Sympatry between Two Wide-ranging Salamander Species

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Abstract.—Understanding how closely related species coexist remains a central problem in community ecology. Habitat characteristics, presence of predators and competitors, and frequency of disturbance all affect the geographic distribution of a species. *Plethodon cinereus* and *P. electromorphus* are two closely related and ecologically similar species that have a large geographic overlap in their distributions. In this study, I had two main goals. First, I wanted to determine how commonly sympatric locations occurred between these two species. To address this goal, I conducted landscape-scale surveys in areas that should contain sympatric locations based on their distributions. My second goal was to determine if the relative number of individuals of each species within sympatric locations was stable over time by monitoring four sympatric locations over three years. In addition, flooding occurred during one year of the study, impacting two of the four monitored sympatric locations; therefore, I wanted to examine whether this disturbance affected the salamander populations at those locations. This flooding event provided a rare opportunity to study the impact of flooding on terrestrial salamanders, a topic about which little is known. I found that sympatric locations occurred less frequently than expected by chance and that some sympatric sites seem to be relatively stable while at others, the relative population size of *P. cinereus* was increasing — and that this shift might be positively affected by flooding. While this study demonstrated that *P. cinereus* and *P. electromorphus* do not occur in sympatry as frequently as expected by chance, the cause for this result is unknown. The most likely factor is that the two species exhibit subtle habitat differences that have not yet been demonstrated. The interactions between *P. cinereus* and *P. electromorphus* are complex, and the patterns observed here could have been generated by any number of mechanisms. Further research on this system could clarify some of these remaining questions.

Understanding how closely related species coexist remains a central problem in community ecology. The amount of overlap between the geographic ranges of closely related species is thought to depend, in part, on the extent to which similar species share the same habitat requirements. Closely related species tend to overlap more than expected by chance, suggesting that species' distributions are more constrained by shared niche requirements and common ancestry than by competition (Harvey and Pagel 1991, Letcher et al. 1994). Conversely, niche similarity may lead to intense competition and eventual exclusion resulting in rare co-occurrence of the two species (Bowers and Brown 1982). The distribution of a species could be affected by any number of mechanisms that could include habitat characteristics and the presence of predators or competitors.

Interspecific competition and territorial aggression seem to be prevalent within the genus *Plethodon* (e.g., Jaeger 1970, Nishikawa 1985, Anthony et al. 1997, Marshall et al. 2004). In some instances, interspecific competition has limited the geographic ranges of competing species (Jaeger 1970, Hairston 1980, Arif et al. 2007) and has led to a variety of evolutionary consequences between sympatric species, such as character displacement (Adams and Rohlf 2000), competitive exclusion (Jaeger 1971, Myers and Adams 2008), and alpha-selection — intense interspecific aggression (Nishikawa 1987, Deitloff et al. 2009). Further, these effects appear to have shaped species distributions at a broad geographic scale, because patterns of community composition are consistent with what is predicted from competitive-based models of community dynamics (Adams 2007).

Fig. 1. Adult *Plethodon cinereus.*

Fig. 2. Adult *Plethodon electromorphus.*

Plethodon cinereus (p. 6 and fig. 1) has a very large geographic range spanning most of the northeastern United States; and, while the geographic range of *P. electromorphus* (Fig. 2) is much smaller, this species has a relatively large geographic range compared to many other species in the genus *Plethodon* (Petranka 1998). In Ohio, the geographic overlap of the ranges of these two species extends throughout most of the state; but, when viewed at a finer scale, the geographic overlap is more accurately described as interdigitation (see Deitloff et al. 2008, figs. 1 and 2). In other words, allopatric locations may be more commonly found than sympatric locations. As suggested in Deitloff et al. (2008), this difference between the coarse- and fine-scale views of the geographic distributions in these two species could lead to differing conclusions about the extent of sympatry. Therefore, I addressed two goals in this study. First, I examined the extent of sympatric locations by conducting landscape-scale surveys (rather than using past distribution maps). Second, I monitored four sympatric sites over three years to determine whether the relative population size of either species changed over time (i.e., whether the condition of sympatry was stable or transient).

During the period when the four sympatric sites were monitored, one of these locations was strongly affected by a flood, another location was weakly affected by the same flood, and two locations were physically undisturbed during the study. This disturbance provided a natural experiment to address the relative impact of flooding on these populations over time. Flooding is a common disturbance of salamander assemblages in both aquatic and terrestrial systems; however, most studies have focused on aquatic and semi-aquatic species. In some instances, individuals that survive flooding can exhibit indications of competitive release (Petranka and Sih 1986); however, other species require a longer time period for recovery (Swanson et al. 1998). The impact of floods on terrestrial salamanders is largely unknown.

