

Niche partitioning along the diet axis in a colour polymorphic population of Eastern Red-backed Salamanders, *Plethodon cinereus*

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Abstract. Eastern Red-backed Salamanders are colour polymorphic and have become a model system for examining ecological separation and the mechanisms for potential divergence in sympatry. Morphs of this species are differentiated along several niche axes including temperature optima, territorial behaviour, and response to predators. We were interested in whether temporal variation in ecological conditions would affect foraging behavior and ultimately diet. The goal of our study was to compare the diets of striped and unstriped *P. cinereus* over a range of seasonal conditions to better understand if the reported differences observed in the fall season at our field site remain consistent through the active season of this species. Diet differences between the two morphs were greatest during spring and fall when salamanders are most abundant at the surface. These diet differences were driven largely by two prey categories. In the spring, striped salamanders ate more oribatid mites and in the fall they consumed more entomobryomorph Collembola. Trade-offs associated with territory acquisition coupled with physiological and morphological differences may explain the observed seasonal niche partitioning related to the diet in this population.

Keywords: aggression, ecological divergence, prey differences, seasonality, sympatry, temporal variation, territoriality.

Introduction

The differing phenotypes of polymorphic species may be subject to different selective regimes within a shared environment which makes these species useful for examining divergence in sympatry. One such polymorphic species is the Eastern Red-backed Salamander, *Plethodon cinereus*, a geographically widespread and ecologically important terrestrial salamander (Burton and Likens, 1975; Hickerson, Anthony and Walton, 2012; Walton, 2013). Red-backed salamanders have served as a model system for many areas of biology including ecology, conservation biology, evolutionary biology, disease ecology, social behaviour, physiology, and foraging behaviour (reviewed in Anthony and Pfingsten, 2013). The species has two common colour phenotypes, a striped morph with a red dorsal band of colour that extends from the head or neck to the tail, and an unstriped morph that lacks the red-stripe and is instead, uniformly black. Other morphs

typically make up less than 1% of any population (Moore and Ouellet, 2014).

The two common morphs (striped and unstriped) are ecologically differentiated and may be responding to differential selection in their shared environment. There has been no comprehensive comparison of polymorphic populations across the range of this species and it is unknown whether morphs have responded similarly to selection in all populations. In general, the morphs differ in their response to disturbance (Fleming et al., 2011), snake predators (Venesky and Anthony, 2007), chytrid fungus (Bd) (Venesky et al., 2015) and in baseline stress levels (Davis and Milanovich, 2010). Additionally, numerous studies suggest that the unstriped morph is better adapted to drier and warmer conditions (Lotter and Scott, 1977; Gibbs and Karraker, 2006; Anthony, Venesky and Hickerson, 2008; Anthony and Pfingsten, 2013; Fisher-Reid and Wiens, 2015; but see Fisher-Reid et al., 2013 and Moore and Ouellet, 2015) and this may affect their social and territorial behaviour. For example, the unstriped morph, which is less aggressive and less likely

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to hold territories (Reiter, Anthony and Hickerson, 2014), may use its ability to tolerate warmer temperatures to forage in drier leaf litter, thus negating the need to hold a territory. Interestingly, the striped morph is able to rehydrate more rapidly than the unstriped morph (Smith, Johnson and Smith, 2015) and this ability may provide an advantage to territorial residents if it allows them to recover more rapidly from hydric stress and to maintain a more consistent presence in their territories.

An important advantage to holding a territory is the access it affords residents to prey. Red-backed salamanders are thought to defend space beneath natural cover objects (i.e. rocks and logs) during dry periods between precipitation events when desiccation-prone arthropod prey become isolated in moist patches beneath cover (Jaeger, 1980; Mathis, 1990, 1991). Geographic variation in territorial behavior may emerge from differences in prey availability or length of the active season (Maerz et al., 2005; Rollinson and Hackett, 2015), but in Ohio, the species is territorial (reviewed in Anthony and Pfungsten, 2013). Red-backed salamanders feed on small invertebrates including ants, mites, and springtails (Collembola). Their diet composition is well known (summarized in Anthony and Pfungsten, 2013), including in Ohio (Ivanov et al., 2011; Paluh et al., 2015), but only two studies have examined prey differences between morphs. Anthony, Venesky and Hickerson (2008) found that the diets of striped individuals were significantly more diverse, and were made up of more energetically profitable prey than those of unstriped salamanders. Paluh et al. (2015) focused on ant species within the diets of the two morphs and found that both the diet, and territories, of striped salamanders contained more ants. In both of these studies, samples were only collected in the fall season.

