

INTERSPECIFIC AGONISTIC BEHAVIORS IN A SALAMANDER COMMUNITY: IMPLICATIONS FOR ALPHA SELECTION

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ABSTRACT: Competition between closely related species can affect behavioral interactions. Intense interspecific competition may favor the evolution of elevated levels of interspecific aggression, termed alpha selection. Salamanders of the genus *Plethodon* exhibit territorial aggression, and in some cases interference mechanisms may have evolved under the process of alpha selection. Throughout Ohio, two closely related and ecologically similar species of salamander, *Plethodon cinereus* (red-backed salamander) and *P. electromorphus* (northern ravine salamander), occur in similar habitats and can be found in sympatry. However, the occurrence of syntopic areas is infrequent compared to the range overlap of each species and seems to be limited by factors other than broad geographic factors. Here, we used salamanders from allopatric and sympatric locations to examine the behavior of both species toward interspecific intruders. We hypothesized that animals in sympatry would exhibit heightened aggression compared to salamanders from allopatric areas. We found support for this hypothesis, indicating that intense interference competition may occur between *P. cinereus* and *P. electromorphus* in sympatry. Further, our results are consistent with the hypothesis of alpha selection at the level of behavioral aggression. These results suggest that sympatry may represent an unstable equilibrium where neither species can gain a competitive advantage.

Key words: Aggression; Alpha selection; Competition; Northern ravine salamander; *Plethodon cinereus*; *Plethodon electromorphus*; Red-backed salamander; Territoriality

CHARACTERISTICS of interspecies interactions have always interested behaviorists. Interspecific relationships, such as competition, have implications for biologically significant behaviors such as habitat use and foraging (Petren and Case, 1996). Many animals that display intraspecific territoriality are also known to display aggressive behaviors towards competitors of other species (Cody, 1969; Hickerson et al., 2004; Nishikawa, 1987; Orians and Willson, 1964). Competition between species may occur for essential resources as well as for territories that contain these resources. The widespread occurrence of interspecific aggression suggests that it has evolved in many contexts and serves a variety of biological roles.

While interspecific aggression requires an investment of time and energy, it may confer a net fitness benefit to individuals that exhibit it. When interspecific competition is more intense than intraspecific competition, several changes in community characteristics may result. One possible outcome of competition

is competitive exclusion, the process where a superior competitor will cause the other competing species to become locally extinct (Gause, 1934; Jaeger, 1974; Lack, 1944). Alternatively, competition can lead to habitat or resource partitioning resulting in character displacement (Brown and Wilson, 1956; Dayan and Simberloff, 2005). Character displacement describes the pattern where two species are phenotypically similar in areas of sympatry but evolve differences in areas of allopatry (Brown and Wilson, 1956). An increase in aggressive behavior can also evolve in response to interspecific competition (Peiman and Robinson, 2007). The evolution of interference traits, such as increased aggressive behavior, in one or both of the interacting species is termed alpha selection (Gill, 1974; Hairston, 1983). Similar to tests of character displacement, evidence of alpha selection can be found by comparing behavior of individuals from allopatry and sympatry, predicting that individuals in sympatry would be more aggressive (Nishikawa, 1987). Knowing whether competitive exclusion, character displacement, or alpha selection occurs in a particular system is of paramount importance for our understanding of species' behavioral interac-

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tions, the resulting community composition, and species coexistence.

