Comparison of the Diets of Sympatric Erythristic and Striped Morphs of *Plethodon cinereus* (Eastern Red-backed Salamander)

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Abstract - *Plethodon cinereus* (Eastern Red-backed Salamander) exhibits 3 distinct color morphs across eastern North America. The ecology of the least-common phenotype (i.e., erythristic morph) is largely unknown and no study has tested for ecological differences between sympatric erythristic and striped morphs. In this study, we compared dietary contents of striped and erythristic *P. cinereus*. We identified 553 prey items from 12 prey groups. Mean number and volume of prey per stomach did not differ between the 2 morphs. Important prey types were similar for both morphs and included Acari, formicids, Collembola, Diptera larvae, and adult Coleoptera. Additional studies regarding erythristic *P. cinereus* ecology will provide a better understanding of the role of this morph in natural populations.

Introduction

Color polymorphism is defined as the occurrence of 2 or more genetically determined distinct color morphs of a single species that occur within an interbreeding population (Ford 1945, Huxley 1955). Many species exhibit color polymorphism, and this characteristic is especially common in amphibians (Hoffman and Blouin 2000, Petranka 1998). Within the family Plethodontidae, the genus *Plethodon* contains at least 9 species that are dimorphic in dorsal coloration (Highton 2004, Petranka 1998). *Plethodon cinereus* (Green) (Eastern Red-backed Salamander), is color polymorphic, and populations of this species vary in color-morph frequency throughout its range, which encompasses the Canadian Maritime provinces and southern Quebec, west into northeastern Minnesota, and south into North Carolina. Renowned for its abundance and large population sizes, *P. cinereus* has been regarded as the most abundant terrestrial vertebrate in the eastern US (Burton and Likens 1975, Petranka 1998), and is a top-down predator that aids in the regulation of nutrient dynamics on the forest floor (reviewed in Walton 2013). Due to its importance in temperate-forest ecosystems, *P. cinereus* has been well studied by ecologists, and is considered a model organism for addressing questions in behavioral, conservation, and disease ecology (Anthony and Pfingsten 2013, Jaeger and Forester 1993, Venesky et al. 2015).

The 2 most prevalent morphs of *P. cinereus* are the striped (red-backed) and unstriped (lead-backed) morphs. The striped morph has a red stripe running down

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the center of a black dorsum, whereas the unstriped morph lacks a red dorsal stripe (Petranka 1998). These 2 morphs are often found in sympatry; however, the ratios at which the 2 morphs occur vary considerably among localities and range from 0% striped to 100% striped (Anthony and Pfingsten 2013, Moore and Ouellet 2015, Pfingsten and Walker 1978). The third, less common, *P. cinereus* phenotype is the erythristic (all-red) morph. This morph does not possess a dorsal stripe and is entirely orange-red with off-white coloration laterally and ventrally. Some erythristic individuals possess black mottling, which is often confined to the tail. The erythristic morph has been found in 4 Canadian provinces and 10 states, and typically co-occurs with the striped morph at low frequencies (rarely >20% of the population) (Moore and Ouellet 2014).

Several studies have characterized the diet of *P. cinereus* (Adams and Rohlf 2000, Anthony et al. 2008, Jaeger 1990, Maerz et al. 2006, Maglia 1996). In general, these studies have indicated that *P. cinereus* is a dietary generalist that feeds opportunistically on a variety of leaf-litter–dwelling invertebrates, with the most numerous prey items identified as Acari (mites), Formicidae (ants), and Collembola (springtails). Although the diet of *P. cinereus* has been described at several localities, few studies have examined dietary differences between *P. cinereus* morphs (but see Anthony et al. 2008, Paluh et al. 2015). Anthony et al. (2008) examined the diet of striped and unstriped *P. cinereus* collected on a single day and found that the diets of striped individuals were significantly more diverse and were made up of more profitable prey (i.e., small, soft bodied prey which are easily digested and pass through the gut quickly; Jaeger 1990), compared to the diets of unstriped salamanders. Further work has suggested these dietary differences may influence mate choice and territoriality in this species, and play a role in maintaining morph frequencies in that population (Acord et al. 2013, Reiter et al. 2014). Ecological data are relatively sparse for erythristic *P. cinereus* morphs, and no study has attempted to examine the dietary differences between striped and erythristic individuals in sympatry.

In this study, we examined dietary contents of striped and erythristic morphs from a single locality in northeast Ohio to: (1) describe the diet of erythristic *P. cinereus* and (2) determine if there is dietary separation between the 2 color morphs occurring in sympatry. We hypothesized that there would be differences between the 2 color morphs in dietary composition, prey importance, and niche breadth (prey diversity).