We were interested in whether variation in temperature and moisture, which the two morphs may respond to in different ways, would affect foraging behavior and ultimately diet. One way to explore this would be to examine

geographic variation in diet between the two morphs and how it relates to different climatic regimes. We chose, instead, to examine how the morphs respond to seasonal shifts in meteorological conditions at a single location where the two morphs coexist in sympatry. In northeastern Ohio (USA), where our study was conducted, red-backed salamanders become active on the forest-floor in late March but become difficult to find as summer approaches. They become active again in September and remain so until November in typical years (Anthony and Pfungsten, 2013). Thus, these salamanders forage in a variety of conditions ranging from cool and wet (in spring and fall) to warm and dry (in summer). The goal of our study was to compare the diets of striped and unstriped *P. cinereus* over a range of conditions to better understand if the reported differences observed in the fall season at this field site (Anthony, Venesky and Hickerson, 2008; Paluh et al., 2015) remain consistent through the active season of this species. We predicted that differences in diet between the morphs would be most pronounced in spring and fall when salamanders are abundant on the forest-floor and presumably are competing for territories, but that these differences would be less pronounced in the summer months when surface activity is curtailed by warm and dry conditions.

Materials and methods

We chose to examine diet differences between striped and unstriped red-backed salamanders over a 13 month period from a single polymorphic population in Summit County, Ohio, USA. This population is comprised of 64% striped and 34% unstriped salamanders (Reiter, Anthony and Hickerson, 2014) which is similar to the frequencies of the two colour morphs in other nearby polymorphic populations (pers. obs.). All stomach contents were collected from salamanders found on a north-facing forested slope within the Cuyahoga Valley National Park (41°13'46.62"N, 81°31'7.77"W). The study area is a mesic hardwood forest typical of the region. Salamanders were found under white ceramic floor tiles (30.5 × 30.5 cm), which had been placed as artificial cover objects in April of 2004 as part of a larger study examining the regulatory role of *P. cinereus* in the forest-floor food web (Hickerson, Anthony and Walton,

2012). Cover objects (288 total) were arranged in arrays of nine tiles per plot in a 3×3 tile square. Each plot (32 total) was 25 m^2 in area. These cover objects allowed us to estimate numbers of surface active salamanders on different dates and to capture specimens for diet analysis.

We used gastric lavage to obtain stomach contents of live salamanders (Fraser, 1976a; Mitchell, Wicknick and Anthony, 1996). We collected stomach contents at least twice monthly from November 2006–December 2007. No stomach contents were collected during January, February, and July because salamanders were not active on the surface of the forest-floor during these months. Stomach contents were collected from 256 salamanders (128 of each of the two phenotypes). On each of the 21 sampling days, equal numbers of striped and unstriped morphs were processed (mean = 11.2; range 4–36 salamanders). Additionally, we size matched individuals of the two morphs on each sampling date to minimize any variation in the diet that could be attributable to body size.

The prey items from each stomach sample were identified, counted and sorted into 34 taxonomic categories using a dissecting scope. The colour morph associated with each sample was unknown to the researcher that counted and identified dietary prey items. Stomach contents from salamanders of all but the smallest size classes (those less than 20 mm snout-vent length, SVL) were incorporated into our analysis, because studies have shown limited differences in diet between age classes (Burton, 1976; Mitchell and Woolcott, 1985; Jaeger et al., 1995). To determine if the number of salamanders examined in this study provided an accurate estimate of diet for each morph, diet accumulation curves were constructed. We used Shannon's Diversity Index to estimate diet breadth for each individual salamander and compared the mean diet breadth for each morph on each sampling day (paired t -test, two-tailed). Diet differences on each of 21 sampling days were calculated by pairing striped and unstriped individuals by size [mean SVL for striped = 33.5 mm (SE = 0.36 mm); for unstriped = 33.3 mm (SE = 0.37 mm)]. We then determined the number of taxonomic prey categories that differed between the two individuals. Differences in prey categories between pairs on a given day were then averaged over the total number of pairs for that day. This approach allowed us to visualize the magnitude of diet difference on each sampling day.

