

Running Head: *PLETHODON HUBRICHTI* CONTACT ZONE ECOLOGY

The Ecology of the Peaks of Otter Salamander (*Plethodon hubrichti*) in the Contact Zone  
with the Redback Salamander (*P. cinereus*)

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Abstract

The Peaks of Otter Salamander *Plethodon hubrichti* is found only in the Peaks of Otter area in the Blue Ridge Mountains of Virginia where its range is completely surrounded by the Redback Salamander *P. cinereus*. In 2005 we conducted a mark-recapture study in the contact zone of *P. hubrichti* and *P. cinereus*. From a 10 × 10 m site a total of 349 (including 131 recaps) *P. hubrichti* and 229 (including 63 recaps) *P. cinereus* were collected. The number of salamanders collected at the surface correlated with the number of days without rainfall prior to a collection event which was indicative of vertical movements in response to dryness at the surface. Vertical movements in response to surface conditions may explain the “shuffle” seen of individuals beneath cover objects. During sequential collection periods, it was most likely that a different individual was found beneath a particular rock rather than the previous resident and that the new resident was not significantly different in size from the previous resident.

Comparisons between the species indicated no difference in habitat use between species as adults and neonates: young animals were found primarily in leaf litter while older animals were found primarily underneath rocks. Likewise linear movements (median = 0.71 and 1 m), and home ranges (median = 0.25 and 0.13 m<sup>2</sup>) were similar between *P. hubrichti*, and *P. cinereus*, respectively. *P. hubrichti*, however, appears to have depressed growth rates and adult densities in sympatry when compared with allopatric populations. Our data and information from the literature suggest a stable contact zone; however, this stability might be altered by timbering or other forms of environmental stress.

Ecology of the Peaks of Otter Salamander (*Plethodon hubrichti*) in the Contact Zone with  
the Redback Salamander (*P. cinereus*)

The ranges of several species of *Plethodon* are completely surrounded by *Plethodon cinereus*. The range boundaries of these similar species are believed to be due to competition with *P. cinereus* (Highton 1972; Jaeger 1974). Several studies have been conducted to determine if this is indeed the case. *Plethodon shenandoah* inhabits the talus areas of three mountains in Shenandoah National Park. Jaeger (1970, 1971a, 1971b, 1972) concluded that *P. cinereus* can competitively exclude juvenile *P. shenandoah* from the preferred, deeper, more moist soil in the forested areas. Another species, *P. hoffmani*, occurs allopatrically with *P. cinereus* in the western part of the Ridge and Valley Province of the central Appalachian Mountains. This species was examined by Fraser (1976a) who concluded that *P. cinereus* was slowly encroaching on *P. hoffmani*. Jaeger et al. (2002), however, examined the same species and considered the contact zone to be static.

Interference competition is thought to be expressed by plethodontid salamanders in the form of agonistic behavior and territoriality (Thurow, 1976; Petranka, 1998). Gergits (1981; cited in Jaeger et al., 1982) stated four conditions that must be met in order to conclude that territoriality exists. Individuals must 1) exhibit site tenacity; 2) defend the area of occupation; 3) advertise their presence, and 4) exclude competitors from the defended area. Many studies have examined *P. cinereus* concerning site attachment (Gergits and Jaeger, 1990), advertisement of sites (Jaeger and Gergits, 1979; Jaeger et al., 1986), aggressive defense of sites (Jaeger, 1981, 1984; Wicknick 1995), and exclusion of intruder from sites (Jaeger et al., 1982). However, many of these studies

were done under laboratory conditions, leaving the exact nature of territoriality of *P. cinereus* in natural habitats in question (Gergits and Jaeger, 1990).

*Plethodon hubrichti* is found only in the Peaks of Otter area in the Blue Ridge Mountains of Virginia and has a range of approximately 8 x 15 km (Pague and Mitchell, 1990). The possibility of competition between *P. hubrichti* and *P. cinereus* was examined by Wicknick (1995). Her results showed that while interspecific competition was likely, both species showed about the same level of competitive success. With the similarity of their competitive success, Jaeger et al. (2002) proposed that the contact zone would be static. Wicknick's (1995) three sites (one allopatric *P. hubrichti*, one allopatric *P. cinereus* and one sympatric site) were reexamined after 10 years by Aasen and Reichenbach (2004) and the proportions of *P. hubrichti* relative to *P. cinereus* were found to have remained static in the sympatric site.

While the contact zone between the two species appears to be static, at least in one area, little has been published on the dynamics of the interaction between the two species. In this study we examine the population dynamics of *P. hubrichti* and *P. cinereus* in the contact zone using data from a mark-recapture study.

#### Materials and Methods

The study site for the mark recapture study was located on the north side of Onion Mountain (37° 29' 56.1", 79° 30' 45.7") at approximately 1035 m in elevation. At this location a 10 m × 10 m area plus a 1 m buffer zone was marked off following the pattern described in Kramer et al. (1993). The site was divided into 121, 1 m<sup>2</sup> subplots each having a flag in the upper left-hand corner with a unique letter/number combination. These subplots were visually divided into 0.5 m × 0.5 m quadrats to gain resolution in the

salamander's capture location. Each quadrat in the subplot was assigned a lower case letter (a, b, c, and d) in a clockwise fashion starting with the top left quadrat. A weather station (Davis Instruments Corp., Hayward, CA) was placed on the site which recorded ambient weather parameters as well as soil moisture and temperature in four different locations (beneath a rock, beneath a log, beneath leaf litter, and amid the leaf litter). All soil probes were located directly adjacent to the study site.

The study site was examined during the day subsequent to a rainfall event on nine occasions between May 13 and October 12, 2005 (average time between collections 19 days, range 6 to 42 days). The entire site was examined by turning rocks and other cover objects and sifting through the leaf litter by hand; all objects were replaced in their original positions. Salamanders were collected and placed in zip-lock bags labeled with the subplot/quadrat capture location as well as whether the animal was found in the leaf litter or under a rock or log. If a salamander was collected beneath a rock, the rock was labeled with a number using a permanent marker and the rock number was noted on the bag containing the salamander. Rocks were numbered consecutively within a subplot basis. Only marked salamanders were collected from the buffer area.

Following examination of the study site, salamanders were measured (snout-vent length, SVL), weighed ( $\pm 0.01$  g), marked (see below), and released in the same location/rock where they were collected. In the fall (Sep. – Oct.) sex was also determined for adult salamanders ( $\approx >40$  mm SVL). Males for both species were characterized by a “football shaped” vent opening with light areas along the sides of the vent. Additionally males had square snouts and swollen nasolabial grooves (Thurow, 1957). Female salamanders of both species had a narrow vent slit, rounded snout and lacked light areas

along the vent (Fig. 1a, b). Twelve salamanders were collected from areas near the study site and returned to the lab for sex evaluation. Correct sexing of individuals based on the above characteristics was verified by passing a strong light through the salamander and visually identifying the presence or lack of testes (Gillette and Peterson 2001).

Salamanders large enough ( $\approx >30$  mm SVL) were given a permanent, unique mark using Visual Implant Elastomer (VIE) (Northwest Technology Inc., Shaw Island, Washington). This marking method has no effect on growth or reproduction on a similar species and provides a permanent, easy to identify mark. Individuals were injected in three of four possible locations (posterior to either front leg or anterior to either hind leg on the ventral side of the individual) (Bailey 2004). Each mark was one of four colors (yellow, red, orange, or green). These colors were chosen because of their ability to fluoresce under ultraviolet (UV) light. The combination of three marks, four locations, and four colors provided 256 possible unique marks. Salamanders collected that were  $<30$  mm SVL were given a generic mark consisting of a single mark on the ventral side of the individual. Neonates were not marked. All salamanders were cooled on ice prior to subcutaneous injection of the elastomer. Individuals were injected using a 0.3 cc syringe directly through the zip-lock bag in which they were contained. All processing was conducted in the field on the collection day. Most marks could be read directly, without the aid of a portable UV light. When marks were difficult to read, the portable UV light was used. Care had to be taken when viewing the marks under UV light since 3 out of the 4 colors changed in appearance under UV light: red looked like orange, orange like yellow, yellow like yellow-green (yellow and green were difficult to distinguish under UV light).