Materials and Methods

Species Co-occurrence.—I conducted landscape-scale surveys of species presence during spring 2007 and fall 2007. To conduct these landscape-scale surveys, I searched for locations within the distributional overlap of *P. cinereus* and *P. electromorphus*. I identified locations only within counties where both species have been found (sympatric counties) according to distribution maps of Ohio (Pfingston and Matson 2003). I chose 21 sympatric counties from northeastern Ohio (from all possible sympatric counties) because this area contained a concentration of townships (subdivisions of counties) where both species have been found (Pfingston and Matson 2003). Within each of these 21 sympatric counties, I identified locations that could contain salamanders by using topographic maps to determine which areas contained wooded habitat. After arriving at a location, if the area was indeed suitable habitat, I searched for salamanders. At each of these locations, I recorded the number of individuals of *P. cinereus* and/or *P. electromorphus* at that location. Each location was searched for a minimum of 20 minutes to determine the presence of salamanders. If any salamanders were found, the area was searched exhaustively (i.e., all cover objects were overturned and the boundaries of each site were delineated by rivers, roads, or non-forested private property). I adapted the distribution maps of Pfingson and Matson (2003) using these locations as well as the locations mentioned below (sites A, B, C, and D), which also were located within sympatric counties (map is described in results). Locations where I found no salamanders might have contained salamanders; however, these areas were not included in the analysis described below and therefore

Fig. 3. Site A, where flooding swept most of the cover objects from the slopes of the ravine into the stream.

Fig. 4. Photograph of a location with allopatric *Plethodon cinereus*. This location was 8 mi NW of Newark in McKean Township, Licking County (40°08'06"N, 82°32'05"W).

did not influence results. I am confident that locations described as being allopatric were indeed allopatric because: (1) Each location was searched exhaustively, and (2) when sympatric locations were identified, minimal search effort found both species (search time as low as 5 min and two total salamanders confirmed the presence of both species). Also, when analyses were calculated excluding sites with fewer than five total salamanders, results were the same. Note that I focused only on counties where both species had been documented, and, thus, had the best chance of finding sympatric locations if they existed.

To test the hypothesis that *P. cinereus* and *P. electromorphus* co-occur less frequently than expected by chance, I used the collection data obtained from the landscape-scale surveys to construct a presence/absence matrix. This matrix was used to determine whether co-occurrence between *P. cinereus* and *P. electromorphus* was best described as segregation, aggregation, or random. I used the C-score index (Stone and Roberts 1990) as a measure of co-occurrence. This index is calculated as:

$$C_{ij} = (r_i - S)(r_j - S)$$

where S is the number of shared sites (sites containing both species) and r_i and r_j are the number of occurrences (row totals) for species i and j. If the C-score was greater than expected by chance, species segregate; if the C-score was smaller than expected by chance, species aggregate. I used EcoSim Version 7.0 (Gotelli and Entsminger 2007) to compare the observed C-score to the average C-score generated from 10,000 randomly constructed assemblages. I used a model where row values were retained so each species only occurred as often as in the observed matrix (fixed sum) and where sites (columns) are equally likely to be represented (equiprobable), eliminating observed differences in species richness of sites in the null assemblages.

Flood.—I located four sympatric sites in Ohio during spring 2004. Site A was ~3 mi E of Lisbon in Elk Run Township, Columbiana County (40°46'04"N, 80°43'33"W); Site B was 10 mi N of Lisbon in Salem Township, Columbiana County (40°49'48"N, 80°49'19"W); Site C was 12 mi NE of Newark in Perry Township, Licking County (40°10'01"N, 82°15'28"W); and Site D was 9 mi N of Newark in Washington Township, Licking County (40°11'27"N, 82°26'38"W). These four sites were monitored during seven collecting trips from spring 2004 to fall 2007. Spring collecting trips in 2004, 2005, and 2007 occurred in early May, and fall collecting trips in 2004, 2005, 2006, and 2007 occurred in late September and early October. These four sites were similar in composition in that they all occurred in temperate deciduous forest in east-central Ohio. During late August and September 2004, severe and frequent rains resulted in flooding of Sites A and B. When Site A was visited on 25 September 2004, I observed that most of the rocks (used as cover objects by salamanders) and leaf litter (used for foraging and refugia during dryer conditions) had been swept into a ravine located within the site (Fig. 3). Salamander habitat at Site B was also disturbed by the flood, but not as severely, and many cover objects remained on the slope. Sites C and D were not flooded during the study period.