In recent years, salamanders of the genus *Plethodon* have become a model system for studying competitive interactions between species. Interspecific competition and territorial aggression within the genus *Plethodon* may be widespread and has been demonstrated for several sympatric species (Anthony et al., 1997; Jaeger, 1970; Marshall et al., 2004; Nishikawa, 1985). As a result of interspecific competition, character displacement (*P. cinereus* and *P. hoffmani*: Adams and Rohlf, 2000), competitive exclusion (*P. cinereus* and *P. shenandoah*: Jaeger, 1971), and alpha selection (*P. jordani* and *P. teyahalee*: Nishikawa, 1987) have all been documented in *Plethodon*. The species occurrence patterns of two *Plethodon* species, *P. cinereus* and *P. electromorphus*, suggest that syntopic areas (locations where both species occur) may be rare (see Fig. 1 in Deitloff et al., 2008); however, the interactions between these two species have not been extensively studied, especially within sympatric areas. Recently, Deitloff et al. (2008) examined the aggressive behaviors of these two species from allopatric populations finding that individuals of both species exhibit aggressive behavior towards conspecific and heterospecific intruders. Understanding these species' behavior patterns in sympatry is crucial for providing insight into how territorial behavior has evolved and how it might impact species' coexistence and community structure.

In this study, we examined interspecific behavioral interactions between sympatric and allopatric individuals of *P. cinereus* and *P. electromorphus*. Our goal was to understand the intensity of interspecific territorial aggression, and suggest how this behavior may influence coexistence. Because alpha selection has been inferred in species pairs where geographic overlap is narrow (Nishikawa, 1985; Wicknick, 1995) and sympatric areas of these two species seems to be infrequent, we hypothesized that *P. cinereus* and *P. electromorphus* in areas of sympatry would display more frequent aggressive behavior, potentially due to alpha selection. To test this hypothesis, we compared the relative degree of aggressive and submissive behaviors dis-

played by territorial residents of both species from sympatric areas to allopatric areas.

MATERIALS AND METHODS

Collection and Maintenance

We collected adult salamanders during daylight hours from 16–19 October 2006. We collected 25 female and 25 male allopatric *P. cinereus* from a forested site 51 km west of Youngstown in Ellsworth Township, Mahoning County (40° 46' 04" N; 80° 43' 37" W), Ohio, USA. Allopatric individuals of *P. electromorphus*, 31 females and 22 males, were collected from a forested site 26 km north of Cambridge in Liberty Township, Guernsey County (40° 09' 04" N; 81° 35' 02" W). Sympatric animals were collected 19 km northeast of Newark in Perry Township, Licking County (40° 10' 01" N; 82° 15' 28" W). A total of 29 female and 29 male sympatric *P. cinereus* and 17 female and 11 male sympatric *P. electromorphus* was collected. After collecting, animals were housed in circular Petri dishes (9 × 1.5 cm) with filter paper dampened with distilled water. Salamanders were transported to Ames, Iowa in coolers. After experiments were conducted, we euthanized salamanders using MS222.

In the laboratory, each salamander was individually housed in a 15 × 1.5 cm circular Petri dish lined with filter paper dampened with distilled water. The salamanders were placed in a refrigerator that was kept at 18–21 C with a 12:12 h light:dark photoperiod. Salamanders were maintained under these conditions for 29 d prior to the onset of the experiments. During this time, we fed the salamanders 10–15 *Drosophila* spp. once per week, moistened the filter paper three times weekly, and replaced filter paper as needed. Behavioral experiments were initiated on 18 November 2006, after the salamanders were given sufficient time to acclimate to laboratory conditions.

We determined the sex of each salamander by visual inspection of the facial region. Males were identified by square snouts and large nasolabial glands; females were identified by rounded snouts; gravid females were identified by the presence of eggs visible through the abdominal wall (Dawley, 1992). Snout-

TABLE 1.—Average snout–vent length (mm \pm 1 SD) of salamanders used in behavioral trials.