The total number of salamanders was correlated with the extent of the dryness prior to the collection day. We correlated the number of dry days 2, 4 and 6 days before the collection day with the total number of salamanders found.

The multimodal nature of histograms based on SVL's for each species per month were used to identify cohorts. Where data were combined across collection periods (May and June), recaptured animals were excluded.

For habitat use comparisons between species and cohorts, the data were divided into spring (May – July) and fall (Aug. – Oct.) time periods. The number of animals captured beneath different cover objects (rock, log, or leaf litter) was compiled. To compensate for multiple captures of uniquely marked animals each individual contributed a total value of 1 regardless of the number of times it was captured. Individuals captured in multiple habitat locations contributed the appropriate fraction for each habitat category based on the number of captures in each habitat. For example, a salamander caught 3 times under a rock and once under a log would be counted at 0.75 rock and 0.25 log. Capture location counts of generically marked salamanders did not include recaptured individuals. Since neonates were not marked, all neonate captured were considered to be unique animals. The data were plotted using bar graphs and were analyzed using the chi-square test.

Population estimates for each species of the 2003 and older cohort (uniquely marked animals) were calculated using the Jolly-Seber method (Program Jolly). Population estimates for the 2004 cohort (generically marked individuals) were calculated using the Schumacher – Eschmeyer method (Krebs, 1999). Survival rates were calculated for the 2003 and older cohort using Program MARK following the



methodology detailed in Cooch and White (2001). Relative survival rates for each species were estimated for the 2004 cohort, where animals could not be uniquely marked due to their small size, by compiling in a  $2 \times 9$  contingency table, the number collected per collection event from the 2004 cohort relative to total collected from the other cohorts excluding neonates. A chi-square test statistic was used to assess homogeneity of these data.

The cumulative ratio of *P. hubrichti* to *P. cinereus* over collection periods was evaluated in two ways to determine the stability of the ratios. One simulated a situation where marking was not conducted and a cumulative ratio was calculated based upon total numbers collected per species over each collection period. The second situation utilized information on marked animals by excluding all recaptures in the cumulative ratios. Both situations were evaluated graphically as well as being tested for homogeneity with a chi-square test.

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

Linear estimates of horizontal movements were calculated for uniquely marked individuals of each species. For both species the maximum linear distance moved by the individual was used in the calculation. Home range estimates for each species were calculated for individuals captured in 3 or more locations using the minimum convex polygon method. When comparisons were done between the species, as with the

measures noted here (home range size and maximum linear distance), normality of the data was first evaluated using the one-sample Kolmogorov-Smirnov test (KS test) followed by the t-test (if the data were normal) 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 parametric and non parametric tests, respectively. SPSS (2004) and SYSTAT (1996) were used in the statistical analyses.

The chronology of salamanders occupying specific rocks was assessed to determine whether salamanders occupy primarily one rock or whether there is essentially a shuffling of salamanders under specific rocks. For example, rock #1 in the subplot f5 was first occupied by *P. cinereus* #18 (45 mm SVL) on 5/26. The next time we sampled our plot (6/3), *P. cinereus* #24 (47 mm SVL) was found under the rock. This was counted as a conspecific change with 0 gap (i.e. the rock was not found unoccupied during a sampling event). On 6/21 the rock was empty, and on 7/8 a *P. hubrichti*, generic mark (25 mm SVL) was found. This was counted as a congeneric change after 1 gap. The rock was empty during the next two sampling dates (8/19 and 9/17) and then on the next sampling date (10/12), *P. cinereus* #18 (45 mm SVL) was found under the rock. This was counted as a congeneric change after 2 gaps. We followed this methodology for every occupied rock on our site. Gaps or time intervals between sampling events averaged 19 days. We then totaled all the times a rock was occupied by the same individual, a congeneric or another conspecific salamander for 0, 1, 2, etc. gaps. By dividing the totals per category just noted by the grand total per species we were able to calculate the probability of, for example, the same individual occupying a rock during the next sampling period or the probability that another conspecific would occupy the rock.

In addition to the probability calculation, the difference in the SVL of salamanders replacing previous residents were evaluated using a paired test comparing the previous resident's SVL with the SVL of individual that replaced it.

The effect of habitat location on the likelihood of recapturing an individual was evaluated for uniquely marked salamanders of each species in the two dominate habitats, rocks and leaf litter. For each species, individuals were divided into four groups: captured once beneath a rock, captured multiple times beneath a rock, captured once in leaf litter, or captured multiple times in leaf litter. Individuals found in multiple habitat locations were categorized in the habitat location where they were found predominantly. When individuals were found equally in both habitats, the animals were excluded (N = 1, *P. hubrichti*; N = 3, *P. cinereus*). The number of individuals in each category was then compiled in a contingency table and then analyzed for homogeneity using a chi-square test. In order to allow for a minimum of two recapture periods, individuals only through the August collection period were used.

Growth rates for 2003 and older cohorts (uniquely marked salamanders) were calculated on an individual basis (change in SVL/days since initial capture). Only individuals with recapture intervals exceeding 90 days were used since these growth rates would represent at least half of the active season (May – Oct.). The growth rates were regressed against SVL and comparisons between species were done using analysis of covariance (ANCOVA). For the 2004 cohort, growth rate (May – Oct.) was determined for each species by regressing SVL against time with the slope being the growth rate (mm SVL/day). Comparisons between species for the 2004 cohort were done using ANCOVA. Growth rates and species comparisons for the 2005 cohort (Aug. – Oct.)

were done as noted for the 2004 cohort. Species comparisons of neonate SVL's when we first encountered them (8/19) were assessed using a Mann-Whitney U-test. Similar comparisons were made between adults of both species using SVL's of individuals captured from September through October.

To compare salamanders captured on our sympatric site with nearby allopatric populations, salamanders of each species were collected from nearby allopatric populations. Salamanders collected were measured (SVL) and weighed ( $\pm 0.01$  g) in the field and then released in the same location. Length comparisons were made between the adult allopatric and sympatric individuals ( $>37$  mm SVL) captured during a similar time period (Sep. – Oct.). A condition index was also calculated for each species using salamanders  $>25$  mm SVL from our sympatric and allopatric sites. First a linear regression was fit to the data, ( $\log(\text{wt.})$  vs.  $\log(\text{SVL})$ ), and then the residuals were compared using a t-test (Jakob et al., 1996).

## Results

A total of 349 *P. hubrichti* (including 131 recaps and 32 neonates) and 229 *P. cinereus* (including 63 recaps and 35 neonates) were captured during the study. For *P. hubrichti*, percent recaptures increased from 3-6% after the first few collection periods to an average of 49% from July to October. Recapture rates for *P. cinereus* were more variable with recapture rates from 25-27% at the beginning of the study to an average of 39% from July to October. The number of salamanders found per collection period ranged from 37 to 112 with the higher numbers being found in late August thru October. The number collected was positively correlated with the number of dry days during a 2 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 (4 and 6 days) the correlations declined but were still significant ( $r = 0.76$  and  $r = 0.75$ , respectively,  $P \leq 0.05$ ). In September and October 17 *P. hubrichti* were identified as male and 25 as female. The smallest *P. hubrichti* identified as being sexually mature was 38 mm SVL. Fourteen *P. cinereus* were identified as male and 21 as female during the same period. The smallest *P. cinereus* identified as being sexually mature was 39 mm SVL. Neither species differs from a 50:50 sex ratio (*P. hubrichti*,  $\chi^2 = 1.52$ ,  $df = 1$ ,  $P = 0.22$ ; *P. cinereus*,  $\chi^2 = 1.40$ ,  $df = 1$ ,  $P = 0.24$ ).

