

000435

FOOD AS A LIMITED RESOURCE IN COMPETITION BETWEEN TWO SPECIES OF TERRESTRIAL SALAMANDERS¹

ROBERT G. JAEGER²

Department of Zoology, University of Maryland, College Park

Abstract. The terrestrial salamander *Plethodon richmondi shenandoah* occurs primarily in areas of talus, apparently excluded from surrounding areas of deep soil by *Plethodon cinereus*. Although the two species are closely related, *P. r. shenandoah* grows to a longer body length and has a broader head. All age classes of *P. r. shenandoah* emigrate out of the talus and are found within 3 m of the talus edge, but only adults which are as large as or larger than the largest *P. cinereus* are able to survive farther than about 3 m from the talus. This distribution is not explained by a tendency for large adults to wander more than juveniles. The large *P. r. shenandoah* in the soil take prey that are significantly larger than prey taken by cohabiting *P. cinereus*, indicating that food may be the limited resource for which competition occurs. Both species are euryphagic and prey upon the same taxa of small animals. Food is periodically limited in availability, but not in abundance. Following a rain, salamanders forage freely and consume a large quantity of prey, based on stomach contents, but prey become increasingly unavailable as the soil and leaf litter dry and the salamanders are restricted to isolated pockets of moisture. Stomachs remain virtually empty until the next rain, at which time they are full again indicating that the abundance of prey is not greatly affected by the intervening dryness. Food may periodically become a limited resource during long dry seasons and as such may affect the survival of the salamanders or their ability to produce eggs.

It is not clear whether interspecific competition is through differential exploitation of the limited resource or through interference. Lack of evidence for interspecific aggression may indicate that the former occurs, although it could not be demonstrated experimentally. Contiguous allopatry between the two species seems to result from an interaction of competitive exclusion and differential tolerance to dryness; *P. cinereus* is presumably a superior competitor for food in the soil and excludes *P. r. shenandoah* to areas of talus which *P. cinereus* cannot enter due to its intolerance of drier conditions in the rocks.

Although there is no universally accepted definition of competitive exclusion, many workers now agree that several factors are involved (Crombie 1947, Morse 1967, Miller 1967, Jaeger 1971a). In a competitive interaction between two species, (1) one species eliminates the other from a habitat due to (2) competition for a vital resource that is (3) jointly utilized by the two species and is (4) in short supply (5) either in abundance or availability to the species. Also of importance are (6) whether the resource is consistently or periodically in short supply, and (7) whether the interspecific competition involved is through interference or exploitation, as discussed by Miller (1969).

In my study of the terrestrial plethodontid salamanders *Plethodon cinereus* and *Plethodon richmondi shenandoah* (redefined as *P. nettingi shenandoah* by Highton 1971), I concluded that competitive exclusion and environmental tolerances of the species interact to delimit their largely allopatric but contiguous distributions. The distributions of the two species (Jaeger 1970) suggest that *shenandoah* is primarily limited to areas of talus slopes due to the presence of *cinereus* in surrounding areas of soil and that the situation is an unstable one, since *cinereus*

is, apparently, still displacing *shenandoah*. *Plethodon cinereus* does not enter the talus due to the dry conditions there, but *shenandoah*, which is more tolerant of the dryness, does not seem to be excluded from the soil due to any discernible intolerance of the physical environment (Jaeger 1971b). Enclosure experiments (Jaeger 1971a) indicate that *Shenandoah's* virtual exclusion from areas of soil outside the talus is due to competitive exclusion by *cinereus*, which is abundant in that habitat. In this paper I shall suggest that food could be a limited resource in this interspecific competition and discuss its relevance to the seven aspects of competitive exclusion enumerated above.

METHODS AND RESULTS

Relationship of body size to distribution

Procedure.—Salamanders were collected on Hawksbill Mountain, Page County, Virginia, by turning rocks and logs and raking leaves, and all specimens found were taken regardless of size. The position of capture of each specimen was plotted on a map of the northeast-facing slope of Hawksbill Mountain in relation to the edge of the talus. Thus, it was later possible to determine whether a particular specimen had been collected inside the talus, in the soil outside the talus but within 3 m of the talus edge, or more than 3 m outside the talus. The salamanders were

¹ Received September 2, 1971; accepted November 26, 1971.

² Present address: Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706.

brought to the laboratory alive and preserved by fixing in 10% formaldehyde for 24 hr, rinsing in water for 24 hr and storing in 65% ethyl alcohol. Body lengths were determined by measuring ventrally from tip of snout to the anterior end of the vent. Head widths were measured directly posterior to the eyes.

Findings.—A comparison of 284 *P. r. shenandoah* and 485 *P. cinereus* shows that for any given body length, *shenandoah* tends to have a greater head width than does *cinereus* (Fig. 1). Also, the former species reaches a 15% greater body length (maximum of 53 mm) than the latter (maximum of 45 mm). An analysis of the distributions of 321 *shenandoah* and 672 *cinereus* (Fig. 2) demonstrates

that while the majority of the former species occurs within the talus, a significant number coexists with *cinereus* in the soil. While collecting was performed up to 150 m from the talus edge, *shenandoah* was located only out to a distance of 80 m from the talus. On the other hand, proportionally few *cinereus* enter the talus, and of all those found there, none was more than a few meters inside the talus edge.

An interesting distribution of body sizes is evident when the *shenandoah* population is partitioned into three microgeographic groups: those inside the talus, those < 3 m outside the talus and those > 3 m outside the talus. The specimens collected from within the talus do not differ in body length or head width significantly by two-tailed t-tests (Table 1) from