Methods

We collected dietary contents of striped (*n* = 29; 18 male, 11 female) and sympatric erythristic (*n* = 25; 10 male, 15 female) *P. cinereus* morphs at the West Woods, Russell Township, Geauga County Park District, OH (41°27'16.2"N, 81°19'47.0"W; Fig. 1). The study site is characterized by silt-loam soils, and the dominant trees are *Acer saccharum* Marshall (Sugar Maple), *Fagus grandifolia* Ehrh. (American Beech), *Acer rubrum* L. (Red Maple), *Liriodendron tulipifera* L. (Tulip Poplar), and *Prunus serotina* Ehrh. (Black Cherry). *Plethodon cinereus* forage in leaf litter during wet conditions, and move under cover to areas that retain moisture and prey

between precipitation events (Jaeger 1980). Therefore, we sampled beneath rocks, logs, and artificial cover (slate floor-tiles from a previous study conducted in 2011) at least 2 days after rainfall, when salamanders had returned to cover objects to escape desiccation. We sampled several days after rain to maximize our ability to capture animals. We searched for salamanders within a 10-ha area of the park on 11 collection days during the period 5 September–22 October 2012. Soil temperature was measured with a waterproof digital soil probe (Update THDP-450 NSF). On collection days, mean soil temperature ranged from 20.6 ºC in early September to 10.5 ºC in late October, and differed by sampling date ($F_{10} = 196.70$, $P < 0.0001$). However, we assume the seasonal decline in soil temperature did not affect our sampling because we were able to find both morphs on each of the 11 collection dates. Air temperature and relative humidity were recorded each sampling day using a digital max/min thermohygrometer (Forestry Suppliers, Inc, MS, USA). We used digital calipers to measure salamander length from the tip of the snout to the anterior angle of the vent (SVL) to the nearest 0.01 mm and an AWS-100 digital balance (American Weigh Scale, Norcross, GA) to measure mass. We determined sex by the shape of the snout—reproductive male *P. cinereus* have an enlarged snout, whereas females possess a blunt snout (Anthony et al. 2008).

We employed gastric lavage to collect diet samples from salamanders during daylight hours. This is a non-lethal procedure in which a small-diameter, flexible
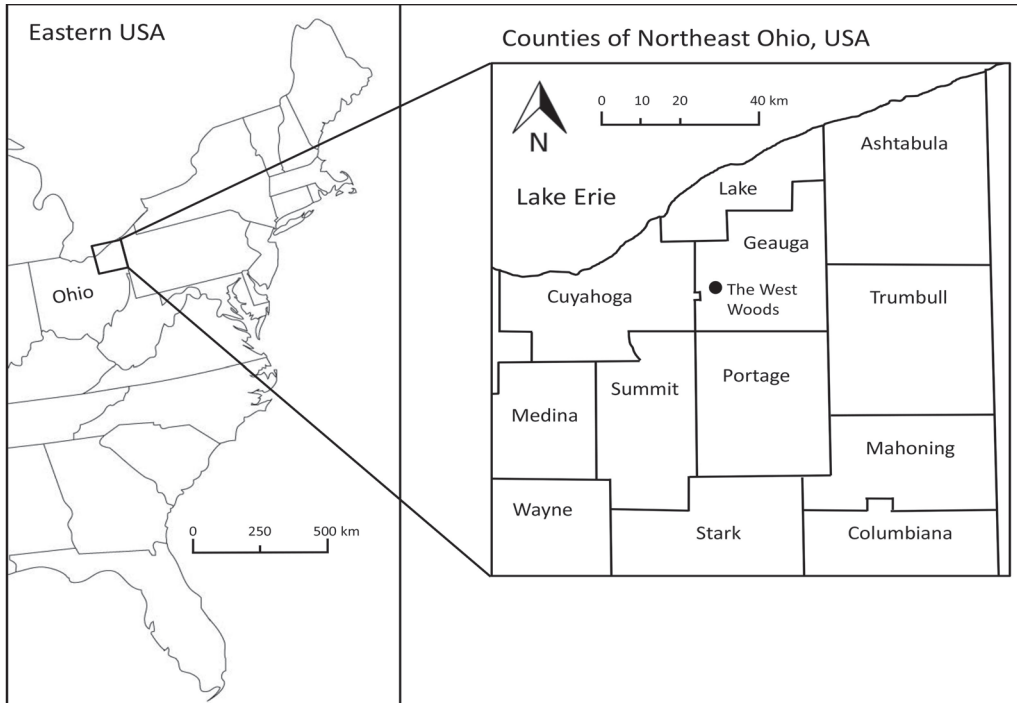