From May through July, 3 cohorts were identifiable for *P. hubrichti*: 2002 and older cohorts (>46 mm SVL), 2003 cohort (34 – 46 mm SVL) and the 2004 cohort (<34 mm SVL) (Fig. 2). In August the 2005 cohort was added as neonates were found. In addition to finding neonates, an egg mass of *P. hubrichti* was followed from late May until the eggs hatched in late July (Fig. 3a,b) (Kniowski and Reichenbach, in press). In August, the 2002 and older cohort blended with the 2003 cohort and so 3 cohorts could be identified from August through the end of the study. In August, salamanders above 38 mm SVL were classified in the 2003 and older cohort, 24 to 38 mm SVL, the 2004 cohort and <24 mm SVL, the 2005 cohort. Minor adjustments to the cohort SVL cutoffs occurred in October due to animal growth.

*P. cinereus* captured in May were classified as follows: salamanders above 42 mm SVL were classified in the 2002 and older cohort; 32 mm to 42 mm SVL, the 2003 cohort and those <30 mm SVL were in the 2004 cohort (Fig. 4). Minor adjustments to the cohort SVL cutoffs occurred in June and July due to animal growth. Beginning in August we could no longer distinguish between the 2002 and older and the 2003 cohort.

Salamanders captured in August through October were classified as follows: >38 mm SVL, the 2003 and older cohort; 24 to 38 mm SVL, the 2004 cohort and <24 mm, the 2005 cohort.

There was a significant difference in habitat use between the three cohorts (2002 and older, 2003, 2004) of *P. hubrichti* in the spring/midsummer season ( $\chi^2 = 30.7$ ,  $df = 4$ ,  $P < 0.001$ ) (Fig. 5a). The 2004 cohort was found primarily in the leaf litter and the older cohorts were found beneath rocks. The same significant trend was found in *P. cinereus* ( $\chi^2 = 35.3$ ,  $df = 4$ ,  $P < 0.001$ ) (Fig. 5b). Comparisons between species indicated no significant differences in habitat use for the 2002 and older cohorts and the 2003 cohorts (2002 and older cohort:  $\chi^2 = 4.93$ ,  $df = 2$ ,  $P = 0.085$ ; 2003 cohort:  $\chi^2 = 0.95$ ,  $df = 2$ ,  $P = 0.62$ ). There was however a significant difference between the 2004 cohorts with *P. hubrichti* being found more commonly beneath rocks than *P. cinereus* ( $\chi^2 = 10.2$ ,  $df = 2$ ,  $P = 0.006$ ) (Fig. 5a, b).

In late summer and fall the capture locations for the 3 cohorts (2003 and older, 2004, 2005) were significantly different in *P. hubrichti* ( $\chi^2 = 47.1$ ,  $df = 4$ ,  $P < 0.001$ ) (Fig. 6a) and in *P. cinereus* ( $\chi^2 = 47.2$ ,  $df = 4$ ,  $P < 0.001$ ) (Fig. 6b). For both species the 2005 cohort was found primarily in the leaf litter and the older cohorts were found beneath rocks. There was no significant difference between the 2003 and older cohorts ( $\chi^2 = 4.36$ ,  $df = 2$ ,  $P = 0.11$ ) or the 2005 cohorts ( $\chi^2 = 5.88$ ,  $df = 2$ ,  $P = 0.053$ ). There was however a significant difference between the 2004 cohorts with *P. hubrichti* being found more commonly beneath rocks than *P. cinereus* ( $\chi^2 = 8.34$ ,  $df = 2$ ,  $P = 0.015$ ) (Fig. 6a, b).

The population estimate for *P. hubrichti* of the 2003 and older cohort was 57 (20-95, 95% confidence intervals (95% CI)) or 0.57 *P. hubrichti*/m<sup>2</sup>. 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 (0.988-0.997, 95% CI) and recapture rate of 0.309 (0.233-0.397, 95% CI). The 2004 cohort population estimate was 147 or 1.47 *P. hubrichti*/m<sup>2</sup> (119–192, 95% CI). The proportion of *P. hubrichti* collected from the 2004 cohort were homogeneous over the collection periods ( $\chi^2 = 5.14$ , df = 8, P = 0.74). The population estimate for *P. cinereus* of the 2003 and older cohort was 46 (10–82, 95% CI) or 0.46 *P. cinereus*/m<sup>2</sup>. 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 (0.984–1.000, 95% CI) and recapture rate of 0.251 (0.175-0.347, 95% CI). The 2004 cohort population estimate was 271 or 2.71 *P. cinereus*/m<sup>2</sup> (184–525, 95% CI). The proportion of *P. cinereus* collected that were from the 2004 cohort were not homogeneous over the collection periods ( $\chi^2 = 23.5$ , df = 8, P = 0.003).

*P. hubrichti* comprised 57% (range 43-77%) of the salamanders found when recaptures were excluded and 61% (range 43-73%) when simple totals were calculated (i.e. recaptures included simulated a situation where salamanders were not marked) (Fig. 7). The cumulative percent for both situations, recaptures excluded and simple totals, changed 15% over the first 3 collection periods; however, over the remaining 6 collection periods the percent changed a maximum of 2% (Fig. 7). The number of salamanders collected per collection period for each species were homogeneous both when recaptures were excluded ( $\chi^2 = 10.9$ , df = 8, P = 0.21) or for simple totals for each species ( $\chi^2 = 8.7$ , df = 8, P = 0.37).

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. There was no significant difference between linear distances moved by the two species ( $U = 634.0$ ,  $P = 0.60$ ,  $N = 75$ ). The median distances moved were 0.71 m (IQR = 0.62 m,  $N = 44$ ) and 1 m (IQR = 1 m,  $N = 31$ ) for *P. hubrichti* and *P. cinereus*, respectively. The median home ranges were also not significantly different for the two species ( $U = 31$ ,  $P = 0.955$ ,  $N = 16$ ). Median home range size was 0.25 m<sup>2</sup> (IQR = 0.31 m<sup>2</sup>,  $N = 9$ ) and 0.13 m<sup>2</sup> (IQR = 0.88 m<sup>2</sup>,  $N = 7$ ) for *P. hubrichti* and *P. cinereus*, respectively.

For rocks originally occupied by *P. cinereus*, replacement by *P. hubrichti* was the most probable event across all gap periods (0, 1, 2) (Fig. 8). Finding the same individual was the second most likely event with 0 gaps; however with 1 gap it was more likely to find a different *P. cinereus*. Similarly, rocks originally occupied by a *P. hubrichti* were most likely occupied by a different *P. hubrichti* regardless of the gap (Fig. 9). Finding the same individual was the second most common occurrence regardless of the gap. There was not significant difference between the SVL's of the resident and replacement salamanders (resident *P. hubrichti* and replacement individuals of the same species,  $t = 0.835$ ,  $df = 50$ ,  $P = 0.408$ ; or replacement by *P. cinereus*,  $t = 1.096$ ,  $df = 27$ ,  $P = 0.283$ ; resident *P. cinereus* and replacement individuals of the same species,  $t = 1.186$ ,  $df = 12$ ,  $P = 0.259$ ) or replacement by *P. hubrichti*,  $t = -0.515$ ,  $df = 24$ ,  $P = 0.611$ ).

There was a significant effect of habitat on the probability of recapturing *P. hubrichti* ( $\chi^2 = 8.3$ ,  $df = 1$ ,  $P = 0.004$ ) and *P. cinereus* ( $\chi^2 = 18.1$ ,  $df = 1$ ,  $P < 0.001$ ). Sixty-one percent ( $N = 39$ ) of *P. hubrichti* and 72% ( $N = 23$ ) of *P. cinereus* captured beneath rocks were recaptured while no individuals were captured more than once in leaf litter.



