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Differences in Prey Availability within the Territories of Striped and Unstriped Eastern Red-backed Salamanders (Plethodon cinereus)

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ARTICLES

Differences in Prey Availability within the Territories of Striped and Unstriped Eastern Red-backed Salamanders (*Plethodon cinereus*)

Polymorphic species provide the opportunity to examine how selection might operate on divergent phenotypes within a single population. As a result, polymorphic species have been the subject of numerous studies aimed at understanding the processes involved in sympatric ecological divergence and speciation (Via 2001; Kusche et al. 2015). Color polymorphic species are common in many plant (Kay 1978) and animal (Gray and McKinnon 2007) taxa and provide a convenient way for researchers to sort individuals by phenotype (Wellenreuther et al. 2014). In animals, color polymorphisms often correlate with other individual features such as aggressive and antipredator behaviors, mating strategies, and physiological tolerances creating "morphs" that are more than simply divergent color phenotypes (McKinnon and Pierotti 2010). Selection acting on the suite of characters comprising morphs within a single population can, in some cases, promote reproductive isolation and eventually speciation (West-Eberhard 1986).

The Eastern Red-backed Salamander (*Plethodon cinereus*) is a fully terrestrial, forest dwelling generalist insectivore that is color polymorphic for the red dorsal stripe from which it derives its common name. In most populations, the red-striped morph predominates, but the unstriped morph is also usually present (Williams et al. 1968; Pfingsten and Walker 1978; Moore and Ouellet 2014). The two color morphs have been variously referred to as "red" and "lead", "red-backed" and "lead-backed", "striped" and "stripeless", and "striped" and "unstriped." We use "striped" to refer to individuals that have a complete or partial red dorsal stripe and "unstriped" for individuals that lack any red pigment (Fig. 1). The color polymorphism has a genetic basis (Highton 1959; Highton 1975) and correlates with a number of behavioral (Venesky and Anthony 2007; Reiter et al. 2014) and physiological traits (Moreno 1989; Smith et al. 2015). Presence of a dorsal stripe also correlates with seasonal activity patterns (Test 1952; Lotter and Scott 1977; Petruzzi et al. 2006; Anthony et al. 2008) and response to disease (Venesky et al. 2015). These correlated traits may provide potential for divergent selection between morphs.

Eastern Red-backed Salamanders have served as a model system for studying sociobiology and territoriality (Jaeger et al. 2016). Territorial behavior in this species varies throughout the range (Wise and Jaeger 2016), and not all populations exhibit territorial behavior (Quinn and Graves 1999; Maerz and Madison 2000). However, in Ohio, and at our field site, the species is territorial (Gall et al. 2003; Hickerson et al. 2004; Deitloff et al. 2008; Anthony and Pfingsten 2013; Reiter et al. 2014; but see Burgett and Smith 2012). For example, of 518 adult salamanders observed under cover at our site, 97.7% were found either alone or paired with an individual of the opposite sex (Anthony et al. 2008). In the laboratory, salamanders from our field site exhibit biting (Thompson 2013) and aggressive postures (Reiter et al. 2014) at levels similar to those reported from known territorial populations in Virginia and New York (Jaeger 1984; Thomas et al. 1989). In territorial populations, adult male and

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Fig. 1. Unstriped (left) and striped (right) Eastern Red-backed Salamanders (*Plethodon cinereus*) from Summit County, Ohio, USA.

female salamanders defend cover objects (rocks and logs) from intraspecific (Mathis 1991a) and interspecifc (Wrobel et al. 1980; Hickerson et al. 2004) competitors for food and space. Because Red-backed salamanders are lungless, they can only forage in the leaf litter surrounding their cover objects when it is sufficiently wet to provide a high humidity microhabitat suitable for cutaneous respiration (Spotila 1972). As the forest floor dries during periods between rainfall events, prey becomes limited in availability within leaf litter (Jaeger 1980) and salamanders retreat to the space beneath cover objects where they can continue to forage. As drying continues, salamanders may be forced underground where foraging opportunities are even more limited (Fraser 1976). The spaces beneath cover provide a consistent high humidity microhabitat and renewable prey resources. Salamanders defend these discrete spaces beneath cover to maintain exclusive access to prey during dry periods. At our field site in northeastern Ohio, the striped morph is more aggressive and maintains more consistent access to cover objects on the forest floor (Reiter et al. 2014). This behavior may explain why the striped morph obtains a more nutritious diet (Anthony et al. 2008) as well as access to higher quality mates (Acord et al. 2013). In this study we sought to determine if prey found within individual territories differed between morphs. We hypothesized that striped salamanders would be found in territories that contained more prey and that these prey would be of higher quality compared to those found in the territories of unstriped salamanders from the same population. For salamanders, high quality prey are soft-bodied (i.e. less chitinous), easily digested, and pass through the gut relatively quickly (Jaeger 1990).