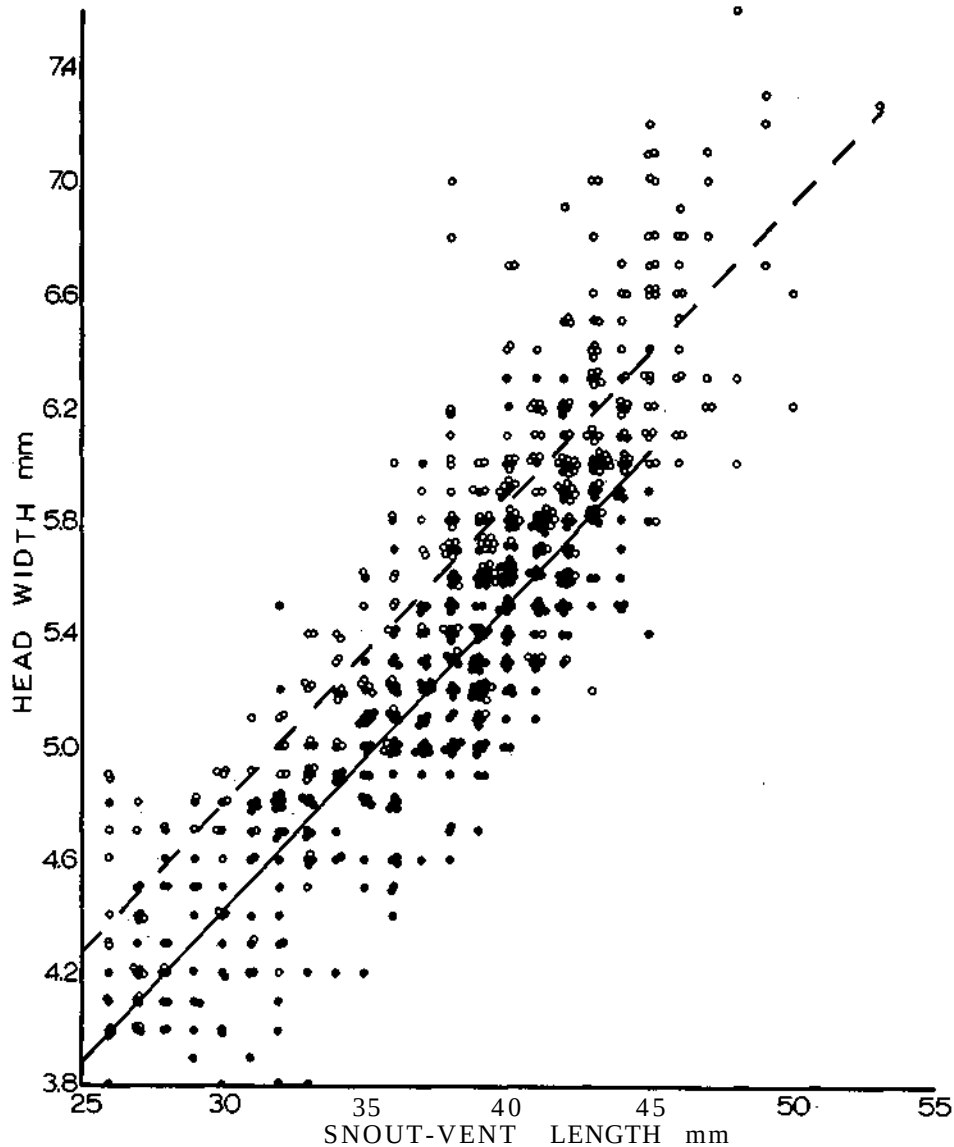


FIG. 1. Regression lines comparing snout-vent lengths and head widths of *P. cinereus* (solid line, solid circles) and *P. r. shenandoah* (dashed line, hollow circles). The maximum length of each species is indicated.

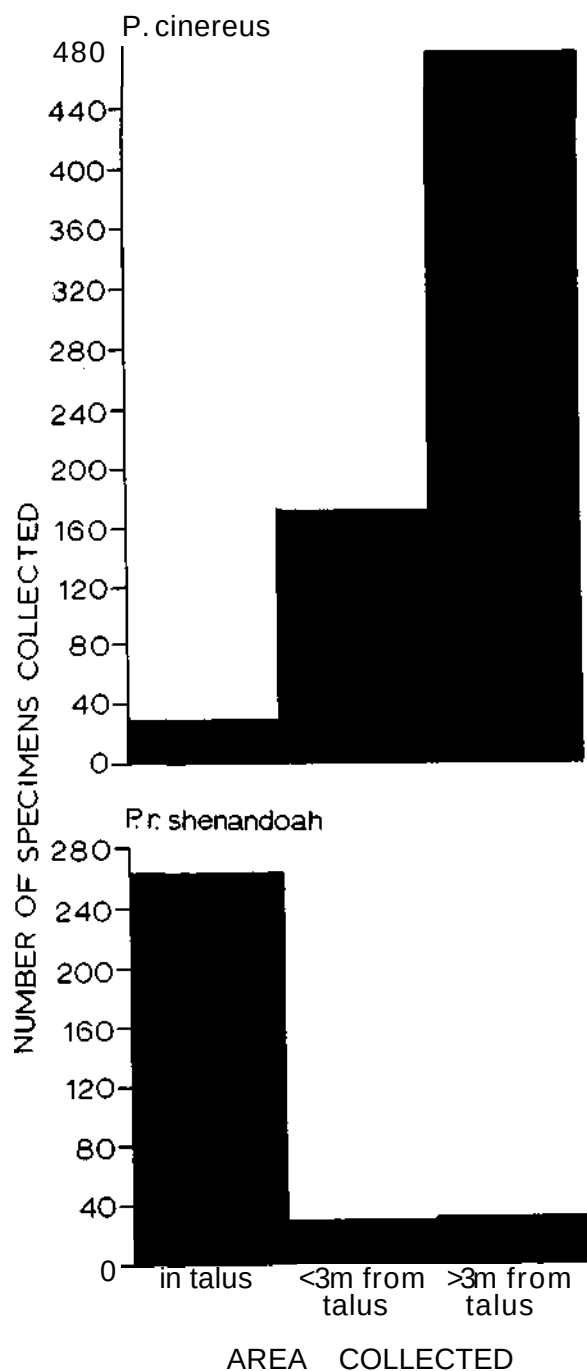


FIG. 2. Number of *P. cinereus* (top) and *P. r. shenandoah* (bottom) collected in the talus, from the talus edge to 3 m outside the talus, and > 3 m outside the talus.

either *cinereus* or conspecifics collected < 3 m outside the talus edge. Also, the *shenandoah* < 3 m outside the talus do not differ significantly from *cinereus* (Fig. 3, Fig. 4). However, those *shenandoah* collected from > 3 m outside the talus edge do differ significantly in both body length and head width from conspecifics within the talus, from conspecifics < 3

TABLE 1. Results of t-tests for snout-vent lengths and for head widths of *P. cinereus* and *P. r. shenandoah*

Comparison of	Snout-vent lengths		Head widths	
	t	P	t	P
<i>shenandoah</i> > 3 m & < 3 m				
from talus edge	3.1	< 0.01 *	3.4	< 0.01 *
<i>shenandoah</i> > 3 m from talus edge and in talus	3.5	< 0.01 *	3.0	< 0.01 »
<i>shenandoah</i> > 3 m from talus & <i>cinereus</i>	5.7	< 0.01 *	7.1	< 0.01 *
<i>shenandoah</i> < 3 m from talus edge and in talus	0.03	> 0.5	1.6	0.1 < P < 0.2
<i>shenandoah</i> < 3 m from talus & <i>cinereus</i>	1.3	0.2	1.4	0.1 < P < 0.2
<i>shenandoah</i> in talus & <i>cinereus</i>	0.2	> 0.5	0.4	> 0.5

*Indicates values at the 5 % level of significance or less.

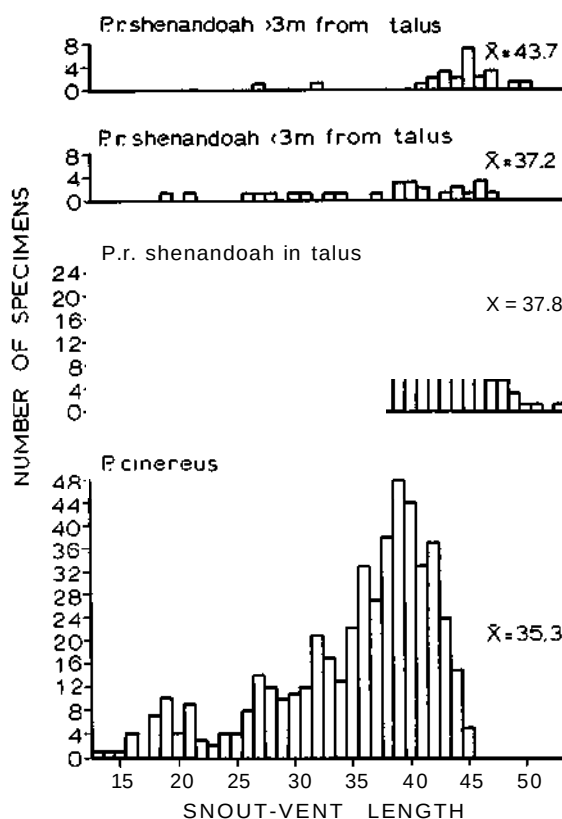


FIG. 3. The number of *P. r. shenandoah* of given snout-vent lengths found (1) > 3 m outside the talus, (2) < 3 m from the talus, (3) in the talus, and (4) the total number of *P. cinereus* of given snout-vent lengths collected. Mean snout-vent length for each group is given.

