

THE ECOLOGY OF THE PEAKS OF OTTER SALAMANDER (*PLETHODON HUBRICHTI*) IN SYMPATRY WITH THE EASTERN RED-BACKED SALAMANDER (*PLETHODON CINEREUS*)

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ABSTRACT.—The Peaks of Otter Salamander, *Plethodon hubrichti*, is found along a 19 km length of the Blue Ridge Mountains, Virginia, USA, often in sympatry with the Eastern Red-backed Salamander, *P. cinereus*. In a sympatric area of Bedford County, Virginia, we conducted a mark-recapture study on a 10 × 10 m site. Surface densities of salamanders increased as the number of days without precipitation prior to a collection event increased. This suggests vertical movements in response to surface moisture. When salamanders returned to the surface after rain, individuals appeared to “shuffle” between rocks and likely, leaf litter. That is, we were more likely to find a different individual beneath a particular rock rather than the previous resident during sequential collection periods. There was no significant difference between the species in microhabitat use by adults; adults were primarily found under rocks. However, neonate and young-of-the-year *P. hubrichti* were found beneath rocks more frequently than *P. cinereus*. Linear movements, home ranges, growth rates and adult survival rates were similar for both species. Density for *P. hubrichti* in sympatry with *P. cinereus* was 0.6/m², which is lower than previously recorded for *P. hubrichti* in allopatry (1.6–3.3/m²). Cumulative ratios of numbers of the two species were stable over nine collection events but showed the least change (≤ 2%) after the third collection. We recommend using ratios of the two species at a series of sympatric sites as one measure to determine whether *P. cinereus* is encroaching upon the distribution of *P. hubrichti*.

Key Words.—Eastern Red-backed Salamander; ecology; Peaks of Otter Salamander; *Plethodon cinereus*; *Plethodon hubrichti*; sympatry

INTRODUCTION

The Peaks of Otter Salamander, *Plethodon hubrichti*, occupies mesic forest habitats along a 19 km length of the Blue Ridge Mountains, Virginia (Pague, C. and J. Mitchell, 1990. The distribution of the Peaks of Otter Salamander (*Plethodon hubrichti*). Unpublished report submitted to the Jefferson National Forest by the Virginia Department of Conservation and Recreation, Division of Natural Heritage, Richmond, VA. 16 p.). In allopatric areas this species dominates the terrestrial salamander community. Of 3441 salamanders sighted from 1995 to 2005 during a timbering impacts study in the Peaks of Otter area of the Blue Ridge Mountains, 94.8% were *P. hubrichti* (Reichenbach and Sattler 2007). In some areas densities can be very high (4.5 salamanders/m²; Kramer et al. 1993).

At the edge of its range, *P. hubrichti* is sympatric with the wide-ranging Eastern Red-backed Salamander, *P. cinereus* (Petranka 1998). These two species are similar in several ways including: (1) foraging on foggy or rainy nights, sometimes on vegetation (Jaeger 1978; Kramer et al. 1993); (2) consuming soft-bodied prey (Mitchell et al. 1996, Arif et al. 2007); (3) limited movements having

home ranges typically < 1 m² (Kramer et al. 1993; Mathis 1991); (4) use of leaf litter, rocks, logs and soil microhabitats (Taub 1961; Kramer et al. 1993; Wicknick 1995); and (5) defending sites (Jaeger et al. 1982; Wicknick 1995). They are also similar in size with adult *P. cinereus* ranging from 6.5–12.5 cm total length (TL) compared with 8–13 cm TL for *P. hubrichti* (Petranka 1998).

Because *P. hubrichti* and *P. cinereus* are similar species, this may lead to interspecific competition in sympatric areas (Wicknick 1995). These competitive interactions may, in part, limit the distribution of *P. hubrichti* (Highton 1972; Jaeger 1974). *Plethodon cinereus* is known to display interference competition in the form of agonistic behavior and territoriality (Jaeger 1971a, 1984). The parapatric distributions of several similar species are thought to be due to competition with *P. cinereus* (Highton 1972; Jaeger 1974). For example, *P. shenandoah* inhabits the talus areas of three mountains in Virginia's Shenandoah National Park. Jaeger (1970, 1971a, 1971b, 1972) concluded that *P. cinereus* can competitively exclude juvenile *P. shenandoah* from preferred, deeper, more moist soil in forested areas, and Griffiths and Jaeger (1998) showed that

P. cinereus inhibited the movements of *P. shenandoah* from source to distant subpopulations. A study by Arif et al. (2007), however, suggests that abiotic factors primarily limit the distribution of *P. hubrichti* instead of competitive interactions with *P. cinereus*.

While the ecophysiological details on what restricts *P. hubrichti* to such a limited area of the Blue Ridge Mountains are not yet fully understood (e.g., abiotic factors and/or interspecific competition with *P. cinereus*), studies on these two species in sympatry and allopatry will begin to unravel those details (Arif et al. 2007). Herein, we add to the limited research conducted to date on these two species in sympatry by using data from a mark-recapture study designed to evaluate: (1) population sizes; (2) survival rates; (3) cumulative ratios of numbers of the two species over collection periods; (4) microhabitat use; (5) movement patterns; and (6) growth rates.

