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COMPETITION AND THE EVOLUTION OF AGGRESSIVE BEHAVIOR IN TWO SPECIES OF TERRESTRIAL SALAMANDERS

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Abstract.—The effects of competition on the evolution of interspecific interference mechanisms were studied by comparing the aggressive behavior of two terrestrial salamander species from two localities that differ in the intensity of interspecific competition.

Plethodon jordani and *P. glutinosus* are closely related, ecologically similar species that are sympatric at intermediate elevations in the southern Appalachian Mountains. Previous removal and transplant experiments showed that interspecific competition is more intense in the northeastern Great Smoky Mountains, where the species are narrowly sympatric, than in the nearby Balsam Mountains, where sympatry is broader.

In laboratory encounters, *P. glutinosus* from the Great Smoky Mountains were more aggressive to heterospecific and conspecific intruders than were *P. glutinosus* from the Balsam Mountains. For *P. jordani,* however, the variation in interspecific and intraspecific aggressive behavior among individuals within populations was as great as the variation between populations. Alpha-selection (i.e., improved competitive ability by the acquisition of interspecific interference mechanisms) has occurred in populations of *P. glutinosus* under conditions of intense interspecific competition. The evolution of aggressive behavior appears to have been influenced by the intensity of intraspecific competition as well.

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Ecologists have long been interested in the evolutionary consequences of interspecific competition. Strictly defined, interspecific competition is a density-dependent decrease in the ability of individuals of one species to survive or reproduce when individuals of a competing species are present (Lotka, 1956). Because natural selection works through differential reproduction of individuals, the intensity of interspecific competition can have a profound effect on the course of evolution within a population.

Several mutually exclusive theories that predict specific evolutionary changes in animal behavior under conditions of intense interspecific competition have been proposed: e.g., character displacement (Brown and Wilson, 1956) vs. character convergence (Moynihan, 1968; Cody, 1969), *K*-selection (MacArthur and Wilson, 1967) vs. alpha-selection (Gill, 1972, 1974). However, the evidence given in support of any particular theory is usually controversial (Arthur, 1982). Behavioral or morphological studies of sympatric species are seldom accompanied by demographic studies of interspecific competition (Arthur, 1982). Because competition is assumed rather than tested, empirical studies of the evolutionary effects of competition are often tautological (Peters, 1976).

The terrestrial salamanders *Plethodon jordani* and *Plethodon glutinosus* provide a unique situation in which to study the evolutionary consequences of interspecific competition because the intensity of competition between them varies among populations. *P. jordani* and *P. glutinosus* are closely related and ecologically similar species (Highton and Henry, 1970*a,* 1970*b*; Highton and Larson, 1979; Hairston, 1980*a,* 1980*b*). Both are terrestrial, nocturnal, generalist predators (Hairston, 1949; Powders and Tietjen, 1974). In the southern Appalachian Mountains, these species are active on the forest floor from May–October (Hairston, 1980*a,* 1980*b*). Courtship occurs from late July–October and females lay eggs the following May (Highton, 1962*b*; Hairston, 1983*a*).

At low elevations in the Blue Ridge Physiographic Province, three cryptic

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species of the *P. glutinosus* complex are found (Highton, 1983; Highton and MacGregor, 1983). *P. jordani* is found at higher elevations (Hairston, 1949), and is restricted to approximately 22 populations (Hairston, 1950; Highton and Henry, 1970*a*; Highton, 1972, 1983). Each population of *P. jordani* is sympatric with *P. glutinosus* at intermediate elevations.

The vertical extent of the zone of sympatry varies among the populations (Hairston, 1949, 1951; Highton and Henry, 1970*a*; Highton, 1972). In the Great Smoky Mountains (hereafter Smoky Mountains or Smokies), the red-cheeked race of *P. jordani* is sympatric with *P. glutinosus* = *P. teyahalee* (Highton, 1983) over a narrow vertical range of only 70–120 m (Hairston, 1951). However, in the nearby Balsam Mountains, the gray-cheeked race of *P. jordani* is sympatric with the same cryptic species of *P. glutinosus* (*P. teyahalee*; Highton, 1983) over a broad vertical range of more than 1,200 m (Hairston, 1949). Hairston (1951) suggested that the narrow zone of sympatry in the Smoky Mountains resulted from strong competition and that interspecific competition must be less severe in the Balsam Mountains where the zone of sympatry is more extensive.

Hairston (1980*a*, 1980*b*) tested the hypothesis that interspecific competition is more intense in the Smokies than in the Balsams with removal and transplant experiments in both areas. After removal of either species from the habitat, the increase in abundance of the remaining species was larger and faster in the Smokies than in the Balsams. These results supported the prediction that interspecific competition is more intense where sympatry is narrow than where it is extensive (Hairston, 1980*a*).