METHODS

Our study was conducted within a 0.1 km² plot of eastern deciduous forest adjacent to the Cuyahoga Valley National Park (CVNP), Summit County, Ohio (41.229393°N, 81.520551°W). The habitat is dominated by *Acer saccharum* (Sugar Maple), *Fagus grandifolia* (American Beech), *Liriodendron tulipifera* (Tulip Poplar), and *Quercus rubra* (Red Oak) (Hickerson et al. 2012). The site was visited afternoons from 18 September 2012 through 9 November 2012. On each sampling day we systematically searched the study area by flipping natural cover objects (e.g., logs or large pieces of bark), until we encountered adult (> 32 mm snout–vent length, SVL; Anthony and Pfingsten 2013) males of *Plethodon cinereus*. Both striped and unstriped color morphs occur at this site, with unstriped individuals comprising about 34% of the population (Reiter et al. 2014). In an effort to reduce the potential for temporal pseudoreplication (e.g., hourly or weekly) and to control for daily changes in invertebrate abundance we attempted to alternate between sampling striped and unstriped territories which resulted in examining equal numbers of each morph's territory on each day. We sampled male, and not female, territories because the territories of female *P. cinereus* tend to overlap, whereas territories of males do not overlap (Mathis 1991b). Additionally, at our field site we almost never observe males co-occurring together under cover (Anthony et al. 2008). We limited our searches to cover objects of at least 25 x 25 cm because this is the minimum size that Red-backed Salamanders use as permanent cover (Mathis 1990).

We assumed that male salamanders captured under cover during the day were territorial residents because males in this population exhibit site fidelity and maintain associations with cover across multiple seasons and years (Anthony and Pfingsten
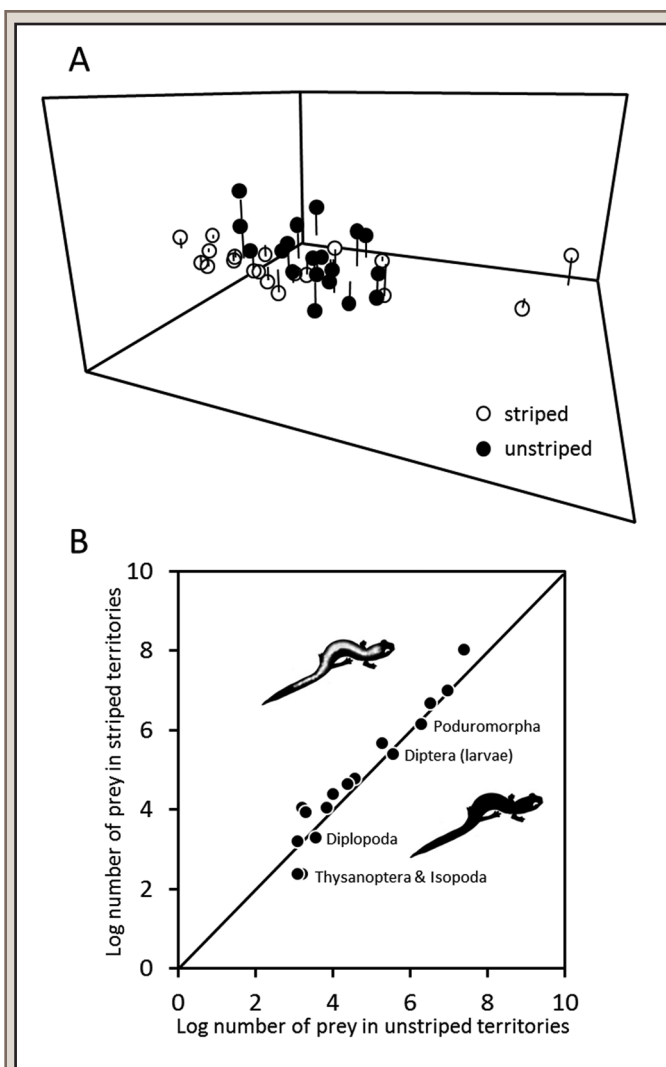