MATERIALS AND METHODS

General field methods.—Our study site was located on the north side of Onion Mountain (Bedford Co., Virginia; 37° 29' 56.1" N, 79° 30' 45.7" W; 1035 m in elevation). A 10 × 10 m area (with a 1 m buffer) was marked off into 1-m² subplots using flags following the pattern described in Kramer et al. (1993). To gain resolution on the salamander's capture location, subplots were visually divided into four 0.5 × 0.5-m quadrats and assigned a lower case letter (a, b, c, and d) in a clockwise fashion starting with the top left quadrat. We placed a weather station (Vantage Pro2, Davis Instruments, Hayward, California, USA) on the site, which recorded ambient weather parameters as well as soil moisture and temperature in four different microhabitats, directly adjacent to the study site (beneath a rock, log, leaf litter, and within the leaf litter). The weather station was operational following the first two collection periods and remained until completion of the study.

We searched our study site during the day subsequent to rainfall on nine occasions from 13 May to 12 October 2005. We conducted the first three surveys at six to eight day intervals to provide a base of marked individuals. The remaining surveys were conducted at 17- to 42-day intervals. We carefully examined the entire site by turning all rocks and other cover objects and sifting through the leaf litter by hand. To minimize site disturbance, we took great care to replace all objects in their original positions. We placed collected salamanders in zip-lock bags labeled with the subplot/quadrat capture location as well as the microhabitat in which they were found (i.e., leaf litter, rock, or log). Rocks with salamanders captured beneath them were numbered using a permanent marker and the rock number was noted on the bag containing the salamander. We collected only marked salamanders

from the buffer area. Following collection, we measured salamanders with a ruler (snout-vent length, SVL) using the method by Wise and Buchanan (1992), weighed salamanders to 0.01 g (Scout Pro SP202, Ohaus Corp., Pine Brook, New Jersey, USA), gave them unique marks (see below), and released them on the same day and location/rock where they were collected.

We gave salamanders ≥ 30 mm SVL a permanent, unique mark using Visual Implant Elastomer (Northwest Technology Inc., Shaw Island, Washington, USA). We injected individuals in three of four possible ventral locations; posterior to either front leg or anterior to either hind leg (Bailey 2004). Using various combinations of four colors (yellow, red, orange, or green) at three marking locations provided 256 unique marks per species. We gave salamanders too small to mark uniquely (< 30 mm SVL) a generic mark consisting of a single mark on the ventral side of the individual. Due to their small size, we did not mark neonates. We first cooled all salamanders on ice and then injected them using a 0.3 cc syringe directly through the zip-lock bag in which they were contained.

Surface population characteristics.—To assess salamander response to surface moisture, we correlated the total number of salamanders captured with the number of days without precipitation prior to the rainfall directly preceding the collection day. Variables included number of dry days within two, four and six days before the collection day. For example, for the number of dry days within two days before our collection day, we would have recorded one of the following possibilities: (1) if both previous days were dry, this would be counted as two dry days; (2) if one of the two previous days had rain, this would be counted as one dry day; and (3) if both previous days had rain, this would be counted as zero dry days. Correlations included data from the last seven collection periods where the weather station was operational.

On a monthly basis, for each species, we identified up to three cohorts (neonates, young-of-the-year: salamanders hatched in 2004, YOY, and adult/juvenile) visually using the multimodal nature of histograms of SVLs (Kramer et al. 1993). We excluded recaptured animals from histograms when data were combined across collection periods due to multiple collections per month (May and June).

We evaluated the cumulative ratio of *P. hubrichti* to total salamanders collected (*P. hubrichti* and *P. cinereus*) over collection periods using two methods. First we simulated a situation where marking was not conducted and cumulative ratios were calculated from total numbers collected per species over each collection period. Second, we used information on marked animals by excluding all recaptures in the cumulative ratios. We then plotted these cumulative ratios over time to assess

how many collections were required to have minimal change (< 5%) in the ratios. The stability of the ratios was also evaluated using the chi-square test.

We estimated population size for uniquely marked adult/juveniles of each species using the Jolly-Seber method (Krebs 1999). We calculated population size for the generically marked YOY cohort using the Schumacher-Eschmeyer method (Krebs 1999). Survival and recapture rates were calculated for the adult/juvenile cohort using Program MARK (Available for free download at: <http://warnercnr.colostate.edu/~gwhite/mark/mark.htm>, last accessed 5 December 2009). We started with the most general model to estimate these rates, which included time varying survival and recapture rates. We then used the Akaike's information criteria to select the most parsimonious model (Cooch, E., and G. White. 2001. Using MARK – A gentle introduction, 2nd edition. Available from <http://www.phidot.org/software/mark/docs/book/> [Accessed 6 May 2002]). We calculated growth rates for adult/juvenile salamanders on an individual basis (change in SVL/days since initial capture). Only individuals with recapture intervals exceeding 90 days were used because these growth rates represent at least half of the active season (May–October). We regressed growth rates against SVL and made comparisons between species using multiple regression analysis (key term in the model being the species*SVL interaction). Because we did not uniquely mark small individuals (YOY and neonates), we determined growth rates (May–October and August–October for the YOY and neonates, respectively) for each species by regressing SVL against time with the slope being the growth rate (mm SVL/day). We made comparisons between the species as noted above except the key term in the model was species*time. We assessed species comparisons of initial neonate SVLs (19 August 2005) using a Mann-Whitney U-test. Similar comparisons were made between adults of both species using SVLs of individuals captured at the end of the active season (September–October).