P. jordani were also transplanted reciprocally between the Balsam and Smoky Mountains (Hairston, 1980*b*). The transplant experiments showed that: 1) Smokies salamanders of both species had a greater impact on salamanders from the Balsam Mountains than Balsam Mountains salamanders had on each other; and 2) Balsams salamanders of both species had even less impact on the abundance of Smokies salamanders than Balsam salamanders had on each other (Hairston, 1980*b*). These results suggested that the competitive abilities (i.e., alpha of the Lotka-Volterra equations) of both species have increased in the Smoky Mountains since the isolates of *P. jordani* were formed.

Hairston (1980*b*, 1983*b*) further suggested that competitive ability may have increased by the evolution of an interspecific interference mechanism, such as aggressive behavior, in the Smoky Mountains population. However, the underlying behavioral mechanism for competition between *P. jordani* and *P. glutinosus* was not revealed by Hairston's (1980*a*, 1980*b*) experiments. Reports of aggression and territorial behavior in other species of *Plethodon* have also suggested that interference competition occurs among terrestrial salamanders (Jaeger, 1981, 1984; Jaeger et al., 1982).

The purpose of the present research was to study the effects of interspecific competition on the evolution of interspecific interference mechanisms by comparing the aggressive behavior of Balsam and Smoky Mountains salamanders. Specifically, I test the hypothesis that the frequency of interspecific aggression is higher between salamanders from populations where interspecific competition is intense (Smoky Mountains) than between salamanders from populations where interspecific competition is less severe (Balsam Mountains). I also test the null hypothesis that the frequency of intraspecific aggression does not differ between salamanders from the two localities. This is a null hypothesis because the relative intensity of intraspecific competition in the two populations cannot be predicted a priori from Hairston's (1980*a*, 1980*b*) experiments.

MATERIALS AND METHODS

Adult males and females of *Plethodon jordani* and *P. glutinosus* were collected from the Balsam and Smoky Mountains during May–August of 1981 and 1982. In the Balsam Mountains, salamanders were collected within 1 km of Hairston's (1980*a*, 1980*b*) study site along Courthouse Creek, Pisgah National Forest, Transylvania County, North Carolina (35°16′22″N, 82°53′20″E). In the Great Smoky Mountains, salamanders were collected along the Heintooga-Roundbottom Road, Great Smoky Mountains National Park, Swain County, North Carolina (35°37′30″N, 83°10′22″E). This site is approximately 8 km east of Hairston's (1980*a*, 1980*b*) study site (which was made inaccessible when the Park road was closed in 1978) and is approximately 50 km northwest of the Balsam study site. Transect data collected at this site over a 10-yr period show that the vertical extent of sympatry is also narrow (less than 50 m) in this area, indicating strong competition (Hairston, 1980*a*).

Salamanders were kept in the laboratory on an artificial 12L:12D photoperiod at an ambient temperature of 15–18°C. Each salamander was placed alone in a covered plastic dish (18.5 cm in diameter and 8 cm high) lined with wet filter paper and was fed 50–75 *Drosophila melanogaster* once per week. Under these conditions, virtually all salamanders of both species gained weight during the study. The salamanders were allowed to habituate to laboratory conditions and to establish residence in their chambers for at least three days prior to testing.

Residents were observed during encounters with heterospecific and/or conspecific intruders (experimental conditions), and in the absence of intruders (control condition). Each resident was observed only once in each condition (i.e., with heterospecific, with conspecific, or alone). However, the same salamander was occasionally used more than once as an intruder. The observations were made in random sequence at two day intervals. All residents were fed approximately 25–30 *D. melanogaster* 48 hr prior to each test in order to control the level of satiation. Only encounters between sympatric adult salamanders of the same sex were included in the analysis. Sex and reproductive state were confirmed by dissection.

Residents and intruders were paired at random with respect to body size. Average body weight of residents and average difference in body weight between residents and intruders did not differ significantly between Balsam and Smokies salamanders of either species in any of the test conditions (*t*-tests, two-tailed, $\alpha = 0.05$). In nature, *P. glutinosus* adults are larger, on the average, than adult *P. jordani* (Hairston, 1983*b*). In all but two encounters, *P. glutinosus* was larger than *P. jordani.*

Encounters were initiated by inverting the chamber of an intruder over the chamber of a resident, so that neither salamander was handled prior to testing. In order to simulate natural nocturnal foraging conditions during laboratory tests, all observations were made under dim, broad spectrum red light at least 0.5 hr after the initiation of the dark phase in the L:D cycle, and 25–30 *D. melanogaster* were added to the resident's chamber at the beginning of each test. Salamanders were observed for 45 min during encounters and for 20 min in the control condition when intruders were absent.