*P. hubrichti* neonates captured in August 2005 were larger (median SVL = 16.5 mm) than *P. cinereus* (median SVL = 14.0;  $U = 43.5$ ,  $P = 0.008$ ,  $N = 29$ ). Neonates grew from August through October at a rate of 0.041 mm/day (0.020-0.062 mm/day, 95% CI) and 0.051 mm/day (0.035-0.073 mm/day, 95% CI) for *P. hubrichti* and *P. cinereus*, respectively. This size difference was maintained throughout the fall (ANCOVA  $F = 13.4$ ,  $df = 1$ ,  $64$ ,  $P = 0.001$ ). The 2004 cohort grew at a rate of 0.079 mm/day (*P. hubrichti*) and 0.078 mm/day (*P. cinereus*). There was no significant difference between the growth rates (ANCOVA  $F = 0.12$ ,  $df = 1$ ,  $238$ ,  $P = 0.73$ ). Growth rates of individuals in the 2003 or older cohort declined significantly as their SVL increased (*P. hubrichti* growth rate (mm/day) = 0.117-0.0022 (SVL, mm),  $r^2 = 0.74$ ,  $t$  for slope = 6.1,  $df = 13$ ,  $P < 0.001$ ; *P. cinereus* growth rate (mm/day) = 0.186-0.0040 (SVL, mm),  $r^2 = 0.66$ ,  $t$  for slope = 4.6,  $df = 11$ ,  $P < 0.001$ ). While the slopes were not significantly different ( $F = 3.56$ ,  $df = 1$ ,  $24$ ,  $P = 0.7$ ; Fig. 10), the more gradual decline in the growth rates of *P. hubrichti* relative to *P. cinereus* translated into a larger size late in the season (Sep. – Oct.) for *P. hubrichti* (median = 48 mm, SVL) as compared to *P. cinereus* (median = 45 mm, SVL) ( $U = 408.5$ ,  $P = 0.006$ ,  $N = 73$ ).

There was no significant difference in the condition of *P. hubrichti* found on our sympatric site ( $N = 103$ ) and those in other allopatric areas ( $N = 47$ ) ( $t = -1.01$ ,  $P = 0.31$ ,  $df = 148$ ). Similarly there was no significant difference in the condition of *P. cinereus* found on our sympatric site ( $N = 67$ ) and the other allopatric area ( $N = 42$ ) ( $t = 0.53$ ,  $P = 0.59$ ,  $df = 65$ ). There was no significant difference in the SVL of *P. hubrichti* found on the allopatric sites (median = 48 mm) and *P. hubrichti* on our sympatric site (median = 48 mm) ( $U = 510$ ,  $P = 0.767$ ,  $N = 67$ ). However, there was a significant difference in SVL

between allopatric *P. cinereus* (median = 42 mm, N = 24) and *P. cinereus* on our sympatric site (median = 45 mm, N = 32; U = 231, P = 0.011, N = 56).

## Discussion

### *General Salamander Biology*

The number of salamanders collected at the surface was affected by the extent of the dryness prior to a collection event. This has been noted for *P. hubrichti* (Kramer et al., 1993), and Kleeberger and Werner (1982) found a significant correlation between horizontal movement and precipitation amount for *P. cinereus*. However, Jaeger (1980) did not see a correlation between surface density of *P. cinereus* and rainfall; there was no change in the above-ground density even over seven-day periods without rain.

Salamanders forage at the surface when there is adequate moisture available (Feder, 1983) because prey are more abundant at the surface relative to underground areas (Fraser, 1976a). During dry periods, salamanders may first move to surface refuges such as rocks and logs but will eventually move underground as the surface dries (Heatwole, 1962; Heatwole and Lim, 1961; Taub, 1961; Fraser, 1976a). While unable to burrow in some substrates, *P. cinereus* readily enlarges existing holes and crevices and burrows in humus where solid objects are present (Heatwole 1960). They remain underground until the surface conditions are adequate for above ground foraging.

Our data suggest that the longer the salamanders remain underground, the greater the number found at the surface when the conditions become favorable. The vertical movement appears largely governed by rainfall. When it rains, the animals re-emerge onto the surface typically at night and then forage, often on vegetation (Kramer, et al., 1993; Jaeger 1978). Upon re-emergence, do salamanders occupy the same rock they left

prior to their vertical migration? Salamanders are known to have homing ability (Madison and Shoop, 1979; Kleeberger and Werner, 1982) and they remain in the same general area (this study; Kleeberger and Werner, 1982; Gergits and Jaeger, 1990; Mathis, 1991; Kramer, et al., 1993). Salamanders are also known to mark their territories with fecal pellets and other pheromonal markers (Jaeger and Gergits, 1979; Jaeger et al., 1986). Under field conditions, these markers might regularly be removed by heavy rainfall and/or through decomposition. Our data suggest that salamanders move vertically when the surface becomes too dry and then re-emerge onto the surface in the same general vicinity (i.e. their home range) they were in before. After foraging, and if the conditions are moist enough, they remain at the surface, typically under a cover object such as a rock. That rock may well be unoccupied versus occupied and hence requiring removal of a resident as the SVLs of our new residents were not significantly different from the original residents. This type of dynamic might produce the regular shuffling of animals we observed under rocks (Figs. 8 and 9) which could result from vertical migrations and losses of territory markers due possibly to rainfall.

Adult salamanders found in leaf litter may involve a different dynamic more difficult to discern than that of salamanders occupying rocks. The lack of recaptured adults in the leaf litter compared with those captured beneath rocks might be explained 3 different ways: 1) these individuals are transients or floaters which do not hold territories (Mathis, 1991) and are looking for habitable unoccupied rocks which may take them out of our collection area, 2) they use burrows or otherwise move vertically (Taub, 1961; Fraser, 1976a) on a more frequent basis than those using rocks and hence are less likely to be found at the surface during the day, and/or 3) they have higher mortality rates

compared to residents of rocks because they are more vulnerable to predators and individuals not holding territories are less likely to forage in optimal manner (Jaeger et al., 1981).

*P. hubrichti* and *P. cinereus* Niche Comparisons

*P. hubrichti* appears very similar to *P. cinereus* with regard to 1) habitat use – small salamanders of both species are primarily found in the leaf litter and then as they increase in size, they shift to primarily occupying rocks, though *P. hubrichti* starts this process at a smaller size relative to *P. cinereus*, 2) reproductive biology – including the number of eggs laid (approximately 10 eggs, data limited for *P. hubrichti*), female brooding behavior (Highton and Savage, 1961), and hatching time (late July, early August), 3) movement patterns – median linear distances moved (0.71 m, *P. hubrichti*; 1.0 m *P. cinereus*) and median home range size (0.25 m<sup>2</sup>, *P. hubrichti*; 0.13 m<sup>2</sup>, *P. cinereus*), and 4) adult survival rates (0.993, *P. hubrichti*; 0.998, *P. cinereus*). Where data are available for allopatric *P. hubrichti* (Kramer, et al, 1993), there do not appear to be any major differences in median linear distance moved (1.0 m) and home range (0.6 m<sup>2</sup>). *P. hubrichti* neonates are larger than *P. cinereus* and the size differential is still noted as adults (median SVL = 48 mm, *P. hubrichti*; 45 mm, *P. cinereus*). The ecological impact of this size difference or that *P. cinereus* is significantly larger in sympatry vs. allopatry while *P. hubrichti* is similar in size both in allopatry and sympatry is unclear. Fraser (1976b) examined two sympatric populations of similar species (*P. hoffmani* and *P. punctatus*) also of dissimilar size and concluded that because life history stages overlap, size alone was unlikely to reduce interspecific competition for food or space. *P. hubrichti* appears to have depressed growth rates and adult densities in

sympatry. *P. hubrichti* in allopatry have recorded growth ranging from 0.08 to 0.11 mm/day for salamanders with SVLs of 31-40 mm and 41-50 mm, respectively. Adult densities in allopatry ranged from 1.6 to 3.3 *P. hubrichti*/m<sup>2</sup> (Kramer et al., 1993; Sattler and Reichenbach, 1998) while in sympatry they were 0.57/m<sup>2</sup>. For *P. cinereus*, the density information could not be compared because of dissimilar data and population estimation methods for assessing densities. The overall similarity between the species is considered to be reflected in comparable competitive status (Wicknick, 1995) which Jaeger (2002) hypothesized would result in a stable contact zone. While densities and growth rates of *P. hubrichti* appear to be depressed in the contact zone, this zone may be static.