m from the talus, and from *cinereus*. Consequently, while only 23.1% of the *cinereus* comprise the largest size range for that species (41-45 mm body length), 62.5% of the *shenandoah* caught > 3 m from the talus fall within that size range. Only 23.1% and 34.4% of the *shenandoah* found < 3 m from the talus and in the talus, respectively, are 41-45 mm in length. Considering body lengths beyond the max-

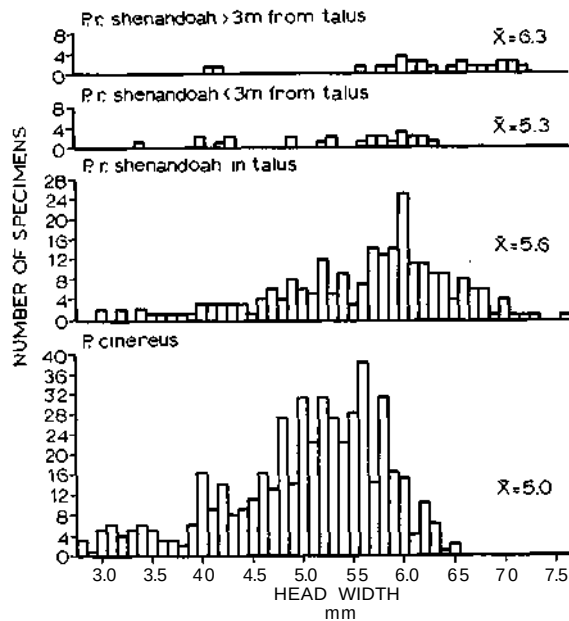


FIG. 4. The number of *P. r. shenandoah* of given head widths found (1) >3 m outside the talus, (2) <3 m from the talus, (3) in the talus, and (4) the total number of *P. cinereus* of given head widths collected. Mean head width for each group is given.

imum size of *cinereus* (46+ mm), 29.2% of the *shenandoah* > 3 m from the talus fall in this range. Thus, 91.7% of the *shenandoah* found > 3 m from the talus are as large as or larger than the longest *cinereus* with which they coexist.

Movements of *P. r. shenandoah*

Two hypotheses can be proposed to explain the coexistence of only very large *shenandoah* with *cinereus* in the soil more than 3 m outside the talus: (1) it is the result of some interspecific interaction with *cinereus*, or (2) large adult *shenandoah* tend to wander more than smaller individuals and, thus, independent of the presence of *cinereus* are found farther outside the talus. Laboratory observations were performed to test the latter hypothesis.

Procedure.—Ten aquaria, 75 cm long by 30 cm wide by 28 cm deep, were arranged in a refrigerator

at 17°C with a day-night lighting based on the normal day length for the time of year (September). Each aquarium contained 7 cm of damp, crushed quartz and 16 glass tubes (artificial burrows) sunk at a 45° angle into the quartz. Each tube was 60 by 13 mm and was encased in a second tube 60 by 15 mm, so that the inner tube could be removed to check for the presence of a salamander without disturbing the animal. The 16 burrows were arranged in two rows of eight each along the length of each aquarium such that each burrow was at the center of a rectangle 9.3 by 15 cm. Into each of five aquaria was placed a *shenandoah* of at least 40 mm snout-vent length while into each of the remaining five aquaria was placed a conspecific of no more than 30 mm. The positions of the salamanders were recorded at 30-min intervals grouped into periods alternating between day and night for 24 days, such that 200 observations were made per animal.

Findings.—In Table 2, the number of moves per 100 hr means that the salamander was found to have changed position in the aquarium a given number of times during the 200 observations. The distance of moves is the sum of straight-line measurements of the distance between the position of a salamander at one observation and its position at a subsequent time. Two-tailed Mann-Whitney U-tests indicate that juveniles and adults did not differ significantly in either the number of moves ($U = 5$, $P = 0.150$) or in the distance of moves ($U = 7$, $P = 0.310$).

Types and sizes of prey utilized by the two species

Procedure.—Salamanders were collected as previously described, but those obtained for stomach analysis were placed in 10% formaldehyde in the field directly after being captured and after incisions were made in their sides so that the stomach contents would fix rapidly. Prey from the stomachs were measured under a binocular dissecting microscope fitted with an ocular micrometer calibrated to 0.1 mm. Prey were counted and measured only if their bodies were still intact, implying that they had been recently ingested. Prey lengths were measured from head to the extreme posterior end and widths were taken at the broadest point of the body. All of the salamanders'

TABLE 2. Movements of juvenile and adult *P. r. shenandoah*

S-V length (mm)	Juveniles		S-V length (mm)	Adults	
	No. of moves/100 hr	Distance (cm) of moves/100 hr		No. of moves/100 hr	Distance (cm) of moves/100 hr
29	16	291	42	2	47
30	38	847	43	45	960
30	18	447	43	11	292
27	16	252	40	6	92
30	17	303	40	7	119
Mean	21.0	428		14.2	302

TABLE 3. Prey found in the stomachs of *P. cinereus* and *P. r. shenandoah*

Prey	<i>P. cinereus</i>		<i>P. r. shenandoah</i>	
	No. of prey	% of prey	No. of prey	% of prey
Insecta				
Diptera	28	2%	5	2%
Coleoptera	57	4%	16	8%
Homoptera	188	12%	2	1%
Hemiptera	20	1%	6	3%
Lepidoptera	3	0% ^a	2	1%
Hymenoptera	35	2%	14	7%
Isopoda	18	1%	5	2%
Collembola	21	1%	5	2%
Orthoptera	6	0%	1	0%
Larvae	452	28%	69	34%
Unidentified adults	45	3%	7	3%
Arachnoidea				
Araneae	30	2%	6	3%
Acarina	636	39%	45	22%
Chilopoda	16	1%	4	2%
Diplopoda	8	0%	5	2%
Gastropoda	22	1%	9	4%
Oligochaeta	0	—	1	0%
Unidentified eggs	29	2	4	2%
Total	1,614		206	

^aPercentages 0.5% or less are recorded as 0%; total absence, by a dash

stomachs were examined during August through October 1968.

Findings.—The types of prey consumed were estimated from 190 *cinereus* and 36 *shenandoah*, the latter taken entirely from within the talus. Both species appear to be euryphagic, although two or three taxa compose the bulk of their diets (Table 3). Homopterans, insect larvae, and mites formed 79% of the diet of *cinereus* while insect larvae and mites composed 56% of the diet of *shenandoah*. The lower percentage of homopterans in the stomachs of *shenandoah* probably reflects the scarcity or unavailability of this group in the talus, due to the paucity of herbaceous plants in that rocky habitat.