We calculated the maximum linear distance moved for uniquely marked salamanders of each species that were recaptured. We used the minimum convex polygon method (Southwood 1978) to determine home range estimates for each species using individuals captured three or more times. When comparisons were done between the species, we first evaluated the normality of the data using the one-sample Kolmogorov-Smirnov test (KS test) followed by a t-test (if the data were normal, $P > 0.05$) or Mann-Whitney U-test (if the data were not normal). Summary statistics included means \pm 1 standard deviation (SD) or medians and interquartile ranges (IQR) for data used in parametric and nonparametric tests, respectively. We used SPSS software (SPSS Inc., Chicago, Illinois, USA) for

statistical analyses with the exception of growth rates and the paired t-test, which were performed using SYSTAT (SPSS Inc., Chicago, Illinois, USA). We performed chi-square analyses using EXCEL (Microsoft Corp., Redmond, Washington, USA).

Microhabitat characteristics and use.—We evaluated ground cover with a 0.5-m quadrat with 36 points placed on the ground as close to the center of each subplot as possible. At each point, we categorized the cover as rock, leaf litter, bare soil, or log, and we calculated a percentage for each category.

For microhabitat use comparisons between species and cohorts, we compiled the number of animals in each cohort captured beneath the two predominant cover objects (rocks and leaf litter). We categorized individuals found in multiple microhabitat locations to the location where they were found most often. We excluded individuals with no dominant microhabitat ($n = 3$, *P. hubrichti*; $n = 4$, *P. cinereus*). Capture location counts of generically marked salamanders did not include recaptured individuals. Because we did not mark neonates, all neonates we captured were considered to be unique animals. The data were plotted using bar graphs.

We evaluated the effect of microhabitat location on the probability of recapturing uniquely marked salamanders of each species found in the two dominant microhabitats: rocks and leaf litter. For each species, we divided individuals into four groups based on whether they were captured: (1) once beneath a rock; (2) multiple times beneath rocks; (3) once in leaf litter; or (4) multiple times in leaf litter. We categorized individuals found in multiple microhabitat locations to the location where they were found most often. We excluded individuals with no predominant microhabitat ($n = 3$, *P. hubrichti*; $n = 4$, *P. cinereus*). The number of salamanders in each category was then compiled in a contingency table and analyzed for homogeneity using a chi-square test. To allow for a minimum of two recapture opportunities, we used data only from individuals captured before September.

We calculated dispersion patterns using the Standardized Morisita's Index (I_p) for August, September, and October, when captures per collection period were highest. When I_p values were less than -0.5, they were considered 95% confident of representing a uniform dispersion pattern (Krebs 1999). Rocks were considered plots (Pielou 1977) and we combined data across species.

To determine whether salamanders primarily occupied one specific rock or whether they moved between several different rocks, we assessed the chronology of salamanders occupying specific rocks. For each rock we compared the current occupant to the most recent previous occupant. For example, rock #1 was first

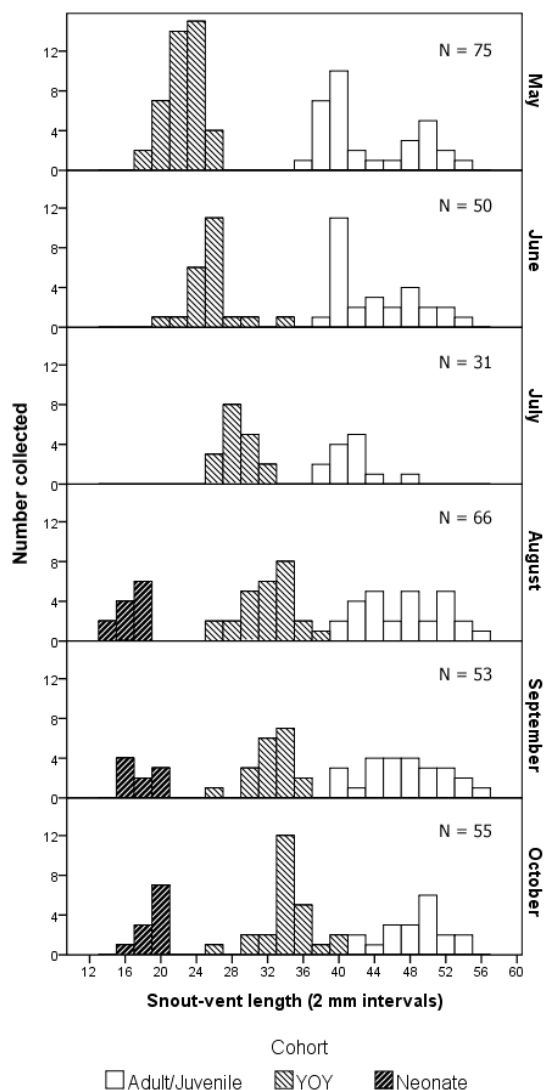


FIGURE 1. Size-class distribution for *Plethodon hubrichti* collected at a 10 X 10-m site in the Blue Ridge Mountains, Virginia, in 2005 (YOY = young-of-the-year hatched in 2004).