The range of *P. cinereus* is not restricted by elevation as the highest elevation in *P. hubrichti*'s distribution (elevation = 1280 m) has a ratio of 0.3 *P. hubrichti* to 1 *P. cinereus* (unpublished data). However, little data have been collected on the effect of climate on the distribution *P. hubrichti*. While definite conclusions were not reached, Thurow (1957) found that *P. cinereus* appeared more resistant to increased temperatures and evaporation rates than *P. hubrichti*. In a similar situation, Hariston (1951) found that climate factors likely restricted the downward (elevation) distribution of *P. jordani* while the upward distribution of *P. glutinosus* was in some way restricted by *P. jordani*. If *P. hubrichti* is restricted by climate, a similar situation may result where the extent of *P. hubrichti*'s range is restricted by climate and it is in some way able to keep *P. cinereus* from entering its range.

#### *Monitoring the Contact Zone*

Ratios of the two species could be used to determine if the contact zone is static.

Ratios at our site favor *P. hubrichti* (61% of total captured); but sites in areas further northeast favor *P. cinereus* (unpublished data). Monitoring the perimeter of *P. hubrichti*'s range, to see if *P. cinereus* is encroaching on *P. hubrichti*, should be done at a selected network of sites where trends in the ratio of the two species would be evaluated over time. While one sample per site could be used to characterize the ratio of these species, ideally three samples per site should be collected in order for the cumulative ratio to stabilize. In addition, marking salamanders would not be necessary (Results - this study).

Limited data in three locations (one allopatric *P. hubrichti*, one allopatric *P. cinereus* and one sympatric site), with one sample taken per location in 1993 (Wicknick, 1995) and then again in 2003 (Aasen and Reichenbach, 2004) indicated the proportions of *P. hubrichti* relative to *P. cinereus* at the one sympatric site were not significantly different over the 10 year time period. This site was located in the primary conservation area for *P. hubrichti* where timbering is not permitted (George Washington and Jefferson National Forests, U.S. Fish and Wildlife Service, Blue Ridge Parkway, 1997). However, large portions of the contact zone between these species is not located in the primary conservation area, but rather in the secondary conservation area where mild forms of timbering, such as shelterwood cuts, are permitted in the National Forest and any form of timbering is permitted on private property. While shelterwood cuts had only minor short-term effects on juvenile age classes of *P. hubrichti*, clearcuts had significant adverse impacts on *P. hubrichti* populations (Sattler and Reichenbach, 1998). Timbering, especially clear cuts, would likely cause an increase in temperature and decrease in moisture of the forest floor. If *P. hubrichti* is restricted by climate, any timbering in the

contact zone would likely favor *P. cinereus* as this species appears more resistant to increased temperatures and evaporation rates (Thurow, 1957) and occurs over a much broader range of environmental conditions.

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Figure Legends

*Figure 1.* Cloacal regions of *P. hubrichti* in reproductive condition. a) Male characterized by “football shaped” vent opening and light areas along the sides of the vent and b) female characterized by a narrow vent slit and no light areas along the sides of the vent.

*Figure 2.* Size distribution (SVL) and cohort assignment for *P. hubrichti* collected.

*Figure 3.* An egg mass of *P. hubrichti* (a) showing eggs suspended in a small cavity beneath a rock May 26, 2005 (rock removed). (b) Neonate hatchlings clustered around remains of the same egg mass July 30, 2005.

*Figure 4.* Size distribution and cohort assignment for *P. cinereus* collected.

*Figure 5.* Habitat location of salamanders captured spring/midsummer (May – July) according to cohort (2002 and older, 2003, 2004); (a) *P. hubrichti*, and (b) *P. cinereus*.

*Figure 6.* Habitat location of salamanders captured late summer/fall (Aug. – Oct.) according to cohort (2003 and older, 2004, 2005); (a) *P. hubrichti*, and (b) *P. cinereus*.

*Figure 7.* Cumulative fraction *P. hubrichti* of total collected. Solid line represents ratio including all individuals collected; dashed line represents ratio including only new (unmarked) individuals.

*Figure 8.* Probability of next capture for rocks previously occupied by *P. cinereus*. Gaps represent collection periods where the rock was unoccupied (mean gap 19 days, range 6 – 42 days; N = 46). *P. cinereus* to same *P. cinereus* (pc – pcs); *P. cinereus* to different *P. cinereus* (pc – pcd); *P. cinereus* to *P. hubrichti* (pc – ph).

*Figure 9.* Probability of next capture for rocks previously occupied by *P. hubrichti*. Gaps represent collection periods where the rock was unoccupied (mean gap 19 days,

range 6 – 42 days; N = 90). *P. hubrichti* to same *P. hubrichti* (ph – phs); *P. hubrichti* to different *P. hubrichti* (ph – phd); *P. hubrichti* to *P. cinereus* (ph – pc).

*Figure 10.* Growth rates in relation to SVL. *P. hubrichti*, closed bullets and solid line (N = 15); *P. cinereus*, open bullets and dashed line (N = 13).



Figure 1.

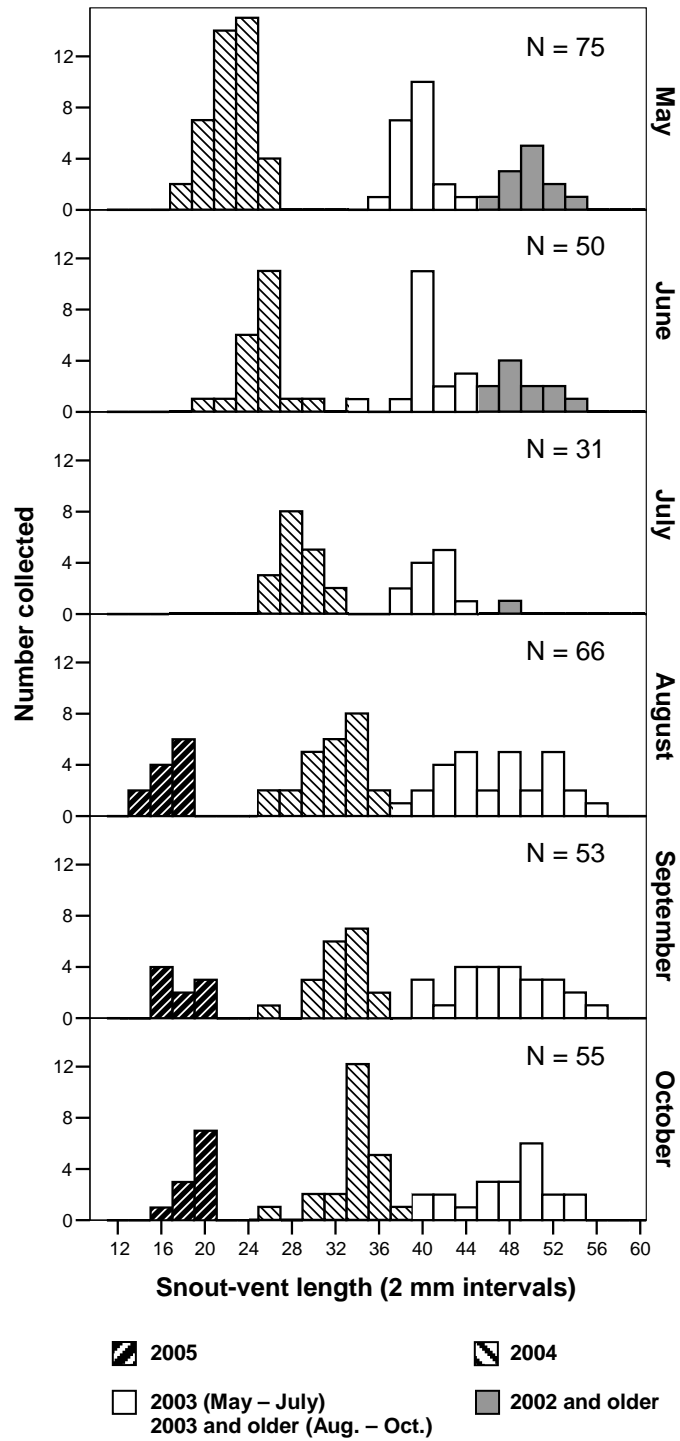


Figure 2.



