Selective Foraging on Ants by a Terrestrial Polymorphic Salamander

DANIEL J. PALUH[1], CAMERON EDDY, KALOYAN IVANOV[2],
CARI-ANN M. HICKERSON AND CARL D. ANTHONY

Department of Biology, John Carroll University, University Heights, Ohio 44118

ABSTRACT.—Numerous authors have studied the diet of the Eastern Red-backed Salamander (*Plethodon cinereus*) and have described this species as a generalist predator of invertebrates. In most studies, prey taxa are identified to the family or order level. Additionally, few studies have directly assessed dietary preference by comparing diet to available prey. We chose an important component of the diet of red-backed salamanders (ants) to test whether salamanders altered their diets temporally and to determine if salamanders preyed on a subset of available ant prey. We identified ant species in salamander diets over a 13 mo period. In the fall season we also compared ants in stomach contents to those available in the surrounding leaf litter to determine if territorial residents of *P. cinereus* selectively forage on different ant species. We found significant temporal differences in ant species incorporated in the diet of *P. cinereus* that were consistent with our detailed examination of salamander ant preference in the fall. Our estimates of prey diversity and richness indicate that salamanders consumed a subset of available ant species. *Aphaenogaster picea*, an abundant species that prefers similar microhabitat characteristics to *P. cinereus*, made up a majority of the ants in the diet. However, our results indicate that *P. cinereus* avoids foraging on *Myrmica punctiventris, Myrmecina americana,* and *Lasius alienus*, ants that are among the most abundant species in the forested areas of northeastern Ohio where the study was conducted. These species are potentially aggressive and/or chemically defended, reducing their profitability as prey. The striped and unstriped morphs of red-backed salamanders foraged similarly on ant taxa, but the striped morph consumed significantly more ants and was found within territories that contained more ants. Our findings suggest selective foraging may be more common among generalist predators than previously considered, and we propose striped and unstriped morphs may represent a trophic polymorphism in *P. cinereus.*

INTRODUCTION

Predators should select prey that are energetically valuable (*e.g.*, large, soft bodied) and avoid prey that are costly to pursue or that possess anti-predator defenses (Stephens and Krebs, 1986). In addition prey selection depends on a number of factors including availability of prey in the environment (Hughes and Croy, 1993; Hughes, 1997) and predator energetic needs relative to the noxiousness of prey (Hileman *et al.*, 1994). For example predators may switch from rare to abundant prey seasonally and such flexibility in foraging behavior has the potential to influence food webs by stabilizing predator-prey cycles (Abrams, 1996; Krivan and Schmitz, 2003). Understanding the role of selective foraging in predator-prey interactions is an important topic in ecology, especially in relation to food web dynamics and energy flow in ecosystems. Nonetheless, few studies have investigated selective foraging behavior of predators in natural ecosystems.

The Eastern Red-backed Salamander, *Plethodon cinereus*, is a fully terrestrial species that occurs in moist forest habitats throughout eastern North America (reviewed in Petranka,

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[1] Department of Biology, Villanova University, Villanova, Pennsylvania, 19085
[2] Virginia Museum of Natural History, Martinsville, Virginia, 24112