occupied by *P. cinereus* #18 on 26 May 2005. The next time we sampled our plot (3 June 2005), *P. cinereus* #24 was found under the rock. This was counted as a conspecific change with zero gap (i.e., the rock was not found unoccupied during a sampling event). On 21 June 2005, the rock was empty, and on 8 July 2005, we found a *P. hubrichti* with a generic mark. We counted this as a congeneric change after one gap. The rock was empty for two sampling dates (19 August 2005 and 17 September 2005) and then on the next sampling date (12 October 2005), we again found *P. cinereus* #18 under the rock. This was counted as a congeneric change after two gaps. We followed this methodology for every occupied rock on our site. Gaps or time intervals between sampling events averaged 19 days. We

calculated the total number of times that a rock was occupied by the same individual, a congeneric or a conspecific salamander for zero, one, two, etc. gaps. We divided the totals per category by the grand total per species allowing us to calculate the probability of the same individual occupying a rock during the next sampling period or the probability that another salamander would occupy the rock. We monitored 46 and 90 rocks that were initially occupied by *P. cinereus* and *P. hubrichti*, respectively. We also evaluated the difference in the SVLs of the current resident to the previous resident using a paired t-test. We used an alpha of 0.05 for all statistical analyses.

RESULTS

Surface population characteristics.—We captured 349 *Plethodon hubrichti* (including 131 recaptures and 32 neonates) and 229 *P. cinereus* (including 63 recaptures and 35 neonates) during the study. Recapture rates for *P. hubrichti* and *P. cinereus* increased from 3% and 9% during the first three collection periods to 49% and 39% from July to October, respectively. The number of salamanders we found per collection period ranged from 37 to 112 with the higher numbers being found in late August–October.

The number of salamanders we collected was positively correlated with the number of days without precipitation during a two-day time period prior to the collection day ($r = 0.89$, $n = 7$, $P = 0.007$). When longer time periods were considered before the collection day (four and six days), the correlation coefficients were still significant but declined relative to the two-day time period prior to the collection day ($r = 0.76$ and $r = 0.75$, respectively, $P \leq 0.05$).



FIGURE 2. Neonate *Plethodon hubrichti* in a nest cavity just after hatching. For details on this nest, which is the first one recorded for this species, see Kniewski and Reichenbach (2006). Photographed by A.B. Kniewski.

From May–July, two cohorts were identifiable for the *P. hubrichti*: individuals > 34 mm SVL represented the adult/juvenile cohort and those ≤ 34 mm SVL were the YOY hatched in 2004 (Fig. 1). In August and September, with the addition of the 2005 neonates (Fig. 2) and changes due to animal growth, salamanders were classified as adult/juvenile (> 38 mm SVL), YOY (25–38 mm SVL), and neonate (< 25 mm SVL). Due to animal growth, in October, cohort SVL cutoffs were adjusted slightly (adult/juvenile > 40 mm SVL, YOY 25–40 mm SVL, neonate < 25 mm SVL).

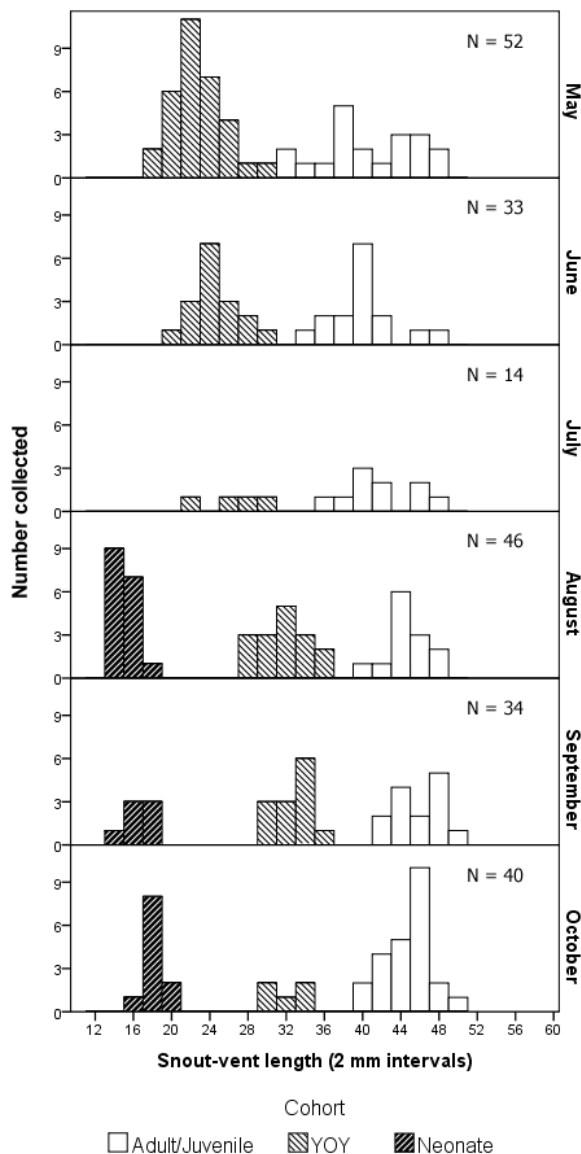


FIGURE 3. Size-class distribution for *Plethodon cinereus* collected at a 10 X 10-m site in the Blue Ridge Mountains, Virginia, in 2005 (YOY = young-of-the-year hatched in 2004).

Plethodon cinereus were classified similarly in May as the adult/juvenile cohort (> 30 mm SVL) and the YOY cohort (≤ 30 mm SVL; Fig. 3). Minor adjustments to the cohort SVL cutoffs occurred in June and July due to animal growth (adult/juvenile > 32 mm SVL, YOY ≤ 32 mm SVL). Beginning in August, we classified salamanders as adult/juvenile (> 38 mm SVL), YOY (25–38 mm SVL), and neonates (< 25 mm SVL).