We recorded the number of surface active salamanders on each diet sampling day by flipping all 288 cover objects in the site. We performed curvilinear regression analyses to test whether date was a predictor of mean numbers of salamanders and/or mean diet differences between the two phenotypes of red-backed salamanders. Since salamanders are known to be active on the forest-floor during spring and fall while retreating to underground refugia in summer and winter (Anthony and Pfingsten, 2013), we specifically tested for a cubic effect in these analyses to tease apart potential seasonal differences in diet. We predicted that niche partitioning along the diet axis would most likely occur when salamanders are abundant on the surface and competition for prey resources is thought to be most intense. We used a linear regression to determine if salamander density predicted differences in diet between phenotypes. Additionally

we used two-tailed paired t -tests (by body size) to compare mean numbers of individual prey categories consumed by striped and unstriped individuals within each season. We targeted these tests to the 10 most common prey taxa consumed in each season. When data failed to meet the assumptions of parametric tests, we employed Wilcoxon signed ranks tests and report Z statistics. We used a nested (morph within season) analysis of similarity (ANOSIM: PRIMER version 5; Primer-E, Ltd., Plymouth, United Kingdom) to explore seasonal differences in diet composition between the two morphs. ANOSIM results are based on Bray-Curtis dissimilarity matrices. All statistics except the ANOSIM were performed using IBM SPSS Statistics Version 21.

Results

Visual inspection of diet accumulation curves revealed that our sample size provided an accurate representation of overall diet of each phenotype at our field site (fig. 1). We counted and identified 4638 individual prey items. Presence/absence of these taxonomic groups of arthropod prey was used to calculate differences in the diets of size matched pairs on each sampling day.

Compared to striped salamanders, unstriped salamanders had significantly more diverse diets (mean Shannon Diversity Index = 1.45 versus 1.30; $t = 2.09$, $P < 0.025$). Differences in diet breadth were greatest in spring and fall

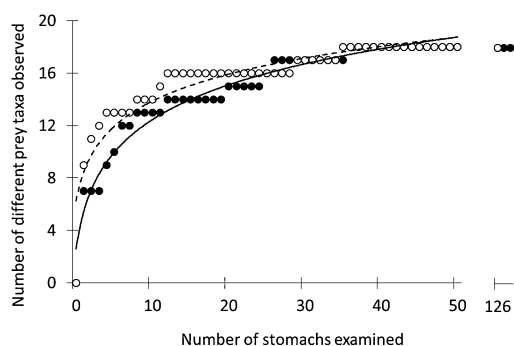


Figure 1. Species accumulation curves for dietary prey items of striped (open circles, dashed line) and unstriped (closed circles, solid line) red-backed salamanders, *Plethodon cinereus*. Very few novel taxa appear in the diets beyond 40 samples suggesting that our sampling was sufficient to obtain overall diet information on this species at our field site.

(fig. 2). Julian date was a significant predictor of salamander surface density which peaks at our field site in late March and again in late October (fig. 3A). Although only 27% of the variation in our diet differences could be predicted by Julian date, we nonetheless found an interesting relationship between salamander density and differences in the diets of the two phenotypes. The diets of striped and unstriped morphs of *P. cinereus* were most different from one another in spring and in fall when salamander den-

sity on the forest-floor is greatest (fig. 3A). This relationship became increasingly clear when we examined salamander density as a predictor of diet differences between colour morphs. We discovered a significant positive linear relationship such that as salamander surface density increased, the magnitude of diet differences also increased (fig. 3B).

ANOSIM revealed no effect of color morphology on composition of the diet within seasons (Global $R = -0.031$, $P = 0.876$). We suspect that ANOSIM failed to detect prey differences between morphs because the test does not allow paired comparisons between size-matched individuals. Our targeted paired tests indicate that diet differences between morphs in spring and fall were driven largely by two prey categories. In the spring, striped salamanders consumed more than twice as many oribatid mites (mean = 2.5 mites/stomach) as unstriped individuals (mean = 1.2 mites/stomach; $t_{29} = 2.6$; $P < 0.025$). In the fall, striped salamanders ate significantly more entomobryomorph Collembola (mean = 1.56 Collembola/stomach) than did unstriped individuals (mean = 1.03 Collembola/stomach; $t_{60} = 2.24$, $P < 0.05$).

