

## TEMPORAL PARTITIONING OF FORAGING IN *PLETHODON METCALFI*

ANDREW N. ASH

Department of Biology, One University Drive, Post Office Box 1510, Pembroke,  
North Carolina 28372-1510, USA, e-mail: aash.ret@uncp.edu

**Abstract.**—I provide evidence for nightly and seasonal patterns of surface activity in the Southern Gray-cheeked Salamander (*Plethodon metcalfi*) and discuss possible explanations for these patterns. From 1979–1997, I made 2,191 observations of this species at five forested sites within 8 km of Highlands, North Carolina, USA, to document surface activity patterns in leaf litter. Data I collected included sex-age class (immature, adult males, adult females), snout-vent length (SVL), and observation time (coded as minutes after sunset, MAS). Immatures, females, and males of this species were active at progressively later times after sunset (73 MAS, 82 MAS and 88 MAS respectively), and these differences were significant. Immature surface activity times did not differ between arbitrarily determined small (16–34 mm SVL) and large (35–49 mm SVL) size classes. The seasonal pattern of surface activity times of all sex-age classes was similar. Mean surface activity time declined from early May (87 MAS) through early August (60 MAS), then increased to mid-August (99 MAS). I suggest that nightly activity is primarily foraging. Two factors, females constraining the foraging times of immatures and males and differences in physiological moisture tolerance related to relative humidity, may cause differences in nightly foraging time by sex-age class. I document seasonal changes in foraging time, but I cannot currently provide an adequate explanation of this pattern. I suggest that availability of food may partly determine intraspecific nightly activity patterns and salamander guild organization.

**Key Words.**—food; litter; plethodontid; resource; salamander; Southern Blue Ridge Mountains; surface activity

### INTRODUCTION

Plethodontid salamander assemblages in North America are major contributors to the energy flow and nutrient cycling dynamics of the forested communities to which they belong (Davic and Welsh 2004; Adams 2007; Semlitsch et al. 2014). These animals are important predators of invertebrates found in leaf litter (Jaeger 1972; Hairston 1987; Hairston et al. 1987; Rooney et al. 2000; Semlitsch et al. 2014), because salamanders exert top-down control of litter invertebrate density and species composition (Wyman 1998; Walton et al. 2006; Walton 2013; Semlitsch et al. 2014; Hickerson et al. 2017). The documented invertebrate responses demonstrate a strong predator-prey interaction in this forest floor system. At least two salamander species, the Eastern Red-backed Salamander (*Plethodon cinereus*) and the Shenandoah Salamander (*Plethodon shenandoah*), have been shown to compete for food (Jaeger 1972).

Researchers have characterized these assemblages as guilds, with 5–11 species of salamanders occupying a given site (Hairston 1981, 1987; Davic and Welsh 2004; Adams 2007; Bruce 2008), and significant numerical dominance by one or two species is common (Davic and Welsh 2004). Repeatedly, researchers have demonstrated or inferred competition between plethodontid salamander species to explain observed distribution patterns. Although the limiting resource

driving competition is unknown in many cases, researchers have proposed food as a possibility (Fraser 1976; Mathis 1991). If the salamander prey base is limited, then competition may influence intraspecific patterns of activity (Marvin 1998) in addition to interspecific guild assembly patterns (Marvin 1998; Adams 2007). Such a possibility might be particularly true of numerically dominant guild members.

I examined patterns of nightly and seasonal activity among sex-age classes of the Southern Gray-cheeked Salamander (*Plethodon metcalfi*). I hypothesized that food resources might be related to observed activity patterns in this species and I provide evidence relating these patterns to possible underlying processes. Foraging is the most common above-ground activity (Petranka 1998; Dodd 2004) as opposed to mating, defense of space, or dispersal. The purpose of this paper is to document and propose explanations of temporal partitioning of nightly above-ground activity between sex-age classes (immature, female and male) of *P. metcalfi*, and to demonstrate seasonal variation in nightly above-ground activity regardless of sex-age class.

### MATERIALS AND METHODS

**Study sites.**—During 11 summers between 1979–1997, I recorded 2,191 sightings of *Plethodon metcalfi* at five sites within 8 km of Highlands, Macon County,

Ash.—Foraging in *Plethodon metcalfi*.

**TABLE 1.** Average selected monthly and annual climate data for Highlands North Carolina, USA, for 23 February 1877 to 30 April 2012 (<https://sercc.com/cgi-bin/sercc/cliMAIN.pl?nc4055>).