FIG. 2. A) Nonmetric multidimensional scaling (nMDS, stress = 0.07) plot depicting variation between prey availability in the territories of striped (open symbols) and unstriped (filled symbols) color morphs of the Eastern Red-backed Salamander, *Plethodon cinereus* (PERMANOVA: $F = 2.169$, $P < 0.0495$). Each symbol denotes available prey from an individual territory sample. The distance between symbols represents the difference in invertebrate community composition. B) Equal probability plot of commonly consumed prey [oribatid and non-oribatid mites; Collembola (Entomobryomorpha, Poduromorpha, and Symphypleona); Diptera larvae; Aranae; Gastropoda; Coleoptera larvae; Pseudoscorpiones; Annelida; Lepidoptera larvae; Diplopoda; Formicidae; Thysanoptera; Isopoda] found in the territories of striped (above the line) and unstriped (below the line) salamanders. Five prey types that were more commonly found in unstriped territories are indicated.

2013). Upon capture of a presumptive resident salamander, we assessed available prey resources by sampling leaf litter within a 1-m² PVC frame centered upon the capture point. To estimate soil invertebrate abundances we collected all of the leaf litter from within the 1-m² area. We then homogenized and subsampled the litter by shaking it in a cloth bag and removing 450 g for analysis. We used Berlese extraction into 70% ethanol (48 h; 40-W bulb) to collect litter and soil invertebrate prey from our leaf litter subsamples. Invertebrates that were within the gape range of *P. cinereus* (a width of 0.2–4.9 mm; Jaeger et al. 1995a) were counted and identified to at least order using a stereo dissecting

TABLE 1. The 15 most abundant invertebrate prey taxa found in the territories of striped and unstriped color morphs of the Eastern Red-backed Salamander (*Plethodon cinereus*). Average dissimilarity between territories for each taxon was calculated with SIMPER analysis. Taxa are listed in order of their contribution to the differences between territories.

Taxon	Average dissimilarity	Percent contribution	Cumulative percent	Mean/Striped territory (SE)	Mean/Unstriped territory (SE)
Oribatida (moss mites)	16.98	36.35	36.35	59.0 (8.6)	31.4 (3.4)
non-oribatid mites	7.99	17.09	53.43	21.2 (4.6)	20.2 (4.2)
Entomobryomorpha (springtails)	5.83	12.48	65.92	15.5 (2.4)	13.1 (2.7)
Poduromorpha (springtails)	4.09	8.75	74.66	9.05 (2.5)	10.3 (2.0)
Symphypleona (springtails)	2.36	5.05	79.71	5.63 (1.3)	3.74 (0.7)
Diptera (fly larvae)	2.11	4.51	84.22	4.32 (1.0)	5.0 (0.9)
Gastropoda (snails)	1.20	2.58	86.80	2.0 (0.7)	1.5 (0.8)
Aranae (spiders)	0.89	1.92	88.71	2.3 (0.4)	1.8 (0.4)
Coleoptera (beetle larvae)	0.69	1.48	90.19	1.6 (0.3)	1.1 (1.1)
Pseudoscorpiones (pseudoscorpions)	0.61	1.31	91.50	1.1 (0.3)	0.9 (0.2)
Annelida (earthworms)	0.59	1.27	92.77	1.1 (0.3)	0.5 (0.3)
Lepidoptera (moth larvae)	0.52	1.11	93.88	1.0 (0.5)	0.5 (0.2)
Diplopoda (millipedes)	0.43	0.92	94.80	0.5 (0.2)	0.7 (0.2)
Hymenoptera (ants)	0.38	0.82	95.62	0.5 (0.2)	0.4 (0.1)
Isopoda (woodlice)	0.29	0.62	96.24	0.2 (0.1)	0.4 (0.3)

microscope. For each resident salamander we measured the snout–vent length (SVL; linear distance from the tip of the snout to the anterior opening of the cloaca, in mm) and mass (with a digital balance, in g). Each salamander capture locality was permanently marked with a flag to ensure that the same cover object was not checked more than once. We maintained a 2-m buffer around each 1-m^2 sampling unit. This sampling protocol created a minimum 25-m^2 area around each cover object. This far exceeds the foraging home range of territorial *P. cinereus* which is approximately 1 m^2 (Leibgold and Jaeger 2007) and ensured that sampled territories did not overlap.