		Nongravid females	Gravid female	Male
<i>P. cinereus</i>	Allopatric	37.7 \pm 3.0	40.4 \pm 3.9	38.9 \pm 3.9
	Sympatric	34.2 \pm 4.9	39.9 \pm 2.8	38.8 \pm 3.5
<i>P. electromorphus</i>	Allopatric	38.5 \pm 5.1	43.1 \pm 6.3	41.9 \pm 7.1
	Sympatric	33.5 \pm 2.9	39.4 \pm 2.1	38.4 \pm 2.7

vent lengths (SVL) were measured to the nearest 0.1 mm using Mitutoyo Digimatic digital calipers (Table 1). Only salamanders greater than or equal to 31 mm SVL were used in behavioral experiments. For all experiments, salamanders were randomly paired, with the constraint that they were the same sex and approximately the same size (within 3 mm SVL). Thus, in our experiment, the mean size of territorial residents was not significantly different from that of intruders ($\bar{X}_{diff} = 2.05 \pm 1.47$ mm; $T = -0.035$, $P = 0.97$, NS).

Behavioral Interactions

In this experiment, we examined interspecific behavioral interactions between salamanders of each species from allopatry and sympatry. We conducted behavioral tests with four different groups as residents: (1) allopatric *P. cinereus*, (2) sympatric *P. cinereus*, (3) allopatric *P. electromorphus* and (4) sympatric *P. electromorphus*. Each resident was tested 3 times (in random order) with: (A) a heterospecific allopatric intruder, (B) a heterospecific sympatric intruder, and (C) a surrogate as a control (a rolled up paper towel approximately the size of a salamander) to account for possible differences in resident responses due to intruder identity. To avoid interobserver biases among resident populations, each observer recorded behavior of residents from each of the four resident groups. In addition the same observer recorded behavior of a particular salamander in each of the three treatments. Behavioral trials were conducted from 18 November to 12 December 2006. We randomly selected which individuals from each group would be residents (allopatric *P. cinereus*: $n = 26$; sympatric *P. cinereus*: $n = 25$; allopatric *P. electromorphus*: $n = 24$; sympatric *P. electromorphus*: $n = 26$). We matched heterospecific intruders to each resident that were the same sex (male, nongravid female, gravid female) and same

size (within 3 mm SVL). Due to restricted numbers within a few groups, some individuals were used as residents and as intruders (allopatric *P. cinereus*, nongravid females: $n = 10$; allopatric *P. electromorphus*, nongravid females: $n = 9$, males: $n = 6$; sympatric *P. cinereus*, nongravid females: $n = 10$; sympatric *P. electromorphus*, nongravid females: $n = 10$, gravid females: $n = 5$, males: $n = 10$). Half of these individuals were randomly chosen to be residents first and the remaining half were residents last, accounting for any differences in behavior resulting from using salamanders as residents and intruders. We randomly chose which residents would be tested on Day 1, 2, 3, and 4 each week. In summary, each resident was tested three times (once/week) and each intruder was used twice (once/week for two of the three weeks, the remaining trial for each resident used a surrogate). Animals that were used as residents and intruders were tested once/week as a resident for all three weeks and also once/week as an intruder for two of the three weeks. These animals were only tested once per day.

On day 1 of the experimental set up, we placed each resident into a Nunc bioassay chamber (24 \times 24 \times 2 cm) lined with a paper towel moistened with distilled water and covered with a transparent lid. We allowed each resident to establish a territory by marking the substrate with its pheromones for 7 d (Jaeger et al., 1986). The intruder was placed into a clean circular Petri dish (15 \times 1.5 cm) with moistened filter paper. We fed residents and intruders on days 2 and 5, and moistened filter paper as needed. On day 8, an intruder was introduced into each resident's chamber using clear polyethylene tubing to reduce stress of handling. We recorded resident behavioral patterns (described below) for 15 min. These observations were made

under dim illumination (60-W bulb reflected off of a white tile floor). The experiment was conducted during daylight hours (0700–1900 h). After the experiment, we placed residents and intruders into separate circular Petri dishes (15 × 1.5 cm) and resumed the care schedule described above. The same protocol was repeated for the second and third trials for each resident.