	Month					Yearly Average
	May	June	July	August	September	
Average Temperature (°C)						
Daily	15.36	18.81	20.25	19.92	17.22	11.31
Daily Minimum	9.22	13.11	14.89	14.67	11.83	5.65
Daily Maximum	21.50	24.50	25.61	25.17	22.61	16.98
						Yearly Total
Precipitation (cm)	15.37	18.03	19.71	18.19	16.56	217.17

North Carolina, USA (35.0526°N, 83.1968°W). The climate of this region is cool, wet, and temperate, with average annual minimum and maximum temperatures of 5.65° C and 16.98° C, respectively. Annual precipitation is 217.17 cm. During the May–August study period, average minimums range from 9.22–14.89° C, average maximums range from 21.50–25.61° C, and monthly precipitation ranges from 15.37–19.71 cm (Table 1).

All sites were in the Nantahala National Forest at elevations of 980–1,260 m. The vegetation was dominated by Mixed Oak Hardwood stands with some White Pine (*Pinus strobus*). I described these sites fully elsewhere (Ash 1988; Ash 1995). Soils and litter were mesic in nature. Litter was often very wet after rain but dried quickly during a 3–4 d period.

**Search parameters.**—My search effort (observer search nights, OSN) varied by year and was summarized during four discreet intervals of data collection (Table 2). My assistants and I did not visit all sites each year. My search effort was plot based (225 m<sup>2</sup>), and observers searched until the entire plot was surveyed. Observers surveyed two plots each night with plot order and search initiation within plot alternated to eliminate time bias. Search effort increased through time and was highest during 1996–1997 when three observers contributed to data collection. Between May and August, observers performed a headlamp-assisted visual search for salamanders nightly from around dusk to as late as 0100, and recorded each sighting time. Sightings were random encounters and should not be construed as first sightings immediately after salamander emergence. Observer movement through a plot from the starting point was systematic to minimize possible double sightings. I determined meteorological time of sunset for each day of search and subtracted time of sunset from each salamander sighting time. I termed this difference minutes after sunset (MAS). Observers measured snout-vent length (SVL) of salamanders to the posterior angle of the vent and to the nearest mm using a field ruler. Due to differences in some yearly protocols, observers did not collect SVLs for all animals. Observers determined the sex and age of individuals as described below.

**Delineation of sex and age classes.**—I designated individuals as adult males, adult females, or immatures. Data I present here and studies by Bruce (1967) and Hairston (1983) allow reasonable estimates concerning SVL at maturity in *P. metcalfi*. The presence of a mental gland on the chin identifies adult males of this species. In the data set I examined, the smallest males with mental glands had SVLs of 45–46 mm. Only two of 413 males in my study had SVLs < 50 mm. Hairston (1983) reported a minimum SVL of 44 mm for males. Bruce (1967) examined several sites and reported minimum male SVL ranges of 47–54 mm; however, he measured to the anterior angle of the vent on formalin-preserved specimens (estimated shrinkage 7–8%, Richard Bruce, pers. comm.). Thus, estimates of Bruce could be low compared to my measurements on live animals to the posterior angle of the vent. I designated 50 mm the minimum SVL for adult males of this species. Bruce (1967) and Hairston (1983) verified adult status by dissection, thus providing the best SVL data for mature females. Bruce (1967) reported that females matured at larger sizes than males, and in no case did they mature at SVLs < 50 mm. Hairston (1983) documented a minimum SVL for adult females of 46 mm. Here, I assumed that salamanders with no mental gland and SVLs in excess of 50 mm were adult females. I assumed individuals with no mental gland and SVLs < 50 mm were immatures of either sex. Having set the upper SVL limit for immatures at 49 mm, I then examined a histogram of recorded immature SVLs (Fig. 1; n = 375) and arbitrarily identified two immature size classes: small (16–34 mm SVL) and large (35–49 mm SVL).

**TABLE 2.** Search effort for the Southern Gray-cheeked Salamander (*Plethodon metcalfi*) at sites near Highlands, North Carolina, USA, as estimated by observer search nights (OSN). OSN totals are summarized over the research spans indicated.

