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COMPETITION LEADS TO AN EXTINCTION-PRONE SPECIES OF SALAMANDER: INTERSPECIFIC TERRITORIALITY IN A METAPOPOPULATION

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Abstract. The Shenandoah salamander, *Plethodon shenandoah*, is a federally endangered species that is restricted to Pleistocene-age talus on three mountains in Shenandoah National Park, Virginia, USA. Each population is surrounded by the red-backed salamander, *P. cinereus*, which defends intraspecific territories on the forest floor. On Hawksbill Mountain, *P. shenandoah* consists of a metapopulation, with a large “source” subpopulation on the top of the mountain and at least five small “sink” subpopulations below. Here we report that *P. shenandoah* is constrained in escaping from the talus into deep soil, and thus in emigrating from source to sink subpopulations, by interspecific territoriality from *P. cinereus*. We performed competitive release experiments during two summers by removing *P. cinereus* from under experimental rocks while leaving territorial residents in place under control rocks. *Plethodon shenandoah* responded by invading experimental rocks significantly more frequently than control rocks in both years. Quadrat analyses indicated that only a small number of individuals escaped from the talus at any given time. Behavioral experiments revealed no significant differences in propensity to bite by the two species, indicating that more subtle tactics are employed by *P. cinereus* in excluding *P. shenandoah* from territorial sites. One sink subpopulation of *P. shenandoah* became extinct in 1970 as a consequence of a severe drought, which affected areas of talus more drastically than areas of deep soil containing *P. cinereus*. Our data now suggest that interspecific territoriality by *P. cinereus* can contribute to the extinction-prone status of *P. shenandoah* by inhibiting movements from source to more distant sink subpopulations.

Key words: aggression; competitive release; density; endangered species; extinction; interspecific territoriality; metapopulation; *Plethodon cinereus*; *Plethodon shenandoah*; salamanders.

INTRODUCTION

Models of metapopulations have been particularly concerned with how extinction rates follow from the interaction of fragmented populations, deterioration of the habitat patches, gene flow among patches, and (in some cases) interspecific competition (Pulliam 1988, Case 1991, Hastings and Harrison 1994, Gaggiotti 1996, Hess 1996). A metapopulation may be defined as a set of subpopulations of a species that are isolated from one another and in which extinctions and colonizations occur (Hastings and Harrison 1994). When extinction occurs in one or more habitat patches, immigration from another patch may reestablish the subpopulation. In some cases, immigration may proceed from a relatively large or stable “source” subpopulation to a smaller or more fragile “sink” subpopulation (Pulliam 1988, Gaggiotti 1996). Interspecific competition between the metapopulation and another species occupying the space between habitat patches can impede movements from source to sinks, and deterioration of the habitat patches can foster extinctions in the

sinks. We here continue a study begun in 1966 by one of us (Jaeger 1970, 1971a, b, 1972, 1980a) to determine whether interspecific competition between two species of salamanders has led to the extinction-prone status of one of them. In this extended study, the competitively inferior species (*Plethodon shenandoah*: the Shenandoah salamander) occurs as a metapopulation in isolated patches of Pleistocene-age talus, while the competitively superior species (*P. cinereus*: the red-backed salamander) occupies forested areas of deep soil that surround each habitat patch of the metapopulation.

One way that interspecific competition can have a major impact on species is through territoriality (sensu Brown and Orians 1970), where intraspecific territoriality is also employed against heterospecifics (Murray 1971). In this case, members of the winning species aggressively defend resource-containing spaces against members of the losing species. Interspecific territoriality has been particularly well documented in avian social systems (Orians and Collier 1963, Dhondt and Eyckerman 1980, review of Red-winged Blackbirds in Searcy and Yasukawa 1995). This form of interference competition may be widespread among salamanders as well, especially species of the family Plethodontidae

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PLATE 1. One of the sink areas of talus on Hawksbill Mountain that contains a subpopulation of *Plethodon shenandoah*.

(reviewed by Mathis et al. 1995), such as the lungless, plethodontid species *P. cinereus* and *P. shenandoah*.