Plethodon hubrichti averaged 57% (range 43–77%) of the salamanders we found when we excluded recaptures and 61% (range 43–73%) when we used simple totals to calculate cumulative ratios (Fig. 4). Both methods of calculating cumulative ratios changed by 15% over the first three collection periods and then declined to a maximum change of 2% over the remaining six collection periods. The proportions of salamanders we found per collection period did not differ between the species when recaptures were excluded ($\chi^2 = 10.9$, $df = 8$, $P = 0.21$) and when using totals ($\chi^2 = 8.7$, $df = 8$, $P = 0.37$).

The population size estimate for the 10×10 m plot of adult/juvenile *P. hubrichti* cohort was 57 (95% CI = 20–95) or 0.6 *P. hubrichti*/m². A constant survival and recapture rate model provided an adequate fit to the data for *P. hubrichti* with a survival rate estimated at 0.993 (95% CI = 0.988–0.997) and recapture rate of 0.309 (95% CI = 0.233–0.397). The YOY cohort population estimate was 147 (95% CI = 119–192) or 1.5 *P. hubrichti*/m². The population size estimate for *P. cinereus* of the adult/juvenile cohort was 46 (95% CI = 10–82) or 0.5 *P. cinereus*/m². A constant survival and recapture rate model provided an adequate fit to the data for *P. cinereus* with a survival rate estimated at 0.998 (95% CI = 0.984–1.000) and recapture rate of 0.251 (95% CI = 0.175–0.347). The YOY cohort population estimate was 271 (95% CI = 184–525) or 2.7 *P. cinereus*/m².

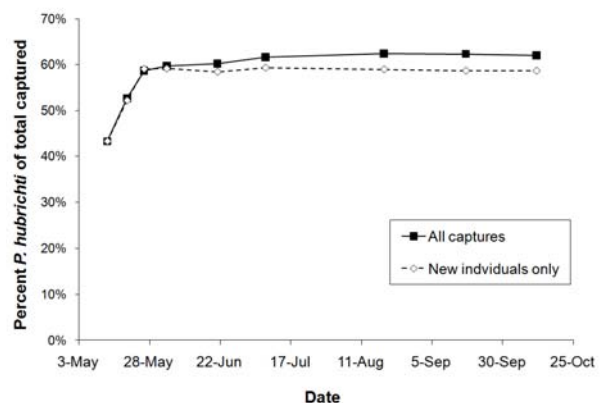


FIGURE 4. Cumulative ratios of *Plethodon hubrichti* collected (% of total salamanders). Solid line represents ratios including all individuals collected; dashed line represents ratios including only new (unmarked) individuals.

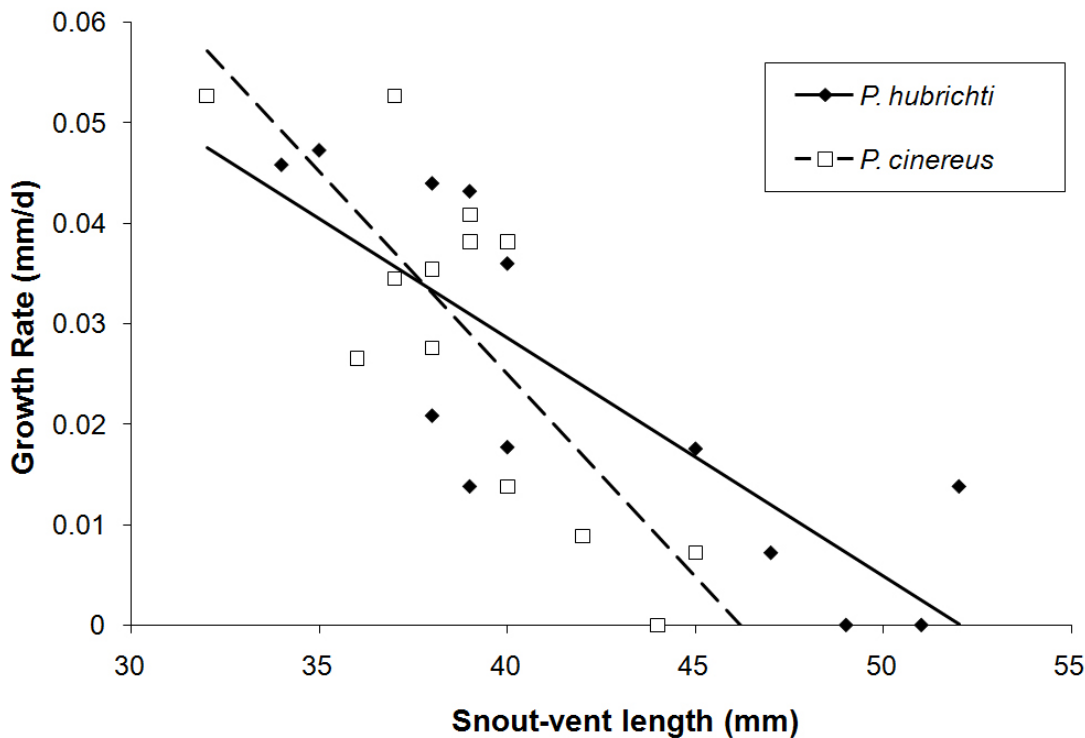


FIGURE 5. Growth rates (mm/day) in relation to SVL (mm) of adult/juvenile *Plethodon hubrichti* and *P. cinereus*.