Search Period	Number of Observers	Search Nights	Percentage of Total
1979–1982	1	39	17
1985–1987	1	39	17
1992–1994	1	66	29
1996–1997	3	87	38
Total		231	

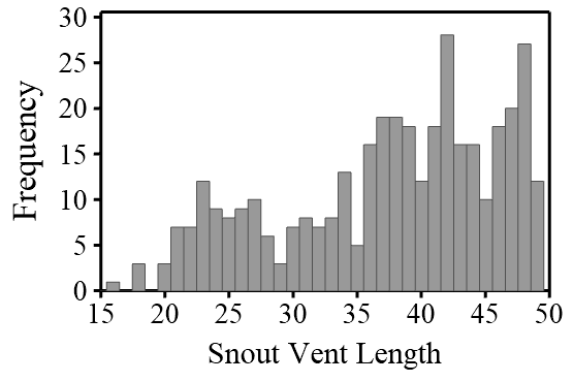


FIGURE 1. Frequency histogram of snout vent length (SVL) of immature Southern Gray-cheeked Salamanders (*Plethodon metcalfi*) at sites near Highlands, North Carolina, USA. Two size classes are recognized: 16–34 mm SVL and 35–49 mm SVL.

**Delineation of biweekly foraging periods.**—To track salamander activity between May and August, I determined first and last dates of salamander sightings for the entire data set. I divided the resulting time interval into eight biweekly periods (14 d per period except for the last which was 16 d; Table 3).

**Statistical analysis.**—I used Minitab 17© statistical software (Minitab Inc., State College, Pennsylvania; USA). I determined a normal distribution and used a parametric data analysis. I employed General Linear Models procedures in Minitab to perform regression-based Analysis of Variance (ANOVA). GLM procedures are robust to differences in cell sizes. I performed multiple comparisons using the Bonferroni Simultaneous Test with an adjusted family  $\alpha = 0.05$ .

An initial ANOVA of MAS predicted by site indicated no significant differences among sites ( $F_{4,2186} = 0.600$ ,  $P = 0.666$ ). I then pooled all sites into a common data set ( $n = 2,191$ ) and performed a two-way ANOVA of MAS testing sex/age class and biweekly period as main effects and the resulting interaction. Such an analysis should reveal significant differences in salamander behavior patterns, if present. I performed ANOVA ( $\alpha$

TABLE 3. Biweekly period start and end dates for surveys of the Southern Gray-cheeked Salamander (*Plethodon metcalfi*) near Highlands, North Carolina, USA.

Biweekly Period	Start date	End date
1	10 May	23 May
2	24 May	6 June
3	7 June	20 June
4	21 June	4 July
5	5 July	18 July
6	19 July	1 August
7	2 August	15 August
8	16 August	31 August

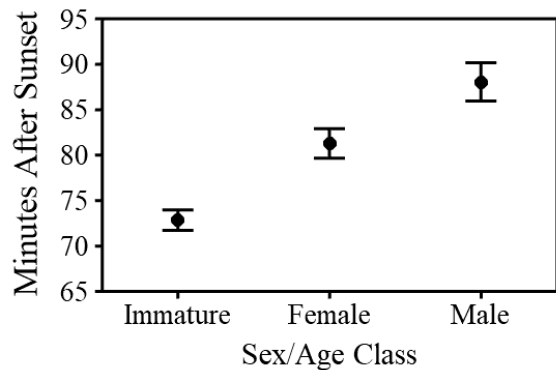


FIGURE 2. Mean ( $\pm 1$  standard error) foraging times in minutes after sunset for Southern Gray-cheeked Salamanders (*Plethodon metcalfi*) based on sex and age classes. All means are significantly different from one another (pairwise  $P \leq 0.00179$  based on Bonferroni adjustment to maintain a familywise  $P \leq 0.05$ ).

$= 0.05$ ) of immature MAS vs. immature size class to reveal differences in immature activity by size.

RESULTS

**Nightly above-ground activity.**—Of the 2,191 observations of *Plethodon metcalfi*, 413 were adult males (19%), 669 were females (30%) and 1,109 were immatures (51%). The relative frequency of sightings of the three sex-age classes was consistent throughout the summer, except for biweekly periods 5 and 6 when observers sighted immatures more often than adults. I found significant differences in MAS for both sex/age class and biweekly period and a non-significant interaction between them (Table 4). Multiple comparisons associated with the ANOVA revealed that the mean activity times of all sex/age classes were significantly different from each of the others (Fig. 2). Immatures were active first, with some appearing above-ground before complete darkness. Females appeared next, and males had the latest activity times. Within immatures for which SVL was recorded ( $n = 375$ ), smaller individuals were active earlier (mean MAS =  $71.12 \pm 3.67$  standard error) and larger individuals

TABLE 4. Analysis of variance of time of sightings in minutes after sunset (MAS) of the Southern Gray-cheeked Salamander (*Plethodon metcalfi*) in relation to salamander sex/age class and bi-weekly period at sites near Highlands, North Carolina, USA.