The salamanders are partitioned into three groups for comparison of sizes of prey taken: the entire *cinereus* sample, *shenandoah* found within the talus, and the few *shenandoah* collected more than 3 m outside the talus. Specimens of the latter species less than 3 m from the talus are not included due to the scarcity of animals available for stomach analysis. *Plethodon r. shenandoah* more than 3 m from the talus took significantly longer prey than either conspecifics in the talus or cohabiting *cinereus*, and *shenandoah* in the talus took significantly longer prey than *cinereus* (Fig. 5, Table 4). Since *shenandoah* specimens tend to have wider heads than *cinereus* of the same length, one would expect a difference in width of prey ingested by these two species in the above groups. Indeed, while *shenandoah* in the talus and > 3 m from the talus did not differ in width of prey, both differed significantly from *cinereus* (Fig. 6, Table 4). However, when stomachs are analyzed from salamanders of both species that are 41 mm or

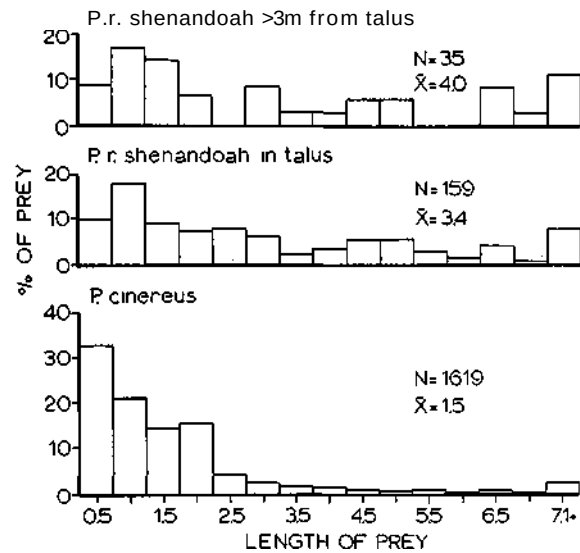


FIG. 5. Percentage of prey of various body lengths found in the stomachs of salamanders of all sizes. Body lengths are grouped in increments of 0.5 mm. Number and mean length of prey are given for each group of salamanders.

longer in snout-vent length (i.e., the largest members of both species), none of the three groups differ significantly among themselves (Table 4) in either length (Fig. 7) or width (Fig. 8) of prey taken. Thus, while the *shenandoah* that coexist with *cinereus* in the soil generally feed upon larger prey than those *cinereus*, comparably large adults of both species do not express a preference for different sizes of prey. Therefore, no foraging strategy exists that might lead to coexistence.

Food as a limited resource

Procedure.—The difference in sizes of prey ingested by *cinereus* and the large *shenandoah* in the soil outside the talus suggests that food may, at times, act as a limited resource. To test for this, *cinereus* was collected at Hawksbill Gap to determine the number of prey taken under various conditions of moisture. The forest floor was divided into a series of ecologically homologous plots and only one plot, chosen at random, was sampled per collecting day. Collections were made on 6 days in 1968 under three different conditions of moisture: dry soil (7 days since the last rain), damp soil (3 days post-rain) and wet soil (less than 1 day following a rain). The number of salamanders sampled for stomach contents was: dry soil of August 27 (26 salamanders), September 4 (25), and October 5 (25); damp soil on August 10 (51); wet soil on September 11 (29) and October 20 (33).

Findings.—The mean number of prey per salamander stomach was inversely proportional to the

TABLE 4. Results of Mann-Whitney U-tests for sizes of prey in the stomachs of *P. cinereus* and *P. r. shenandoah*

Size of salamanders	Samples compared	Prey length		Prey width	
		z^a	P	z^a	P
All body lengths	<i>shenandoah</i> > 3 m from talus	1.67	=0.05	0.02	=0.50
	& <i>shenandoah</i> in talus	4.91	< 0.001	4.64	< 0.001
	<i>shenandoah</i> > 3 m from talus & <i>cinereus</i>	8.34	< 0.001	3.14	< 0.001
41 mm or greater body lengths	<i>shenandoah</i> in talus & <i>cinereus</i>	0.60	0.27	1.16	0.12
	<i>shenandoah</i> > 3 m from talus	0.77	0.22	0.05	0.48
	& <i>shenandoah</i> in talus	1.62	>0.05	1.30	0.10

^aValues of z are derived from V since samples are large.

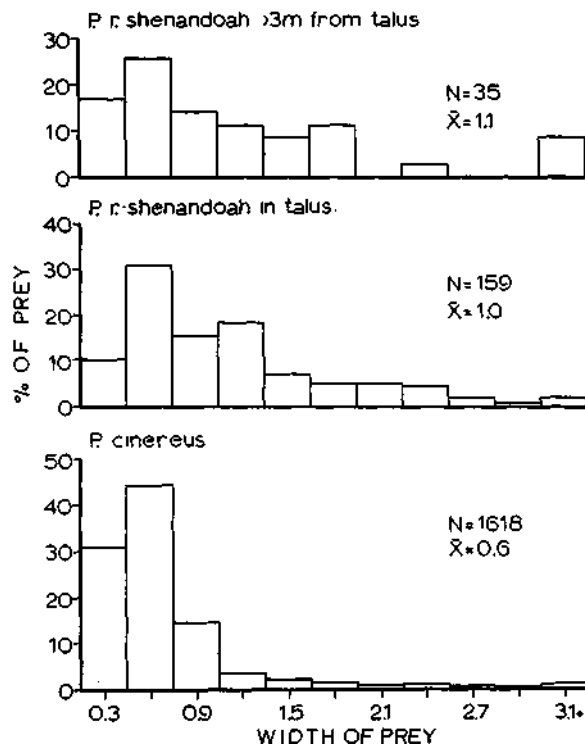


FIG. 6. Percentage of prey of various body widths found in the stomachs of salamanders of all sizes. Body widths are grouped in increments of 0.3 mm. Number and mean width of prey are given for each group of salamanders.

amount of time following a rain (Fig. 9). When the data for the 3 dry-soil days are grouped and the same is done for the 2 wet-soil days, the mean number of prey per stomach was: dry, 1.9 for 76 salamanders; damp, 4.6 for 51 salamanders; wet, 20.1 for 62 salamanders. When comparing these groups of data by one-tailed Mann-Whitney U-tests, the z values, derived from U due to the large sample sizes, indicate that the number of prey ingested is significantly different at the 1% level of probability among each pair of conditions of moisture: for dry vs. damp soil, $z = 4.58$ ($P < 0.001$); for dry vs. wet soil, $z = 9.19$

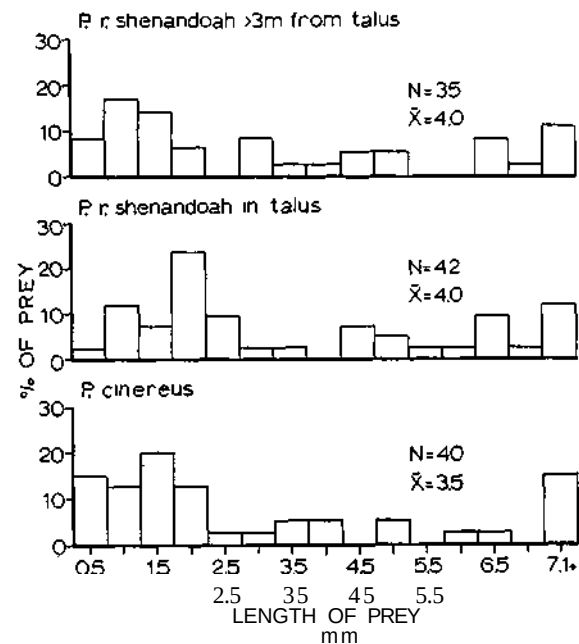


FIG. 7. Percentage of prey of various body lengths found in the stomachs of salamanders with body lengths of 41 mm or greater. Prey lengths are grouped in increments of 0.5 mm. Number and mean length of prey are given for each group of salamanders.

($P < 0.001$); for damp vs. wet soil, $z = 6.36$ ($P < 0.001$). Thus, it appears that prey vary either in abundance or availability in relation to the dryness of the soil.