Neonates of *P. hubrichti* captured in August were larger (median SVL = 16.5 mm, IQR = 1.3, $n = 12$) than *P. cinereus* neonates (median SVL = 14.0 mm, IQR = 2.0, $n = 17$; $U = 43.5$, $n = 29$, $P = 0.008$). There were no significant differences in neonate growth rates from August–October (species*time interaction $F = 0.9$, $df = 1, 63$, $P = 0.34$) with *P. hubrichti* and *P. cinereus* growing at 0.041 and 0.051 mm/day, respectively. For the YOY cohort, there were no significant differences between the growth rates (species*time interaction $F = 0.24$, $df = 1, 242$, $P = 0.63$) of *P. hubrichti* (0.078 mm/day) and *P. cinereus* (0.081 mm/day). Growth rates of individuals in the adult/juvenile cohort declined significantly as their SVL increased (*P. hubrichti* growth rate (mm/day) = $0.123 - 0.002$ (SVL), $r^2 = 0.67$, t for slope = 4.7, $df = 11$, $P < 0.001$; *P. cinereus* growth rate (mm/day) = $0.186 - 0.004$ (SVL), $r^2 = 0.66$, t for slope = 4.6, $df = 11$, $P < 0.001$). While the slopes were not significantly different ($F = 2.7$, $df = 1, 22$, $P = 0.1$; Fig. 5), *P. hubrichti* growth rates declined more gradually than *P. cinereus*. The difference in growth rates is reflected by the significantly larger size of *P. hubrichti* relative to *P. cinereus* captured at the end of the active season: September and October (median SVL = 48 mm, IQR = 6.5, $n = 41$ and median SVL = 45 mm, IQR = 3.0, $n = 32$ for *P. hubrichti* and *P. cinereus*, respectively; $U = 408.5$, $n = 73$, $P = 0.006$).

The median distance moved was 0.71 m (IQR = 0.62,

$n = 44$) and 1.00 m (IQR = 1.00, $n = 31$) for *P. hubrichti* and *P. cinereus*, respectively. The median home range for *P. hubrichti* was 0.25 m² (IQR = 0.31, $n = 9$) and 0.13 m² (IQR = 0.88, $n = 7$) for *P. cinereus*. There were no significant differences between linear distances moved ($U = 634.0$, $n = 75$, $P = 0.60$) and home range sizes ($U = 31$, $n = 16$, $P = 0.95$) for the two species.

Microhabitat characteristics and use under moist conditions.

—The ground cover at our site consisted of 11% rocks, 58% leaf litter, 27% bare ground, and 4% logs. Comparisons within each species indicated that significantly more salamanders in the neonate and YOY cohorts were found in the leaf litter than the adult/juvenile cohort, which preferred rocks ($\chi^2 = 45.1$, $df = 2$, $P < 0.001$, *P. hubrichti*, Fig. 6a; $\chi^2 = 53.6$, $df = 2$, $P < 0.001$, *P. cinereus*, Fig. 6b). Comparisons between species indicated no significant differences in microhabitat use by adult/juvenile cohorts ($\chi^2 = 1.6$, $df = 11$, $P = 0.21$). There was, however, a significant difference between the YOY and neonate cohorts with *P. hubrichti* being found under rocks and in leaf litter while *P. cinereus* were found primarily in leaf litter ($\chi^2 = 8.0$, $df = 1$, $P = 0.005$, YOY; $\chi^2 = 5.7$, $df = 1$, $P = 0.017$, neonates; Figs. 6a, b).

Microhabitat had a significant effect on the probability of recapturing *P. hubrichti* ($\chi^2 = 8.5$, $df = 1$, $P = 0.004$)

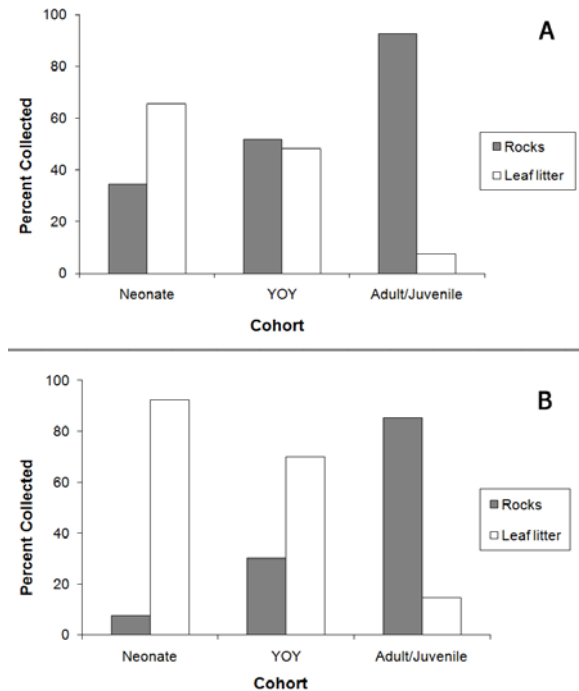


FIGURE 6. Microhabitat location of salamanders captured according to cohort (neonate; young-of-the-year hatched in 2004, YOY; adult/juvenile); (a) *Plethodon hubrichti*, and (b) *P. cinereus*.

and *P. cinereus* ($\chi^2 = 18.1$, $df = 1$, $P < 0.001$). Sixty-two percent ($n = 65$) of *P. hubrichti* and 73% ($n = 33$) of *P. cinereus* captured beneath rocks were captured more than once, while no salamanders were captured multiple times in the leaf litter.