Figure 1. Map showing the location of Ohio within the eastern US. The inset map depicts the counties of northeastern Ohio; the location of our field site is in the western part of Geauga County, OH.

tube is inserted through the mouth and into the stomach, and dietary items are flushed out with water (Bondi et al. 2015, Fraser 1976). We collected dietary samples from salamanders ≥30 mm SVL. To minimize the possibility of detecting variation in diets attributed to differences in body size, we size-matched salamanders by collecting striped and erythristic individuals of similar SVL (mm) on each sampling day (size range = 30.7–41.9 mm). Additionally, we attempted to collect equal numbers of both morphs on each sampling day; however, the frequency of the erythristic morph is low in this population (10–15%). To ensure independence of data, we toe-clipped sampled salamanders before releasing them at their capture location and did not sample any recaptured individuals. We placed dietary samples in 1.5-mL centrifuge tubes containing 70% ethanol for storage at John Carroll University, University Heights, OH.

We examined all dietary samples under a dissecting stereomicroscope. We organized all invertebrate specimens into morphospecies, counted them, and identified each to the lowest taxonomic resolution possible (usually order). We used morphospecies (i.e. invertebrates that were assumed different species based upon their distinct morphological differences) in our prey community composition analyses in an attempt to prevent artificially simplifying the data set and missing important dietary differences that would be masked by only analyzing orders of litter invertebrates. We measured length and width of each prey item to the nearest 0.01 mm and estimated volume as a prolate spheroid using the equation (Dunham 1983):

$$\text{Prey volume} = (4\pi/3)\,(\text{length}/2)\,(\text{width}/2)^2$$

We employed non-metric multidimensional scaling (nMDS) to illustrate dietary variation between the 2 phenotypes. We used 1-way analysis of similarity (ANOSIM) to detect any statistical differences in dietary composition between morphs and sex, and examined numbers of each morphospecies per sample in this analysis. Both the nMDS and ANOSIM results were based on Bray-Curtis dissimilarity matrices (PRIMER version 5). We calculated Shannon diversity index (H') to represent niche breadth for each dietary sample. We compared diversity indices between morphs using 2-tailed *t*-tests (SPSS version 21).

We used the equation:

$$I_x = [(n_x/N) + (v_x/V) + (f_x/F)]\,/3$$

to calculate importance values (I_x) for the 12 prey groups that individually accounted for >1% of the total invertebrates consumed by striped and erythristic *P. cinereus*, where n_x, v_x, and f_x represent the number, volume, and frequency (number of stomachs containing that prey), respectively, of each prey group, and N, V, and F represent the sums of those values across all prey types in the stomachs examined. Importance values range between 0 and 1 and provide a measure of importance of each prey group in an organism's diet (Anderson and Mathis 1999, Powell et al. 1990). We calculated the importance values at the taxonomic resolution of order so they would be comparable to results from other diet studies of *P. cinereus*. We used 2 separate χ^2 tests to compare the number (i.e., total number of prey across all stomachs) and frequency (i.e., number of stomachs with a given prey type) and 2-tailed

t-tests to compare total volume and number of the most-common prey groups between morphs (SPSS version 21). We natural log-transformed all data [LN(x + 1)] to improve adherence to normality, and adjusted degrees of freedom for cases in which there was violation of equal variance.

Results

We identified 553 prey items, representing 12 commonly occurring categories of invertebrates, from 54 salamanders. Within these prey categories, striped morphs (*n* = 29) consumed 289 invertebrates, while erythristic morphs (*n* = 25) consumed 264 invertebrates. Dietary contents were similar between morphs. For both striped and erythristic morphs, numerically the most common prey items consumed were Acari, Collembola, and Formicidae (Table 1, Fig. 2). These 3 prey groups made up 69% of the diet of striped and 71% of the diet of erythristic salamanders. The 3 most important categories of prey were consumed in the following proportions for each morph: striped and erythristic morphs consumed Acari (41% and 39%), Collembola (16% and 22%), and Formicidae (12% and 10%), respectively. Volumetrically important prey items for both salamander phenotypes were Formicidae, Coleoptera, and Hemiptera (Table 1, Fig. 2). Mean number (striped = 9.10, erythristic = 8.88; $Z = 0.21$, $P = 0.83$, 2-tailed) and mean volume of prey per dietary sample (striped = 44.98 mm^3, erythristic = 51.15 mm^3; $Z = 0.36$, $P = 0.720$, 2-tailed) did not differ between morphs. When we examined the number, frequency, and volume of important taxa as determined by our I_x values, we found no differences with regard to morphs. The total number of prey consumed ($\chi^2_7 = 11.56$, $P = 0.75$), frequency of prey in stomachs ($\chi^2_7 = 4.23$, $P = 0.116$), and volume ($F_7 = 0.34$, $P = 0.945$) of important prey taxa were similar for striped and erythristic *P. cinereus*.

