microhabitats beneath small and large surface retreats. Larger retreats are associated with lower temperatures, higher moisture, and an increase in prey abundance (Keen, 1984; Mathis, 1990; Jaeger et al., 1995). Therefore, these larger retreats may be valuable to terrestrial plethodontid salamanders because of their increased quality or quantity of microhabitats compared to smaller retreats.

Although the size of plethodontid salamanders showed a positive association with the area of surface retreats, the amount of variation explained by these models was low. These data suggest that area of retreats cannot fully explain the variation in size of salamanders using retreats. Although other studies have found larger retreats to be associated with abiotic variables that are important to terrestrial salamanders (e.g., temperature; Mathis, 1990), the area of retreats may not always correlate to higher quality habitat. Therefore, other variables may contribute to this unexplained variation such as time (a recently established retreat might have a different microhabitat com-

pared to an older retreat) or canopy coverage above each retreat. These factors should be included in future studies to elucidate this relationship.

Elevation was a significant predictor of the size (SVL and mass), number, and presence of terrestrial salamanders, and I found the relationship between mass, number of salamanders, and retreat area varied with elevation. At the highest elevations, the increase in salamander mass or number as a function of retreat area was the lowest (Fig. 2E,H); larger or more salamanders were able to use smaller retreats compared to low or mid elevations. Therefore, the abiotic environment may explain inconsistencies among studies with respect to salamander use of retreat sizes; warmer and drier habitats may show a strong positive relationship between size and number of salamanders, whereas cooler and moister habitats would show a weakly positive or null relationship. Future studies can elaborate on these patterns by measuring key microhabitat characteristics (e.g., moisture, temperature) along with salamander retreat use.

Salamanders and Retreat Type.—Plethodontid salamanders used all three types of surface retreats; however, they were located beneath logs and bark piles more often and rocks less often than expected based on the available retreat frequencies, suggesting bias toward woody objects. Although some rocks were deeply imbedded into the forest floor, the inability to turn larger objects did not have an influence on my results because these occurred at a low frequency. An explanation for the inconsistencies among studies of salamander use of retreat types is that the use of retreats is not always tested against the available distribution. Therefore, favoritism toward a particular retreat may represent only the distribution of available retreats.

Multiple Salamanders under Retreats.—When multiple salamanders used the same surface retreat, I found the identity of salamanders, on both the genus and species levels, was no different from expected based on the pool of species at each study site. The similar use of retreats among taxa is consistent with the similarity in habitat requirements (e.g., temperature or moisture) and the spatial overlap for terrestrial species (Grover, 2000). Additionally, I found that salamanders under the same retreat had more similar SVLs than expected. This pattern suggests these surface retreats provided enough space, moisture, and/or prey items to allow cohabitation of similar sized salamanders. Furthermore, my data show that area of retreats is positively correlated with the number of salamanders. Although I did not find a significant difference in average salamander size among groups of salamanders, larger salamanders were typically found alone; in fact, 81% ($N = 129$) of salamanders that were at least 50 mm did not share a surface retreat with any another salamander.

Results of this study indicate the importance of larger, woody, retreats for terrestrial salamanders, especially at lower elevations. A thorough understanding of retreat use is of ecological importance and can direct forest management by providing detailed information on the relationship between salamander presence and abundance and different retreat sizes or types (see Grover, 1998; Strojny and Hunter, 2009).

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APPENDIX 1. Latitude, longitude, site number, and species encountered for each site.

