

INTERSPECIFIC AGGRESSION IN OHIO *PLETHODON*: IMPLICATIONS FOR COMPETITION

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ABSTRACT: Interspecific competition between closely-related and ecologically similar species may limit geographic ranges and fine-scale sympatry, especially when one species is aggressive toward another species. Throughout Ohio, two closely-related salamander species, *Plethodon cinereus* and *P. electromorphus*, can be found in similar habitats. While the distributions of the two species generally overlap through much of this region, a finer-scale examination of their distributions indicates that many areas within the zone of sympatry contain only one or the other species. This geographic pattern suggests that the two species are interacting. In this study, we examined the behavioral responses of individuals from allopatric populations of both species to provide an initial understanding of their interactions. This study represents interactions between 'novel' biotic stimuli, as individuals from allopatry have not previously encountered members of the congeneric species. We found that allopatric populations of *P. electromorphus* exhibited all typical behaviors recorded in other *Plethodon* species and that both species from Ohio exhibited aggressive behavior. We found that when animals were tested in intraspecific trials, *P. cinereus* was more aggressive than *P. electromorphus* and that *P. electromorphus* was more submissive than *P. cinereus*. However, these two species did not differ in behavior during interspecific trials, except that *P. electromorphus* spent more time in escape behavior (EDGE). Therefore, we conclude that *P. electromorphus* likely would act submissively if encountering *P. cinereus* for the first time in the field. These results imply that *P. electromorphus* may not be able to expand its range into areas occupied by *P. cinereus*, and, in turn, *P. cinereus* may be able to successfully expand its range into areas presently occupied by *P. electromorphus*.

Key words: Aggression; Competition; *Plethodon cinereus*; *Plethodon electromorphus*; Salamander; Territoriality

THE COMPETITIVE interactions of closely-related species have long been considered important determinants of community composition. Both field and laboratory experiments have documented the prevalence of interspecific competition across a diverse array of ecological communities (reviewed in Schluter, 2000), and have shown how species interactions can affect local adaptation and patterns of evolutionary diversification (Adams, 2004; Jastrebski and Robinson, 2004; Schluter and McPhail, 1992). Species interactions can also limit species geographic boundaries and the extent of distributional overlap among competitors (Hairston, 1949, 1980*a,b*; Jaeger, 1970). Under some circumstances, spatial gradients in competitive ability can lead to abrupt shifts in competitive dominance, resulting in sharp parapatric distributions with limited geographic overlap of competitors (Bull, 1991; Case et al., 2005). Therefore, behavioral interactions between closely-related species may regulate the extent

of distributional overlap between them and when species interactions occur, sharp boundaries delimiting species ranges may result.

Both ecological theory and empirical research suggest that behavioral interactions can have an appreciable effect on species co-occurrence patterns. While determining the effects of behavioral interactions in the field is difficult (but see Griffis and Jaeger, 1998), examining behavioral responses of potential competitors in controlled laboratory and semi-controlled field experiments provides considerable insight into how behavioral interactions within and between species affect community composition. In recent years, salamanders of the genus *Plethodon* have become a model system for studying behavioral interactions. These terrestrial salamanders are widely distributed in the forests of eastern and western North America, and extensive ecological research suggests that interspecific competition may be widespread (Anthony et al., 1997; Marshall et al., 2004). Some species in this genus develop territories under and around cover objects on the forest floor

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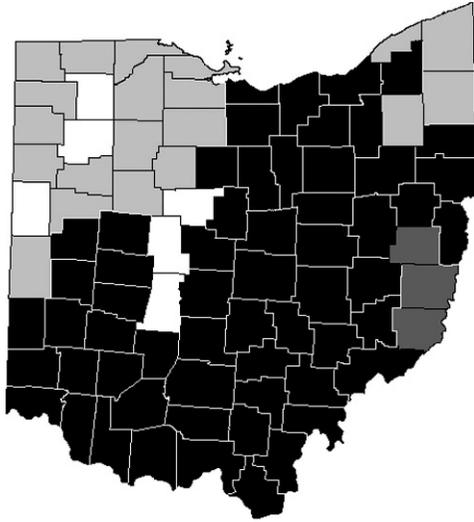


FIG. 1.—Geographic distributions of *Plethodon cinereus* and *P. electromorphus* in Ohio (maps adapted from Ohio Department of Transportation, 2007, using collection data in Pfingston and Matson, 2003). Counties where only *P. cinereus* was found are shown in light gray, counties where only *P. electromorphus* was found are shown in dark gray, and sympatric counties are shown in black. White counties represent areas where neither species was found.