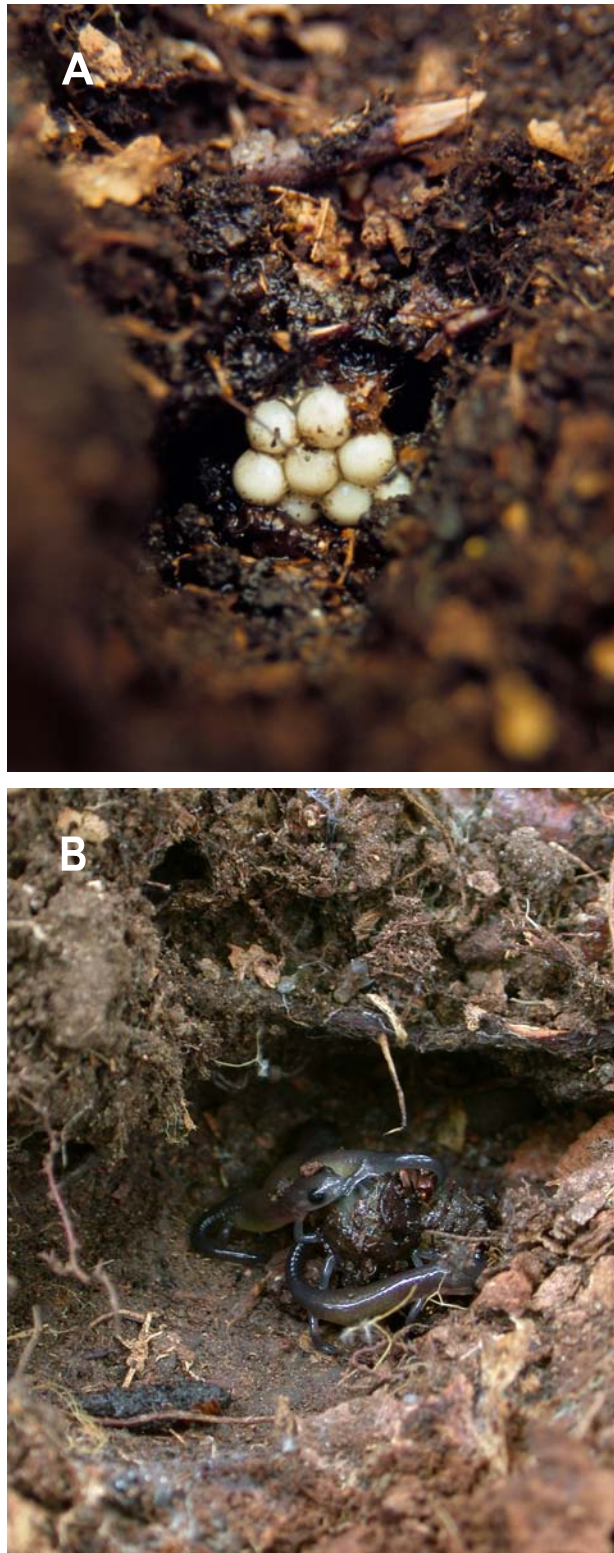


Figure 3.

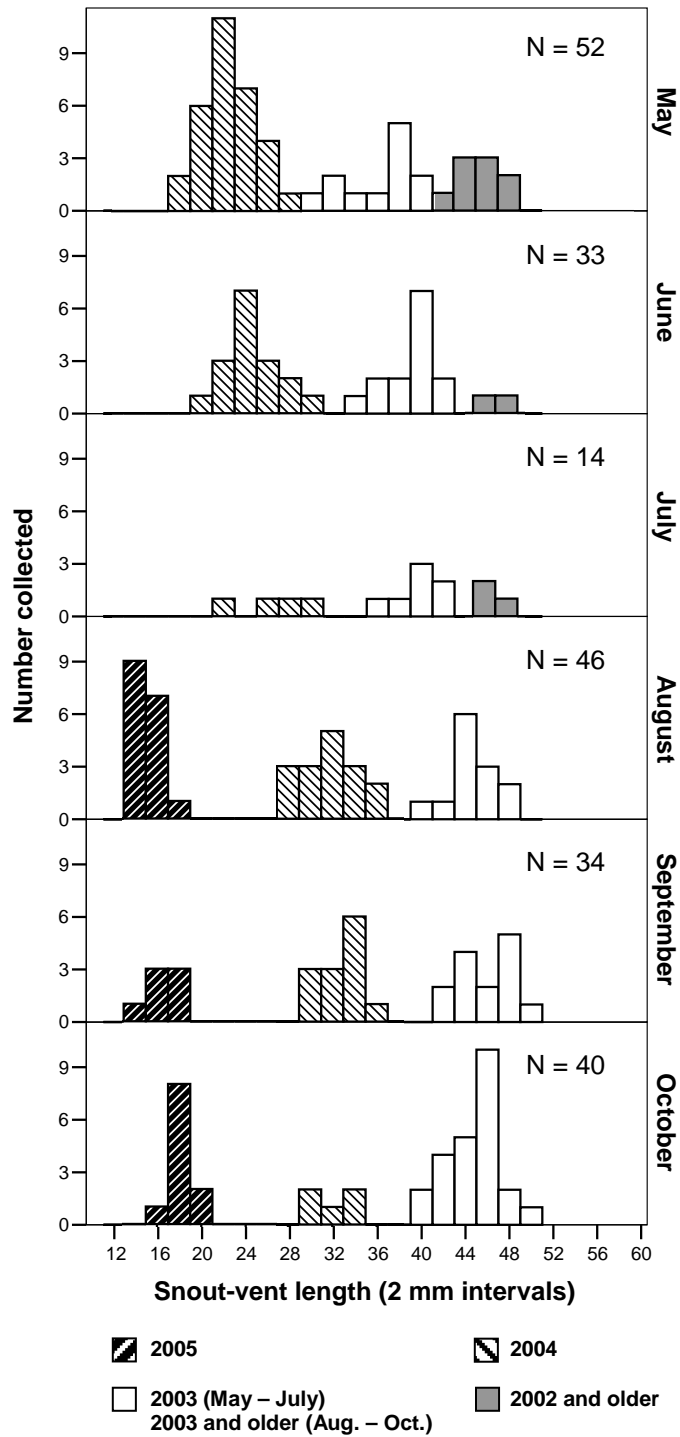


Figure 4.