During encounters, the frequencies of 10 behavior patterns were recorded for the resident salamander. Brief operational definitions of these behavior patterns follow:

Non-aggressive Behavior Patterns

1) PURSUE FLY: a salamander takes at least one step toward a fly before striking at it.

2) EAT FLY: a salamander ingests a fly.

3) NOSETAP: a salamander presses its nasolabial cirri against the substrate, the intruder, fecal material, or itself.

4) APPROACH: a salamander moves directly toward an intruder (i.e., in a direction that, if continued, would eventually result in contact with the intruder).

5) CONTACT: a salamander touches

an intruder with any part of its body other than its mouth.

6) TURN HEAD: a salamander turns its head directly toward an intruder.

Aggressive Behavior Patterns

1) SNAP: a salamander opens its jaws and snaps them shut. SNAPs may occasionally produce an audible sound.

2) LUNGE: a salamander moves rapidly and directly toward an intruder, but stops before making contact.

3) CHASE: a salamander moves rapidly and directly toward a retreating intruder.

4) BITE: a salamander contacts an intruder with its mouth. Biting may cause injuries such as skin lacerations or loss of up to 25% of the tail.

In the absence of intruders, only the frequencies of PURSUE FLY, EAT FLY, NOSETAP, APPROACH, and SNAP were recorded. When intruders are absent, APPROACH is defined as movement toward an arbitrary reference point in the experimental chamber, and SNAP is performed after the ingestion of prey. Although SNAP occurs in both aggressive and non-aggressive contexts, no effort was made to distinguish its context during encounters. All instances of SNAP were assumed to be aggressive when an intruder was present and to be non-aggressive when an intruder was absent. Analyses of aggressive behavior were performed both with and without SNAP to assure that these assumptions did not affect the interpretation of results. Omission of SNAP from the analyses did not affect the significance level of any statistical comparison between the populations.

Sixty-five interspecific encounters between sympatric Smoky Mountains salamanders (40 *P. jordani* residents and 25 *P. glutinosus* residents) and 56 interspecific encounters between sympatric Balsam Mountains salamanders (29 *P. jordani* and 27 *P. glutinosus* residents) were observed. In intraspecific encounters, 15 pairs of *P. jordani* and 16 pairs of *P. glutinosus* from the Smoky Mountains, and 21 pairs of *P. jordani* and 19 pairs of *P. glutinosus* from the Balsam Mountains were observed. Eighteen *P. jordani* and 12 *P. glutinosus* from the Smoky Mountains, and 19 *P. jordani* and 18 *P. glutinosus* from the Balsam Mountains were observed in the absence of intruders. These data were used to test the ten hypotheses listed in Table 1.

The frequencies of individual behavior patterns did not differ significantly between males and females for either species under any test conditions (Mann-Whitney U-tests, two-tailed, $\alpha = 0.05$). Separate analyses of behavior patterns by sex are not presented.

For each species, and for each condition, the frequencies of aggressive and non-aggressive behavior patterns performed by salamanders from the Balsam vs. Smoky Mountains were compared using principal component analysis (PCA) as a summarizing statistic. For intraspe-

TABLE 1. A summary of the null hypotheses tested for *P. glutinosus* and *P. jordani*. In all, 10 null hypotheses were tested, using principal component analysis to summarize variation in aggressive and non-aggressive behavior.

A) Interspecific aggression
  1) There are no differences in the frequencies of aggressive behavior performed by salamanders from the Balsam and Smoky Mountains in the presence of heterospecifics.
  2) There are no differences in the frequencies of non-aggressive behavior performed by salamanders from the Balsam and Smoky Mountains in the presence of heterospecifics.

B) Intraspecific aggression
  1) There are no differences in the frequencies of aggressive behavior performed by salamanders from the Balsam and Smoky Mountains in the presence of conspecifics.
  2) There are no differences in the frequencies of non-aggressive behavior performed by salamanders from the Balsam and Smoky Mountains in the presence of conspecifics.

C) Control: intruders absent
  1) There are no differences in the frequencies of non-aggressive behavior performed by salamanders from the Balsam and Smoky Mountains in the absence of intruders.

TABLE 2. Factor loadings of individual behavior patterns on the first principal components of aggressive and non-aggressive behavior for *Plethodon jordani* and *Plethodon glutinosus* during interspecific and intraspecific encounters. Principal components were calculated for A) aggressive and B) non-aggressive behavior patterns separately. Salamanders from the Balsam and Smoky Mountains are included in each analysis. Note that all behavior patterns load strongly and positively on most of the principal components.