Dispersion patterns were uniform for salamanders under rocks for the months of August, September, and October, $I_p = -0.81$, -0.65 , -0.54 , respectively. This indicates that it was most likely to find only one salamander under a rock. Rocks found occupied by salamanders were rarely vacant for long periods of time, as shown by the reduced height of bars as gaps increased in Figs. 7 and 8. For rocks originally occupied by a *P. cinereus*, replacement by a *P. hubrichti* was most likely across zero, one, and two gap periods (Fig. 7). Finding the same individual was second most likely with zero gaps while finding a different *P. cinereus* was the second most likely occurrence with one gap. Rocks originally occupied by a *P. hubrichti* were most likely occupied by a different *P. hubrichti* regardless of the gap number (Fig. 8). Finding the same individual was the second most common occurrence for one and zero gaps. There was no significant difference between the SVLs of the resident and replacement salamanders (resident individuals of *P. hubrichti* and replacement salamanders of the same species, $t = 0.835$, $df = 50$, $P = 0.408$, 40.9 and 42.2 mm mean resident and replacement SVLs or replacement by *P. cinereus*, $t =$

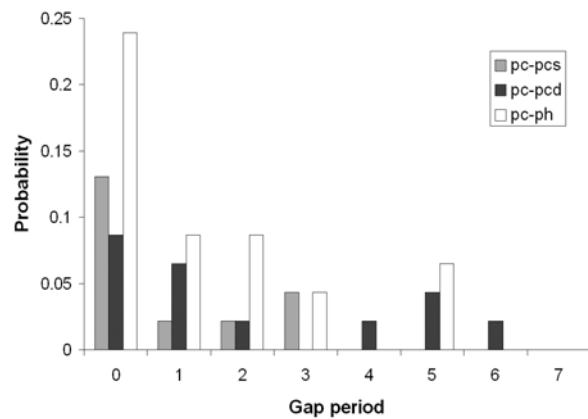


FIGURE 7. Probability of capturing the same individual or another salamander for rocks previously occupied by *Plethodon cinereus*. Gaps represent collection periods where the rock was unoccupied (mean gap 19 days, range 6–42 days; $n = 46$). *Plethodon cinereus* to same *P. cinereus* (pc-pcs); *P. cinereus* to different *P. cinereus* (pc-pcd); *P. cinereus* to *P. hubrichti* (pc-ph).

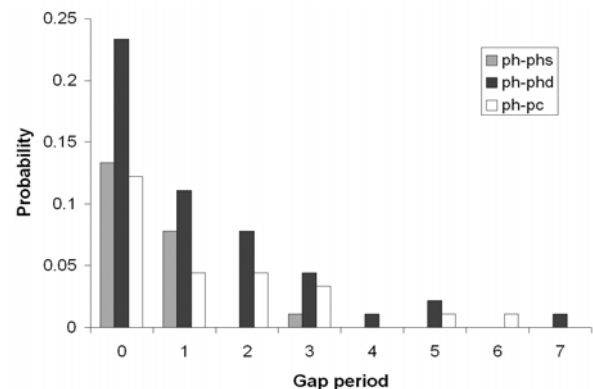


FIGURE 8. Probability of capturing the same individual or another salamander for rocks previously occupied by *Plethodon hubrichti*. Gaps represent collection periods where the rock was unoccupied (mean gap 19 days, range 6–42 days; $n = 90$). *Plethodon hubrichti* to same *P. hubrichti* (ph-phs); *P. hubrichti* to different *P. hubrichti* (ph-phd); *P. hubrichti* to *P. cinereus* (ph-pc).

1.096, $df = 27$, $P = 0.283$, 37.7 and 39.8 mm mean resident and replacement SVLs; resident individuals of *P. cinereus* and replacement salamanders of the same species, $t = 1.186$, $df = 12$, $P = 0.259$, 38.7 and 41.2 mm mean resident and replacement SVLs or replacement by *P. hubrichti*, $t = 0.515$, $df = 24$, $P = 0.611$, 38.1 and 37.0 mm mean resident and replacement SVLs).

DISCUSSION

Salamander ecology.—Positive correlation between surface densities of salamanders and time interval between rainfall events, as found in this study, has been noted for *P. hubrichti* (Kramer et al. 1993; Reichenbach and Sattler 2007) and is likely due to hunger. Prey are more abundant at the surface relative to underground

areas (Fraser 1976b). During dry periods, salamanders may first move to surface refuges such as rocks and logs (Jaeger 1980a), but tend to eventually move underground as the surface dries further (Taub 1961; Heatwole 1962; Fraser 1976a). The longer they stay underground, presumably the more hungry they become. After it rains salamanders re-emerge onto the surface, typically at night, and forage on plants, in leaf litter, and under cover objects (Jaeger 1978, 1980b, 1980b; Kramer et al. 1993). Directly after rain, when leaf litter is wet, salamanders at our site appear to be moving between rocks as they shuffle between rocks and leaf litter while foraging. We infer that hostile takeover of rock territories did not occur because the SVLs of new occupants were not significantly different from the original occupant (Mathis 1990). We presume that as the leaf litter dries between rainfall events that salamanders holding territories would abandon the leaf litter (Jaeger 1980b; Jaeger et al. 1995) and move back to particular sites (Gergits and Jaeger 1990; Wicknick 1995) that have been marked (e.g., fecal pellets and other pheromonal markers; Jaeger and Gergits 1979; Jaeger et al. 1986; Simons and Felgenhauer 1992).