In our prey-community composition analyses, individual morphospecies (75 categories) did not vary between the 2 *P. cinereus* color morphs (global R = 0.191; $P = 0.203$; Fig. 3), or between genders (global R = -0.025, $P = 0.158$). Within each color morph there were no gender differences in total prey consumed (erythristic, $t_{23} = 1.23$, $P = 0.234$; striped, $t_{27} = 1.18$, $P = 0.248$). Estimates of niche breadth did

Table 1. Importance values (I_x) for dominant-prey categories (i.e., those that made up greater than 1% of the total number of invertebrates for each morph) of striped and erythristic morphs of Eastern Red-backed Salamander. The 6 most-important prey categories (*) for each phenotype were calculated from (in parentheses) the total number of each prey type (n_x), the total volume of each prey type (v_x) and the frequency (f_x) of each prey type.

Prey taxon	Striped (*n* = 29)	Erythristic (*n* = 25)
Acari	0.409* (118, 47.57, 23)	0.405* (95, 69.36, 12)
Formicidae	0.306* (35, 371.75, 17)	0.255* (24, 293.75, 12)
Collembola	0.261* (50, 44.85, 17)	0.270* (55, 56.78, 14)
Coleoptera	0.165* (11, 319.89, 8)	0.197* (13, 335.09, 8)
Diptera (larvae)	0.159* (32, 40.09, 10)	0.112 (13, 7.29, 7)
Hemiptera	0.114* (5, 267.55, 5)	0.100 (3, 256.61, 3)
Diptera	0.111 (11, 33.88, 8)	0.130* (14, 23.86, 8)
Lepidoptera (larvae)	0.059 (2, 178.92, 2)	0.125* (5, 235.98, 5)

not differ between phenotypes (mean H' striped = 1.38, mean H' erythristic = 1.41, $t_{39.56} = -0.107$, $P = 0.915$).