THE COMPETING SPECIES

Plethodon shenandoah occurs in north-facing talus above 900 m on three mountains in Shenandoah National Park, Virginia, USA (Highton and Worthington 1967). Due to its restricted distribution, it is a federally listed endangered species (Federal Register, 54 FR 34464, 8/18/1989). *Plethodon cinereus*, which is widely distributed in forests throughout eastern North America (Highton 1972), surrounds each of the three isolates of *P. shenandoah* at an average density of 2.3 red-backed salamanders/m² of the forest floor (Jaeger 1979). The three extant populations of *P. shenandoah* apparently are relicts of a more widely distributed species during the Pleistocene (Highton and Worthington 1967). Since the Pleistocene, *P. cinereus* has spread from lowland habitats into the mountains, probably due to changing climatic conditions (Highton 1972). Jaeger (1970, 1971a, b) demonstrated that *P. cinereus* on Hawksbill Mountain competitively dominates *P. shenandoah* in competition for prey (Jaeger 1972, 1980b), confining the latter species to a few, relatively dry talus

refuges. The sink subpopulations of *P. shenandoah* on Hawksbill Mountain (see maps in Jaeger 1970) are at risk from (1) perturbations that cause drying in the talus (Jaeger 1971a) and (2) deterioration of the habitat refuges due to soil eroding into the talus (followed by invasions of *P. cinereus*: Jaeger 1970). One isolated subpopulation of *P. shenandoah* on Hawksbill Mountain became extinct in 1970 during a drought (Jaeger 1980a). Thus, *P. shenandoah* on Hawksbill Mountain forms a metapopulation consisting of a source subpopulation at the top of the mountain and at least five sink subpopulations isolated in areas of talus below (map in Jaeger 1970: Fig. 1). During the spring of 1970, Jaeger (1980a) estimated the total number of *P. shenandoah* in the source subpopulation to be ~70 000 salamanders, while the sink subpopulations contained as few as ~400 salamanders. Movement of *P. shenandoah* from source to nearby sinks appears to be common, because Shenandoah salamanders have been commonly found in areas of deep soil between the source and nearby sinks (map in Jaeger 1970: Fig. 4). However, movement of *P. shenandoah* from the source to more distant sinks (map in Jaeger 1970: Fig. 2) is severely limited by competition from *P. cinereus*, which inhabits the deep soil between them (Jaeger 1971b, 1972). Shenandoah salamanders appear to move across the talus edge into the deep soil throughout the nonwinter months, because it has been found sympatric with red-backed salamanders outside of the talus from April through October.

Subsequent studies found that adult males and females of *P. cinereus* defend intraspecific territories (Mathis 1989), defending foraging (Gabor 1995) and perhaps courtship (Mathis 1991) sites; the largest individuals in the population tend to gain access to these sites (Mathis 1990) and may defend them as intersexual pairs even outside of the courtship seasons (Mathis 1991, Jaeger et al. 1995). Individuals show site attachment (Gergits and Jaeger 1990a) and home to the original site when displaced (Kleeberger and Werner 1982). Residents advertise their territories with pheromones (Jaeger and Gergits 1979, Simon and Madison 1984, Jaeger et al. 1986, Horne and Jaeger 1988), defend them with visual agonistic displays and biting (Jaeger 1981, 1984), and can expel ~90% of conspecific intruders (Jaeger et al. 1982).

To test the general hypothesis that *P. cinereus* also defends territories against *P. shenandoah*, thus limiting movements from source to sink subpopulations, we (1) conducted competitive release experiments during two summers on Hawksbill Mountain, (2) estimated the densities of the two species in the narrow area of sympatry at the talus-soil interface, and (3) conducted an experiment to test for interspecific aggression.

PREDICTIONS, METHODS, AND RESULTS

Does interspecific territoriality occur?

Prediction.—If interspecific territoriality occurs, we predicted that Shenandoah salamanders would occupy

cover objects in the deep soil outside the talus significantly more frequently when red-backed salamanders were absent than when they were present (competitive release experiment).