1998). The species has been used to address questions in ecology, evolution, conservation biology, and disease ecology (reviewed in Anthony and Pfingsten, 2013) and has also served as a model organism in the field of behavioral ecology (reviewed in Jaeger and Forester, 1993). *Plethodon cinereus* functions as a top predator in forest-floor food webs. Several studies have demonstrated that this species not only has strong direct trophic effects but also affects multiple trophic levels through indirect channels via trophic cascades (Walton, 2005; Walton and Steckler, 2005; Walton *et al.*, 2006; Walton, 2013) and behavioral interactions with guild members (Hickerson *et al.*, 2004; Hickerson *et al.*, 2012). Individuals of *P. cinereus* are territorial with residents establishing territories under natural cover objects (*i.e.,* rocks and logs; Mathis, 1990). Prey items are obtained under these cover objects during dry periods, and territorial residents forage in the surrounding leaf-litter during moist conditions (Mathis, 1990). Territorial behavior in this species may vary geographically (Quinn and Graves, 1988), but in Ohio, where the current study was conducted, populations of *P. cinereus* are territorial (Gall *et al.*, 2003; Hickerson *et al.*, 2004; Deitloff *et al.*, 2009; Anthony and Pfingsten, 2013). Most populations of *P. cinereus* exhibit color polymorphism, and the two most prevalent phenotypes are the striped and unstriped morphs (Petranka, 1998). Previous work suggests the two morphs are differentiated along ecological niche axes including temperature (Lotter and Scott, 1977), pH optima (Mitchell and Woolcott, 1985), territorial behavior (Reiter *et al.*, 2014), and diet (Anthony *et al.*, 2008). The striped morph is thought to be the more territorial of the two morphs, and as a consequence, gains access to higher quality prey (Anthony *et al.*, 2008; Reiter *et al.*, 2014). Therefore, morphs in this species may represent a case of within-population trophic polymorphism as has been described between habitat types (upland versus lowland) in this species (Maerz *et al.*, 2006).

Numerous studies have examined and characterized the diet of *Plethodon cinereus* (*e.g.,* Jameson, 1944; Jaeger, 1990; Maglia, 1996; Adams and Rohlf, 2000; Maerz *et al.*, 2006). These studies have shown that *P. cinereus* consumes a variety of small forest-floor invertebrates (Burton, 1976) and most studies list mites, ants, springtails, flies, isopods, termites, and beetles as important components of the diet (reviewed in Anthony and Pfingsten, 2013). Most dietary studies have identified prey to the order or family level but such an approach has the potential to miss important ecological information. For example Maerz *et al.* (2005) showed red-backed salamanders utilized up to 11 nonnative prey species, but these species augmented rather than replaced native prey in the diet. Similarly, Ivanov *et al.* (2011) found a nonnative ant species was the second most important prey in the diet of red-backed salamanders at a disturbed urban site in northeastern Ohio. In both of these studies, order or family level resolution would have missed these key findings. An additional shortcoming of many dietary studies is the lack of data on prey availability during foraging bouts. Such data are often logistically difficult to collect because predators may cover large areas during foraging or because it is not clear where or when predators are encountering prey. Red-backed salamanders provide an ideal system with which to explore predator selectivity because territorial residents are known to forage within discrete territories surrounding cover objects, while nonterritorial floaters (Mathis, 1991) may forage over wider areas. Additionally, laboratory studies have shown red-backed salamanders select prey that maximize their energy intake (Jaeger and Barnard, 1981; Jaeger *et al.,* 1981).

Ants are an important component of terrestrial ecosystems and have been described as ecosystem engineers due to their abundance (Hölldobler and Wilson, 1990) and ability to physically and chemically alter the soil environment which indirectly influences plants and other ground dwelling organisms (Folgarait, 1998). In northeastern Ohio ants are an important component of the diet of red-backed salamanders, comprising up to 33% of

prey taken (Ivanov *et al.*, 2011). The proportion of ants in the diet of these salamanders varies by region [*e.g.*, Virginia, 5.5% (Jaeger, 1990); Tennessee, 21% (Maglia, 1996)] and by color morph [striped morph, 19%; unstriped morph, 25% (Anthony *et al.*, 2008)], but it is unknown how this variation relates to availability of ants in the foraging environment. For example do ants make up a greater proportion of the diet of the unstriped morph because that morph prefers to feed on ants, or because ants make up a greater proportion of available prey? Ants also vary in energy content (*e.g.*, size) and anti-predator defenses (*e.g.*, chemical defenses), but it is unknown how these traits relate to consumption by predators.

The goal of the present study was to determine if *P. cinereus* is a true generalist predator or a selective forager on ants in northeast Ohio. In an effort to document seasonal diet preferences, we examined the ant species found in the diets of salamanders over a 13 mo period. During the fall we also compared ant species consumed by salamanders to those found within the surrounding leaf litter to determine whether individuals of *P. cinereus* selectively forage on ant species within their territories. We hypothesized salamander stomach contents would contain a subset of the resident ant fauna found within their territories due to differential energy profitability (*i.e.*, size) and natural history (*i.e.*, aggression, chemical ecology, habitat preferences). We also hypothesized the two color morphs would exhibit different dietary preferences, with striped *P. cinereus* consuming more profitable ant prey or gaining access to territories containing more ants or more energetically profitable ant species.