A) Aggressive behavior patterns:

	Interspecific encounters		Intraspecific encounters	
	P. jordani	*P. glutinosus*	*P. jordani*	*P. glutinosus*
Snap	0.697	0.606	0.673	0.726
Lunge	0.753	0.809	0.466	0.915
Chase	0.745	0.279	0.796	0.921
Bite	0.922	0.794	0.931	0.888

B) Non-aggressive behavior patterns:

	Interspecific encounters		Intraspecific encounters	
	P. jordani	*P. glutinosus*	*P. jordani*	*P. glutinosus*
Pursue fly	0.782	0.694	0.782	0.731
Eat fly	0.770	0.851	0.747	0.698
Nosetap	0.526	0.389	0.574	0.574
Approach	0.591	0.797	0.823	0.753
Contact	0.288	0.413	0.529	0.767
Turn head	0.643	0.740	0.762	0.730

cific and interspecific encounters, separate principal component analyses of aggressive behavior patterns (i.e., SNAP, LUNGE, CHASE, BITE) and non-aggressive behavior patterns (i.e., PURSUE FLY, EAT FLY, NOSETAP, APPROACH, CONTACT, TURN HEAD) were performed for each species. For the control condition a principal component analysis of the non-aggressive behavior patterns was performed for each species. In all, there were 10 PCA's and 10 first principal components. For each species and for each treatment, the first principal component was calculated from the combined data for both the Balsam and Smoky Mountains populations.

The PCA solutions were calculated from the Pearson product-moment correlation matrices without rotation, using the Cyber 6000 version of SPSS, subprogram Factor (Nie et al., 1975). For each salamander, one factor score on each first principal component was calculated. A factor score is the sum over all behavioral variables of the observed values of each variable weighted by the factor loading of that variable on the first component of the PCA solution. The factor loadings vary between 1.0 and −1.0.

The loadings of individual behavior patterns on the first principal components of aggressive and non-aggressive behavior for *P. jordani* and *P. glutinosus* are shown in Table 2. All aggressive behavior patterns loaded strongly (i.e., factor loadings close to the maximum value of +1.0) on most of the first principal components of aggressive behavior. All non-aggressive behavior patterns loaded strongly on most of the first principal components of non-aggressive behavior.

TABLE 3. Factor loadings of individual non-aggressive behavior patterns on the first principal components of non-aggressive behavior for *P. jordani* and *P. glutinosus* in the absence of intruders (control). Salamanders from the Balsam and Smoky Mountains are included in each analysis. Note that feeding behavior patterns loaded more strongly than other behavior patterns on the first principal components.

Non-aggressive behavior patterns	Control: Intruders absent	
	P. jordani	*P. glutinosus*
Pursue fly	0.787	0.793
Eat fly	0.835	0.907
Nosetap	−0.212	0.357
Approach	0.408	0.055
Snap	0.474	0.282

TABLE 4. Mean factor scores on the first principal components of aggressive and non-aggressive behavior for *P. glutinosus* residents from the Balsam and Smoky Mountains during interspecific and intraspecific encounters and in the absence of intruders, and the probability (P) that means differ between populations (t-tests, $\alpha = 0.05$). (N = number of encounters observed).

	Balsams	Smokies	P
A) Interspecific encounters	$N = 27$	$N = 25$	
1. Aggressive behavior[1]	−0.2875	0.3105	0.018*
2. Non-aggressive behavior	−0.2892	0.3123	0.031*
B) Intraspecific encounters	$N = 19$	$N = 16$	
1. Aggressive behavior	−0.2359	0.2801	0.163
2. Non-aggressive behavior	−0.0824	0.0978	0.611
C) Control	$N = 18$	$N = 12$	
1. Non-aggressive behavior	0.0920	−0.1380	0.584

[1] One-tailed test.
* Significant difference.

Table 3 shows the loadings of individual behavior patterns on the first principal components of non-aggressive behavior for *P. jordani* and *P. glutinosus* residents from both areas in the absence of intruders. In general, covariation among non-aggressive behavior patterns is less apparent when intruders are absent than during intra- or interspecific encounters. Feeding behavior patterns loaded more strongly than other behavior patterns on the first principal components of non-aggressive behavior (Table 3). In all PCAs, the second and subsequent principal components accounted for non-significant proportions of the total variance (i.e., all eigenvalues <1.0).

The average factor scores on the first principal components of interspecific aggressive behavior for the Balsam and Smoky Mountains populations were compared by t-tests (one-tailed, $\alpha = 0.05$). The one-tailed test is justified by the a priori prediction that aggression will be more frequent among Smoky Mountains salamanders. All other average factor scores were compared by two-tailed t-tests, because no difference between populations was predicted.