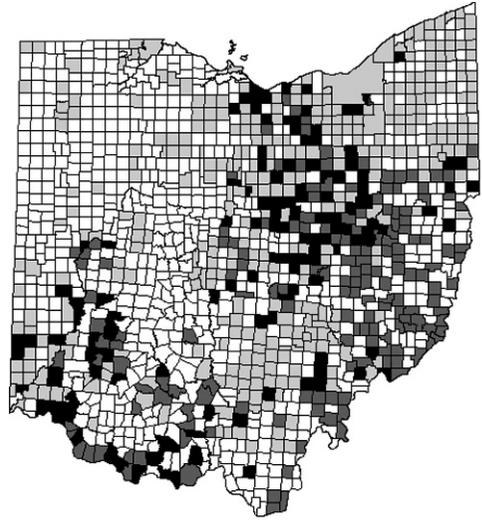


FIG. 2.—Geographic distributions of *Plethodon cinereus* and *P. electromorphus* in Ohio showing township boundaries (maps adapted from Ohio Department of Transportation, 2007, using collection data in Pfingston and Matson, 2003). Townships where only *P. cinereus* was found are shown in light gray, townships where only *P. electromorphus* was found are shown in dark gray, and sympatric townships are shown in black. White townships represent areas where neither species was found.

(Jaeger, 1981; Jaeger et al., 1995; Mathis, 1991), which provide a source of food and moisture during dry conditions when both are critical for survival (Jaeger et al., 1981; Mathis, 1990). In addition, salamanders defend their territories in intraspecific encounters (reviewed in Jaeger and Forester, 1993).

Territorial aggression between individuals of different salamander species has been demonstrated for several ecological communities (Anthony et al., 1997; Jaeger, 1970; Nishikawa, 1985), and in some instances, it appears to have restricted the geographic ranges of species that are potential competitors (Hairston, 1980a; Jaeger, 1970). Most of our knowledge of interspecific competition in *Plethodon* is found between species whose contact zones are quite narrow (<500 m), and in many locations are parapatric (Highton, 1995). These include territorial aggression between small-bodied species of *Plethodon*: (1) *P. cinereus* vs. *P. shenandoah* (Griffis and Jaeger, 1998; Jaeger, 1970), (2) *P. cinereus* vs. *P. hubrichti* (Arif et al., 2007; Wicknick, 1995), (3) *P. cinereus* vs. *P. hoffmani* (Adams, 2000; Adams and Rohlf, 2000; Jaeger et al., 2002),

(4) *P. cinereus* and *P. nettingi* (Adams et al., 2007) and between large-bodied species of *Plethodon*: (1) *P. jordani* vs. *P. teyahalee* (Hairston, 1980a; Nishikawa, 1985), (2) *P. albagula* vs. *P. ouachitae* (Anthony et al., 1997), (3) *P. kentucki* vs. *P. glutinosus* (Marvin, 1998). By contrast, we know much less about species interactions where the distributions of species overlap across a large geographic area.

In southeastern Ohio, the geographic overlap between *P. cinereus* and *P. electromorphus* is considerably greater than what exists between other species in the *P. cinereus* species complex suggesting sympatry at the coarse geographic scale (Fig. 1). However, when viewed at a more fine scale, the two species do not always co-occur. An example of this fine scale difference can be viewed when examining species co-occurrence in townships (geographical subdivisions of counties) (Fig. 2). The geographic distributions of *P. cinereus* and *P. electromorphus* may more accurately be described as an interdigitation of distributions, meaning that allopatric locations of each species are more commonly

found than sympatric locations. The higher frequency of allopatric areas compared to sympatric areas within the overlap zone may indicate that sympatry is not stable. Therefore, the scale, fine or coarse, at which species distributions are examined will change interpretations about the extent of co-existence between *P. cinereus* and *P. electromorphus*.