METHODS

TEMPORAL SHIFTS IN DIET

From November 2006 to November 2007, salamander stomach contents were collected from 256 surface active individuals found under artificial cover objects placed within the Cuyahoga Valley National Park (CVNP; see Hickerson *et al.*, 2012 for a site description). On each of 21 sampling days, equal numbers (mean = 11.2; range 2–36 salamanders per sampling day) of size-matched striped and unstriped salamanders [striped mean (SE) SVL = 33.5 (0.36) mm; unstriped = 33.3 (0.37) mm] were collected. Stomach contents were removed in the field via gastric lavage from the live specimens following Fraser (1976). We sampled in every month except January, February, and July because salamanders were not surface active during these months. For our analyses we divided the diet samples into three seasons [spring – Julian dates 84–138 (six dates); summer – Julian dates 150–257 (six dates); and fall – Julian dates 271–357 (nine dates)].

STOMACH CONTENT – TERRITORY COMPARISONS

During September and October 2013, 20 striped and 20 unstriped adult *Plethodon cinereus* were collected under natural cover objects (*i.e.*, logs and rocks) adjacent to the CVNP near Peninsula, Ohio (41° 13′ 37.8″ N, 81° 31′ 34.4″ W). Adults of this species are territorial in Ohio (Gall *et al.*, 2003; Hickerson *et al.*, 2004) and larger adults are more likely to hold territories (Anthony and Pfingsten, 2013). Individuals reach adult size at 32–34 mm SVL (Anthony and Pfingsten, 2013), but we only collected individuals greater than 37 mm SVL to increase the likelihood of collecting territorial salamanders. The upper limit of home range size of adult red-backed salamanders is <5 m^2 (Kleeberger and Werner, 1982) and can be as small as 1 m^2 (Mathis, 1991). Specimens were collected at least 10 m apart from one another to ensure no territories were overlapping. Each salamander was held in a marked 50 ml centrifuge tube and placed in an ice cooler to prevent further digestion of

stomach contents until being transported back to the laboratory and euthanized in a chloretone solution. Specimens were then dissected, and stomach contents were collected and placed in marked vials with 70% EtOH. We utilized euthanasia and dissection, rather than gastric lavage, for the territory – stomach content comparisons because time constraints did not allow us to collect leaf litter for the Winkler samples and stomach pump the salamanders while we were in the field. Ants were separated from other prey items, identified to species using available taxonomic keys (Coovert, 2005 and Ellison *et al.*, 2012), and counted. Ant specimens were deposited in CDA's invertebrate collection at John Carroll University and salamanders were deposited in the Collection of Vertebrates at the Cleveland Museum of Natural History.

We used Winkler litter extraction to collect ants within each of the 40 salamander territories (20 striped and 20 unstriped) used in the diet study. Litter samples were obtained by collecting the surface material delimited by a 1 m^2 plastic frame, which was centered on the location where each of the 40 resident *P. cinereus* were found. The average territory size of resident *P. cinereus* is approximately 1.15 m^2 (Liebgold and Jaeger, 2007). This approach allowed us to collect the potential prey items within each salamander foraging territory (Mathis, 1990). The litter contained a layer of leaves and detritus that were scraped from the more compact soil of the forest-floor and sifted on site through a sieve with a 1 cm grid to exclude large fragments. The litter was then transported to the laboratory and placed into mesh bags and suspended inside Winkler extractors for 72 h, which is an adequate time for the collection of most individual ants in a sample (Bestelmeyer *et al*,. 2000, Krell *et al.*, 2005). All extracted materials were stored in 70% EtOH. Each sample was sorted; ants were separated from other prey items and identified and counted as above. Salamander and litter collections were conducted at least 3 d after moderate rainfall to increase the likelihood of finding salamanders associated with cover within their territories.