To quantify aggression and submission, we used a set of behaviors that are commonly exhibited by *Plethodon* during encounters. Three of these behaviors were described in Jaeger (1984) to evaluate aggressive and submissive behavior patterns among competitors. All trunk raised (ATR) behavior describes a threat posture when all legs are extended downward such that the head and trunk are raised above the substrate. Flattened (FLAT) behavior describes the submissive posture of the entire body pressed against the substrate. Biting (BITE) occurs when one salamander grasps another with its open mouth. The fourth behavior that we examined was edging (EDGE), which occurs when the salamander walks along the periphery of the experimental chamber with its snout or part of its body pressed or tapping against the side of the chamber; it is presumed to be an attempt to escape from the chamber (Wise and Jaeger, 1998). Specifically, we recorded the total time in seconds that residents spent in ATR, FLAT, and EDGE; and the number of bites administered to the intruder.

Data Analysis

Because behavioral data are often considerably variable and nonnormal, nonparametric approaches are typically used to assess statistical patterns in these data (e.g., Jaeger, 1984). A more powerful statistical alternative is to use standard statistical designs, but determine the significance of effects through randomization (Adams and Anthony, 1996). For our analyses, we implemented this alternative using a generalized linear mixed model (LMM) to test our hypothesis that sympatric animals would be more aggressive than allopatric animals. Our approach contained a two-factor ANOVA model with resident group (allopatric *P. cinereus*, sympatric *P. cinereus*, sympatric

P. electromorphus, allopatric *P. electromorphus*) and intruder group (allopatric, sympatric, surrogate) as fixed effects. In addition, because the same individual was presented with each type of intruder, a random effect of individual was included to account for the considerable variation among individuals. Using this model, the explained sums of squares (SS) for each factor was obtained, and the least-squares (LS) means for each group were estimated. From the LS means, all pair-wise differences between groups (*D*) were calculated, and used as a measure of group differences (see e.g., Collyer and Adams, 2007). To assess significance of these terms, we performed residual randomization (Gonzalez and Manly, 1998) following the procedure outlined in Adams and Collyer (2007) and Collyer and Adams (2007).

With residual randomization, population differences and differences due to other model effects are accounted for and preserved throughout the procedure. This is in contrast to standard randomization, where the order of individuals is shuffled irrespective of main effects or covariates. Therefore, when multiple factors are present in a model, residual randomization is superior to the standard approach, as it does not conflate variation due to main effects (e.g., differences among populations) with the error variation among individuals (see discussions in Adams and Collyer, 2007; Collyer and Adams, 2007; Freedman and Lane, 1983; Gonzalez and Manly, 1998). This approach also has higher statistical power as compared to standard permutation and restricted randomization procedures (see Anderson and ter Braak, 2003). In our analyses, the residual randomization procedure was performed 9999 times, and the proportion of random values (plus the observed) greater or equal to the observed value was treated as the significance of the effect (for statistical details, see Collyer and Adams, 2007). In this analysis we observed that when the intruder effect was significant, this difference was due to differences toward surrogate individuals (results not reported). Because of this, we ran the model a second time with the surrogate treatment removed from the intruder effect (i.e., using only allopatric and sympatric salamander intruders).

RESULTS

To test our hypothesis that sympatric salamanders would be more aggressive, we compared differences in behavior among the four resident groups and towards the two intruder types using a generalized linear mixed model with residual randomization to assess significance (Table 2). Residents of the four groups showed a significant difference in time spent in ATR and EDGE, but not in FLAT or number of bites (Table 3). Residents did not behave differently toward allopatric and sympatric intruders (Table 3), and as such these data were subsequently pooled for the following pair-wise comparisons. Sympatric residents of *P. cinereus* exhibited significantly more ATR than allopatric residents of *P. cinereus* ($D = 126.6$; $P_{\text{rand}} = 0.023$) and *P. electromorphus* ($D = 265.2$; $P_{\text{rand}} = 0.0002$; Fig. 1). Sympatric residents of *P. electromorphus* displayed more ATR than allopatric *P. electromorphus* ($D = 229.9$; $P_{\text{rand}} = 0.0003$;