Plethodon cinereus is known to exhibit variation in levels of territoriality and aggression across its range. Individuals in Virginia exhibit high levels of aggression, while individuals in Michigan exhibit very little aggression (Quinn and Graves, 1999; Wise, 1995). Ohio is intermediate geographically, but the amount of aggression that individuals express in this area is unknown. In addition, *P. cinereus* has been shown to exhibit aggression towards unrelated competitors (beetles: Gall et al., 2003; centipedes: Anthony et al., 2007; Hickerson et al., 2004). While considerable information is known about the ecology and behavior of *P. cinereus*, little is known about *P. electromorphus*. *Plethodon electromorphus* was described on the basis of genetic data to be distinct from its sister species, *P. richmondi* (Highton, 1999). An anecdotal study of *P. richmondi* suggested that this species is considerably less aggressive and less territorial relative to other species of *Plethodon* (Thurrow, 1975). Jewell (1991) compared the behavior of *P. electromorphus* to *P. cinereus* from northwestern West Virginia, but small sample sizes precluded statistical analyses and firm conclusions about behavioral differences between the two species could not be made. Therefore, the occurrence of these two species in Ohio provides a unique opportunity to document the behavioral interactions of species that show a large distributional overlap with little fine-grained sympatry. By examining behavior of allopatric animals, we can better understand the behavioral interactions between these two species if individuals of allopatric populations should meet during novel encounters.

In this study, we investigated the behavior that would occur when individuals of *P. cinereus* and *P. electromorphus* encounter each other during novel interactions, as would happen if individuals of one species tried to invade an area occupied by the other species.

We used individuals of both species collected from allopatric sites (areas within townships that are contiguous geographic localities where only *P. cinereus* or *P. electromorphus* can be found) to address this question. To understand the behavior of each species in Ohio, we have two descriptive objectives. These objectives were (1) to determine whether *P. electromorphus* exhibits similar aggressive and submissive behaviors as other species of *Plethodon* (behaviors are described below) and (2) whether *P. cinereus* in Ohio exhibits similar levels of aggression recorded in other areas of its range. We then tested four specific hypotheses. First, we examined intraspecific interactions testing the hypotheses that (1) allopatric residents of *P. cinereus* are more aggressive intraspecifically than are allopatric residents of *P. electromorphus*, and (2) allopatric residents of *P. electromorphus* are more submissive intraspecifically than allopatric residents of *P. cinereus*. Second, we studied interspecific interactions by testing the hypotheses that (3) allopatric residents of *P. cinereus* are more aggressive interspecifically, and (4) allopatric residents of *P. electromorphus* are more submissive. While the first and second hypotheses and the third and fourth hypotheses are related, one hypothesis does not automatically follow from the other. For example, individuals of one species may show more aggressive behavior than individuals of the other species, while the frequency of submissive behaviors is similar between the two. Therefore, we specifically tested four separate, but related hypotheses. Collectively, the results for these four hypotheses inform on the species interactions that may occur in a natural setting.

MATERIALS AND METHODS

Collection and Maintenance

We obtained salamanders during a series of daylight collecting trips on 16–20 October 2005. Individuals of *Plethodon cinereus* were obtained from a forested site 52 km west of Youngstown in Ellsworth Township, Mahoning County, Ohio, U.S.A. (40° 46' 04" N; 80° 43' 37" W). Individuals of *P. electromorphus* were collected from a forested site 26 km north of Cambridge in Liberty Township,

Guernsey County, Ohio, U.S.A. (40° 09' 04" N; 81° 35' 02" W). We collected 24 females and 29 males of *P. cinereus* and 27 females and 25 males of *P. electromorphus*. Animals were housed in circular Petri dishes (9 × 1.5 cm) with a substrate of filter paper dampened with distilled water. Salamanders were transported to Ames, Iowa in coolers for temperature control. After the experiments were conducted, we euthanized the salamanders using MS222.

In the laboratory, salamanders in their individual Petri dishes were placed in a refrigerator and stored at 18–21 C on a 12:12 h light:dark cycle. Salamanders were maintained for 32 days prior to the onset of the experiments. During this time, we fed the salamanders 10–15 *Drosophila* once per week, moistened the filter paper three times weekly, and replaced filter paper as needed. With the exception of four animals, salamanders ate well and remained healthy during the acclimation period. Behavioral experiments were initiated in late November 2005. Between experiments, salamanders were kept on the same care schedule as stated above.