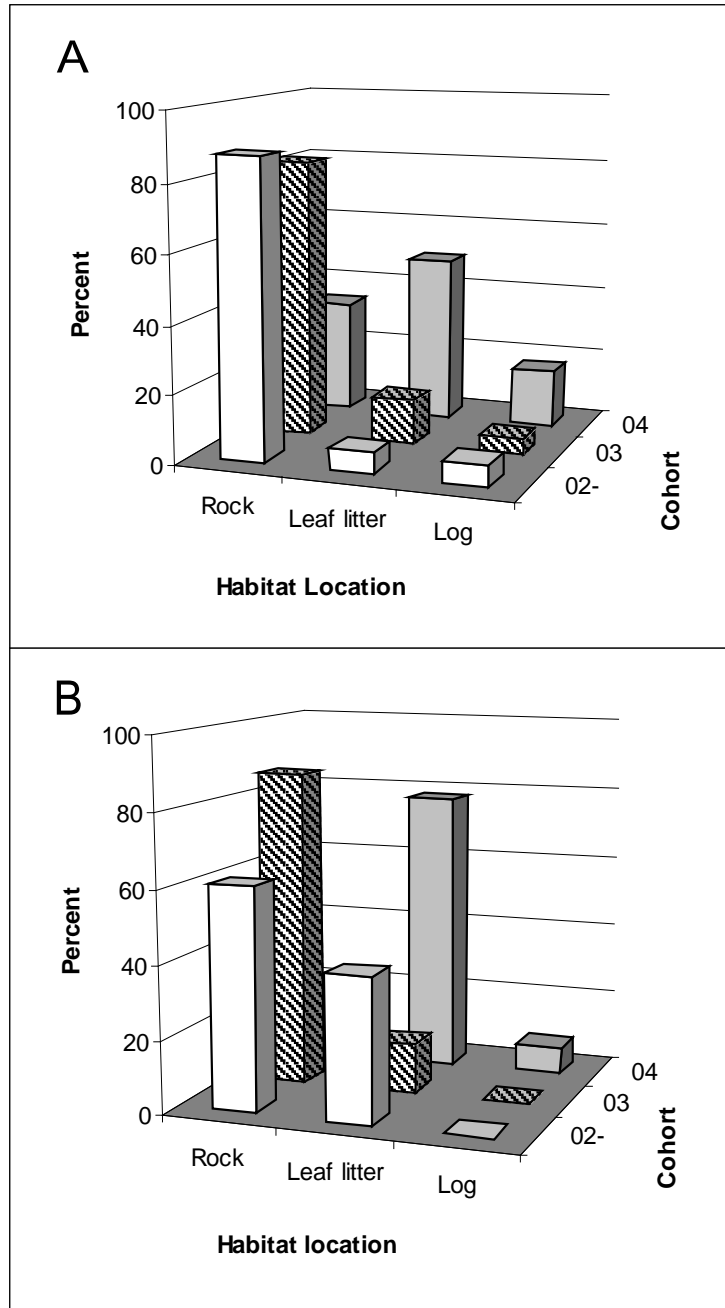


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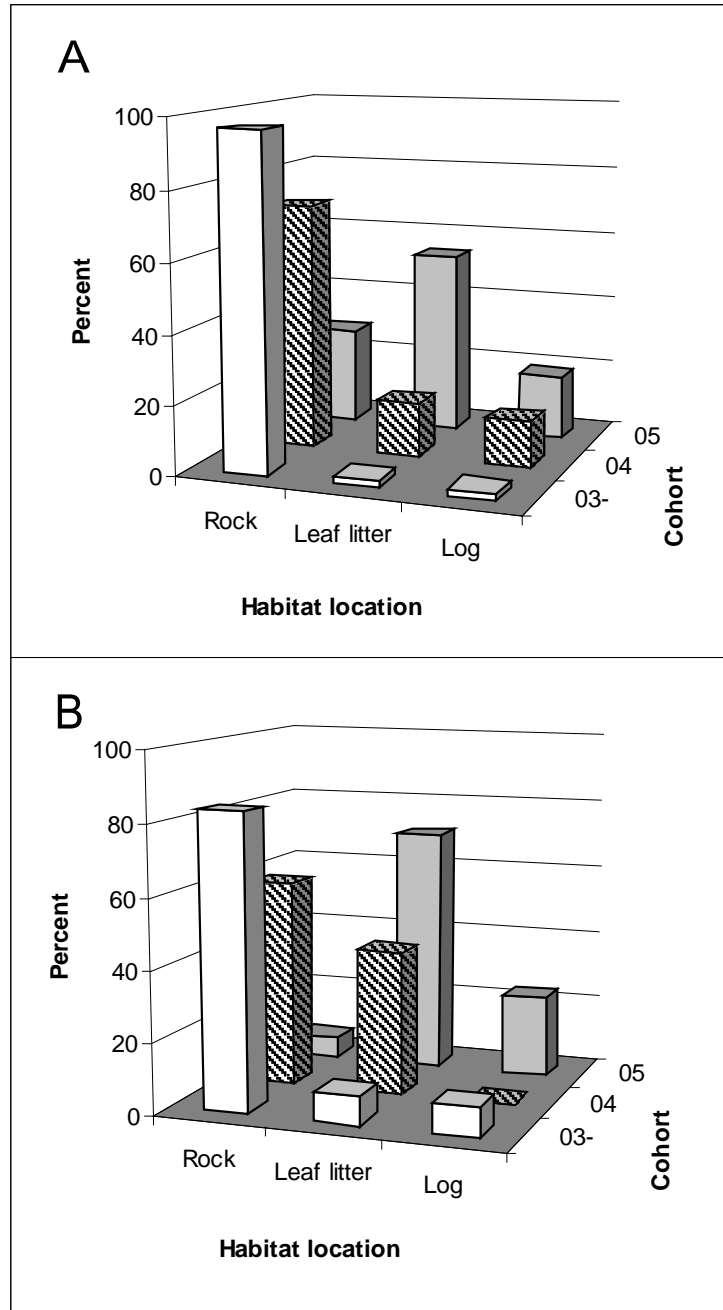


Figure 6.