Methods.—We conducted competitive release experiments from 5 June to 7 August 1991 and from 12 May to 30 July 1992 in four areas where deep soil (occupied by *P. cinereus*) extends into the talus on Hawksbill Mountain (maps of study area in Jaeger 1970). Individuals of *P. cinereus* were located under natural cover objects (rocks) within 10 m of the talus' edge in these deep soil areas (very few individuals of *P. shenandoah* have been found farther than 10 m from the talus' edge; Jaeger 1972). We selected only cover objects that were large enough (range 215–940 cm²) to house multiple salamanders if they were tolerant of cohabiting (the largest salamander would be 53 mm snout-vent length (SVL) and 7.6 mm head width; Jaeger 1972). We randomly assigned cover objects, in 1991, to either experimental (*P. cinereus* removed: $n = 50$) or control (*P. cinereus* not removed: $n = 50$) treatments. These same 100 cover objects were reinvestigated in 1992. There was no significant difference between treatments for either distance from the edge of the talus ($\bar{X}_{\text{exp}} = 4.8$ m, $\bar{X}_{\text{con}} = 3.8$ m, $W_x = 1373$, $P = 0.398$; Mann-Whitney test, two-tailed, $\alpha = 0.05$) or size of cover object ($\bar{X}_{\text{exp}} = 577.4$ cm², $\bar{X}_{\text{con}} = 579.7$ cm², $W_x = 1295$, $P = 0.756$). Each salamander from both treatments was placed in a box made of Plexiglas with a cushion of foam (Wise and Buchanan 1992) for measurement. We measured its SVL through the clear Plexiglas using dial calipers (0.1 mm precision). Control animals were returned to their cover objects in the original positions. Animals from the experimental treatment were relocated to Hawksbill Gap, 0.75 km from the study site, because individuals of *P. cinereus* can "home" to their original sites when moved up to 90 m (Kleeberger and Werner 1982). We made no attempt to remove the pheromones of these displaced animals from the soil under the cover objects. We uniquely marked the cover objects with flags and did not disturb them for 3 d to allow recovery following initial handling of the salamanders. Then each cover object was turned and checked for the presence of salamanders 3–8 d after each rainfall, when food availability decreases in the leaf litter (Jaeger 1980b) and cover objects are more likely to be occupied (Jaeger 1979). We removed subsequent individuals of *P. cinereus* that occupied the experimental cover objects to maintain those sites free of that species. Mathis (1990) monitored similarly manipulated cover objects every 2 d for 28 d without apparent disturbances to red-backed salamanders.

For *P. shenandoah*, we recorded the number of days to invasion, the number of individuals invading, and their SVL in both experimental and control treatments. For *P. cinereus*, we recorded the SVL for each original

resident and each subsequent conspecific invader in the experimental treatment.

All statistical comparisons were two tailed with $\alpha = 0.05$. We used chi-square tests of independence to compare the numbers of *P. shenandoah* that invaded experimental and control sites in 1991 and 1992, with expected values being equiprobable. We compared times (in days) to invasion and SVL of invading *P. shenandoah* between experimental and control treatments by nonparametric Mann-Whitney tests (Siegel and Castellan 1988), because the assumptions of normality and homoscedasticity of data were not met. In the experimental treatment, we compared SVL of the original residential *P. cinereus* with the SVL of the (1) first invading *P. shenandoah* using a paired *t* test (parametric assumptions met), and (2) first invading conspecific using nonparametric Wilcoxon signed-ranks test (parametric assumptions not met).

The exact number of days to invasion was unknown, because the experimental design did not allow us to sample cover objects on a daily basis. Thus, our data represent rough estimates, but the statistical inferences are valid because experimental and control treatments were sampled on the same days.

Results.—During 1991, *P. shenandoah* occupied significantly more of the experimental cover objects ($n = 21$) than the control cover objects ($n = 7$): $\chi^2 = 7.0$, $df = 1$, $P = 0.008$. During 1992, *P. shenandoah* again occupied significantly more of the experimental cover objects ($n = 13$) than the control cover objects ($n = 3$): $\chi^2 = 6.25$, $df = 1$, $P = 0.012$. Time to invasion by *P. shenandoah* was analyzed for 1991 only, because all cover objects had a known start date with a resident of *P. cinereus*. The time to first invasion (from day 0) was significantly shorter for experimental cover objects (40 ± 23 d [mean ± 1 SD], $n = 50$ rocks) than for control cover objects (52 ± 17 d, $n = 50$ rocks): Mann-Whitney test, $W_x = 835.5$, $P = 0.0043$.

For experimental cover objects, the first invading individuals of *P. shenandoah* and the original residential *P. cinereus* did not differ significantly in SVL (Table 1A). However, the first invading individuals of *P. cinereus* were significantly smaller in SVL than the original residents (Table 1B). The *P. shenandoah* that invaded experimental vs. control cover objects in 1991 and 1992 did not differ significantly in SVL (Table 2).

We pooled the data for SVL for all Shenandoah salamanders (first plus subsequent invaders) found in 1991 and 1992. Mean SVL was 38.8 ± 7.2 mm, and adults comprised ~86% of the 56 individuals, based on extrapolations from Saylor's (1966) data for size at sexual maturity of *P. cinereus*.

Inferences.—We infer that *P. cinereus* defends territories against *P. shenandoah*, based on differential numbers of Shenandoah salamanders that invaded experimental vs. control treatments and the differential times to invasion. The invading Shenandoah salamanders were mostly adults but were not significantly large-

TABLE 1. Sizes of resident and invading salamanders under experimental cover objects in 1991.