Source	df	Adjusted SS	Adjusted MS	F	P
Sex/age class	2	73,028	36,514	24.85	< 0.001
Bi-weekly period	7	258,135	36,876	25.10	< 0.001
Interaction	14	22,947	1,639	1.120	0.338
Error	2,167	3,184,165	1,469		

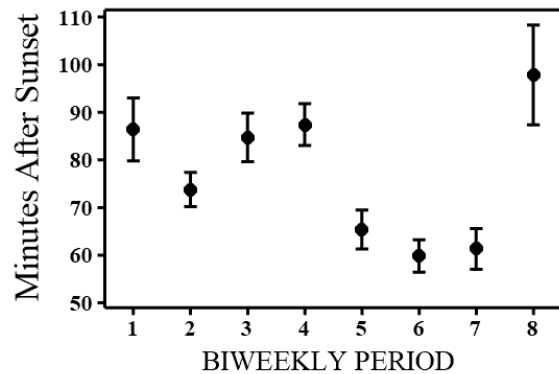
were active later (mean MAS = 73.30 ± 2.51). The differences in activity times between the two immature size classes were not significant ( $t = 0.497$ ,  $df = 373$ ,  $P = 0.620$ ). The trend in immature size classes is similar to the pattern seen when immatures are compared with adults as smaller individuals are active somewhat earlier than larger individuals.

**Seasonal variation in above-ground activity times.**—Salamanders showed a marked temporal pattern in MAS through the summer (Fig. 3). Mean MAS declined during July and early August and then rose to values similar to those of May and June by mid-August. Salamanders were active earlier in mid-late summer than they were in either early summer or very late summer. Pairwise comparisons between biweekly periods produced several significant results (Table 5).

**DISCUSSION**

**Nightly surface activity.**—*Plethodon metcalfi* may engage in several above-ground activities: foraging, defense of space, dispersal, and reproductive activity. Reproductive activity begins in early August and continues through September (Organ 1958; Hairston 1983) and is easily identified. My field notes do not specify any reproductive observations in this data set. Beyond reproduction, I cannot distinguish the other three activities. Dispersal activities must occur but are relatively uncommon. Among plethodontid adults, home range/ territorial fidelity is high (Nishikawa 1985; White 2000; Jaeger et al. 2016), and dispersal behavior is minimal (Madison and Shoop 1970; Ousterhout and Liebgold 2010). Perhaps agonistic and/or foraging activities account for the great majority of my observations.

Assuming defense of resources in *Plethodon metcalfi*, a possible mechanism is intraspecific partitioning of resources through competition mediated by



**FIGURE 3.** Foraging times in mean minutes after sunset (± one standard error) for the Southern Gray-cheeked Salamander (*Plethodon metcalfi*) as a function of biweekly period. Sex and age classes have been pooled due to their independence from biweekly period as indicated by a lack of interaction in the corresponding ANOVA (see Table 4).

agonistic interactions. Researchers have documented competition for this species (Hairston 1981; Nishikawa 1985) and congeners in eastern habitats (Mathis 1990; Gabor and Jaeger 1995; Griffis and Jaeger 1998; Marvin 1998; Jaeger et al. 2016). Territoriality is the most commonly invoked mechanism of competitive resource defense in several plethodontid species, including *P. metcalfi* (Hairston 1981; Nishikawa 1985; Gabor and Jaeger 1995; Marvin 1998). Marvin (1998) demonstrates that aggressive resource defense in the Cumberland Plateau Salamander (*Plethodon kentucki*) includes both interspecific and intraspecific interactions, and that intraspecific interactions are often the most intense.

**Possible intraspecific partitioning of foraging.**—Temporal partitioning of nightly activity by different sex and age classes of *Plethodon metcalfi* might be explained by defense of limited food resources. Food can be an object of competition in plethodontids (Fraser

**Table 5.** Mean foraging times of the Southern Gray-cheeked Salamander (*Plethodon metcalfi*) at sites near Highlands, North Carolina, USA, in minutes after sunset (MAS) pooled over sex/age class for the eight biweekly periods. A plus sign (+) indicates a positive significant difference to the compared biweekly mean and minus sign (-) indicates a negative significant difference to the compared biweekly mean (pairwise  $P \leq 0.00179$  based on Bonferroni adjustment to maintain a familywise  $P \leq 0.05$ ).