During visits to each site, I collected adult *P. cinereus* and *P. electromorphus* and recorded the number of individuals of each species. During fall 2004, Sites B and C were searched until approximately 25 salamanders of each species were collected for other research. Therefore, this collecting season was not included in the analyses

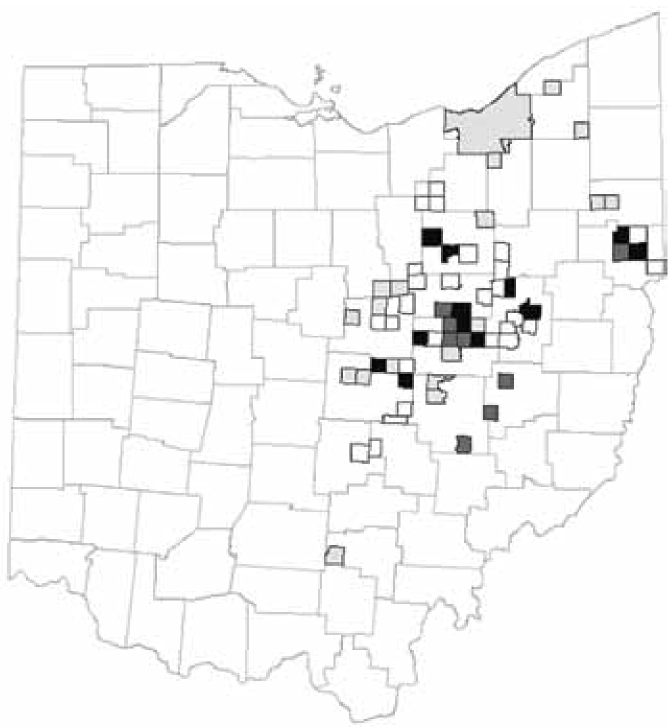

Fig. 5. Results of landscape surveys of *Plethodon cinereus* and *P. electromorphus* in Ohio showing surveyed townships outlined in black (maps adapted from Ohio Department of Transportation 2007). Townships with sympatric locations are filled with black, allopatric *P. cinereus* locations with light gray, and allopatric *P. electromorphus* locations with dark gray. Townships where I found no salamanders are white.

and is reported only because this was the collection that occurred immediately after the flood and Site A contained only one salamander. All collecting was conducted at 0700–1100 h, and all salamanders were captured by hand. All sites during each collection season were searched exhaustively (all cover objects were overturned and the boundaries of each site were delineated by rivers, roads, or non-forested private property). Therefore, the area at each site that was searched was the same for each collection season. Unfortunately, time spent collecting salamanders was not recorded for the first collecting season (spring 2004). Three people collected salamanders during this season and each site was searched for approximately 1–2 h (3–6 collecting h/site). For all other collecting seasons, two people collected salamanders, and collection effort per site was similar (Site A: 3 h each collection season; Site B: 2–4 h; Site C: 2.5–4 h; Site D: 2 h). The goal of this paper was to estimate the relative number of individuals of *P. cinereus* and *P. electromorphus*, so actual population sizes were not estimated. Instead, the number of individuals of each species encountered was used to calculate the proportion of *P. cinereus* at each site for each season, and this measure is referred to as "relative population size." To determine if this proportion changed significantly over time, I compared the proportion found during the second through seventh collecting seasons (post-flood) to the proportion found during the first collecting season (pre-flood) using chi-square tests with $\alpha = 0.05$.

Results

Species Co-occurrence.—I found 20 allopatric locations for *P. cinereus* (Fig. 4), nine allopatric locations for *P. electromorphus* (two locations were within the same township), and 12 sympatric locations; I did not find any salamanders in 27 townships. For the adapted map (Fig. 5), each township was coded as containing allopatric *P. cinereus*, allopatric *P. electromorphus*, both species (sympatric), or neither species. *Plethodon cinereus* and *P. electromorphus* co-occurred less frequently than was expected by chance (C-score = 180; P = 0.0008). Therefore, the distributions of *P. cinereus* and *P. electromorphus* in regard to the presence of the other species would be best described as segregation, as opposed to aggregation or random.

Flood.—Over the course of this study, *P. cinereus* was more common than *P. electromorphus* at all monitored sympatric sites. At both flood sites (A and B), I recorded a temporal pattern in which *P. cinereus* significantly increased in relative population size compared to *P. electromorphus* (Table 1). Furthermore, in fall 2004 (immediately after the flood), I found only one adult *P. cinereus* and no *P. electromorphus* at Site A. At the non-flooded sites (C and D), relative population sizes of *P. cinereus* and *P. electromorphus* did not change significantly (Table 1). More specifically, at Site C, a non-significant increase in *P. cinereus* occurred until fall 2006, when the relative population sizes were similar to the first collecting season. While the change was not significant at Site D, no *P. electromorphus* were found during the final collecting season.