We compared available prey communities within the sampled territories of striped and unstriped individuals of *P. cinereus* using a permutational multivariate analysis of variance (PERMANOVA) in the program PAST (version 2.16; Hammer et al. 2001). The important invertebrate prey were identified with a similarity of percent analysis (SIMPER; PAST version 2.16) which provides the relative contribution of each taxon to the differences between territories. To illustrate prey community variation between morphs we used non-metric multidimensional scaling (nMDS). PERMANOVA, nMDS plots and SIMPER results were based on Bray-Curtis dissimilarity matrices. The statistical program PRIMER (version 5) was used to create the nMDS plot. To further illustrate differences in total prey between the territories of striped and unstriped salamanders, we created an equal probability plot using the 15 most commonly consumed prey at this site (94.5% of all prey consumed, Stuczka 2011; Stuczka et al. 2016). To estimate nutritional quality of prey within territories, we compared the numbers of soft-bodied prey (Jaeger 1990; Mitchell et al. 1996) found in the two territory types. We calculated Shannon's Diversity Indices for available prey in each individual territory. The index allowed us to estimate the niche breadth available to each salamander. Mean niche breadth and total number of available prey were compared between morphs using *t*-tests. We applied a two-tailed test when comparing niche breadths because previous studies reported conflicting results in the diet breadth in the two morphs. We applied one-tailed

tests when comparing total number of prey and prey quality within territories because we had clear directional predictions based on behavioral and diet differences between morphs for these comparisons (Reiter et al. 2014 for behavior; Anthony et al. 2008 and Paluh et al. 2015 for diet). When data did not meet the assumptions we used non-parametric tests. We performed *t*-tests in SPSS version 17.0 (SPSS, Inc., Chicago, Ilinois).

RESULTS

Striped (N = 19) and unstriped (N = 19) salamanders did not differ in mass (mean striped = 0.76 ± 0.02 g; unstriped = 0.77 ± 0 .04 g; *P* = 0.94) or in SVL (mean striped = 37.2 ± 0.40 mm; unstriped = 36.9 ± 0.57 mm; *P* = 0.64). We extracted and identified 4190 invertebrates from the leaf litter surrounding the 38 territories. Territories of both color morphs were dominated by mites, springtails, fly larvae, spiders, snails, beetle larvae, pseudoscorpions, earthworms, moth larvae, and millipedes. Mites and springtails made up 85.8% of the invertebrates identified. The territories of striped salamanders contained 32% more prey than unstriped territories (mean 127 versus 93 prey items per territory, *t* = 1.68, *P* = 0.052). Our PERMANOVA revealed significant variation between available prey in the territories of striped and unstriped salamanders (*F* = 2.17, *P* = 0.0495, Fig 2A). SIMPER analysis revealed that mites and springtails contributed nearly 80% of the differences between striped and unstriped territories. Of the 15 most influential taxa identified in our SIMPER analysis, 11 were more abundant in striped territories (Table 1). Prey that were more common within the territories of unstriped salamanders included poduromorph springtails, fly larvae, millipedes, isopods, and thrips (Fig. 2B). There were no differences in the numbers of soft-bodied prey between territories (striped mean = 41.4 prey; unstriped = 37.5 prey; *t* = 0.51; *P* = 0.31). Our estimates of niche breadth, as measured by Shannon's Diversity Index, did not differ between the territories of striped (H' = 1.66) and unstriped (H' = 1.78) salamanders (*t* = 1.7, *P* = 0.10).