Fig. 1). Allopatric *P. cinereus* spent more time in ATR than allopatric *P. electromorphus* ($D = 138.5$; $P_{\text{rand}} = 0.018$; Fig. 1). Sympatric residents of *P. electromorphus* showed more EDGE behavior than *P. cinereus* from allopatry ($D = 53.9$; $P_{\text{rand}} = 0.016$) and sympatry ($D = 45.4$; $P_{\text{rand}} = 0.006$; Fig. 2). All other pair-wise comparisons between groups were not significant. In summary, sympatric individuals of both species exhibited more aggressive behavior and less submissive behavior than individuals from allopatry.

DISCUSSION

Studying interspecific competition can aid in understanding the stability of multi-species communities. Through the process of alpha selection, species can evolve higher levels of aggression as a result of intense interference competition. The goal of this study was to determine whether enhanced interspecific aggression was exhibited by sympatric sala-

TABLE 2.—Residents' responses to allopatric and sympatric interspecific intruders. The behaviors all trunk raised (ATR) and biting (BITE) are considered to be aggressive behaviors, and flattened body (FLAT) and edging behavior (EDGE) are considered submissive behaviors.

Resident		Intruder					
Allopatric <i>P. cinereus</i>	Behavior	Allopatric <i>P. electromorphus</i>			Sympatric <i>P. electromorphus</i>		
		Mean	Median	Range	Mean	Median	Range
	ATR (s)	260.0	265	0-625	301.8	322	0-860
	FLAT (s)	4.0	0	0-75	43.4	0	0-900
	EDGE (s)	27.4	0	0-227	14.4	0	0-92
	BITE (number)	0.16	0	0-1	0.52	0	0-7
Sympatric <i>P. cinereus</i>	Behavior	Allopatric <i>P. electromorphus</i>			Sympatric <i>P. electromorphus</i>		
		Mean	Median	Range	Mean	Median	Range
	ATR (s)	377.7	390	0-870	437.4	460	0-855
	FLAT (s)	56.7	0	0-900	26.0	0	0-528
	EDGE (s)	18.4	0	0-259	40.3	0	0-297
	BITE (number)	0.36	0	0-5	1.40	0	0-12
Allopatric <i>P. electromorphus</i>	Behavior	Allopatric <i>P. cinereus</i>			Sympatric <i>P. cinereus</i>		
		Mean	Median	Range	Mean	Median	Range
	ATR (s)	130.5	57	0-686	154.2	78	0-660
	FLAT (s)	47.9	0	0-424	70.0	0	0-679
	EDGE (s)	55.0	4.5	0-385	53.6	0	0-236
	BITE (number)	0.71	0	0-10	0.21	0	0-3
Sympatric <i>P. electromorphus</i>	Behavior	Allopatric <i>P. cinereus</i>			Sympatric <i>P. cinereus</i>		
		Mean	Median	Range	Mean	Median	Range
	ATR (s)	360.7	411	0-800	358.6	424	0-891
	FLAT (s)	16.3	0	0-184	34.9	0	0-826
	EDGE (s)	61.2	25	0-331	94.4	34	0-460
	BITE (number)	0.42	0	0-3	0.40	0	0-7

TABLE 3.—Results for randomizations using the linear mixed model where resident group (allopatric *P. cinereus*, sympatric *P. cinereus*, allopatric *P. electromorphus*, and sympatric *P. electromorphus*) and intruder (allopatric interspecific or sympatric interspecific) were the two factors. Sum of squares (SS), mean sum of squares (MS), and *P*-values are provided. See Table 2 for behavioral descriptions.