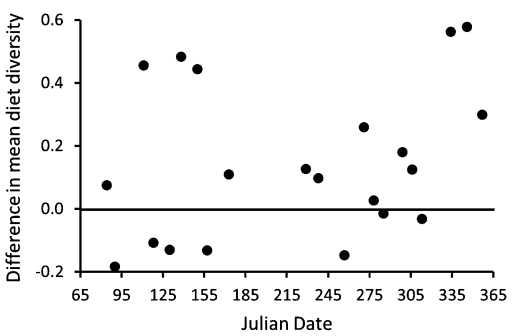


Figure 2. Difference in mean diet diversity (Shannon's Diversity Index) between striped and unstriped salamanders on each of 21 sampling dates. Points above the horizontal line are instances where mean diet diversity of unstriped salamanders was greater than that of striped salamanders.

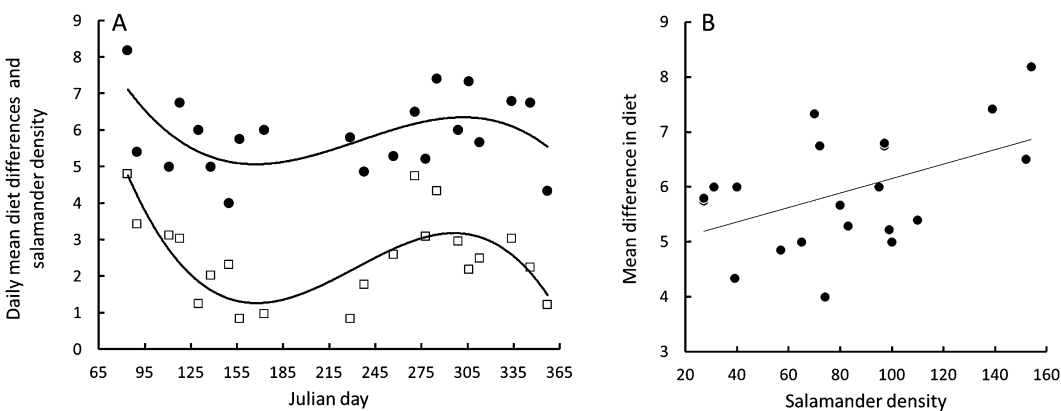


Figure 3. (A) Daily mean difference in diet (closed circles, solid line) and salamander density (open squares, dashed line) per 9-tile plot. All points represent daily means. Upper line: $R^2 = 0.274$, $F_{3,17} = 2.143$, $P = 0.133$. Lower line: $R^2 = 0.603$, $F_{3,17} = 8.615$, $P < 0.002$. (B) Relationship between daily mean difference in diet and salamander density. Each point represents a daily mean difference in diet. Salamander densities reflect total number of red-backed salamanders observed in constrained cover object searches on each stomach content collection day. $R^2 = 0.228$, $F_{1,19} = 5.597$, $P < 0.05$.

Discussion

Red-backed salamanders are territorial, defending space beneath rocks and logs against intraspecific (Mathis, 1990) and interspecific intruders (Lancaster and Jaeger, 1995; Hickerson, Anthony and Wicknick, 2004). These territories provide residents with a predictable source of prey (Jaeger, 1979), especially during times when the surrounding forest-floor is too dry to forage in. Differences in cover object use and aggression of striped and unstriped *P. cinereus* has been documented in our study population. Reiter, Anthony, and Hickerson (2014) found that striped residents in the field held territories for longer, and were recaptured more often than unstriped residents. In the laboratory, striped salamanders were more aggressive and less submissive than unstriped salamanders. These results suggest that the striped morph in this population may be more territorial than the unstriped morph and this difference in behavior may allow the morphs to access different prey types during the seasons when this species is most surface active (spring and fall). During the cool, wet conditions of spring and fall, densities of surface active salamanders at our field site increase markedly with numbers exceeding 5 per m². In the summer months, warm temperatures and dry conditions restrict surface activity and the number of salamanders found approaches zero at our site. This activity pattern stands in contrast to that observed in mountainous portions of the range of *P. cinereus* where the species remains surface active from spring through the fall (Jaeger, 1980). Since surface activity in north-eastern Ohio is limited in duration, this may set the stage for increased competition for territories and prey during these relatively brief periods of activity. Fraser (1976a, 1976b) suggested that in mountainous regions, the densities of similarly sized sympatric species of *Plethodon* may not be high enough to promote competition because they resurface at staggered intervals during favorably wet conditions. It is possible, that at our field site, both morphs are physiologically stressed by the end of both winter

and summer and are forced to resume activity at the same time during spring and fall to forage. This results in the high surface densities of both morphs observed in spring and fall (Anthony, Venesky and Hickerson, 2008; Anthony and Pfingsten, 2013) and may contribute to the observed diet differences.