Discussion

The first goal of this study was to examine the extent of sympatry between *P. cinereus* and *P. electromorphus* in Ohio, and I addressed this goal by conducting landscape-scale surveys. I found that allopatric sites of *P. cinereus* are more common than sympatric sites and allopatric sites of *P. electromorphus*, that co-occurrence was less than expected by chance, and that, at sympatric sites, *P. cinereus* is more abundant. The second goal of this study was to monitor sympatric locations to determine if the condition of sympatry was stable over time. I found that at one location, local extinction of *P. electromorphus* might have occurred (Site D); at one location, the relative number of each species remained approximately the same (Site C); and at two locations, the relative population size of *P. cinereus* increased over time (Sites A and B), but the site remained sympatric.

Flooding occurred at the two sites where *P. cinereus* increased, suggesting that flooding could affect relative population sizes of each species. Furthermore, *P. cinereus* returned more quickly after the flood to Site A than *P. electromorphus*. At Site B, where flooding occurred but did not destroy the entire terrestrial habitat, the community changed significantly, but this change occurred over a longer time period. This major disturbance appeared to affect the population of *P. electromorphus* more than the population of *P. cinereus*. Evidence suggests that flooding influences the relative population size of these species through one of three, non-mutually exclusive mechanisms: (1) Enhanced competitive exclusion of *P. electromorphus* by *P. cinereus*, (2) a change of environmental characteristics at the flooded sites, making these sites unsuitable for *P. electromorphus*, or (3) a slower rate of reestablishment for *P. electromorphus* relative to *P. cinereus*.

To my knowledge, this is the first study that examined the effects of flooding on terrestrial salamanders. Natural disturbance events, such as flooding, provide rare opportunities to study population dynamics that cannot be understood with laboratory experiments. Flooding can disrupt populations of terrestrial salamanders in multiple ways, including damaging the physical environment by removing cover objects that are required for their survival, decreasing population sizes of potential competitors and predators, or temporarily removing all individuals.

In this system, local distribution patterns reveal that complex interactions occur between these two species and possibly with the environment or other species (such as predators) not studied. Competition often plays some role in the interactions of species, but the importance of its effects in a community are context-dependent and other factors are important as well (Tello et al. 2008), For example, disturbance history (Hyde and Simons 2001) and predation (Connell 1975) can suppress densities to chronically low levels, so that shared resources never become limiting — which would promote co-occurrence. Unfortunately, the effect of predators on communities of *Plethodon* is understudied and should be examined. A full understanding of

Table 1. Number of individuals (n) of each species collected during sampling periods and the proportion of total individuals that were *P. cinereus* (%Pc). At Site A during fall 2006 and 2007, the proportion of *P. cinereus* to *P. electromorphus* is significantly greater during the first collection season indicating the impact of the flood on relative population sizes. In addition, at Site B where minor flooding occurred, the proportion of *P. cinereus* to *P. electromorphus* is significantly greater during fall 2006 and 2007. P-values (P) from chi-square tests are provided.

	P. cinereus (*n*)	*P. electromorphus* (*n*)	%Pc	P
Site A: Flood Site				
Spring 2004	34	8	0.81	—
Fall 2004	1	0	—	—
Fall 2005	32	4	0.89	0.23
Fall 2006	33	1	0.97	0.02*
Spring 2007	15	1	0.94	0.19
Fall 2007	40	3	0.93	0.04*
Site B: Weak flooding				
Spring 2004	23	9	0.72	—
Fall 2004**	25	22	0.53	—
Spring 2005	27	5	0.84	0.12
Fall 2006	58	2	0.97	<0.0001*
Spring 2007	22	5	0.81	0.27
Fall 2007	17	1	0.94	0.03*
Site C: No flooding				
Spring 2004	49	13	0.79	—
Fall 2004**	25	25	0.50	—
Spring 2005	28	3	0.90	0.12
Fall 2006	82	28	0.75	0.25
Site D: No flooding				
Spring 2004	25	3	0.89	—
Fall 2004	8	1	0.89	0.97
Spring 2007	7	0	1.00	0.36

* Indicates significant differences between the percent of *Plethodon cinereus* during first collecting season and subsequent collecting seasons.

** The number of salamanders collected was intentionally approximately 25 for each species. These collecting seasons were omitted from analyses.

the role of competition, predation, and environmental conditions in regulating populations requires broad spatial and temporal studies (Petranka and Sih 1986) and was beyond the scope of this investigation. Future studies should lead to an understanding of the relative influence of competition, predation, and disturbance in the community dynamics of terrestrial salamanders.

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Male *Sphaerodactylus thompsoni* from a locality off the Alcoa Road, north of Cabo Rojo. This individual is on a limestone rock that typifies the preferred substrate of this species in the area.