Our study is one of few that have examined available prey within the territories of Eastern Red-backed Salamanders and the only study to have compared total prey availability in the territories of striped and unstriped color morphs of this species. Gabor (1995) tested the hypothesis that larger territorial residents would be found in territories that were more food rich. She found significant positive correlations between salamander size and total prey found in the territory. She concluded that larger salamanders gain access to higher quality territories and that this is due to the advantage that larger salamanders have in aggressive territorial contests (Mathis 1991a; Townsend and Jaeger 1998). Striped and unstriped salamanders in our samples did not differ in body size (as measured by SVL and mass) and so it is possible that differences in prey availability within territories between morphs is due to differences in territory holding potential. Specifically, the ability of striped salamanders to maintain access to territories with an abundance of prey may result from differences in aggression between the two morphs. Reiter et al. (2014), using the same population studied here, showed that striped salamanders were both significantly more aggressive and significantly less likely to exhibit submissive behaviors during staged laboratory contests. Additionally, striped salamanders showed a clear "residency effect" in which resident salamanders were significantly more aggressive than intruders, a phenomenon predicted by territoriality theory (Parker 1974; Reiter et al. 2014). In contrast, unstriped salamanders behaved similarly as residents and as intruders. Furthermore, Reiter et al (2014) showed that differences in behavior in the laboratory scaled up to measurable differences on the forest floor: striped salamanders maintained more consistent presence in their territories and unstriped salamanders were more likely to play the role of territorial "floaters" (i.e., those that are unable to hold territories [Mathis 1991b]). Differences in aggressive behavior and territoriality between the two morphs might also help to explain why the unstriped morph shows a greater proclivity to disperse (Grant and Liebgold 2017), a tactic that makes sense for individuals that are at a disadvantage in territorial disputes. Such differences in behavior may have important consequences for access to prey. For example, Dalallio (2013) found that when unstriped salamanders were paired with striped salamanders in laboratory mesocosms, they were forced into subterranean retreats. In a natural setting, this would presumably limit access by unstriped salamanders to prey.

Our results show that even when unstriped salamanders are active at the surface, they occupy territories that are less prey rich and may contain different prey communities than territories of striped individuals. This may have effects on fitness of territory holders in two ways. First, differences in the assimilation efficiencies of various types of prey translate directly to differences in available energy for territorial residents. Soft-bodied prey, such as springtails and insect larvae, should pass through the gut more rapidly and with greater efficiency than heavily armored prey, such as millipedes and isopods (Jaeger and Barnard 1981). It is interesting to note that in Virginia, striped and unstriped salamanders do not differ in assimilation efficiency (Bobka et al. 1981), but it is unknown whether the two morphs differ in Ohio. In our samples, we found no differences in the numbers of soft-bodied prey between territory types, but of the five prey types that were more abundant in unstriped territories, two were particularly well armored (isopods and millipedes) and two were rarely found in the diet of salamanders (of either morph) at this site (poduromorph springtails and Thrips [Stuzcka 2011]). Red-backed salamanders have been shown to forage optimally (preferring soft-bodied to armored prey; Jaeger et al. 1995b), so gut contents at any given time should reflect an optimal diet solution to available prey. The ability to forage optimally might explain why striped salamanders have been shown to consume more ants (a well-armored prey taxon) in some studies (Paluh et al. 2015) but not others (Anthony et al. 2008). As the forest floor dries, territorial residents are limited to foraging under cover, and if the environment becomes dry enough, ants and other armored prey may be the only (and thus optimal) prey available. Thus, when soft-bodied prey become rare in the environment, the quantity of prey within a territory may become more important than the quality of available prey. The options for non-resident floaters during exceptionally dry periods may be even more limited, illustrating the advantage to maintaining access to prey-rich territories.

A second way in which prey quality may influence fitness of the territory resident is through access to mates. In choosing mates, female red-backed salamanders assess territory quality (Karuzas et al. 2004) and possibly mate quality (Walls et al. 1989) via sampling the diet signature left in fecal pellets (termed "fecal inspection"; Walls et al. 1989). Female red-backed salamanders have also been shown to directly respond to skin secretions that are altered by diet quality (Chouinard 2012). Thus red-backed salamanders are able to determine quality of prey within territories and, to some extent, the diet of territorial residents. Compared to unstriped salamanders, striped males attract larger and presumably more fecund females (Anthony et al. 2008; Acord et al. 2013), but when presented with fecal pellets from striped and unstriped salamanders, females made no distinction (Acord et al. 2013). Given that our results suggest that differences in prey availability, but not necessarily quality, exist between striped and unstriped territories, perhaps it is not surprising that no differences in pellet quality were detected by these researchers. Whether salamanders can detect levels of prey abundance within a territory via indirect means remains to be determined.