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-vent lengths (SVL) were measured to the nearest 0.1 mm using Brown and Sharpe Mark IV digital calipers (*P. cinereus*: $\bar{X}_{\text{nongravid}} = 40.1 \text{ mm} \pm 4.2 \text{ SD}$, $\bar{X}_{\text{gravid}} = 43.5 \pm 3.0$, $\bar{X}_{\text{male}} = 41.4 \pm 3.7$; *P. electromorphus*: $\bar{X}_{\text{nongravid}} = 36.3 \pm 5.1$, $\bar{X}_{\text{gravid}} = 44.8 \pm 5.2$, $\bar{X}_{\text{male}} = 47.3 \pm 5.1$). Only adult salamanders (SVL > 32 mm; Saylor, 1966) were used in behavioral experiments. Salamanders were used only once during each experiment. Resident salamanders during experiment 1 were the same individuals as resident salamanders during experiment 2. For all experiments, salamanders were randomly assigned to resident or intruder groups. Then residents and intruders were randomly paired, with the constraint that pairs were of the same sex (male, gravid female, and nongravid female) and were sized-matched in an effort to reduce the fighting advantage of

larger animals (Mathis, 1990). Residents and intruders were not significantly different in size ($\bar{X}_{\text{Resident}} - \bar{X}_{\text{Intruder}} = -0.1 \pm 3.4$; $T = -0.39$, $P = 0.70$, $df = 86$, NS).

Experiment 1: Intraspecific Interactions

In the first experiment, we examined intraspecific interactions for each species. Behavioral trials were conducted from 22 November–9 December 2005. On day 1, we randomly selected one salamander from each conspecific pair (*P. cinereus*: $n = 23$; *P. electromorphus*: $n = 24$) to be the 'resident' and placed it into a transparent Nunc bioassay chamber (24 × 24 × 2 cm) lined with a paper towel moistened with distilled water and with a transparent lid. We allowed each resident to establish a territory by marking the substrate with its pheromones for 7 d (Horne and Jaeger, 1988; Jaeger et al., 1986; Wise and Jaeger, 1998). The other member of the pair was termed the 'intruder' and remained in a circular Petri dish (15 × 1.5 cm). We fed residents and intruders on days 2 and 5, and moistened filter paper as needed. On day 8, a conspecific intruder was introduced into the resident's chamber using clear polyethylene tubing to reduce stress of handling. Each trial began when the intruder entered the resident's chamber. We recorded resident and intruder behavioral patterns (described below) for 900 s (15 min). These observations were made under dim illumination (60-W bulb reflected off a white tile floor). All trials were conducted during daylight hours (0900–1800 h) and within a temperature range of 18–24 C. After the experiment, we placed residents and intruders into Petri dishes (15 × 1.5 cm circular) and resumed the care schedule described above.

To quantify aggressive and submissive behaviors, we used a set of behaviors that are commonly exhibited by *Plethodon* during encounters. These behaviors were described by Jaeger (1984) and used to evaluate aggressive and submissive behavior among competitors. Specifically, we recorded the total time in seconds that residents spent in all-trunk-raised (ATR) threat posture, flat (FLAT) submissive posture, and edge behavior (EDGE), and the number of bites administered to the intruder. EDGE 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).

To address our first descriptive objective, we examined whether *P. electromorphus* exhibits similar aggressive and submissive behaviors as other *Plethodon*, by comparing our observations with the behavioral descriptions by Jaeger (1984). We then qualitatively compared the time that *P. electromorphus* spent in ATR to previous studies of *Plethodon* to determine if *P. electromorphus* exhibited ATR at comparable frequencies to other species. Regarding our second objective, we included *P. cinereus* in this comparison to determine if its level of aggression compared to published records for other populations of *P. cinereus*.

To test our first two hypotheses, whether *P. cinereus* was more aggressive and whether *P. electromorphus* was more submissive during intraspecific encounters, we recorded time spent in ATR, FLAT, and EDGE behaviors and the frequency of bites (bites/trial) during intraspecific interactions. We analyzed our results by (1) using a two-tailed Wilcoxon Rank-Sum test (Z) with a sequential Bonferroni correction (Rice, 1989, 1990) to compare the time residents of *P. cinereus* and residents of *P. electromorphus* spent in ATR, FLAT, and EDGE and (2) using a two-tailed Wilcoxon Rank-Sum test (Z) to compare the frequency of bites administered by residents of each species.

Experiment 2: Interspecific Interactions

In the second experiment, we examined interspecific interactions between the two species. Behavioral trials were conducted from 3–20 January 2006 allowing time for the animals to become reacclimated to laboratory conditions. Residents from the first experiment were also used as residents during interspecific trials, but were paired with a heterospecific intruder. However, our second experiment contained fewer trials (*P. cinereus* as resident: $n = 20$; *P. electromorphus* as resident: $n = 20$), because one resident of each species died between the first and

second experiments and because the two smallest *P. cinereus* and three largest *P. electromorphus* were excluded due to size asymmetry making it impossible for us to assign them to matched pairs. The remaining experimental protocol was identical to that described for the intraspecific trials (in experiment 1), with the exception that heterospecific intruders were introduced rather than conspecifics.