As a quantitative representation of aggressive and non-aggressive behavior, factor scores on first principal components are preferable to the frequencies of the individual behavior patterns for three reasons: i) because no two behavior patterns can be performed simultaneously, an additive representation of the behavior patterns may more accurately reflect the intensity of aggressive behavior than an analysis of single behavior patterns; ii) only ten statistical tests (Table 1) are required to distinguish the behavior of the two populations of both species in all three of the test conditions, whereas analysis of each behavior pattern separately would require 25 tests for each species; iii) factor scores conform to a multivariate-normal distribution with zero mean and unit variance, and can be analyzed by parametric statistics.

RESULTS

Plethodon glutinosus: *Interspecific Encounters*

The average factor scores on the first principal components of aggressive and non-aggressive behavior for *Plethodon glutinosus* residents from the Balsam and Smoky Mountains are shown in Table 4. The first principal component of aggressive behavior during interspecific encounters explained 43.2% of the total aggression variance (eigenvalue = 1.73). *P. glutinosus* from the Smoky Mountains had significantly higher factor scores on the first principal component of interspecific aggressive behavior than *P. glutinosus* from the Balsam Mountains (Table 4). During interspecific encounters, LUNGE, CHASE, and BITE were exhibited more frequently by Smokies *P. glu-*

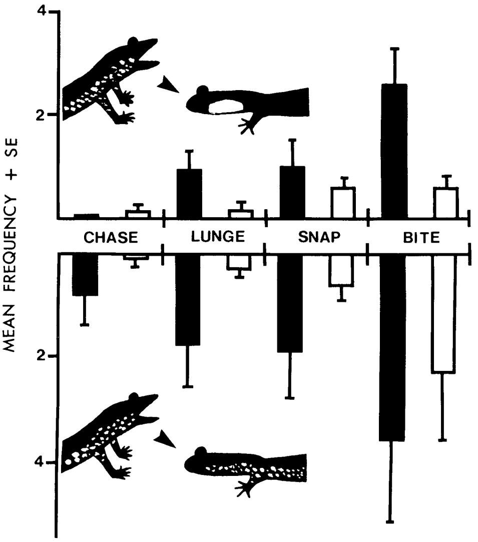

FIG. 1. Average frequency (+1 SE) of aggressive behavior patterns exhibited by *Plethodon glutinosus* residents from the Smoky and Balsam Mountains A) during encounters with sympatric *P. jordani*; and B) during encounters with sympatric conspecifics. Solid bars = Smoky Mountains; open bars = Balsam Mountains. Note that most solid bars are higher than open bars. The salamanders in the legend illustrate the species of the resident and the intruder. *P. jordani* is shown with a white cheek, and *P. glutinosus* is shown with white spots. Residents are symbolized by upright posture and intruders by prostrate posture.

tinosus than by Balsams *P. glutinosus* (Fig. 1A).

The first principal component of non-aggressive behavior explained 45.2% of the total non-aggression variance for *P. glutinosus* during interspecific encounters (eigenvalue = 2.71). Smoky Mountains *P. glutinosus* exhibited significantly higher factor scores on the first principal component of non-aggressive behavior than Balsam Mountains *P. glutinosus* (Table 4). The average frequencies of all individual non-aggressive behavior patterns were higher for Smoky Mountains *P. glutinosus* than for Balsam Mountains *P. glutinosus* (Table 5).

Plethodon glutinosus: *Intraspecific Encounters*

The average factor scores on the first principal components of aggressive and non-aggressive behavior for *Plethodon glutinosus* residents from the Balsam and Smoky Mountains during intraspecific encounters are shown in Table 4. The first principal component of aggressive behavior explained 75% of the total aggression variance (eigenvalue = 3.00), and the first principal component of non-aggressive behavior explained 50.6% of the non-aggression variance (eigenvalue = 3.04).

Neither the aggressive nor the non-aggressive factor scores on the respective first principal components differed significantly between the Balsam and Smoky Mountains populations (Table 3). The average frequencies of all individual non-aggressive behavior patterns, except TURN HEAD, were higher for Smokies *P. glutinosus* than for Balsams *P. gluti-*

TABLE 5. Mean frequencies ($\bar{x}$) and standard errors (SE) of non-aggressive behavior patterns exhibited by *P. glutinosus* residents from the Balsam and Smoky Mountains during 45 min encounters with sympatric congeneric and conspecific intruders.