In summary, although our study is of a single population of a widespread species, it adds to a growing body of evidence that the striped morph of *P. cinereus* maintains a territorial advantage over the unstriped morph. We found that prey quantity, but not necessarily quality, differed between territories of the two morphs, with the striped morph residing in territories with more abundant prey. At our site in northeastern Ohio, weak positive assortative mating by color morph has been reported (Anthony et al. 2008; Acord et al. 2013). Because mate choice may rely, in part, on territory quality, differences between morphs may be one avenue by which assortative pairings by color, a critical first step in the process of sympatric divergence, could occur.

LITERATURE CITED

ACORD, M. E., C. D. ANTHONY, AND C. M. HICKERSON. 2013. Assortative mating in a polymorphic salamander. Copeia 2013:676–683.

ANTHONY, C. D., AND R. A. PFINGSTEN. 2013. Eastern red-backed salamander, *Plethodon cinereus*. *In* R. A. Pfingsten, J. G. Davis, T. O. Marson, G. L. Lipps, Jr., D. Wynn, and B. J. Armitage (eds.), Amphibians of Ohio. Ohio Biol. Surv. Bull. New Series 17:335–360.

———, M. D. VENESKY, AND C. M. HICKERSON. 2008. Ecological separation in a polymorphic terrestrial salamander. J. Anim. Ecol. 77:646–653.

BOBKA, M. S., R. G. JAEGER, AND D. C. MCNAUGHT. 1981. Temperature dependent assimilation efficiencies of two species of terrestrial salamanders. Copeia 1981:417–421.

BURGETT, A. A., AND G.R. SMITH. 2012. Differential responses of eastern red-backed salamanders (*Plethodon cinereus*) to conspecifics and centipedes. Curr. Herpetol. 31:78–86.

CHOUINARD, A. J. 2012. Rapid onset of mate quality assessment via chemical signals in a woodland salamander (*Plethodon cinereus*). Behav. Ecol. Sociobiol. 66:765–775.

DALALLIO, E. A. 2013. Assessing climate change effects on competitive interactions of the federally endangered Shenandoah salamander (*Plethodon shenandoah*). Master's Thesis, Towson University, Towson, Maryland. 59 pp.

DEITLOFF, J., D. C. ADAMS, B. F. M. OLECHNOWSKI, AND R. G. JAEGER. 2008. Interspecific aggression in Ohio *Plethodon*: implications for competition. Herpetologica 64:180–188.

FRASER, D. F. 1976. Empirical evaluation of the hypothesis of food competition in salamanders of the genus *Plethodon*. Ecology 57:459–471.

GABOR, C. R. 1995. Correlational test of Mathis' hypothesis that bigger salamanders have better territories. Copeia 1995:729–735.

GALL, S. B., C. D. ANTHONY, AND J. A. WICKNICK. 2003. Do behavioral interactions between salamanders and beetles indicate a guild relationship? Am. Midl. Nat. 149:363–374.

GRANT, A. H., AND E. B. LIEBGOLD. 2017. Color-biased dispersal inferred by fine-scale genetic spatial autocorrelation in color polymorphic salamander. J. Hered. 108(5):588–593.

GRAY, S. M., AND J. S. MCKINNON. 2007. Linking color polymorphism maintenance and speciation. Trends Ecol. Evol. 22:71–79.

HAMMER, O., D. A. T. HARPER, AND P. D. RYAN. 2001. Past: paleontological statistics software package for education and data analysis. Paleontol. Electron. 4:1–9.

HICKERSON, C. M., C. D. ANTHONY, AND B. M. WALTON. 2012. Interactions among forest-floor guild members in structurally simple microhabitats. Am. Midl. Nat. 168:30–42.

———, ———, AND J. A. WICKNICK. 2004. Behavioral interactions between salamanders and centipedes: competition in divergent taxa. Behav. Ecol. 15:679–686.