Mountain range	Latitude	Longitude	Site number	Species encountered	
Balsam Mountains	35.6208	-83.1825	1	<i>Plethodon jordani</i> × <i>metcalfi</i> , <i>Desmognathus wrighti</i>	
	35.6175	-83.1839	2	<i>P. jordani</i> × <i>metcalfi</i> , <i>Eurycea wilderae</i> , <i>D. wrighti</i> , <i>D. ocoee</i> + imitator	
	35.6158	-83.1831	3	<i>P. jordani</i> × <i>metcalfi</i>	
	35.6147	-83.1822	4	<i>P. jordani</i> × <i>metcalfi</i> , <i>D. wrighti</i> , <i>D. ocoee</i> + imitator	
	35.5944	-83.1914	5	<i>P. jordani</i> × <i>metcalfi</i> , <i>E. wilderae</i> , <i>D. wrighti</i> , <i>D. ocoee</i> + imitator	
	35.5636	-83.1617	6	<i>P. metcalfi</i> , <i>D. ocoee</i> + imitator, <i>D. santeetlah</i>	
	35.5836	-83.1794	7	<i>P. jordani</i> × <i>metcalfi</i> , <i>D. wrighti</i> , <i>D. ocoee</i> + imitator	
	35.5817	-83.1764	8	<i>P. jordani</i> × <i>metcalfi</i> , <i>D. wrighti</i> , <i>D. ocoee</i> + imitator, <i>Gyrinophilus porphyriticus danielsi</i>	
	35.6997	-83.0981	14	<i>P. serratus</i> , <i>P. teyahalee</i> , <i>E. wilderae</i> , <i>D. wrighti</i>	
	35.7011	-83.1086	15	<i>P. jordani</i> × <i>teyahalee</i> , <i>E. wilderae</i>	
	35.7033	-83.11	16	<i>P. jordani</i> , <i>P. serratus</i> , <i>E. wilderae</i> , <i>D. wrighti</i>	
	35.7019	-83.1225	17	<i>P. jordani</i> , <i>D. wrighti</i> , <i>D. ocoee</i> + imitator	
	Great Smoky Mountains	35.5208	-83.8536	9	<i>P. jordani</i> , <i>D. wrighti</i> , <i>D. ocoee</i> + imitator
		35.5208	-83.8544	10	<i>P. jordani</i> , <i>P. serratus</i> , <i>D. wrighti</i> , <i>D. ocoee</i> + imitator
		35.5208	-83.8722	11	<i>P. jordani</i> , <i>P. serratus</i> , <i>E. wilderae</i>
		35.5167	-83.8819	12	<i>P. jordani</i> , <i>D. ocoee</i> + imitator
		35.5206	-83.8631	13	<i>P. jordani</i> , <i>P. serratus</i> , <i>E. wilderae</i> , <i>D. ocoee</i> + imitator, <i>G. porphyriticus danielsi</i>
35.6125		-83.2431	18	<i>D. ocoee</i> + imitator	
35.6200		-83.2389	19	<i>D. ocoee</i> + imitator	
35.6297		-83.2347	20	<i>P. jordani</i> × <i>metcalfi</i> , <i>D. wrighti</i> , <i>D. ocoee</i> + imitator	
35.5625		-83.5667	21	<i>E. wilderae</i> , <i>D. ocoee</i> + imitator	
35.5628		-83.5661	22	<i>P. jordani</i> , <i>D. wrighti</i>	
35.5814		-83.7347	23	<i>P. glutinosus</i> , <i>P. jordani</i> , <i>P. serratus</i>	
35.5672		-83.7294	24	<i>P. jordani</i> , <i>E. wilderae</i> , <i>D. wrighti</i> , <i>D. ocoee</i> + imitator, <i>G. porphyriticus</i>	
35.6364		-83.4947	25	<i>P. jordani</i> , <i>D. wrighti</i> , <i>D. ocoee</i> + imitator	
35.6069		-83.450	26	<i>P. jordani</i> , <i>D. ocoee</i> + imitator	
35.6536		-83.4422	27	<i>D. wrighti</i> , <i>D. ocoee</i> + imitator	
35.6361		-83.7489	28	<i>P. serratus</i> , <i>P. ventralis</i>	
35.6389		-83.7478	29	<i>P. glutinosus</i> , <i>P. ventralis</i>	
35.7111		-83.3842	30	<i>P. serratus</i> , <i>P. ventralis</i>	
35.7111		-83.3853	31	<i>P. serratus</i> , <i>P. ventralis</i>	
35.6894		-83.3964	32		
35.5342		-83.3039	33	<i>E. wilderae</i>	
35.5083		-83.5233	34	<i>P. jordani</i> , <i>P. serratus</i>	
35.5319		-83.4544	35	<i>P. jordani</i>	
35.5833		-83.3983	36	<i>P. jordani</i> , <i>D. ocoee</i> + imitator, <i>D. santeetlah</i>	
35.5256		-83.3719	37	<i>P. jordani</i> , <i>E. wilderae</i> , <i>D. wrighti</i>	
35.6058		-83.8111	38	<i>P. serratus</i>	
35.6997		-83.5081	39		
35.7094		-83.3075	40	<i>P. jordani</i> , <i>E. wilderae</i> , <i>D. ocoee</i> + imitator	

APPENDIX 2. Total captures (number found under retreat sites) and the range, mean, and standard deviation (SD) for SVL and mass for each species. SVL measurements are shown in millimeters, whereas mass was measured in grams.

Genus	Species	N	SVL range	Mean SVL (SD)	Mass range	Mean mass (SD)
<i>Desmognathus</i>	<i>imitator</i> + <i>ocoee</i>	85 (81)	21.27–58.93	39.57 (7.93)	0.30–3.70	1.50 (0.77)
	<i>santeetlah</i>	3 (2)	34.52–51.10	41.47 (8.77)	1.20–3.00	2.07 (0.90)
	<i>wrighti</i>	63 (55)	14.55–32.00	23.43 (2.91)	0.20–0.80	0.37 (0.12)
<i>Plethodon</i>	<i>glutinosus</i>	4 (3)	17.91–59.39	39.84 (21.11)	0.30–5.50	2.83 (2.86)
	<i>jordani</i>	222 (209)	15.29–68.90	44.48 (9.91)	0.10–5.05	2.21 (1.13)
	<i>jordani</i> × <i>metcalfi</i>	110 (105)	15.13–65.00	43.83 (13.11)	0.10–6.00	2.29 (1.40)
	<i>jordani</i> × <i>teyahalee</i>	28 (28)	20.89–62.83	46.56 (10.99)	0.30–5.00	2.57 (1.33)
	<i>metcalfi</i>	29 (28)	13.65–58.80	47.75 (10.69)	0.10–4.00	2.29 (0.95)
	<i>serratus</i>	19 (16)	11.43–49.10	33.53 (9.25)	0.20–2.50	1.14 (0.72)
	<i>teyahalee</i>	8 (7)	32.86–72.41	59.75 (15.59)	0.90–9.20	5.59 (2.91)
	<i>ventralis</i>	27 (23)	18.38–46.05	35.60 (5.29)	0.75–3.00	1.57 (0.58)
	<i>wilderae</i>	23 (17)	22.83–41.28	33.92 (4.99)	0.30–1.90	0.84 (0.36)
	<i>porphyriticus</i>	3 (3)	45.99–64.45	57.61 (10.11)	2.00–4.40	3.53 (1.33)