Behavior	Factor	df	SS	MS	<i>P</i>
ATR (s)	Resident	3	1,660,879.0	553,626.0	0.0001*
	Intruder	1	73,154.0	73,154.0	0.21
FLAT (s)	Resident	3	40,848.0	13,616.0	0.52
	Intruder	1	6424.0	6424.0	0.57
EDGE (s)	Resident	3	55,534.0	18,511.0	0.03*
	Intruder	1	4905.0	4905.0	0.27
Bite (number)	Resident	3	9.4	3.1	0.57
	Intruder	1	10.4	10.4	0.12

* Significant difference.

manders as compared to allopatric salamanders. We compared the behavioral interactions of *P. cinereus* and *P. electromorphus* from allopatric and sympatric populations towards heterospecific intruders. In general, residents did not exhibit differences in aggressive or submissive behavior towards the different types of intruders. Thus, we conclude that residents cannot distinguish from which population (allopatric or sympatric) heterospecific intruders originated. Pair-wise comparisons of our focal groups revealed that animals from sympatric populations did exhibit greater levels of aggression than allopatric populations of the same species. Therefore, we found support for the hypothesis that heightened aggression was occurring in sympatry, possibly as a result of alpha selection. It should be noted, however, that this experi-

ment examined only one population each from sympatry and allopatry of each species. Therefore, our conclusions can only be conservatively drawn about these populations. Determining whether these findings apply to interactions of these species generally and over the extent of their range of overlap requires examining a greater number of sympatric locations and will be the focus of future research.

Alpha selection has also been inferred for other species of *Plethodon*. For example, in the eastern portion of the Great Smoky Mountains where *P. teyahalee* and *P. jordani* co-occur, interspecific competition is very intense, and Nishikawa (1985) suggested that alpha selection has occurred in *P. teyahalee*. Alpha selection, by definition, is an evolutionary process, and thus, requires a genetic shift

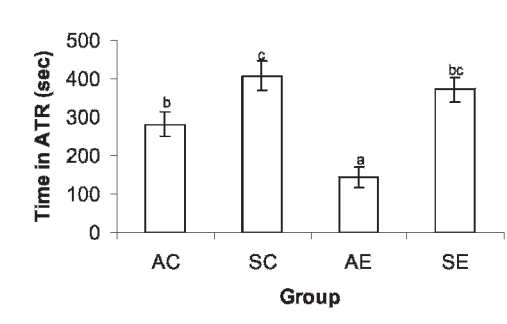


FIG. 1.—Comparison of time spent in the aggressive display (ATR) between sympatric and allopatric *Plethodon cinereus* and *P. electromorphus*. The following abbreviations are used: AC for allopatric *P. cinereus*; SC for sympatric *P. cinereus*; AE for allopatric *P. electromorphus*; and SE for sympatric *P. electromorphus*. Different lower case letters above each bar indicate statistical differences at $P = 0.05$.

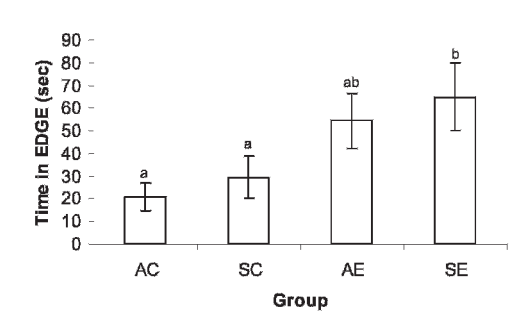


FIG. 2.—Comparison of time spent in the submissive edging (EDGE) behavior between sympatric and allopatric *Plethodon cinereus* and *P. electromorphus*. The following abbreviations are used: AC for allopatric *P. cinereus*; SC for sympatric *P. cinereus*; AE for allopatric *P. electromorphus*; and SE for sympatric *P. electromorphus*. Different lower case letters above each bar indicate statistical differences at $P = 0.05$.