Biweekly period	Dates	Mean MAS	Compared with biweekly period							
			2	3	4	5	6	7	8	
1	10–23 May	87				S+	S+	S+		
2	24 May - 6 June	74		S-	S-		S+	S+	S-	
3	7–20 June	85				S+	S+	S+	S-	
4	21 June - 4 July	88				S+	S+	S+		
5	5–18 July	65							S-	
6	19 July - 1 August	60							S-	
7	2–15 August	61							S-	
8	16–31 August	97								

1976; Mathis 1991), with larger animals gaining access to higher quality foraging areas (Mathis 1991). Foraging may occur in pulses associated with moist litter after rainfall. Such moisture-related activity patterns could magnify pressure on food resources on nights when litter is moist, necessitating temporal partitioning. Immature, female, and male *Plethodon metcalfi* forage at successively later periods during the evening and these differences are significant. Further, this pattern is independent of, and does not interact with, a seasonal pattern of foraging whereby individuals forage earlier in the evening during late summer than they do in either early summer or early fall. Females might control the foraging order because they are the largest sex-age class (by mass) in unaltered forests (Ash et al. 2003) and are defending food resources.

Immatures (the smallest individuals) may be forced to forage first near dusk, when they are exposed to less competition with adults (particularly females) but are perhaps more susceptible to diurnal predators. Immatures active at dusk might be less likely to forage cursorily to avoid predation. *Plethodon cinereus* decreased foraging activity as light intensity increased and displayed a more cursorial search pattern in the dark (Placyk and Graves 2001). Greater exposure to diurnal predators may further reduce foraging success of immature *Plethodon metcalfi*. *Plethodon cinereus* avoids experimental substrate treatments that mimic the presence of garter snakes (Madison et al. 1999) indicating predator avoidance is a concern. Furthermore, foraging success is reduced in Ozark Zigzag Salamanders (*Plethodon angusticlavias*) after experimental exposure to stresses related to predation (Watson et al. 2004). Although foraging early may increase predation risk and require a less cursorial search pattern, it affords immature *Plethodon metcalfi* reduced foraging overlap with adults.

Female salamanders forage after the immatures and generally after dark. For a great part of each summer only about half the females in the population are foraging because the other half are below ground guarding clutches (Hairston 1983, 1987). Nonetheless, observers sighted females about 1.5 times as often as males. Observers might have identified males with minimal mental glands as females, affecting the reported ratio slightly. A 1:1 sex ratio in *Plethodon metcalfi* is likely (Riedel et al. 2012) and allows the conclusion that females are foraging more often than males. Females need to avoid predation and to maximize energy intake over a two-year period to produce a viable clutch (Hairston 1983; Petranka 1998). These requirements potentially explain both female foraging as soon as it is safely dark and that females forage more often than males. Additionally, females may exclude males from foraging until later in the evening because of their

greater mass (Ash et al. 2003; Mathis 1990).

Males forage last and do not forage as often as females based on the relative occurrence of their sightings. I explain this pattern by exclusion of males to later foraging times by females on a given night and a lesser need to accumulate energy reserves compared to females. Moisture relations could also help explain the observed pattern. Adults have smaller surface to volume ratios than immatures because of their larger body sizes. Smaller adult ratios indicate that adults could forage longer and thus have later average foraging times than immatures on nights when relative humidity or litter moisture levels are low.

**Moisture relations and relative humidity effects.**—Environmental factors in relation to physiological tolerances may control nightly activity patterns in amphibians and reptiles (Toft 1985). A likely physiological factor in *P. metcalfi* is environmental moisture and/or relative humidity. Cutaneous respiration in plethodontids requires that their skin is moist. Foraging time in the Allegheny Mountain Dusky Salamander (*Desmognathus ochrophaeus*) is positively correlated with water loss rates and inversely correlated with vapor pressure gradients (Feder and Londoss 1984).