HIGHTON, R. 1959. The inheritance of the color phases of *Plethodon cinereus*. Copeia 1959:33–37.

———. 1975. Geographic variation in genetic dominance of the color morphs of the red-backed salamander, *Plethodon cinereus*. Genetics 80:363–374.

JAEGER, R. G. 1980. Fluctuations in prey availability and food limitation for a terrestrial salamander. Oecologia 44:335–341.

———. 1984. Agonistic behavior of the red-backed salamander. Copeia 1984:309–314.

———. 1990. Territorial salamanders evaluate size and chitinous content of arthropod prey. *In* R. N. Hughes (ed.), Behavioral Mechanisms of Food Selection, pp. 111–126. Springer-Verlag, Berlin, Germany.

———, AND D. E. BARNARD. 1981. Foraging tactics of a terrestrial salamander: choice of diet in structurally simple environments. Am. Nat. 117:639–664.

———, B. GOLLMAN, C. D. ANTHONY, C. R. GABOR, AND N. KOHN. 2016. Behavioral Ecology of the Eastern Red-backed Salamander: 50 Years of Research. Oxford University Press, New York, New York. 248 pp.

———, J. SCHWARZ, AND S. E. WISE. 1995b. Territorial male salamanders have foraging tactics attractive to gravid females. Anim. Behav. 49:633–639.

———, J. A. WICKNICK, M. R. GRIFFIS, AND C. D. ANTHONY. 1995a. Socioecology of a terrestrial salamander: juveniles enter adult territories during stressful foraging periods. Ecology 76:533–543.

KAY, Q. Q. N. 1978. The role of preferential and assortative pollination in the maintenance of flower color polymorphisms. *In* A. J. Richards (ed.), The Pollination of Flowers by Insects, pp. 175–190. Academic Press, London, UK.

KUSCHE, H., K. R. ELMER, AND A. MEYER. 2015. Sympatric ecological divergence associated with a color polymorphism. BMC Biol. 13, 82.

LIEBGOLD, E. B., AND R. G. JAEGER. 2007. Juvenile movements and potential inter- age class associations of red-backed salamanders. Herpetologica 63:51–55.

LOTTER, F., AND N. J. SCOTT, JR. 1977. Correlation between climate and distribution of the color morphs of the salamander *Plethodon cinereus*. Copeia 1977:681–690.

MAERZ, J. C., AND D. M. MADISON. 2000. Environmental variation and territorial behavior in a terrestrial salamander. *In* R. C. Bruce, R. G. Jaeger, and L. D. Houck (eds.), The Biology of Plethodontid Salamanders, pp. 395–406. Plenum Publishing Corp., New York.

MATHIS, A. 1990. Territoriality in a terrestrial salamander: The influence of resource quality and body size. Behaviour 112:162–174.

———. 1991a. Large male advantage for access to females: evidence of male-male competition and female discrimination in a territorial salamander. Behav. Ecol. Sociobiol. 29:133–138.

———. 1991b. Territories of male and female terrestrial salamanders: costs, benefits, and intersexual spatial associations. Oecologia 86:433–440.

MCKINNON, J. S., AND M. E. PIEROTTI. 2010. Colour polymorphism and correlated characters: genetic mechanisms and evolution. Mol. Ecol. 19:5101–5125.

MITCHELL, J. C., J. A. WICKNICK, AND C. D. ANTHONY. 1996. Do timber harvesting practices affect Peaks of Otter salamander (*Plethodon hubrichti*) populations? Amphib. Rept. Conserv. 1:15–19.

MOORE, J. D., AND M. OUELLET. 2014. A review of colour phenotypes of the eastern red-backed salamander, *Plethodon cinereus*, in North America. Can. Field Nat. 128:250–259.

MORENO, G. 1989. Behavioral and physiological differentiation between the color morphs of the salamander, *Plethodon cinereus*. J. Herpetol. 23:335–341.

PALUH, D. J., C. EDDY, K. IVANOV, C. M. HICKERSON, AND C. D. ANTHONY. 2015. Selective foraging on ants by a terrestrial polymorphic salamander. Am. Midl. Nat. 174:265–277.

PARKER, G. A. 1974. Assessment strategy and the evolution of fighting behaviour. J. Theoret. Biol. 47:223–243.