that programs levels of behavior across generations. Evidence for a genetic shift in behavior was not provided here or in past studies of alpha selection (Nishikawa, 1985, 1987). Testing the heritability of aggressive behavior in *Plethodon* via common garden experiments is nearly impossible due to the difficulty of obtaining viable egg clutches from gravid females and because hatchlings require three or more years to reach maturity (Nagel, 1977). However, other studies in *Plethodon* have shown that behaviors can have a genetic basis. For example, Gibbons et al. (2005) examined foraging behavior and found that this behavior does exhibit a significant genetic component. Thus, it is at least plausible that aggressive and territorial behaviors may have a genetic component as well. An alternative hypothesis to alpha selection that may explain the observed pattern is a nongenetic response, where the behavioral shift in aggression from allopatry to sympatry is instead due to an environmental effect. For example, if overall salamander density in sympatry is greater than density of either species in allopatry and/or if food supply is decreased in sympatry relative to allopatry, salamanders may be more likely to fight for the limited food supply (hungrier salamanders fight more for food). This rationale would also apply to other resources such as cover objects. This alternative hypothesis could be examined by determining differences in abundance of salamanders and the availability of resources at this sympatric location compared to the allopatric locations. However, unquantified observations in this study suggest that these differences do not occur.

Our results suggest that the two species may be separated in sympatry by unique exploitation of some aspects of the multidimensional niche. If these two species are partitioning resources in some way, we would predict that in areas of sympatry, aspects of diet or habitat usage would overlap, but that we would find that each species is excluding the other from some portion of the niche that could be utilized by the other species. Further studies comparing the ecological competition between these two species, such as types of prey each species consumes, will provide evidence that could corroborate or refute this hypothesis. Any characteristic that would

reduce niche-overlap would promote coexistence. For example, advertisement of territories that is received by individuals of both species would reduce the potential for costly aggressive interactions (Jaeger, 1981).

Allopatric *P. cinereus* is more aggressive than allopatric *P. electromorphus*, as evidenced by greater levels of aggressive behavior (ATR) exhibited by *P. cinereus* and more submissive behavior (EDGE) by *P. electromorphus*, supporting species-specific differences. These results corroborate prior behavioral studies of these two species (Deitloff et al., 2008). Pre-existing differences in behavior of allopatric populations could also have influenced the subsequent sympatric interactions and led to the necessity of increased aggression in *P. electromorphus*. We emphasize, though, that further studies could determine which of these alternative hypotheses best describe the data presented here.

Not only can we examine competition in sympatry, but we can use this information to generate hypotheses regarding the long term stability of sympatric areas. For instance, one species may have a competitive advantage and will eventually exclude the other (Diamond, 1975; Jaeger et al., 2002). Alternatively, the possibility of alpha selection would suggest that this sympatric zone has occurred at least long enough for evolution to occur. By monitoring this and other sympatric populations, we could distinguish whether the abundance of each species is relatively stable or if one species is steadily declining. In general, if competitive ability of one species has improved due to an increase in aggressive behavior, this species may steadily exclude the other so long as it can gain a large numerical advantage (Gill, 1974). Eventually, exclusion of the second species could occur. However, if the second species can also increase its competitive ability to maintain a comparable number of individuals, it will not be excluded (King and Moors, 1979). If neither species can gain significant numerical advantage over the other, either an unstable equilibrium where population sizes fluctuate or the stable coexistence of the two species can result (Gill, 1974). While population sizes may fluctuate at a sympatric area, neither species will be able, definitively, to exclude the other species from

an area. Due to the intensity of interference, either species may be able to restrict the movement of the other into allopatric areas.

Identifying characteristics of inter-species competition and the mechanism regulating elevated aggressive behavior is of great interest in ecology and evolutionary biology. Here, we identified that, in sympatry, *P. cinereus* and *P. electromorphus* have elevated aggressive behavior which may provide support for the hypothesis of alpha selection. If alpha selection is occurring, these two species likely compete for some limiting resources. Furthermore, alpha selection suggests that neither species has been able to competitively exclude the other from sympatric areas. Determining if sympatric areas are examples of unstable equilibrium or stable coexistence and how interspecific competition affects stability of sympatry is important in understanding how competition affects community change over time and species coexistence patterns.

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