There are two conditions that could lead to alternate interpretations of the results. One is that the number of prey in the stomach merely reflects the size of the prey eaten. Thus, a salamander of a given size could eat a few large prey and obtain the same amount of caloric input as one that eats a larger number of smaller prey. If such a differential selection for size of prey occurred, then those salamanders collected on dry days should have fed on larger prey than those collected on damp and wet days. The mean lengths of prey consumed by these three groups of salamanders were: dry soil, 1.7 mm; damp soil, 2.0 mm; wet soil, 1.6 mm. The salamanders

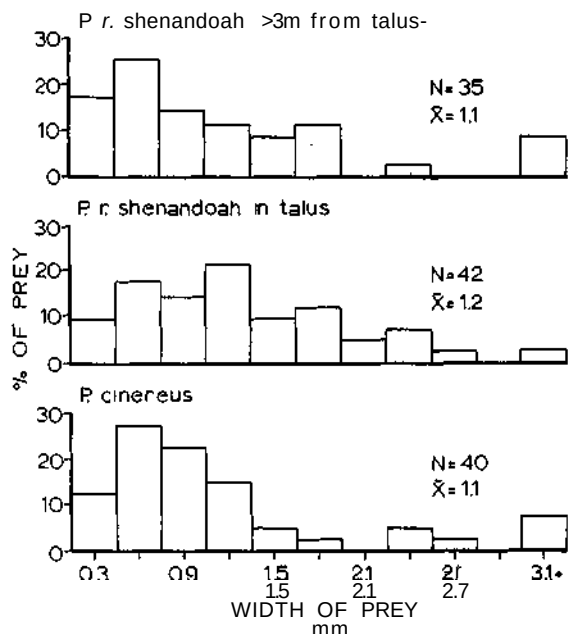


FIG. 8. Percentage of prey of various body widths found in the stomachs of salamanders with body lengths of 41 mm or greater. Prey widths are grouped in increments of 0.3 mm. Number and mean width of prey are given for each group of salamanders.

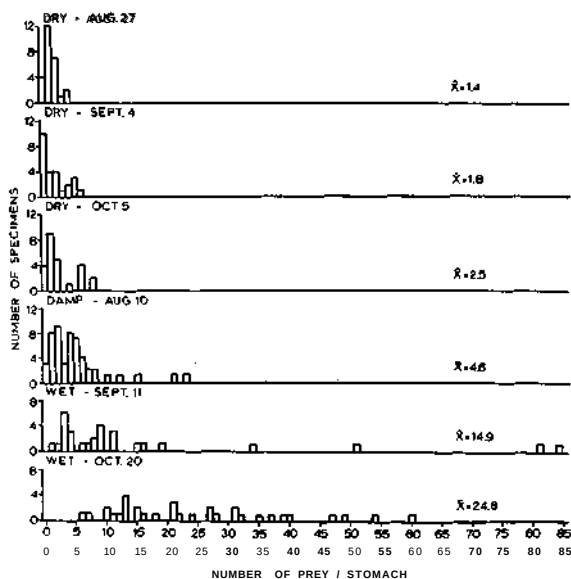


FIG. 9. Number of prey per stomach of *P. cinereus*. The salamanders were collected on 3 dry days, 1 damp day, and 2 wet days in 1968.

taken from dry soil did not consume prey of a larger mean length than those taken on damp soil, and the former ingested prey of almost the same mean length as those collected on wet soil. Therefore, the first interpretation may be rejected.

The second interpretation is that the *cinereus* collected under the three conditions of moisture were not of the same range of lengths. It is possible that

smaller salamanders were obtained on dry soil than on damp or wet soil. These smaller specimens, then, could have filled their stomachs to capacity with fewer prey than the larger salamanders collected under more-moist conditions. The mean snout-vent lengths of the three groups do vary: dry soil, 28.9 mm; damp soil, 31.6 mm; wet soil, 34.4 mm. However, due to large variances, two-tailed t-tests do not reveal significant differences among these means: dry vs. damp soil, $t = 0.2523$ ($P > 0.5$); dry vs. wet soil, $t = 0.5735$ ($P > 0.5$); damp vs. wet soil, $t = 0.3010$ ($P > 0.5$). The second interpretation, then, does not seem to be valid.

Predation experiment

Since *cinereus* and *shenandoah* are hypothesized to be in competition for a limited resource and since food appears to be limited during dry periods, one might expect that *cinereus*, the more successful species outside the talus (Jaeger 1970), is behaviorally more adept at exploiting the available food supply. The following experiment was designed to test, in a simplified environment, the hypothesis that *cinereus* could consume a larger number of prey than could *shenandoah* in a given period of time.

Procedure.—Four aquaria were used, each 41 by 21 by 25 cm. Into each was placed damp soil to a depth of 23 cm covered by a 2-cm layer of leaf litter, both of which had been previously sterilized by heating to 150°C for 24 hr. Ten burrows were bored into the soil in each aquarium, one-half being 1.5 cm in diameter and the other half 0.5 cm. The aquaria were covered with glass and placed in an illuminated refrigerator at 17°C. Ten *cinereus* were introduced into one aquarium and 10 *shenandoah* into the other. Five specimens of each species were placed into each of the other two aquaria. The salamanders had been collected 5 days previously at Hawksbill Mountain, and adults of approximately equal sizes were chosen. The animals were allowed to habituate to the aquaria for 4 days; on the fifth day, 15 termites per salamander were scattered in the leaf litter of each aquarium (150 prey per aquarium). Ten hours later, the soil was removed and the salamanders were sacrificed. The salamanders' stomachs were removed and opened and the number of termites per stomach recorded. Termites were used because laboratory observations show that they are preferred prey by these species of salamanders and because the heads are not easily digested and remain in the stomachs for a long period of time.

Findings.—Both *cinereus* and *shenandoah* are very efficient in capturing and ingesting prey. The single-species sample of *cinereus* consumed a mean of 12.3 prey per salamander, or 82% of the original 15 prey per salamander introduced. The single-species sample of *shenandoah* consumed a mean of 13.2, or

88%, of the prey. The *cinereus* under mixed-species conditions took a mean of 13.3 (89%), while the *shenandoah* under mixed-species conditions captured 14.9 (99%) of the prey available per salamander. Under each condition, a number of the salamanders did not feed while others ate from 1 to 61 termites. The results do not indicate that, under the highly artificial conditions of the experiment, *cinereus* is competitively superior to *shenandoah* in obtaining prey. Two-tailed Kolmogorov-Smirnov two-sample tests give the following values: comparing single-species samples of *cinereus* and *shenandoah*, $K_D = 2$ ($P = 0.21$); mixed-species samples of the two species, $K_D = 2$ ($P = 0.21$); single- and mixed-species samples of *cinereus*, $K_D = 3$ ($P = 0.58$); single- and mixed-species samples of *shenandoah*, $K_D = 2$ ($P = 0.21$). This experiment does not necessarily refute the hypothesis that *cinereus* excludes *shenandoah* due to superior exploitation of prey, because of the artificiality of laboratory conditions; however, it provides no evidence to support the hypothesis.

Interference

One possible explanation for the distributions of *cinereus* and *shenandoah* (Jaeger 1970) is that some sort of interference is occurring, in the sense of Miller (1967, 1968). That is, some sort of aggression by *cinereus* or avoidance of *cinereus* by *shenandoah* may keep the latter species restricted to the talus. To test this hypothesis, two sets of observations were made.

Procedure.—Five animals of each species, between 35- and 40-mm snout-vent length, were placed in an aquarium 75 by 30 by 28 cm. A substrate of damp soil was provided, but no burrows were available. Observations on interanimal behavior were made for 6 hr a day, over a period of 4 days. All observations were in a dark, walk-in refrigerator at 17°C with only a 40-w red light for illumination.