To test our third and fourth hypotheses regarding differences in behavior during interspecific encounters, we compared interspecific encounters in the same manner described above for intraspecific encounters.

RESULTS

Salamander behavior did not correlate with either the time of day or the temperature in which they were tested (results not shown). Regarding our first descriptive objective, we observed *P. electromorphus* performing all the typical *Plethodon* behaviors described in Jaeger (1984). By addressing our second objective, we also observed *P. cinereus* exhibiting aggressive behaviors at rates comparable to other studies (discussed below).

When testing our first two hypotheses, comparing behavior of residents of *P. cinereus* and *P. electromorphus* during intraspecific trials (experiment 1), residents of *P. cinereus* spent significantly more time in ATR than did residents of *P. electromorphus* (Table 1). Furthermore, *P. electromorphus* spent significantly more time in FLAT behavior and EDGE behavior than residents of *P. cinereus* (Table 1). Residents of *P. cinereus* and *P. electromorphus* did not differ in the frequency of bites (Table 1).

To address our third and fourth hypotheses, we compared behavior of residents of *P. cinereus* to that of residents of *P. electromorphus* behavior when presented with a heterospecific intruder (interspecific trials: experiment 2). Residents of *P. cinereus* and residents of *P. electromorphus* did not differ in the amount of time they spent in ATR or FLAT and did not differ in the frequency of bites during interspecific trials (Table 2). Conversely, they did significantly differ in

TABLE 1.—Average time (s) spent by residents in ATR, FLAT, EDGE and frequency of biting (bites/trial) during intraspecific trials (experiment 1).

Behavior	Resident				Z	P
	<i>P. electromorphus</i>		<i>P. cinereus</i>			
	mean	range	mean	range		
ATR	10.5	0–101	64.4	0–387	1.69	0.046*
FLAT	426.8	0–900	178.7	0–9	2.88	0.002*
EDGE	62.6	0–478	13.6	0–851	2.02	0.022*
Bites	0.25	0–2	0.86	0–9	0.54	0.587

* Significant difference with sequential Bonferroni

the amount of time spent in EDGE behavior (Table 2).

DISCUSSION

In this study, we examined the behavioral interactions of adults of two salamander species whose geographic overlap is considerably greater than what is seen among other species in the *P. cinereus* species complex. We compared the behavior of *P. cinereus* and *P. electromorphus* with two descriptive objectives and four specific hypotheses. Our two objectives were in regard to the general behaviors of both species. *Plethodon electromorphus* exhibited all behaviors typical of *Plethodon* during intraspecific and interspecific behavioral trials (Objective 1). The range of mean time spent in ATR (during 900 s) from other studies using *Plethodon* is 0 s to 757 s (*P. cinereus*, 12 s to 757 s: Jaeger et al., 2002; Nunes and Jaeger, 1989; Wicknick, 1995; Wise and Jaeger, 1998; Wise, 1995; this study; *P. hoffmani*, 0 s to 8 s: Jaeger et al., 2002; and *P. hubrichti*, 90 s to 113 s: Wicknick, 1995). When compared to other congeners, *P. electromorphus* seemed to exhibit ATR at the lower end of the range of this genus in general. Similarly, our population of *P.*

cinereus exhibited ATR at comparable, but lower rates to most other populations (Objective 2). This implies that, similar to salamanders in other geographic locations, salamanders in this region used aggressive behavior in their behavioral encounters, but perhaps at a lower frequency.

Our four hypotheses examined the behavioral interactions of *P. cinereus* and *P. electromorphus*. Our first two hypotheses concerning intraspecific encounters were supported, because we found that *P. cinereus* was more aggressive towards conspecific intruders than *P. electromorphus*, and *P. electromorphus* was more submissive towards intruders. However, our third and fourth hypotheses were not supported. *Plethodon cinereus* and *P. electromorphus* did not differ in aggression or in FLAT behaviors during interspecific trials, but we found that *P. electromorphus* did exhibit escape behavior more frequently than *P. cinereus*.