Discussion

This is the first study to describe the diet of the erythristic morph of *P. cinereus*, and our results demonstrate that sympatric striped and erythristic morphs have similar diets during the autumn season. Weather conditions during our study (mean temperature = 18.1 °C; mean relative humidity = 72.2%) were appropriate for *P. cinereus* to forage on abundant invertebrate prey (Jaeger 1980). Both striped and erythristic salamander diets were numerically dominated by Acari. Formicids were also important prey items for both morphs at our field site, and although striped
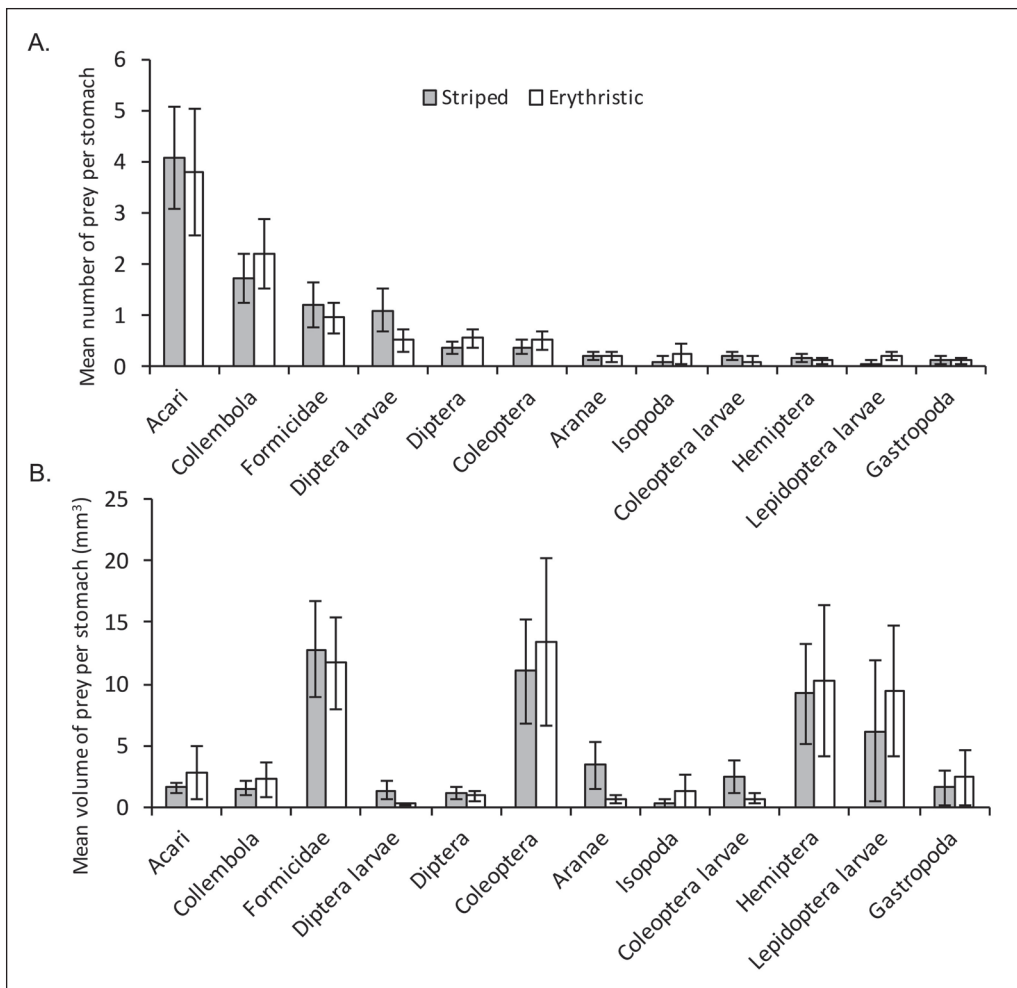

Figure 2. Diet differences between striped (gray bars, *n* = 29) and erythristic (white bars, *n* = 25) Eastern Red-backed Salamanders. Mean number (A) and volume (B) of prey consumed by each morph (± 1 SE). There were no differences in mean number or volume of prey between the 2 morphs.

salamanders consumed more formicids than erythristic salamanders, this difference was not significant. Previous studies have shown that the striped morph of *P. cinereus* consumes more formicids than the unstriped morph (Anthony et al. 2008, Paluh et al. 2015). Paluh et al. (2015) suggested that because ants are an important dietary source for *P. cinereus*, the striped morph may maintain territories that offer greater foraging opportunities on formicids. Therefore, striped *P. cinereus* may have higher-quality territories than the erythristic morph at the West Woods site due to the abundance of ants in their diet; however, further research is needed to measure ant abundance in the morph territories to verify this hypothesis. In our study, the erythristic morph consumed more Collembola than the striped morph. This result differs from findings reported by Anthony et al. (2008), which indicated that the striped morph consumed more Collembola than the unstriped morph at a location ~32 km away from our field site.

Interestingly, diplopods and isopods were neither abundant nor important prey categories at our field site (Table 1, Fig. 2), a result that also differs from the report by Anthony et al. (2008). For example, isopods made up about 5.5% of the diets of *P. cinereus* in the Cuyahoga Valley (CV) where Anthony et al. (2008) conducted their diet study, but at our field site, isopods made up only 3% of the diet, and less than 1% when we removed from the calculation the single individual that consumed 5 isopods. It is possible that the prey community in the CV differs from that of West
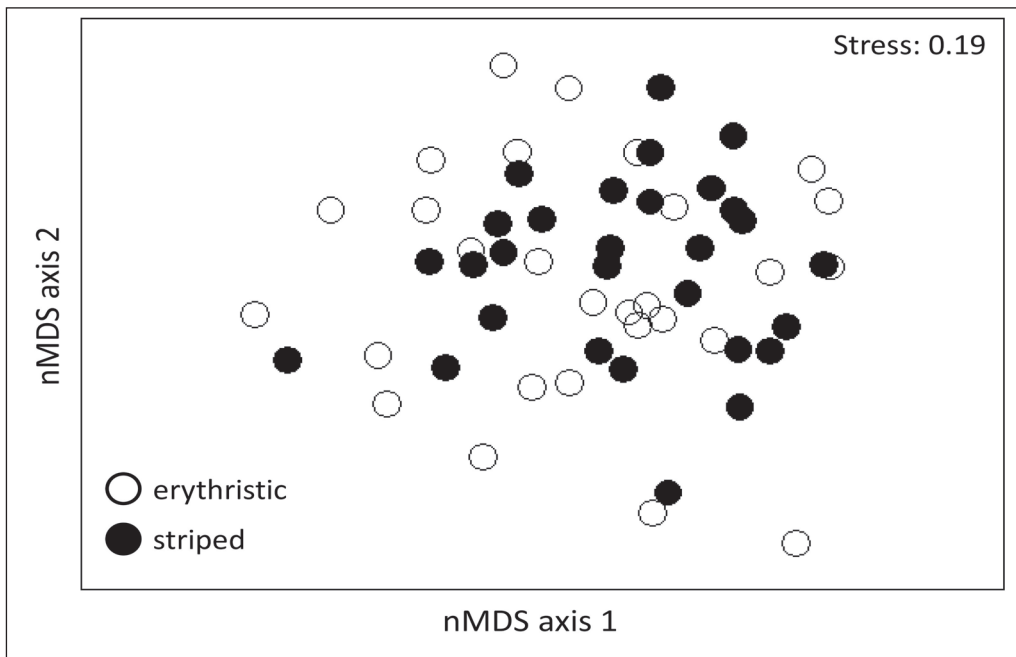