Adult salamanders found primarily in leaf litter represent a different dynamic than those found primarily under rocks. We explain the lack of recaptured adults found primarily in leaf litter in three ways: (1) these individuals may have been transients or floaters that do not hold territories (Mathis 1991) and their movements may have taken them out of our collection area; (2) they may have used burrows or otherwise moved vertically (Taub 1961; Fraser 1976a, b) more frequently than those using rocks and therefore were less likely to be found at the surface during the day; and/or (3) they may have had higher mortality rates compared to residents of rocks because they were more vulnerable to predators.

Ecology of *P. hubrichti* in sympatric areas.—Data from our 10 × 10 m site indicate that *P. hubrichti* is similar to *P. cinereus* with regard to: (1) microhabitat selection under moist conditions where young individuals of both species were found predominantly in the leaf litter, and as they increase in size, they shift to primarily occupying rocks. This is similar to what Jaeger et al. (1995) found for *P. cinereus*, although *P. hubrichti* starts this process at a younger age relative to *P. cinereus*; (2) movement patterns as shown by median linear distances moved and median home range size; (3) growth rates; and (4) adult/juvenile survival rates. In contrast, *P. hubrichti* neonates and adults are significantly larger than *P. cinereus* neonates and adults, which is similar to what Wicknick (1995) found for adults of the same species. Size difference is one way interspecific competition may be lessened if the size difference allows for resource partitioning (i.e., food) as was seen with adult *P. hoffmani* and *P. punctatus* (Fraser

1976b). Resource partitioning with regard to food, though, was not seen for *P. cinereus* and *P. hubrichti* in sympatry (Arif et al. 2007).

Adult *P. hubrichti* densities at 13 allopatric sites ranged from 1.6 (Sattler and Reichenbach 1998) to 3.3 salamanders/m² (Kramer et al. 1993, mark-recapture data reanalyzed for adults only using Jolly-Seber methodology). In contrast, the density of *P. hubrichti* in sympatry with *P. cinereus* was 0.6/m² (this study). However the combined density for both species at our site (1.1 salamanders/m²), is comparable to nearby densities for *P. hubrichti* in allopatry noted above. The combined density suggests the species split available resources when sympatric. To confirm that *P. hubrichti* populations are depressed due to *P. cinereus*, removal studies could be conducted where *P. cinereus* is removed from experimental plots to see if *P. hubrichti* numbers increase similar to what Hairston (1980) found when *P. jordani* was removed from plots with *P. glutinosus*.

Monitoring *P. hubrichti* in sympatric areas.—We suggest establishing multiple monitoring sites throughout sympatric areas in the perimeter of the range of *P. hubrichti*. The sympatric areas have been hypothesized to be static (Jaeger et al. 2002) based upon research done by Wicknick (1995) and more recently Arif et al. (2007). Limited data at one site, with one sample taken in 1993 (Wicknick 1995) and another in 2003 (Aasen and Reichenbach 2004), indicated that proportions of *P. hubrichti* relative to *P. cinereus* were not significantly different after a 10-year period. This site was located in the primary conservation area for *P. hubrichti* where timbering is not permitted (George Washington and Jefferson National Forests. 1997. Habitat conservation assessment for the Peaks of Otter salamander (*Plethodon hubrichti*). U.S. Fish and Wildlife Service, Unpublished report. 28 p.). There is, however, a large portion of the sympatric zone located in the secondary conservation area. Here, forms of timbering such as shelterwood cuts, which do not completely remove the forest canopy, are permitted on national forest lands and any form of timbering is permitted on private property. Shelterwood cuts had only minor, short-term effects on juvenile age classes of *P. hubrichti* (Sattler and Reichenbach 1998) while clearcuts had significant, long-term, adverse impacts on *P. hubrichti* populations (Reichenbach and Sattler 2007). Both types of timbering reduced diet quality for *P. hubrichti* (Mitchell et al. 1996). Timbering, especially clearcuts, may increase temperature and decrease moisture on the forest floor (Covington 1981; Ash 1995). This might favor *P. cinereus* as this species may be more resistant to increased temperatures and evaporation rates (anecdotal information in Thurow 1957; Arif et al. 2007).

At these monitoring sites, trends in the ratios of

numbers of these two species could be one variable evaluated over time. Although further validation is needed, our data can be used as guidance for the number of samples to collect. We showed that one sample was adequate to characterize the ratios of the two species in our 10 × 10 m area, though with three samples the cumulative ratios were more stable. Data from this study also indicate that multiple samples of salamanders would not have to be marked as the ratios based on cumulative totals of salamanders collected were not significantly different from ratios calculated with recaptures excluded. The ability to leave salamanders unmarked allows for significant time savings in the field. In this study, it took two of us typically three hours to check the leaves and cover objects in our 10 × 10 m site. Depending on the number of animals collected, it would take us an additional three to six hours to take measurements and mark salamanders with elastomer. While more research is needed to determine all the factors affecting the distribution of the *P. hubrichti*, monitoring the ratio of *P. hubrichti* to *P. cinereus* in sympatric areas would provide one simple measure for assessing the stability of this zone.

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