For a second set of observations, seven plastic trays, 30 by 16 by 9 cm with 6 cm of damp, crushed quartz in each, were covered and placed in a dark

refrigerator at 17°C. A glass tube was sunk at a 45° angle at either end of each tray. The tubes were 60 by 13 mm and were slid into tubes 60 by 15 mm to facilitate observations. One *cinereus* and one *shenandoah*, between 35 and 40 mm snout-vent length, were placed in each tray by randomly distributing them between the two tubes. Each tray was checked hourly for periods of 3-10 hr over a span of 30 days, and the glass tube that each salamander occupied was noted. If both specimens were not simultaneously inside tubes but one or both were resting on the quartz substrate, the observation was disregarded. Thus, I could ascertain whether members of the two species would inhabit separate burrows more often than they would cohabit in a single burrow.

Findings.—Twenty-four hours of observations on interspecific interactions did not reveal any form of aggression. Although occasionally a salamander would move when stepped on by either a conspecific or a member of the other species, there appeared to be no avoidance of contact by either species. This supports observations made over a period of 4 years that the two species can coexist in the same aquarium for many months without any sign of aggression or infliction of bodily injury.

The paired-salamander observations also did not provide convincing evidence for interference (Table 5). Chi-squared values in all seven tests indicate that the pairs did not randomly distribute themselves between the two burrows. This may be due to either some form of interaction or a burrow preference by both species. Further chi-squared tests for interaction yield the following results: (1) in tests 2, 4, and 7, the distribution of one species did not significantly affect that of the other, indicating that the individuals exhibited preferences for particular burrows; (2) in tests 1 and 3, interference seemed to occur since the salamanders were in separate burrows more often than would be expected by chance; (3) in tests 5 and 6, the animals were in the same burrows more often than would be expected by chance, providing a situation just the opposite of interference.

TABLE 5. Results of seven interference tests where *P. cinereus* and *P. r. shenandoah*, when paired, were allowed to choose either the same burrow or different burrows

Burrow no.	<i>cinereus</i> in burrow 1 <i>shenandoah</i> in burrow 2	<i>shenandoah</i> in burrow 1 <i>cinereus</i> in burrow 2	Both species in burrow 1	Both species in burrow 2	χ^2 for randomness	χ^2 for interaction
1	13	47	36	4	47.6 ($P < .001$)	6.3 ($.01 < P < .02$)
2	26	23	33	18	4.7 ($.02 < P < .05$)	0.0 ($P > .50$)
3	15	47	3	35	46.7 ($P < .001$)	9.8 ($.001 < P < .01$)
4	16	47	16	21	26.5 ($P < .001$)	3.4 ($.05 < P < .10$)
5	17	9	49	25	35.8 ($P < .001$)	21.0 ($P < .001$)
6	19	6	35	40	28.9 ($P < .001$)	27.5 ($P < .001$)
7	32	15	33	20	9.6 ($.001 < P < .01$)	0.6 ($.30 < P < .50$)

DISCUSSION

Exclusion of P. r. shenandoah from the soil

I previously concluded that *P. cinereus* appears to exclude *P. r. shenandoah* from the soil outside the talus such that *shenandoah* is now primarily restricted as a geographical relict within areas of talus. Such a conclusion was based on three types of evidence: (1) observations that *shenandoah* is mostly found in isolated pockets of soil within the talus that are unavailable to *cinereus* but that are ecologically similar to the soil outside the talus (Jaeger 1970); (2) experiments in the laboratory indicating that *shenandoah* does not express a preference for rocky or dry situations in contrast to soil and would probably invade the soil in the absence of *cinereus* (Jaeger 19716); (3) enclosure experiments showing that *shenandoah* survives equally as well as *cinereus* in the soil in the absence of the latter but survives poorly in the presence of *cinereus* (Jaeger 1971a).

The vital resource

We may find an hypothesis for the question of what is the vital resource for which competition occurs in the distribution of the sizes of those few *shenandoah* individuals that are found cohabiting with *cinereus* in the soil outside the talus. The *shenandoah* that occur within an arbitrarily determined 3-m area just outside the talus prove to be insignificantly different in both snout-vent length and head width from conspecifics found inside the talus and also insignificantly different in both respects from *cinereus* with which they occur. This indicates that all age classes of *shenandoah* leave the talus, probably due to random wandering, and settle into the preferred habitat of soil such that slightly more than 10% of all salamanders found there are of this species. Farther than 3 m from the talus, though, *shenandoah* comprises only about 5% of the salamander population, and these *shenandoah* prove to be significantly larger in both body length and head width than cohabiting *cinereus* and the *shenandoah* just outside of and in the talus. The hypothesis may now be proposed that food is the resource for which competition occurs, since (1) the very large *shenandoah* that live more than 3 m from the talus have the ability to consume prey that are larger than those ingested by the generally smaller *cinereus*, and thus the two would avoid competition, and (2) those same *shenandoah* are obviously not transients, since they are found up to 80 m from the talus edge (see map in Jaeger 1970), and must survive with *cinereus* for long periods of time. The *shenandoah* close to the talus are probably transients and this 3-m area, or some distance approximating it, seems to act as a filter. Those *shenandoah* leaving the talus that are in the same size range as *cinereus* may be prevented

from escaping farther from the talus due to competition from *cinereus*. The very large adults of *shenandoah* are able to escape into the soil because their greater head size allows selection of larger prey. However, these large adults would not be able to reproduce successfully, as their young would be in the same size range as young *cinereus* and competition would result. Indeed, while newly hatched *shenandoah* were found in isolated patches of soil inside the talus (Jaeger 1970), none were found outside the talus. Thus, a population of *shenandoah* cannot become permanently established in the soil, since only the largest emigrants from the talus can survive. Random wandering provides an important component of the invasion by *shenandoah* of the physically superior soil habitat of *cinereus*. However, it appears from laboratory observations that adults do not have a greater propensity for wandering than do juveniles. Differential movement alone cannot account for the preponderance of large *shenandoah* more than 3 m from the talus.

Interspecific competition for food is far from a new idea, and Lack (1955), among others, felt that it is probably the most important resource for which such competition occurs in animals. However, Dumas (1956) postulated that *Plethodon vehiculum* and *P. dunni* do not compete for food when sympatric, since an adverse physical environment limits their population sizes, and Vernberg (1953) pointed out that the *cinereus* in his study area suffered severe winter mortality. In contrast, Grobman (1944) noted that in eastern North America, when sympatry occurs between species of the genus *Plethodon*, it usually consists of one large species paired with a small one, such as *P. cinereus* sympatric with the much larger *P. glutinosus* and *P. richmondi* with the larger *P. wehrlei*. This situation is similar to the coexistence of *cinereus* with only larger *shenandoah* in the soil around the talus on Hawksbill Mountain and may indicate that competition for food is a widespread occurrence among terrestrial salamanders.

Joint utilization of prey by the two species of salamanders

A number of workers have suggested that salamanders are euryphagic predators (Jameson 1944, Hairston 1949, Duellman 1954, Avery 1968), although the taxa of prey taken vary macro- and micro-geographically, temporally, and with the moisture content of the soil (Jaeger, unpublished). My own observations show a broad diversity of prey in the stomachs both of *cinereus* and *shenandoah* collected on the same days. Unfortunately, I was unable to obtain enough specimens of *shenandoah* from outside the talus at critical times to compare with sympatric individuals of *cinereus*. However, those *shenandoah* collected inside the talus showed a response to

prey similar to that of *cinereus*, at least at the ordinal and higher taxa, and both species crop prey from virtually all the groups of small animals available in their habitats. The amount of each taxon taken by the two species probably reflects the comparative abundance of that taxon in and out of the talus. For example, the stomachs of *cinereus* contained about 12 times the number of homopterans as those of *shenandoah*; most of the homopterans consist of aphids that *cinereus* obtains by climbing the stalks of plants at night. However, herbaceous plants are less abundant in the talus, and, thus, the aphids feeding on them are not generally available to *shenandoah*. The more indiscriminate use of prey by *shenandoah* may suggest that prey are more limited in the talus than in the soil where *cinereus* occurs, as generally hypothesized by Emlen (1968). With such a wide diversity of prey taken by the two species, it seems unlikely that they might specialize at the species level when in sympatry.