Residents and invaders	SVL (mm)	n or n'	t or T ⁺	P
A) Original resident (<i>P. cinereus</i>)	36.4 ± 6.8	21	1.46	0.16
Invader (<i>P. shenandoah</i>)	39.6 ± 6.3	21		
B) Original resident (<i>P. cinereus</i>)	37.6 ± 5.8	26	227.0	0.01*
Invader (<i>P. cinereus</i>)	32.8 ± 8.0	26		

Note: Snout-vent length (SVL: mean ± 1 SD) of (A) original resident *P. cinereus* and first invading *P. shenandoah* (paired *t* test, *n* = number of salamanders) and (B) original resident *P. cinereus* and next invading *P. cinereus* (Wilcoxon signed-ranks test, *T*⁺; *n'* = number of nonzero values).

* Significant difference at $\alpha = 0.05$.

er than the territorial red-backed salamanders, even though *P. shenandoah* reaches a maximum SVL of 53 mm while *P. cinereus* reaches a maximum SVL of 45 mm (Jaeger 1972). However, invading red-backed salamanders were significantly smaller than the original conspecific residents, which supports Mathis' (1990) inference that red-backed salamanders tend to be non-territorial floaters until they reach nearly maximum adult size.

Do Shenandoah salamanders inhabit spaces between territories of red-backed salamanders?

Prediction.—*Plethodon shenandoah* prefers to reside in the deep-soil habitat outside the talus and is more tolerant of desiccation than is *P. cinereus* (Jaeger 1971a). However, *P. cinereus* has a density of 1–4 salamanders/m² in the deep-soil habitat (Jaeger 1979, see Mathis 1991 for a similar density at another forested locality) and is aggressive toward congeners (Lancaster and Jaeger 1995) as well as conspecifics (Jaeger 1981). Thus, Shenandoah salamanders that leave the talus and become sympatric with red-backed salamanders may be excluded from cover objects by territorial red-backed salamanders (see *Does interspecific territoriality occur?*: Results above) but may be able to maintain a high density in the leaf litter, which dries between rainfalls, by foraging between the territorial boundaries of *P. cinereus*. We predicted that a random survey of the area of sympatry outside the talus would locate significantly more Shenandoah salamanders in the leaf litter than under cover objects.

Methods.—To determine the densities and locations of both species of salamander, in August 1992 we placed 1-m² quadrats in the deep soil habitat where the

competitive release experiment had been performed. The quadrats were confined to an area that extended 30 m along the talus' edge and 15 m away from that edge. We selected the location of each of 50 quadrats by randomly choosing a distance along the talus (1–30 m) and out from the talus (1–15 m), for a total of 450 possible quadrat sites. Complete randomization was constrained in that no two quadrats were adjacent to each other (to avoid between-quadrat disturbances) and that 25 quadrats were located 1–7 m and 25 were located 8–15 m from the talus' edge. We sampled the quadrats in random order by turning all cover objects and leaf litter in an attempt to locate all salamanders therein. All cover objects, leaf litter, and animals were replaced in the quadrats immediately after sampling.

We measured the distance from the talus' edge to the far end of each quadrat, soil depth (mean of five measurements, one at each corner and one in the center of each quadrat, using a 107-cm long steel soil probe), and determined the species, SVL, and location (under cover object or in the leaf litter) of each animal within the quadrat. We used linear regression (assumptions met by the residuals) to explore the relationship between distance from the talus and depth of soil and a binomial test (equiprobable expected) to compare the number of Shenandoah salamanders under rocks and in the leaf litter. Analyses were two-tailed with $\alpha = 0.05$.

Results.—We located 60 individuals of *P. cinereus* ($\bar{X} = 1.2$ individuals/m²) and seven of *P. shenandoah* ($\bar{X} = 0.1$ individuals/m²). Five of the seven Shenandoah salamanders were adults; for all seven, one was 1–7 m from the talus' edge, six were 7–11 m, and none was 11–15 m from the edge. Six Shenandoah salamanders were under cover objects and one was in the leaf litter (binomial test: $P = 0.124$). The soil depth within the quadrats increased significantly with distance from the talus ($R^2 = 0.32$, $P < 0.001$).

Inferences.—We infer that relatively few Shenandoah salamanders coexist with *P. cinereus* in the deep soil habitat at any given time. Those that do occur there are primarily adults (see the competitive exclusion experiment above) that do not progress far from the talus' edge, which conforms to the findings of Jaeger (1970).

TABLE 2. Snout-vent length (SVL: mean ± 1 SD) of all individuals of *P. shenandoah* that invaded control and experimental cover objects in 1991 and 1992.