Understanding the allopatric behaviors of each of these species is important, as levels of behavioral aggression among populations of *Plethodon* are known to vary by geographic locality (Nishikawa, 1985; Wise, 1995). Within *P. cinereus*, some populations such as those

TABLE 2.—Average time (s) spent by residents in ATR, FLAT, EDGE and frequency of biting (bites/trial) during interspecific trials (experiment 2).

Behavior	Resident				Z	P
	<i>P. electromorphus</i>		<i>P. cinereus</i>			
	mean	range	mean	range		
ATR	27.3	0–150	75.3	0–526	0.49	0.142
FLAT	330.6	0–286	134.3	0–811	2	0.034
EDGE	57.4	0–900	5.6	0–80	2.42	0.002*
Bites	0.052	0–1	0.3	0–4	0.58	0.564

* Significant difference with sequential Bonferroni

found at Hawksbill Mountain, Virginia, are highly aggressive (Griffis and Jaeger, 1998; Jaeger, 1970; Wise, 1995), while other populations, such as those in the upper peninsula of Michigan, are considerably less aggressive and apparently less territorial (Quinn and Graves, 1999; Wise, 1995). Qualitatively, our population represents intermediate levels of aggression when compared to some other populations of *P. cinereus* (Wise, 1995).

Plethodon electromorphus exhibited more submissive behavior compared to *P. cinereus*. In general, *Plethodon* is considered to be aggressive and territorial (Jaeger and Forrester, 1993). Nevertheless, variation in levels of aggression and territoriality within and between species has been identified. Within the *P. cinereus* species group, several species exhibit relatively low levels of aggressive behavior (*P. electromorphus*: this study; *P. hoffmani*: Jaeger et al., 2002; *P. nettingi* and *P. richmondi*: Thurrow, 1975), while other species exhibit relatively high levels of aggressive behavior (*P. hubrichti*: Arif et al., 2007; Wicknick, 1995; *P. serratus*: Camp, 1999; *P. shenandoah*: Griffis and Jaeger, 1998).

Interspecific interactions in our study represent the situation in which an individual of each species encounters an individual of the other species for the first time; in other words, it is a 'novel' interaction. Because neither species was significantly more aggressive interspecifically than the other, we encounter difficulty when predicting which species would be the 'winner' of novel interactions. Conversely, our data (EDGE) suggest that *P. electromorphus* would be more submissive in natural habitats. The aggressive superiority of *P. cinereus* suggests that it may be competitively superior (Jaeger et al., 2002). Therefore, we cautiously predict that *P. cinereus* would be the 'winner' during these interactions. To increase our understanding of the behavioral interactions between these two species in the field, we can also examine their behavior when found sympatrically. Behavioral experiments on other pairs of sympatric *Plethodon* have shown heightened aggression (alpha selection sensu Gill, 1974) associated with interspecific interactions (Nishikawa, 1985). If these results are comparable to our species pair, we hypothesize that individuals from sympatric

sites may exhibit heightened aggression towards congeners due to familiar competition (e.g., prior experience) with congeneric individuals. Alpha-selection is not universal in sympatric *Plethodon*, however, as other species pairs do not follow this pattern. For example, although *P. kentuckyi* and *P. glutinosus* exhibit aggression towards conspecifics and heterospecifics, intense aggression occurs only towards conspecifics, presumably because intraspecific competition is greater than interspecific competition (Marvin, 1998). In this situation, intraspecific aggression may facilitate coexistence of competing species (Genner et al., 1999). Understanding the interactions within sympatric sites will be important in determining the extent of competitive interactions between these two species.

In summary, we draw the following inductive inferences: (1) *P. electromorphus* exhibits typical behaviors and is intermediate relative to other *Plethodon* species in the level of aggression exhibited; (2) *P. cinereus* is intermediately aggressive relative to other populations of *P. cinereus*; (3) *P. cinereus* is intraspecifically more aggressive than *P. electromorphus*, but this is not true for interspecific interactions; (4) *P. electromorphus* is more submissive than *P. cinereus* in intraspecific behavioral interactions and in edging behavior during interspecific encounters. Further studies are needed to determine if competition influences the behavioral interactions between these two species. We now have a better understanding of the aggressive behaviors *P. cinereus* and *P. electromorphus* in allopatric zones and the interactions that could occur if these species were to come into contact for the first time. When strong species interactions occur, these interactions are expected to generate sharp boundaries delimiting species ranges; however, other factors may influence presence or absence of species at specific locations and the amount of range overlap between them.

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