	Interspecific encounters				Intraspecific encounters			
	Balsams		Smokies		Balsams		Smokies	
Behavior	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Nosetap	15.37	3.34	23.28	4.59	12.05	2.76	13.19	2.94
Eat fly	7.59	0.78	9.60	1.02	7.68	1.37	8.06	1.59
Turn head	6.33	0.83	6.52	0.83	5.84	0.92	4.19	0.90
Pursue fly	3.19	0.52	4.68	0.64	3.58	0.69	4.56	1.13
Approach	3.07	0.52	5.88	1.03	3.26	0.69	5.38	1.74
Contact	0.63	0.18	1.56	0.47	0.58	0.25	1.13	0.51

TABLE 6. Mean factor scores on first principal components of aggressive and non-aggressive behavior for *P. jordani* residents from the Balsam and Smoky Mountains during interspecific and intraspecific encounters and in the absence of intruders, and the probability (P) that means differ between populations (t-test, $\alpha = 0.05$). (N = number of encounters observed).

	Balsams	Smokies	P
A) Interspecific encounters	$N = 29$	$N = 40$	
1. Aggressive behavior[1]	0.0481	−0.0349	0.736
2. Non-aggressive behavior	−0.0533	0.0386	0.695
B) Intraspecific encounters	$N = 21$	$N = 15$	
2. Aggressive behavior	0.1137	−0.1592	0.396
2. Non-aggressive behavior	−0.1973	0.2762	0.172
C) Control	$N = 19$	$N = 18$	
1. Non-aggressive behavior	0.0124	−0.0131	0.939

[1] One-tailed test.

nosus during intraspecific encounters (Table 5). The frequencies of all aggressive behavior patterns were higher during encounters between *P. glutinosus* from the Smoky Mountains than between Balsams *P. glutinosus* (Fig. 1B).

Plethodon jordani: *Interspecific Encounters*

P. jordani from the Balsam and Smoky Mountains did not differ significantly in average factor scores on the first principal component of aggressive behavior during interspecific encounters (Table 6). The sample sizes were higher for *P. jordani* than for *P. glutinosus,* and the first principal component of aggressive behavior accounted for a greater proportion (61.4%) of the variance (eigenvalue = 2.46). The average frequencies of SNAP and CHASE during interspecific encounters were higher for Smokies *P. jordani* than for Balsams *P. jordani,* but LUNGE and BITE were exhibited more frequently by Balsam *P. jordani* (Fig. 2A).

There were also no differences between populations in the average factor scores on the first principal component of non-aggressive behavior (Table 6), which explained 38.8% of the non-aggression variance (eigenvalue = 2.33). The average frequencies of individual non-aggressive behavior patterns were not consistently higher for *P. jordani* from either population (Table 7).

Plethodon jordani: *Intraspecific Encounters*

Table 7 shows the average factor scores on the first principal components of aggressive and non-aggressive behavior for Balsam and Smoky Mountains *P. jordani* during intraspecific encounters. There were no differences between populations in the average factor scores on the first principal component of aggressive behavior (54.2% of the variance, eigenvalue = 2.17; Table 6). The average frequency of LUNGE was higher during encounters between Smokies *P. jordani,* but SNAP, CHASE, and BITE were more frequent during encounters between Balsams *P. jordani* (Fig. 2B). The first principal component of non-aggressive behavior explained 50.6% of the non-aggression variance (eigenvalue = 3.04). The average factor scores on the first principal component of non-aggressive behavior did not differ significantly between populations (Table 6). The average frequencies of all individual non-aggressive behavior patterns, except PURSUE FLY, were higher during encounters between Smokies *P. jordani* than during encounters between Balsam *P. jordani* (Table 7).

Control Observations: Intruders Absent

For *P. glutinosus,* the average factor scores on the first principal component of non-aggressive behavior (33.2% of to-

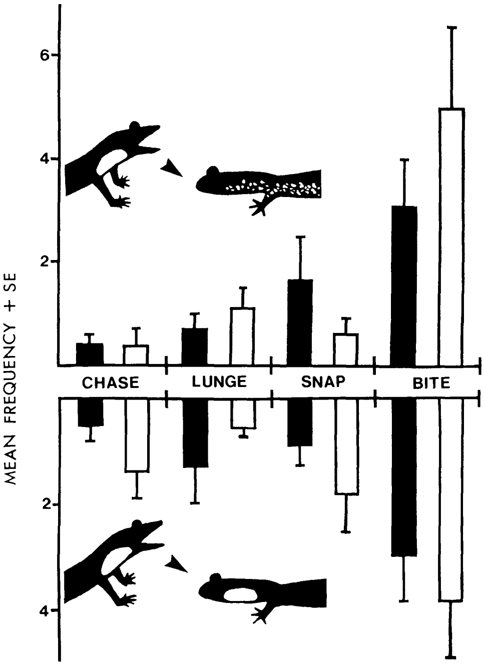

Fig. 2. Average frequency (+1 SE) of aggressive behavior patterns exhibited by *Plethodon jordani* residents from the Smoky and Balsam Mountains A) during encounters with sympatric *P. glutinosus*; and B) during encounters with sympatric conspecifics. Solid bars = Smoky Mountains; open bars = Balsam Mountains. Note that there are no consistent differences between solid and open bars. See Figure 1 for explanation of legend.

tal variance, eigenvalue = 1.66) did not differ significantly between the Balsam and Smoky Mountains populations when intruders were absent (Table 4). The average frequencies of all individual behavior patterns, except SNAP, were higher for Balsam Mountains *P. glutinosus* than for Smoky Mountains *P. glutinosus* in the absence of intruders (Table 8).