Year	Control		Experimental		<i>W</i> _s	<i>P</i>
	SVL (mm)	<i>n</i>	SVL (mm)	<i>n</i>		
1991	38.7 ± 8.4	11	39.9 ± 5.6	27	149.0	0.987
1992	38.8 ± 9.9	4	36.6 ± 9.0	13	22.0	0.651

Note: Mann-Whitney test, *W*_s.

Our prediction that Shenandoah salamanders are largely restricted to the leaf litter, rather than residing under cover objects, was not supported.

Are Shenandoah salamanders losers because they are aggressively inferior?

Prediction.—Because red-backed salamanders are able to inhibit *P. shenandoah* from occupying cover objects on the forest floor (competitive release experiment above), even though the latter species is larger in body size (Jaeger 1970), we predicted that *P. cinereus* would exhibit significantly more aggressive behavior in laboratory encounters. In particular, we predicted significantly higher rates of biting by *P. cinereus*, as individuals from our research locality are known to bite conspecifics frequently during territorial encounters (Gabor and Jaeger 1995).

Methods.—We staged interactions between individuals in a controlled laboratory environment to mimic territorial residents and intruders. Salamanders were allowed to establish territories in separate chambers that contained an artificial cover object supplied with a food source. After the invading animal was introduced, we monitored the behavior of both animals.

We collected 30 adult *P. cinereus* and 60 adult *P. shenandoah* on Hawksbill Mountain from 11–13 June 1992, and from collection to testing maintained them in separate Petri dishes in The Pinnacles Natural Resources Laboratory in Shenandoah National Park. The mean size of the *P. cinereus* (40.5 ± 1.9 mm SVL) was significantly smaller than both the *P. shenandoah* used as residents (43.1 ± 3.9 mm SVL, Mann-Whitney test, $W_x = 187.5$, $P = 0.0002$) and the *P. shenandoah* used as invaders (42.5 ± 3.5 mm SVL, Mann-Whitney test, $W_x = 609.0$, $P = 0.0083$). The two groups of *P. shenandoah* did not differ significantly in SVL (Mann-Whitney test, $W_x = 473.0$, $P = 0.565$). The Petri dishes (150×25 mm) contained filter paper (changed every 5–7 d) dampened with spring water. We fed the salamanders live tubifex worms (Tubificidae) and kept them on a natural photoperiod at 17° – 19°C .

Five days prior to testing, each future resident was allowed to establish a territory (as in Gabor and Jaeger 1995) in an experimental chamber (polystyrene cell culture dish, $245 \times 245 \times 20$ mm) containing a moistened paper towel on the bottom and an opaque cover object (60×15 mm circular disc raised 1 cm on stilts) in the center. Every 2 d, we placed ~15 tubifex worms under the cover objects so that the salamanders would associate them with food. Because *P. shenandoah* is a federally endangered species, all tests were performed in sterile chambers and the Shenandoah salamanders were subsequently returned to their original points of capture.

We employed one control and three experimental conditions: (1) resident *P. cinereus* invaded by *P. shenandoah* ($n = 29$), (2) resident *P. shenandoah* invaded by *P. shenandoah* (for intraspecific levels of aggres-

sion: $n = 29$), (3) a surrogate replica of a salamander as a resident invaded by *P. shenandoah* (control: $n = 30$), and (4) resident *P. shenandoah* invaded by *P. cinereus* ($n = 30$). Unequal sample sizes were due to the death of one Shenandoah salamander during the experiment. The surrogate in condition 3 consisted of a rolled piece of brown, wetted paper towel approximately the size and shape of a salamander (Gabor and Jaeger 1995). It allowed us to compare the behavior of invading *P. shenandoah* toward residents in conditions 1 and 2 with the behavior of invading *P. shenandoah* toward an inanimate object in condition 3. So that we could compare differential behavior within individuals (related samples: Siegel and Castellan 1988), we tested each red-backed salamander once in condition 1, as resident, and once in condition 4, as invader, in random sequence. The 60 Shenandoah salamanders were randomly partitioned into 30 residents and 30 intruders. Each resident was tested once in condition 2 and once in condition 4, in random sequence, and each intruder was tested once in each of conditions 1, 2, and 3, in random sequence.

Although asymmetric body sizes may affect the outcomes of territorial conflicts (Maynard Smith and Parker 1976), and do so in contests between red-backed salamanders (Wise and Jaeger 1998), we did not match residents and intruders in our experiment for size or sex. We did this because (1) *P. shenandoah* reaches a significantly longer body length and a significantly broader head width than does *P. cinereus* (Jaeger 1972), and (2) we wished to mimic conditions in the forest, where adults of both sexes and a variety of sizes might interact in contests for cover objects on the forest floor.