Figure 3. Nonmetric multidimensional scaling (nMDS) plot depicting variation in species composition found in stomach contents of striped (black symbols) versus erythristic (white symbols) Eastern Red-backed Salamanders. Each symbol represents an individual diet sample. Symbols that are farther from one another indicate greater differences in dietary composition relative to symbols that are closer together.

Woods (WW), where our study was conducted. We know for example, the relative abundance of diplopods and isopods present in leaf litter from the Cuyahoga Valley was found to be higher than at West Woods in the fall (mean number of millipedes CV = 0.440, WW = 0.204, $F_{1,28}$ = 5.35, P = 0.025; mean number of isopods CV = 0.478, WW = 0.262, $F_{1,28}$ = 4.12, P = 0.048; C.M. Hickerson, unpubl. data). Similarly, although our estimates of niche breadth did not differ between striped and erythristic *P. cinereus* morphs, the mean diversity (H') of prey found in all salamander guts combined at the West Woods was 1.40 compared to 2.54 at Cuyahoga Valley. Therefore, the diversity of prey consumed was lower for both morphs in our study compared to the morphs examined by Anthony et al. (2008)—a difference that may reflect differences in prey availability at the 2 sites and one that may also be attributed to more exotic invertebrate species at the CV field site (C.-A.M. Hickerson, pers. observ.).

Our results do not support our initial hypothesis that sympatric striped and erythristic *P. cinereus* diets would differ in important prey taxa (as examined by calculating importance values), prey diversity, and prey composition. This finding is in contrast to the results of previous studies on striped/unstriped *P. cinereus* polymorphism, which have demonstrated a significant divergence in diet (Anthony et al. 2008, Paluh et al. 2015). The striped/unstriped morphs differ in microhabitat use, thermal optima, and metabolic rates (Fisher-Reid et al. 2013, Lotter and Scott 1977, Moreno 1989, Petruzzi et al. 2006). Additionally, the CV *P. cinereus* population mates assortatively by color (Acord et al. 2013, Anthony et al. 2008). Various mechanisms may drive the maintenance of color polymorphism in populations that differ in the dominant *P. cinereus* morphs (i.e., striped and erythristic).

Studies have suggested that the erythristic *P. cinereus* morph is a Batesian mimic of the terrestrial eft stage of *Notophthalmus viridescens* (Rafinesque) (Eastern Newt), which exhibits bright orange coloration and is toxic to potential predators (Brodie 1968, Brodie and Brodie 1980, Kraemer and Adams 2013, Kraemer et al. 2015, Tilley et al. 1982). This strategy may help maintain the striped/erythristic color polymorphism. For example, if predators perceive erythristic *P. cinereus* as aposematic in coloration, this morph may be afforded additional foraging opportunities at the surface that are unavailable to striped morphs. Due to these extra foraging opportunities, erythristic morphs at our field site may be able to maintain a similar diet to striped morphs, which appear to be a superior competitor in striped/unstriped populations (Anthony et al. 2008, Paluh et al. 2015). We suggest further research is needed to examine other sympatric populations of erythristic and striped morphs to verify the lack of dietary divergence, as well as test for differences in other ecological traits and identify the presence or absence of assortative mating between these 2 morphs.

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