In the absence of intruders, the first principal component of non-aggressive behavior for *P. jordani* explained 35% of the total variance (eigenvalue = 1.75). The average frequencies of individual non-aggressive behavior patterns in the absence of intruders were not consistently higher for *P. jordani* from either population (Table 8). *P. jordani,* like *P. glutinosus,* showed no significant difference between populations in the average factor scores on the first principal component of non-aggressive behavior in the absence of intruders (Table 6).

Discussion

From these experiments, there is evidence that alpha-selection has occurred in *P. glutinosus* under conditions of strong interspecific competition in the Smoky Mountains. The frequencies of aggressive behavior elicited by heterospecific competitors were higher for *P. glutinosus* from the Smoky Mountains than for *P. glutinosus* from the Balsam Mountains.

The frequencies of non-aggressive behavior were also higher for Smokies *P. glutinosus* than for Balsams *P. glutinosus* during interspecific encounters. During encounters, aggressive salamanders were more active than less aggressive salamanders. However, the difference in non-aggressive behavior between the popu-

Table 7. Mean frequencies ($\bar{x}$) and standard errors (SE) of non-aggressive behavior patterns exhibited by *P. jordani* residents from the Balsam Mountains and Smoky Mountains during 45 min encounters with sympatric congeneric and conspecific intruders.

	Interspecific encounters				Intraspecific encounters			
	Balsams		Smokies		Balsams		Smokies	
Behavior	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Nosetap	10.93	2.31	16.02	2.57	3.33	0.77	8.73	3.05
Eat fly	7.41	0.89	7.40	0.80	7.67	1.71	7.73	1.80
Approach	6.72	1.34	6.57	1.10	3.10	0.82	3.67	1.32
Turn head	5.76	0.84	5.52	0.64	2.86	0.69	4.73	0.78
Pursue fly	4.14	0.59	4.02	0.58	3.86	0.94	4.73	1.13
Contact	1.38	0.40	2.97	0.81	0.33	0.16	1.00	0.36

TABLE 8. Mean frequencies ($\bar{x}$) and standard errors (SE) of non-aggressive behavior patterns exhibited by *P. jordani* and *P. glutinosus* residents from the Balsam and Smoky Mountains during 20 min observations in the absence of intruders.

	P. jordani				*P. glutinosus*			
	Balsams		Smokies		Balsams		Smokies	
Behavior	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Eat fly	12.53	1.40	12.94	1.45	12.28	0.85	11.17	2.21
Pursue fly	7.53	1.00	6.72	0.62	6.00	0.60	5.67	0.86
Nosetap	2.47	0.72	5.00	1.15	3.00	0.82	2.25	0.65
Approach	1.21	0.39	1.22	0.29	0.94	0.15	0.50	0.15
Snap	1.05	0.28	1.72	0.45	1.06	0.45	1.25	0.68

lations of *P. glutinosus* only occurred during encounters with heterospecifics. There were no differences in the frequencies of non-aggressive behavior patterns when intruders were absent. Thus, differences in non-aggressive behavior between populations cannot account for the observed differences in aggressive behavior between the populations.

For *P. glutinosus,* variation in intraspecific aggression was similar to variation in interspecific aggression. During intraspecific encounters, the frequencies of aggressive behavior exhibited by Smokies *P. glutinosus* were higher than the frequencies of aggressive behavior exhibited by Balsam *P. glutinosus,* but the difference was not significant. For intraspecific aggressive behavior, the difference between population means and the standard errors of factor scores were comparable to the difference between population means and the standard errors for interspecific aggressive behavior. Intraspecific differences in aggressive behavior probably fell short of significance because of the smaller number of observations of intraspecific encounters (35 intraspecific observations vs. 52 interspecific observations).

There is no evidence from these experiments that alpha-selection has occurred in the Smoky Mountains population of *Plethodon jordani.* In all test conditions, there were no significant differences in aggressive or non-aggressive behavior between *P. jordani* from the Balsam and Smoky Mountains.