Testing began on day 6 (sufficient time for *P. cinereus* to establish a territory by pheromonal marking: Jaeger 1981, 1984) by introducing the invader randomly into one of the four corners of the chamber. The resident was handled similarly and was placed in the corner diagonally opposite to the invader with the food-rich cover object halfway between them. Each salamander was placed under a habituation cup (60×15 mm) for 10 min and then released and observed for 15 min of interactions, using a digital stopwatch. We chose 15 min for the interactions because Gabor and Jaeger (1995) found that territorial residents of *P. cinereus* from our locality inflicted $\bar{X} = 1.93$ bites/15 min (range 0–36) on invading conspecifics, and we wished to minimize aggressive damage to the federally endangered *P. shenandoah* in our experiment. We recorded the number of bites and the total amount of time that biting occurred for each salamander. We also recorded the amount of time that each individual spent in the “all trunk raised” threat posture (Jaeger 1984, Jaeger and Schwarz 1991), the “flat” submissive posture (Jaeger 1984), and within 2 cm of the tubifex worms under the cover object. The sex of each individual was determined by the shape of the salamander’s snout.

TABLE 3. Biting behavior of *Plethodon cinereus* (*cin*) and *P. shenandoah* (*shen*) in paired laboratory encounters of territorial residents and intruders.

Null hypotheses	Results	Statistic	P
A) No significant difference among invading <i>shen</i> in time spent biting residents of <i>shen</i> , <i>cin</i> , and control	Bites to <i>shen</i> : median = 0 s (0–3 s) Bites to <i>cin</i> : median = 0 s (0–2 s) Bites to control: median = 0 s (0 s)	$F_r = 0.71$	0.715
B) No significant difference between invading <i>cin</i> and <i>shen</i> in time spent biting residents of <i>shen</i>	Bites by <i>cin</i> : median = 0 s (0–2 s) Bites by <i>shen</i> : median = 0 s (0–2 s)	$W_x = 380.5$	0.407
C) No significant difference between numbers of invading <i>shen</i> and <i>cin</i> that bit residents of <i>shen</i>	4 of 29 <i>shen</i> bit 7 of 30 <i>cin</i> bit	Fisher's test	0.506
D) No significant difference in time that residents of <i>shen</i> spent biting invading <i>shen</i> and <i>cin</i>	Bites to <i>shen</i> : median = 0 s (0–16 s) Bites to <i>cin</i> : median = 0 s (0–12 s)	$T^+ = 31.5$	0.894
E) No significant difference in time that residents of <i>cin</i> and <i>shen</i> spent biting invading <i>shen</i>	Bites by <i>cin</i> : median = 0 s (0–4 s) Bites by <i>shen</i> : median = 0 s (0–16 s)	$W_x = 361.0$	0.262
F) No significant difference between numbers of residential <i>shen</i> and <i>cin</i> that bit intruding <i>shen</i>	8 of 30 <i>shen</i> bit 3 of 29 <i>cin</i> bit	Fisher's test	0.181
G) No significant regression for <i>shen</i> invaders in time spent biting as a function of their SVL relative to SVL of resident <i>cin</i>		$R^2 = 0.070$	0.164
H) No significant regression for <i>shen</i> residents in time spent biting as a function of their SVL relative to SVL of invading <i>cin</i>		$R^2 = 0.016$	0.511

Note: F_r = Friedman's test, W_x = Mann-Whitney test, T^+ = Wilcoxon test, R^2 = linear regression. All times measured in seconds.

We used the nonparametric Mann-Whitney test (two-tailed) to analyze behavioral differences between species and between sexes within species. For individuals of *P. shenandoah* used twice as residents (in conditions 2 and 4), we employed the nonparametric Wilcoxon test (two-tailed) for related samples. For individuals of *P. shenandoah* used three times as intruders (in conditions 1, 2, and 3), we employed the nonparametric Friedman's test for related samples. We also used Fisher's exact test to compare between species the numbers of individuals that bit (invading *P. shenandoah* vs. invading *P. cinereus* that bit territorial residents of *P. shenandoah*, and territorial residents of *P. shenandoah* vs. territorial residents of *P. cinereus* that bit invading *P. shenandoah*). We employed linear regression to compare time spent biting as a function of relative body size (SVL of invader minus SVL of resident). Alpha was 0.05 in all tests.

Results.—In no analysis did *P. shenandoah* and *P. cinereus* demonstrate significant differences in amounts of time spent biting opponents, either as invaders (Table 3A, B) or as residents (Table 3D, E). Also, the numbers of individuals that bit in contests did not differ significantly between the species for invaders (Table 3C) or for residents (Table 3F). The body lengths of *P. shenandoah*, relative to those of *P. cinereus*, did not significantly affect the amount of time devoted to biting as invaders (Table 3G) or as residents (Table 3H).