Further evidence that interspecific competition for food occurs is found in the analysis of stomach contents of *cinereus* versus the very large *shenandoah* that live in the soil more than 3 m from the talus. These *shenandoah* take significantly longer and wider prey than the *cinereus* with which they coexist and significantly longer prey than those taken by *shenandoah* in the talus. This again suggests that individuals of similar size from the two species prey upon the same size and type of organisms and that only the very largest *shenandoah* are removed from this competition and can cohabit with *cinereus*. It does not appear that the two species innately select different sizes or types of prey based on some factor other than their own comparative body proportions. When only the very largest salamanders of both species are compared (41+ mm snout-vent length), the prey ingested no longer differ significantly in either length or breadth at the 5% level of significance. There are probably an insufficient number of *cinereus* in this size range to provide competition severe enough to exclude the large adult *shenandoah* from the soil. Finally, there seems to be no habitat distinction between members of the two species when cohabiting that might lead to partitioning of the niche. Likewise, I cannot discern a temporal difference in utilization of the surface of the soil, probably because the similar preferences for soil moisture (Jaeger 19716) coordinate burrowing and surfacing of the two species.

Food as a limited resource

It seems improbable that euryphagic salamanders feeding on apparently ubiquitous insects and other soil organisms would ever be faced with a limited supply of food. Yet moisture plays an important role in determining the number of prey that a salamander

can capture. During wet weather, their stomachs are engorged with prey, with fewer prey present when the soil is damp and virtually absent during times of dryness. At the same time, the sizes of both salamanders and prey on the ground's surface do not change significantly from dry to damp to wet conditions. Thus, the physical environment is the ultimate factor in determining whether or not food is limited in supply. This subject is now being investigated in greater detail.

Currently, information is inadequate to prove that food is a limited resource. Data are needed concerning the amount of food the salamanders need to survive and reproduce, and the length of time that they can go without food, or on a minimal amount of it, before either survival or reproduction is affected. It may now be possible to determine the number of calories ingested by *cinereus* under various conditions of moisture and compare that data with the estimated energy budget as derived by Merchant (1970) for that species. This will help to determine whether food is *limited* for long enough periods to be *limiting* to the population.

Circumstantial evidence does indicate that food is limited in supply. Jaeger (1971a) demonstrated that *shenandoah* encounters significant mortality over the course of a summer when forced into competition with *cinereus* in the soil. At such a time the salamanders are subjected to their highest metabolic rate and probably require a considerable amount of food; this is demonstrated by the salamanders during wet weather when they continue to pack their stomachs with food for as many days as wet conditions allow. The frequent need for food may explain the tendency for these species to remain on the surface of the ground, where they are subjected to predation by shrews (Jaeger 1971a), when they are well adapted to fossorial life. Apparently a continuously fossorial existence does not provide an adequate supply of food, since the salamanders are not morphologically adapted for digging for prey but must rely on incidentally available burrows and cracks where prey seem to be scarce.

Availability of prey

Huffaker (1966) felt that food could be in short supply when the predator does not have the capacity to locate or utilize it efficiently. In the case of *cinereus* and *shenandoah*, prey are not limited in abundance, since there are ample prey available in the stomachs of the salamanders immediately following a rain. There is a relative rather than an absolute lack of food, a factor suggested by Birch and Battaglia (1957) in relation to the abundance of *Drosophila*. The availability of food is related to the behavior of the species, based on field observations. During and shortly after rains, both species of sal-

amanders wander in leaf litter during the day and climb plants and trunks of trees at night. During this time they are able to seek out large numbers of prey and feed heavily upon homopterans, especially aphids, while arboreal. As drying occurs, movement in the leaf litter is still possible, but the salamanders are denied access to the arboreal insects due to low humidity in the air, although climbing is still accomplished during very foggy nights. Eventually they are restricted to patches of moisture beneath rocks and logs where prey are quickly exterminated. Finally, the animals are forced into subterranean holes, during drought, where food is also minimal (Jaeger, unpublished). These observations agree with those of Heatwole (1962) who found *cinereus* to be inactive on the surface of the ground during times of low humidity. During the retreat by the salamanders to patches of moisture, the prey are still relatively abundant in the habitat, but they are not available to the salamanders until the next rain or heavy fog.

Periodicity of prey availability

It is thus evident that food is limited to these species on a periodic basis, not a continuous one, due to the periodicity of rainfall. Hutchinson (1957) felt that when competition occurs it probably does so intermittently, and Gilbert, Reynoldson, and Hobart (1952) commented on the periodicity of competition in relation to Gause's hypothesis. The length of time that prey are limited in availability varies from year to year and from season to season. On Hawksbill Mountain, winter provides a paucity of prey but during this time the salamanders are underground and metabolize very slowly. Spring and early summer are usually, but not always, quite wet, and it is at this time that both species of salamanders lay their eggs. Newly hatched young of both species are seen in middle to late summer. From late summer through fall it is not uncommon for a month to pass with insufficient rainfall to moisten the soil, as occurred, for example, in October 1963 (0.04 inches total) and September 1970 (1.27 inches total). Fall may be a critical period for both species, since food at this time may be essential to prepare eggs for the spring lay; Saylor (1966) showed that eggs of *cinereus* require 2 years in which to accumulate enough yolk for deposition. Competition for food at this time may be severe enough to inhibit fecundity, perhaps enough so to put *shenandoah* at a reproductive disadvantage. Insufficient food was hypothesized to inhibit fecundity in a pond snail by Eisenberg (1970) and in a number of other organisms by Wynne-Edwards (1962).

Exploitation and interference

One species may competitively exclude another because the former is superior in exploiting a limited

resource. In other cases, interference may occur when the successful species is able to limit access by a competitor to the limited resource, perhaps through interspecific aggression or territoriality. Miller (1967) proposed that interference may occur when the information transferred in intraspecific interactions is extended to interspecific interactions. Species that lack sophisticated intraspecific communicatory displays (in the broadest sense of the term) tend to compete through exploitation.

Interference has been proposed for a number of species (Orians and Collier 1963, for birds; Penn and Fitzpatrick 1963, for crawfishes; Miller 1964, for gophers; Murie 1971, for voles; Simmons 1951), but it has not been well demonstrated in salamanders. Indeed, Stewart and Bellis (1970) found that the two species of salamanders which they studied were distributed randomly with regard to one another. My observations on interactions between *cinereus* and *shenandoah* in the laboratory also reveal no indication of interspecific aggression, while tests for interspecific spacing provide conflicting results. It is possible, though, that some form of subtle interaction occurs, as these species appear to have an intraspecifically well-developed system of olfactory communication.

Reynoldson (1966) concluded that differential exploitation of a limited food supply leads to exclusion among species of lake-dwelling triclads. My experiment on predatory success provided no evidence that, under simplified laboratory conditions, *cinereus* is better able to capture prey than is *shenandoah*. However, in the absence of observable evidence of interference, I feel that differential exploitation is the more likely mechanism governing the exclusion of *shenandoah* from the soil by *cinereus*.