In another set of observations (Nishikawa, 1985), I compared the responses of individual salamanders of both species to sympatric heterospecifics with their responses to sympatric conspecifics. In matched observations, Balsam *P. jordani* were significantly less aggressive to heterospecifics than they were to conspecifics. However, in *P. jordani* from the Smoky Mountains, where interspecific competition is more intense, heterospecifics and conspecifics elicited equal frequencies of aggressive behavior. For *P. jordani,* the frequencies of aggressive behavior elicited by heterospecifics, relative to conspecifics, were greater in the Smoky Mountains population.

In *P. glutinosus* from the Balsam Mountains, heterospecifics and conspecifics elicited equally low frequencies of aggression. In *P. glutinosus* from the Smoky Mountains, heterospecifics and conspecifics elicited equally high frequencies of aggression (Nishikawa, 1985).

Hairston's (1980*a*, 1980*b*) removal experiments showed that interspecific competition limits the abundance of salamanders in both the Balsam and Smoky Mountains and that interspecific competition is more intense in the Smoky Mountains. Hairston's (1980*b*, 1983*b*) transplant experiments suggested that alpha-selection had improved the competitive abilities of both species in the Smoky Mountains. I suggest that the greater intensity of interspecific aggression among Smoky Mountains salamanders is the mechanism for the greater competitive impact of Smoky Mountains salamanders on each other and on the abundances of Balsam salamanders in Hairston's experiments.

Assuming that some aspect of aggressive behavior (e.g., stimulus recognition) is at least partially heritable, I suggest that the difference in interspecific aggression between the populations may have resulted from natural selection under different intensities of interspecific competition. Although heritable differences in simple behavior patterns have been observed in other vertebrate species (DeFries and Hegmann, 1970; Arnold, 1981*a*, 1981*b*), behavioral differences may also result from non-genetic processes such as learning. For these salamanders, this alternative is virtually impossible to test experimentally because of the difficulty in obtaining viable egg clutches from gravid females and because of the 4–5 yr period required for hatchlings to reach maturity (Highton, 1962*a*; Hairston, 1983*a*).

Gill (1972, 1974) defined alpha-selection as natural selection for improved competitive ability under conditions of interspecific competition. In his definition, improved competitive ability explicitly refers to the acquisition of interference mechanisms such as aggressive behavior. Given the assumption of heritability, the differences in aggressive behavior between populations of *P. jordani* and *P. glutinosus* strongly suggest that alpha-selection has occurred under conditions of increased interspecific competition in the Smoky Mountains.

Although alpha-selection appears to have occurred in both species, it is interesting to note that the behavioral mechanism for increased interspecific aggression differs between the species. In *P. glutinosus,* the frequency of aggression elicited by intruders (regardless of species) varies geographically with the intensity of interspecific competition. In *P. jordani,* the species-specificity of aggression varies geographically with the intensity of interspecific competition (Nishikawa, 1985).

This difference in aggressive behavior between species may be related to differences between species in population density and relative abundance. *P. jordani* is found at high population densities throughout higher elevations in the southern Appalachian Mountains (Highton and Henry, 1970*a*; Merchant, 1972; Hairston, 1980*a,* 1980*b*), and intraspecific aggression has been reported in several different populations (Organ, 1958; Hutchison, 1959; Arnold, 1972, 1976, 1977). In sympatric populations, the ratio of *P. jordani* to *P. glutinosus* is 6–8 to 1 (Hairston, 1980*a,* 1980*b*). Thus, intraspecific interactions should have a greater effect than interspecific interactions on the ability of *P. jordani* to survive and reproduce.

In the Balsam Mountains, where interspecific competition is less severe, *P. jordani* are more aggressive to conspecific intruders than they are to heterospecific intruders (Nishikawa, 1985). This is expected if intraspecific competition is relatively more intense than interspecific competition in the Balsam Mountains. Under conditions of stronger interspecific competition in the Smoky Mountains, *P. glutinosus* elicits aggression from *P. jordani* at a frequency that is equal to the frequency of intraspecific aggression (Nishikawa, 1985).

P. glutinosus exists at lower population densities than *P. jordani* throughout the southern Appalachian Mountains (Highton and Henry, 1970*a*; Merchant, 1972; Hairston, 1980*a,* 1980*b*). In sympatric populations, the less abundant *P. glutinosus* individuals should be influenced to a greater extent by interspecific interactions than by intraspecific interactions. Under conditions of intense interspecific competition, *P. glutinosus* is more aggressive to both congeneric and conspecific intruders. This suggests either that: 1) intraspecific aggression has increased as a general consequence of alpha-selection for interspecific aggression; or 2) for *P. glutinosus,* intraspecific competition is more intense in the Smoky Mountains than in the Balsam Mountains.

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