Invading individuals of *P. shenandoah* did not differ significantly in time spent threatening residents of *P. cinereus* (median = 349 s, range 53–819 s), of *P. shenandoah* (median = 346 s, range 0–845 s), or the sur-

rogate control (median = 303 s, range 129–644 s): Friedman's $F_r = 2.55$, $P = 0.279$. They also did not differ significantly in submission toward residents of *P. cinereus* (median = 0 s, range 0–175 s), residents of *P. shenandoah* (median = 0 s, range 0–91 s), or the surrogate control (median = 0 s, range 0–12 s): $F_r = 1.45$, $P = 0.485$. There was no significant difference in time spent near the food source when with *P. cinereus* (median = 0 s, range 0–250 s), with *P. shenandoah* (median = 13 s, range 0–109 s), or with the surrogate control (median = 11 s, range 0–144 s): $F_r = 4.21$, $P = 0.122$.

When in chambers inhabited by *P. shenandoah*, there was no significant difference in time spent in threat by invading *P. shenandoah* (median = 346 s, range 0–845 s) and by invading *P. cinereus* (median = 459 s, range 145–879 s): Mann-Whitney $W_x = 360.5$, $P = 0.259$. There also was no significant difference in time spent in submission by invading *P. shenandoah* (median = 0 s, range 0–91 s) and by invading *P. cinereus* (median = 0 s, range 0–53 s): $W_x = 463.5$, $P = 0.666$. However, time spent near the food supply was significantly greater for invading *P. shenandoah* (median = 13 s, range 0–109 s) than for invading *P. cinereus* (median = 0 s, range 0–266 s): $W_x = 565.0$, $P = 0.049$.

Residents of *P. shenandoah* did not differ significantly in time threatening invading *P. shenandoah* (median = 458 s, range 0–862 s) vs. invading *P. cinereus* (median = 387 s, range 0–790 s) (Wilcoxon's $T^+ = 174.0$, $P = 0.229$), in time submissive toward them (toward invading *P. shenandoah*, median = 0 s, range 0–114 s; toward invading *P. cinereus*, median = 0 s, range 0–182 s: $T^+ = 52.0$, $P = 0.308$), or in time near

the food source (with invading *P. shenandoah*, median = 55 s, range 0–412 s; with invading *P. cinereus*, median = 33 s, range 0–269 s: $T^+ = 199.5$, $P = 0.497$).

When comparing the behavior of residents of *P. cinereus* and *P. shenandoah*, when invaded by *P. shenandoah*, there was no significant difference in time spent in threat (for residential *P. cinereus*, median = 375 s, range 0–842 s; for residential *P. shenandoah*, median = 485 s, range 0–862 s: Mann-Whitney $W_x = 352.5$, $P = 0.211$) or in submission (for residential *P. cinereus*, median = 0 s, range 0–206 s; for residential *P. shenandoah*, median = 0 s, range 0–114 s: $W_x = 525.0$, $P = 0.172$). However, time spent near the food source was significantly greater for residents of *P. shenandoah* (median = 55 s, range 0–412 s) than for residents of *P. cinereus* (median = 17 s, range 0–264 s): $W_x = 281.0$, $P = 0.020$.

When comparing sexes within species, we found no significant differences for either species as residents or intruders with the following exception: when invading territories held by *P. cinereus*, males of *P. shenandoah* spent significantly more time in threat (median = 517 s, range 262–819 s, $n = 12$) than did conspecific females (median = 279 s, range 53–780 s, $n = 17$): Mann-Whitney $W_x = 171.0$, $P = 0.002$.

Inferences.—We cannot refute the null hypothesis that the two species are equally aggressive in interspecific encounters. Thus, the competitive dominance of *P. cinereus* over *P. shenandoah* in the forest (cf. competitive release experiment above) cannot be explained by differences in willingness to bite. Indeed, Shenandoah salamanders were significantly more successful than red-backed salamanders in gaining access to the food-rich cover objects in the chambers, both as residents and as intruders.

DISCUSSION

In the forest, *P. shenandoah* was better able, during both summers, to occupy cover objects where *P. cinereus* had been removed than where *P. cinereus* was present. Thus, red-backed salamanders defend their territories against Shenandoah salamanders. The quadrat study revealed that there was not a large number of Shenandoah salamanders living in the leaf litter waiting to occupy “empty” cover objects. The relatively rapid occupancy of empty cover objects in the competitive release experiment, however, suggests that Shenandoah salamanders will occupy available cover objects when they are not guarded by red-backed salamanders. Because *P. cinereus* aggressively defends territories against conspecifics by biting (under laboratory conditions: Jaeger 1981, Gabor and Jaeger 1995; on the forest floor: Gergits and Jaeger 1990b) and against juveniles of *P. glutinosus* (Lancaster and Jaeger 1995), we predicted that this species would be a “better biter” in interspecific defense against *P. shenandoah*. Our behavioral experiment did not reveal such a difference.