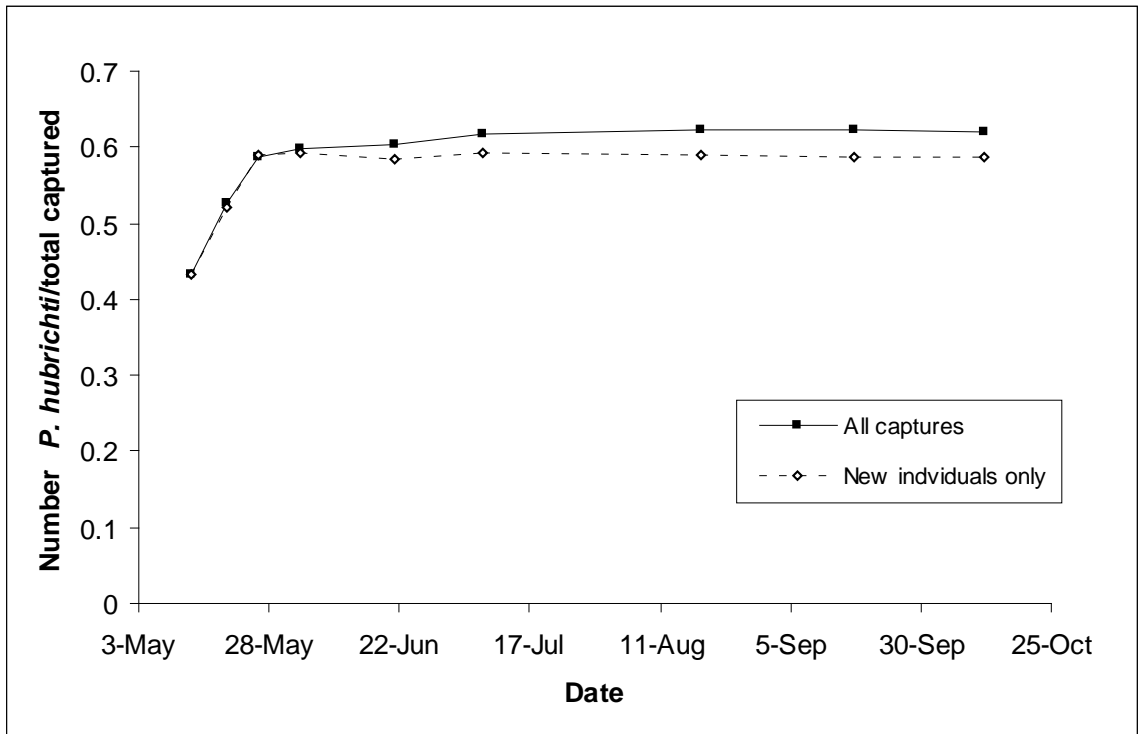


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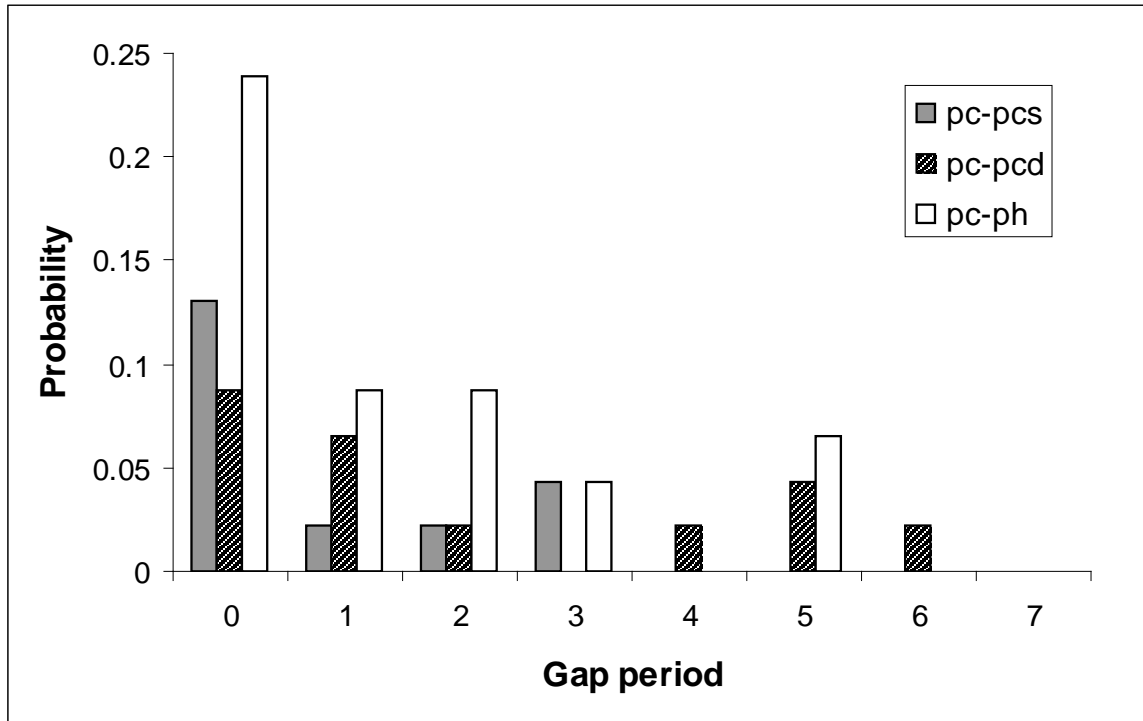


Figure 8.

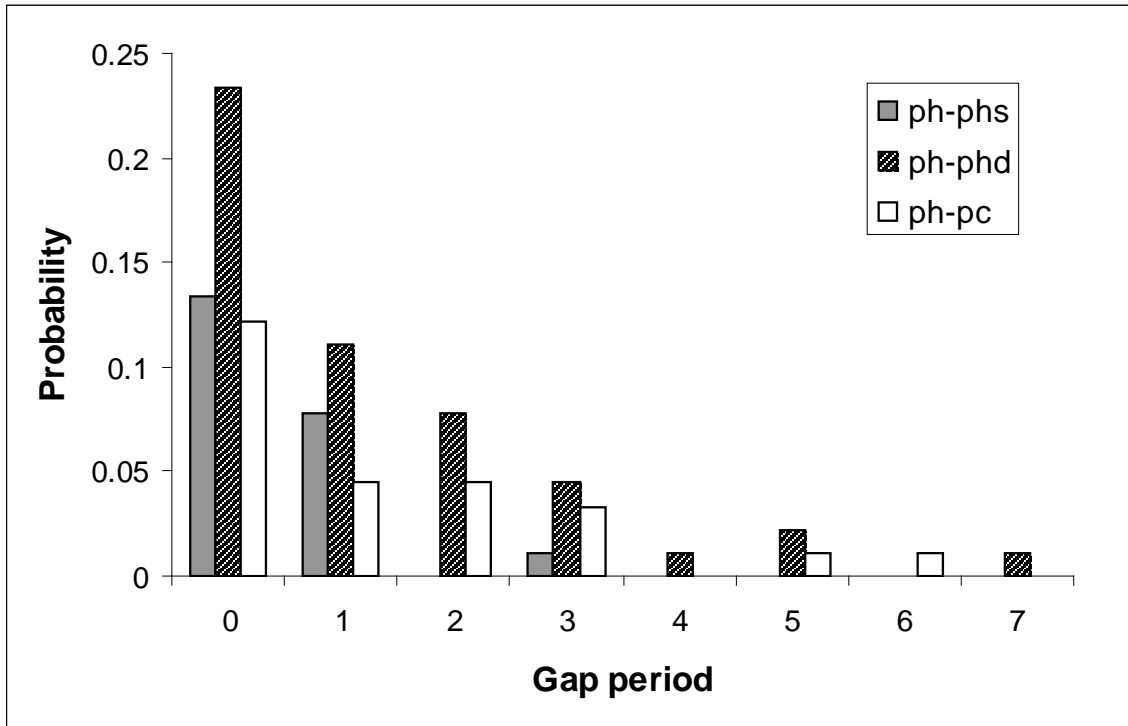


Figure 9.

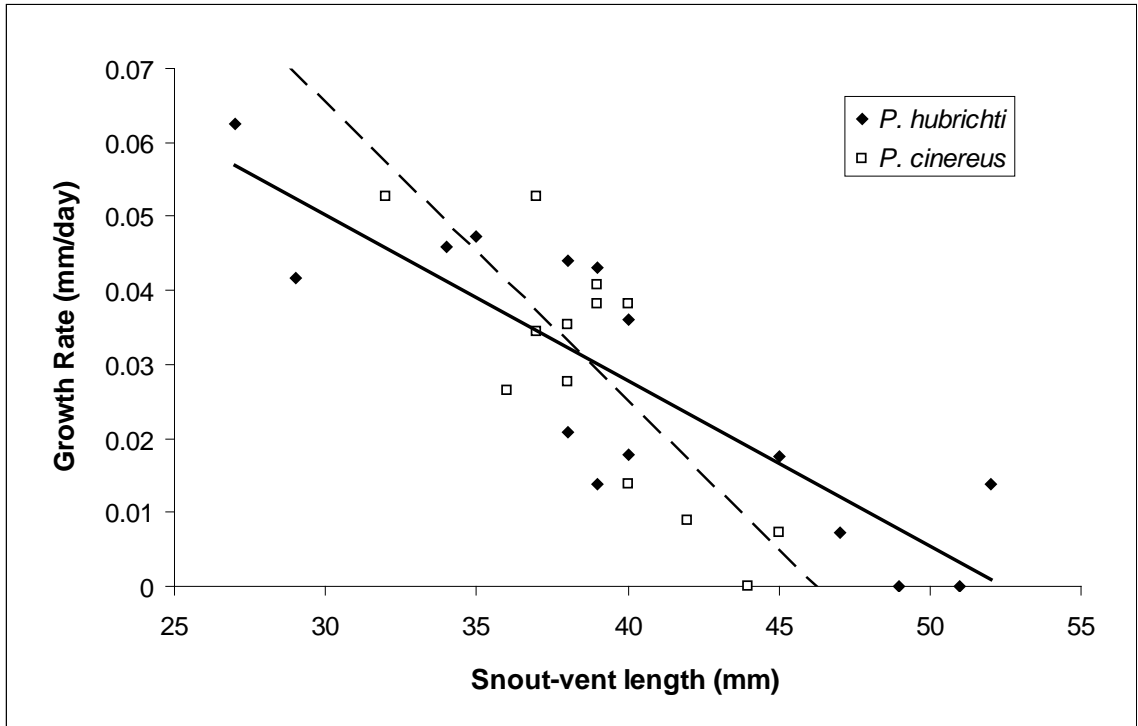


Figure 10.