PETRUZZI, E. E., P. H. NIEWIAROWSKI, AND F. B. MOORE. 2006. The role of thermal niche selection in maintenance of a colour polymorphism in redback salamanders (*Plethodon cinereus*). Front. Zool. 3:10–18.

PFINGSTEN, R. A., AND C. F. WALKER. 1978. Some nearly all black populations of *Plethodon cinereus* (Amphibia, Urodela, Plethodontidae) in northern Ohio. J. Herpetol. 12:163–167.

QUINN, V. S., AND B. M. GRAVES. 1999. Space use in response to conspecifics by the red-backed salamander (*Plethodon cinereus*, Plethodontidae, Caudata). Ethology 105:993–1002.

REITER, M. K., C. D. ANTHONY, AND C. M. HICKERSON. 2014. Territorial behavior and ecological divergence in a polymorphic salamander. Copeia 2014:481–488.

SPOTILA, J. R. 1972. Role of temperature and water in the ecology of lungless salamanders. Ecol. Monogr. 42:95–125.

SMITH, G. R, T. JOHNSON, W. O. SMITH. 2015. Effects of colour morph and season on the dehydration and rehydration rates of *Plethodon cinereus*. Amphibia-Reptilia 36:170–174.

STUCZKA, A. M. 2011. Differences in the foraging behaviors of two color morphologies of the eastern red-backed salamanders, *Plethodon cinereus*. M.S. Thesis. John Carroll University, University Heights, Ohio. 55 pp.

———, C. M. HICKERSON, AND C. D. ANTHONY. 2016. Niche partitioning along the diet axis in a colour polymorphic population of eastern red-backed salamanders, *Plethodon cinereus*. Amphibia-Reptilia 37:283–290.

TEST, F. H. 1952. Spread of the black phase of the red-backed salamander in Michigan. Evolution 6:197–203.

THOMAS, J. S., R. G. JAEGER, AND E. A. HORNE. 1989. Are all females welcome? Agonistic behavior of male red-backed salamanders. Copeia 1989: 915–920.

THOMPSON, K. A. 2013. Behavioral interactions between *Plethodon cinereus* and *Eurycea bislineata* within a forest to stream ecotone. M.S. Thesis. John Carroll University, University Heights, Ohio. 57 pp.

TOWNSEND, V. R. JR., AND R. G. JAEGER. 1998. Territorial conflicts over prey: Domination by large male salamanders. Copeia 1998:725–729.

VENESKY, M. D., AND C. D. ANTHONY. 2007. Antipredator adaptations and predator avoidance for two color morphs of the eastern red-backed salamander, *Plethodon cinereus*. Herpetologica 63:450–458.

———, A. HESS, J. A. DEMARCHI, A. WEIL, J. MUNROE, C. M. HICKERSON, AND C. D. ANTHONY. 2015. Morph specific differences in disease prevalence and pathogen-induced mortality in a terrestrial polymorphic salamander. J. Zool. 295:279–285.

VIA, S. 2001. Sympatric speciation in animals: the ugly duckling grows up. Trends Ecol. Evol. 16:381–390.

WALLS, S. C., A. MATHIS, R. G. JAEGER, AND W. F. GERGITS. 1989. Male salamanders with high quality diets have faeces attractive to females. Anim. Behav. 38:546–548.

WELLENREUTHER, M., E. I. SVENSSON, AND B. HANSSON. 2014. Sexual selection and genetic colour polymorphisms in animals. Mol. Ecol. 23:5398–5414.

WEST-EBERHARD, M. J. 1986. Alternative adaptations, speciation, and phylogeny (a review). Proc. Natl. Acad. Sci. 83:1388–1392.

WILLIAMS, E. E., R. HIGHTON, AND D. M. COOPER. 1968. Breakdown of polymorphism of the red-backed salamander on Long Island. Evolution 1:76–86.

WISE, S. E., AND R. G. JAEGER. 2016. Seasonal and geographic variation in territorial conflicts by male red-backed salamanders. Behaviour 153:187–207.

WROBEL, D. J., W. F. GERGITS, AND R. G. JAEGER. 1980. An experimental study of interference competition among terrestrial salamanders. Ecology 61:1034–1039.