After 27 yr of research (beginning with Jaeger 1970),

we are now beginning to understand how one species can limit dispersion, from source to sinks, in another species’ metapopulation through interspecific competition. Individuals of *P. shenandoah* emigrate from the source subpopulation on the top of Hawksbill Mountain and become sympatric with *P. cinereus* for a short distance (up to ~11 m) from the talus–deep soil interface. In that area of sympatry, *P. shenandoah* maintains a low density (~0.1 individual/m²) relative to that of *P. cinereus* (~1.2 individuals/m² in our study). However, dispersal by Shenandoah salamanders beyond 11 m appears to be prevented through territorial defense of cover objects by *P. cinereus*. Cover objects are important to both species because rocks and logs provide patches of moisture on the forest floor during dry periods between rainfalls (Jaeger 1980b). Because salamanders are amphibians (and thus are subject to desiccation) and plethodontid salamanders are lungless (and thus respire primarily through the skin), patches of moisture are essential to both Shenandoah salamanders and red-backed salamanders when foraging on the forest floor during dry periods (Jaeger 1980b). Territorial defense of cover objects by red-backed salamanders thus appears to inhibit dispersal of Shenandoah salamanders beyond the 11-m zone of competition. One of the sink subpopulations of *P. shenandoah* is within this zone of competition (map of source and this sink in Jaeger 1970: Fig. 4), while other sink subpopulations lie farther down the side of the mountain outside of this zone of competition (maps in Jaeger 1970: Figs. 1 and 2). These more distant sink subpopulations, then, probably receive few or no immigrants from the source subpopulation. One of these distant sink subpopulations became extinct in autumn 1970 during a drought and had not been re-established by the end of Jaeger’s (1980a) yearly censuses in 1979. Jaeger and D. E. Barnard (*unpublished data*) found no evidence that this sink patch of talus had been re-colonized as late as 1994. Federal permit restrictions for studies of the endangered Shenandoah salamander have not allowed recent censuses of other sink subpopulations.

At the present time, *Plethodon shenandoah* on Hawksbill Mountain appears to conform to a “core–satellite” case of a metapopulation (sensu Harrison 1991, Doak and Mills 1994). That is, the source (core) subpopulation at the top of the mountain is relatively large in both area inhabited and number of Shenandoah salamanders present, such that the species would be little impacted even if all of the sink (satellite) subpopulations were to go extinct. Looking into the distant future, though, one might consider *P. shenandoah* on this mountain to be a nonequilibrium metapopulation (sensu Harrison 1991, Doak and Mills 1994). In this sense, the areas of talus containing both the source and the sink subpopulations are disintegrating slowly through erosion (Jaeger 1970). Thus, what appears presently to be a stable metapopulation may, in the long term, be a slowly declining metapopulation. Because

of the slow disintegration of all areas of talus containing this species, and the long-term dim prospects for the survival of the species (Jaeger 1980a), *P. shenandoah* was listed as a federally endangered species in 1989.

Empirical studies of how interspecific competition affects a metapopulation are relatively rare (Hastings and Harrison 1994). The research program on the interactions between *P. cinereus* and *P. shenandoah* demonstrates how complex such studies can be. This research program required field observations to determine distributions and dispersion patterns (Jaeger 1970, Highton 1972) and population fluctuations (Jaeger 1980a) of the two species, field experiments on competitive exclusion (Jaeger 1971b, Mathis 1990) and resource limitation (Jaeger 1972), and laboratory experiments on agonistic behavior within and between species (e.g., Jaeger 1981, 1984, Gabor and Jaeger 1995). Even so, we still do not understand the behavioral interactions that allow red-backed salamanders to exclude Shenandoah salamanders from favorable territorial sites on the forest floor. Highton (1972) proposed that *P. shenandoah* was the first of the two species to inhabit mountainous areas such as Hawksbill Mountain, followed by later invasion from *P. cinereus* moving into the mountains from lowland habitats. *Plethodon shenandoah* is presently restricted to a metapopulation of a source and a few sink subpopulations in areas of talus as a consequence of that invasion by a competitively superior species. Thus, our study provides an example of how interspecific competition, through interspecific territoriality, can lead to the extinction-prone status of a fragmented population.

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