Additionally, both unstriped individuals of *P. cinereus*, and unstriped species within the *Plethodon cinereus* species group, have more costal grooves (i.e. trunk vertebrae) than their striped counterparts (Fisher-Reid et al., 2013; Fisher-Reid and Wiens, 2015). An increase in body elongation is thought to be an adaptation for burrowing (Williams, Highton and Cooper, 1968). Grooves also function in transport of water over the body (Lopez and Brodie, 1977) so an increase in the number of grooves may improve performance in drier conditions. It could be that tolerance to dry conditions and body elongation allows the unstriped morph to forage in suboptimal habitat (e.g. drier leaf litter and subterranean burrows) thereby avoiding intraspecific competition with the striped morph for prey and for mates during warm and dry conditions. It is thought that the best foraging opportunities for terrestrial plethodontids are at the surface of the forest floor (Jaeger, 1972, 1980) and that these opportunities rapidly decline below the surface (Fraser, 1976a). However, below ground foraging, though perhaps not optimal, does occur. Red-backed salamanders taken up to 100 cm below the surface have been found with prey in their guts (Caldwell and Jones, 1973; Caldwell, 1975), so it is possible that subterranean foraging sites, and drier leaf litter, may represent alternatives for the unstriped morph at our field site. This very pattern of subterranean burrow use by the unstriped morph has been documented in a Virginia population in which striped male *P. cinereus* were able to suppress surface activity of unstriped males in laboratory mesocosms (Dallalio, 2013).

The differences that we observed in prey types consumed between the morphs is consistent with a scenario where the striped morph

is more territorial and maintains exclusive access to defended cover objects. In our study, the striped morph ate more entomobryomorph Collembola and oribatid mites, groups that are most active in upper layers of litter or on the surface (Coleman, Crossley and Hendrix, 2004). A previous study reported similar findings in a sample taken in the fall at this site in which striped salamanders consumed more Collembola and mites compared to unstriped individuals (Anthony, Venesky and Hickerson, 2008). Collembola are small, lightly armored prey that provide salamanders with an easily digestible resource (Jaeger, 1990). Salamanders invest more in the defense of territories that contain high quality prey (Gabor and Jaeger, 1995). Perhaps the cost of territorial defense for unstriped salamanders outweighs the benefit of access to high quality prey. The unstriped morph can tolerate warmer and drier conditions relative to the striped morph (Lotter and Scott, 1977; Moreno, 1989), and as a result may be able to forage more broadly in space.

We found that unstriped salamanders had significantly more diverse diets than striped salamanders. If unstriped salamanders are foraging in suboptimal habitats (e.g., dry leaf litter, underground), they may encounter more varied prey and this could contribute to the differences that we observed. Our individual estimates of diet breadth ranged from 0.56 to 2.2 and are notably lower than those reported in other studies (summarized in Anthony, Venesky and Hickerson, 2008). This difference probably reflects seasonality in diet, with lower diversity of prey taken in summer and winter, and the larger number of prey categories (34) used to estimate diversity in the current study. Regardless of general differences in magnitude, it is interesting to note that Anthony, Venesky, and Hickerson (2008) reported a wider diet breadth for the striped morph, while the current study shows the opposite trend, a finding that highlights the importance of sampling across seasons.

Given that diet differences, such as we have observed here, can give rise to adaptive morphological change within *P. cinereus* (Maerz, Myers and Adams, 2006) and between competing species within the *P. cinereus* species group (Adams and Rohlf, 2000), morphological comparisons between morphs should be an area of future research. For example, examining head shape or jaw morphology in the context of diet differences or aggression between the two morphs at polymorphic and monomorphic sites would be a logical next step. Aggressive behavior in *Plethodon* has been linked to the evolution of a more robust jaw (Adams, 2004) and diets dominated by small prey have been shown to favor a slower, stronger jaw (Adams, 2000). Thus, we predict that, relative to the unstriped morph, striped salamanders should have more robust jaw morphology that is also efficient in capturing smaller prey such as Collembola and mites. Likewise, comparisons of costal groove numbers between morphs at polymorphic sites might shed light on the role of subterranean foraging and help to explain maintenance of the colour polymorphism in *P. cinereus*.

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