Contiguous allopatry between potential competitors

The distributions of *cinereus* and *shenandoah* on Hawksbill Mountain seem to be determined by a combination of interspecific competition and physical factors, primarily moisture. Contiguous allopatry, on a microgeographic scale, occurs along the edge of the talus, and the distributions of the salamanders conform to the included niche model (Hutchinson 1957, Miller 1967), as discussed by Jaeger (1971a).

A number of other contiguously allopatric species apparently are similarly affected by interactions of competition and physical factors, although the parameters affecting the fundamental and realized niches vary. Bovbjerg's (1970) study of two species of crayfish, one distributed in streams, the other in ponds, gives results similar to those I propose to govern the distributions of *cinereus* and *shenandoah*. Also, Connell's (1961) and Morris' (1969) studies on barnacles and rodents, respectively, again dem-

onstrate interactions between competition and physical aspects of the environment. Other examples may exist for blackbirds (Miller 1968) and gophers (Kennedy 1959), to name a few. It appears, then, that contiguous allopatry between a wide diversity of species may be explained by the included niche model. Potential competitors are able to survive through a balance of competitive superiority by one species (inhabiting both its fundamental and realized niches) with a wider ecological tolerance by the other species (inhabiting only its realized niche), as is demonstrated by *cinereus* and *shenandoah*.

ACKNOWLEDGMENTS

I wish to thank E. Raymond Schaffner of the National Park Service, whose cooperation made this research possible, and my wife, Linda, whose vocalized discomfort did not inhibit her collecting ability. The manuscript was kindly read by Jack Hailman, Douglass Morse, Richard Highton, and Douglas Fraser. Richard Miller offered helpful criticism and ideas. This paper formed part of a dissertation submitted in partial fulfillment of the requirements for the Ph.D. degree at the University of Maryland. The research was supported in part by the Department of Zoology, University of Maryland, and by N.S.F. grants GB-3235 and GB-7299 to Richard Highton.

LITERATURE CITED

- Avery, R. 1968. Food and feeding relations of three species of *Triturus* (Amphibia Urodela) during the aquatic phases. *Oikos* 19:408-412.
- Birch, L., and B. Battaglia. 1957. The abundance of *Drosophila willistoni* in relation to food in natural populations. *Ecology* 38:165-166.
- Bovbjerg, R. 1970. Ecological isolation and competitive exclusion in two crayfish (*Orconectes virilis* and *Orconectes immunis*). *Ecology* 51:225-236.
- Connell, J. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42:710-723.
- Crombie, A. 1947. Interspecific competition. *J. Anim. Ecol.* 16:44-73.
- Duellman, W. 1954. The salamander *Plethodon richmondi* in southwestern Ohio. *Copeia* 1954:40-45.
- Dumas, P. 1956. The ecological relations of sympatry in *Plethodon dunni* and *Plethodon vehiculum*. *Ecology* 37:484-495.
- Eisenberg, R. 1970. The role of food in the regulation of the pond snail, *Lymnaea elodes*. *Ecology* 51:680-684.
- Emlen, J. M. 1968. Optimal choice in animals. *Amer. Natur.* 102:385-389.
- Gilbert, O., T. Reynoldson, and J. Hobart. 1952. Gause's hypothesis: an examination. *J. Anim. Ecol.* 21:310-312.
- Grobman, A. 1944. The distribution of the salamanders of the genus *Plethodon* in eastern United States and Canada. *Ann. N.Y. Acad. Sci.* 45:261-316.
- H Hairston, N. 1949. The local distribution and ecology of the plethodontid salamanders of the southern Appalachians. *Ecol. Monogr.* 19:47-73.
- Heatwole, H. 1962. Environmental factors influencing local distribution and activity of the salamander *Plethodon cinereus*. *Ecology* 43:460-472.
- Highton, R. 1971. Distributional interactions of eastern North American salamanders of the genus *Plethodon*. In press. In P. Holt [ed.] *The distributional history of the biota of the southern Appalachians*. Part III: Vertebrates. Res. Div. Monogr. 3, Virginia Polytechnic Inst.
- Huffaker, C. 1966. Competition for food by a phytophagous mite: the roles of dispersion and superimposed density-independent mortality. *Hilgardia* 37:533-561.
- Hutchinson, G. 1957. Concluding remarks. *Cold Spring Harbor Symp. Quant. Biol.* 22:415-427.
- Jaeger, R. 1970. Potential extinction through competition between two species of terrestrial salamanders. *Evolution* 24:632-642.
- . 1971a. Competitive exclusion as a factor influencing the distributions of two species of terrestrial salamanders. *Ecology* 52:632-637.
- . 1971b. Moisture as a factor influencing the distributions of two species of terrestrial salamanders. *Oecologia* 6:191-207.
- Jameson, E. 1944. Food of the red-backed salamander. *Copeia* 1944:145-147.
- Kennerly, T. 1959. Contact between the ranges of two allopatric species of pocket gophers. *Evolution* 13:247-263.
- Lack, D. 1955. The mortality factors affecting adult numbers, p. 47-55. In J. Cragg and N. Pirie [ed.] *The numbers of man and animals*. Publ. for Inst. of Biol. by Olivier and Boyd, Edinburgh.
- Merchant, H. 1970. Estimated energy budget of the red-backed salamander, *Plethodon cinereus*. Ph.D. Thesis. Rutgers Univ., New Brunswick, N.J.
- Miller, R. 1964. Ecology and distribution of pocket gophers (Geomyidae) in Colorado. *Ecology* 45:256-272.
- . 1967. Pattern and process in competition. In J. Cragg [ed.] *Advances in ecological research* 4:1-74.
- . 1968. Conditions of competition between redwings and yellowheaded blackbirds. *J. Anim. Ecol.* 37:43-62.
- . 1969. Competition and species diversity, p. 63-70. In *Diversity and stability in ecological systems*. Brookhaven Symp. in Biol. 22.
- Morris, R. 1969. Competitive exclusion between *Microtus* and *Clethrionomys* in the aspen parkland of Saskatchewan. *J. Mammal.* 50:291-301.
- Morse, D. 1967. Foraging relationships of brown-headed nuthatches and pine warblers. *Ecology* 48:94-103.
- Murie, J. 1971. Behavioral relationships between two sympatric voles (*Microtus*): relevance to habitat segregation. *J. Mammal.* 52:181-186.
- Orians, G., and G. Collier. 1963. Competition and blackbird social systems. *Evolution* 17:449-459.
- Penn, G., and J. Fitzpatrick. 1963. Interspecific competition between two sympatric species of dwarf crawfishes. *Ecology* 44:793-797.
- Reynoldson, T. 1966. The distribution and abundance of lake-dwelling triclads—towards a hypothesis. In J. Cragg [ed.] *Advances in ecological research* 3:1-71.
- Sayler, A. 1966. The reproductive ecology of the red-backed salamander, *Plethodon cinereus*, in Maryland. *Copeia* 1966:183-193.
- Simmons, K. 1951. Interspecific territorialism. *Ibis* 93:407-413.
- Stewart, G., and E. Bellis. 1970. Dispersion patterns of salamanders along a brook. *Copeia* 1970:86-89.
- Vernberg, F. 1953. Hibernation studies of two species of salamanders, *Plethodon cinereus cinereus* and *Eurycea bislineata bislineata*. *Ecology* 34:55-62.
- Wynne-Edwards, V. 1962. Animal dispersion in relation to social behaviour. Hafner, New York. 653 p.