Although moisture or a wet environment is not the proximate effect that governs plethodontid activity, it is a good general indicator. Water loss can restrict plethodontid surface activity to wet nights and limit activity during dry periods (Feder 1983). In the Eastern Red-backed Salamander (*Plethodon cinereus*), most foraging occurs within several days of rainfall (Fraser 1976; Placyk and Graves 2001). Jaeger (1980) specified that foraging in this species peaked within 3 d of rain. Days since rain reduced surface activity time in the Western Slimy Salamander (*Plethodon albagula*) (Peterman and Semlitsch 2014). Surface activity in the Southern Red-legged Salamander (*Plethodon shermani*) is strongly associated with recent rain (Connette and Semlitsch 2013; Connette et al. 2015). Increases in environmental vapor pressure deficit greatly reduces the probability of sighting both *P. metcalfi* and the Southern Appalachian Salamander (*Plethodon teyahalee*; Riddell and Sears 2015). These findings imply that plethodontid foraging patterns can be constant through time or pulsed, depending on patterns of rainfall. Because adult *P. metcalfi* are larger than immatures and because they have smaller surface area to volume ratios, possibly they can maintain dermal moisture and be active longer than immatures on a given night resulting in later mean activity times. I cannot explain differences in male and female activity times using this logic because males and females have similar SVLs (male  $59.99 \pm 0.42$ , female  $60.41 \pm 0.43$ ) although females tend to be more massive (Ash et al. 2003).

At least two factors, which can operate independently or interactively, control resource partitioning in many reptiles and amphibians (Toft 1985). These factors can be behavioral or physiological (Toft 1985). Hairston (1980a,b; 1981) demonstrates that competition and microclimate tolerances (temperature and moisture) mediate resource partitioning between the Northern Slimy Salamander (*Plethodon glutinosus*) and *P. metcalfi* (which was then classified as *Plethodon jordani*). I suggest that intraspecific nightly activity patterns in *P. metcalfi* are controlled by moisture tolerances working interactively with partitioning of foraging activity.

Experimental verification of my tentative explanation of nightly foraging patterns is necessary. An experimental removal of adult females from forested plots might cause immatures and males to shift their foraging times, thus demonstrating the effect of females. Environmental moisture/humidity regimes should also be monitored to assess impacts on foraging activity.

**Salamander guild organization.**—Researchers have portrayed salamander assemblages in forested communities as guilds (Davic and Welsh 2004) that exploit forest litter invertebrates as a food resource (Jaeger 1972; Hairston 1987; Rooney et al. 2000; Semlitsch et al. 2014). Physiological constraints commonly affect resource partitioning in reptiles and amphibians (Toft 1985). *Plethodon metcalfi* is the dominant member (92% of all observations) of a five-species guild in the Southern Blue Ridge Mountains (Ash 1997, Davic and Welsh 2004). If partitioning of nightly above-ground activity within such a dominant Southern Blue Ridge Mountain guild member is connected to foraging, defense of food resources, and relative humidity requirements, then these processes might explain the organization of the entire guild or possibly other similar guilds (Davic and Welsh 2004).

**Seasonal variation in foraging time.**—*Plethodon metcalfi* apparently forages earlier in the evening during late summer, a seasonal pattern that has been demonstrated for encounter rates for two large plethodontids (*P. metcalfi* and *P. teyahalee*; Hairston 1987), and for recapture frequency in a small plethodontid, *P. cinereus* (Maerz and Madison 2000). Monthly precipitation and temperatures both reach maximums in July and August; perhaps a moister environment allows higher relative humidity in early evening even though evening temperatures might be comparatively high. Higher relative humidity might allow earlier foraging by salamanders, particularly immatures. Additional research is necessary to determine the cause of the seasonal activity patterns of *P. metcalfi* documented here.

**Acknowledgments.**—I thank the individuals and institutions that made this work possible. Funding was provided by cost-share research agreements numbers 18–656, 11–175, and 11–260 between the Highlands Biological Station and the U.S. Forest Service, by U.S. Forest Service research grant No. 29–193 through the Southeastern Forest Experiment Station, and by grants-in-aid from the Highlands Biological Station. Stephen Boyce, Richard Bruce, and John Hendee assisted in the procurement of funding. Mary Ash and Cyndi White assisted in data collection. The Highlands Biological Station and the University of North Carolina Pembroke provided facilities and housing. The staff of the Highlands Biological Station provided assistance and support. Richard Bruce and John Roe provided ideas for and criticism of early versions of the manuscript.

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**ANDREW N. ASH** has been a professional Ecologist in North Carolina since 1977. Since 1989 he has been a Professor in the Department of Biology at the University of North Carolina at Pembroke, USA. He retired from this position in June 2019. Dr. Ash's research concerns plethodontid salamander ecology in relation to forest management. He works at the Highlands Biological Station (HBS) where he has maintained an ongoing program since 1979. Over the years, Dr. Ash has served HBS in several capacities: as a member of the Board of Scientific Advisors, as a member of the Highlands Biological Foundation, and he is currently a member of the Board of Directors. (Photographed by Lisa Kelly)