<center>STATISTICAL ANALYSES</center>

We used one-way analysis of similarity (ANOSIM; PRIMER version 5) to explore seasonal patterns in diet composition, differences between morphs, and to compare prey consumed by territory residents to prey found within their territories. We corrected for sampling differences between foraging salamanders and our Winkler extractors by dividing Winkler results by 4.67. This value was estimated by dividing the maximum number of ants in a Winkler sample (70) by the maximum number found in a salamander's gut (15). The correction is conservative in that it makes it more difficult to detect differences between diet and Winkler samples. We used nonmetric multidimensional scaling (nMDS) to illustrate the variation between stomach contents and available prey. Both the nMDS and ANOSIM results are based on Bray-Curtis dissimilarity matrices. Relative abundance, species richness, and Simpson's index of diversity ($D = 1/(\sum P_i^2)$) were calculated for each stomach and territory sample. Stomach and corrected territory measures were compared using paired *t*-tests (SPSS version 21). We used unpaired *t*-tests to compare the total number of ants consumed by each of the color morphs as well as the total number of ants found in the territories of each morph. Nonparametric statistics were used when the data were not normally distributed.

<center>RESULTS</center>

<center>TEMPORAL SHIFTS IN DIET</center>

We collected and identified 481 individual ants from 172 stomachs of *Plethodon cinereus* over three seasons. There were a total of thirteen ant species identified from the stomach

contents across all seasons combined. We found no effect of salamander color morphology on ant species composition in the diet (Global R = −0.005; P = 0.835). However, our data analysis does suggest there are slight seasonal differences in ant species in the diets of *P. cinereus* (Global R = 0.026, P = 0.058), with less dietary overlap between spring and summer (R = 0.058, P = 0.004) compared to other seasons (fall/spring R = 0.021, P = 0.166; fall/summer R = 0.019, P = 0.184). *Aphaenogaster picea* and *Stenamma impar* were common in diets of salamanders in the summer and fall and the most common ant species in diet in spring was *Stenamma schmittii* (Fig. 1). *Stigmatomma pallipes* and *Stenamma impar* were absent in the guts of *P. cinereus* in the spring, while *Myrmica punctiventris*, *Myrmecina americana* and *Lasius alienus* were not incorporated in the diet during the fall season (Fig. 1). Interestingly, *Myrmecina americana* was a common prey species except in the fall. These results are consistent with the detailed analysis in which we examined salamander preference and avoidance of ants in the fall season.

<center>STOMACH CONTENT – TERRITORY COMPARISONS</center>

All stomach contents and litter samples contained invertebrates, except for a single unstriped *P. cinereus* that had an empty stomach. The diet and territory data for this individual were excluded from our analysis. Thirteen ant species were observed within the stomach contents and territories of *P. cinereus* with nine ant species shared between territories and stomach contents (Fig. 2; Table 1). There were a total of 86 individual ants obtained from the stomach samples of *P. cinereus* and 332 ants from salamander territories.

Our statistical analyses suggest resident salamanders prey on a subset of the available ant taxa. We found fewer ant species in stomachs (mean = 1.08 species) compared to those available in the associated territories (mean = 2.24 species, $T = 6.33$, P < 0.0001). Similarly, we recorded a significantly less diverse assemblage of ants within salamander stomachs compared to territories ($D_{stomachs} = 1.01$, $D_{territories} = 1.65$, $T = 4.61$, P < 0.0001). These differences were reflected in our analysis of similarity, which revealed significant variation between diets and available prey (Global $R = 0.190$, $P = 0.001$, Fig 3). This was true for both the striped ($R = 0.176$, P = 0.001) and unstriped morphs ($R = 0.172$, P = 0.004). There were, however, no significant differences between ant species eaten by striped and unstriped salamanders ($R = 0.027$, P = 0.143) or between ant species found in the territories of the two morphs ($R = -0.001$, P = 0.460). Striped salamanders consumed significantly more ants than did unstriped salamanders (mean of 3.4 versus 1.2 ants per stomach; z = 1.99; P = 0.046) and this may have resulted from there being significantly more ants in the territories of striped salamanders (mean of 10.7 versus 6.7 ants per territory; z = 2.09; P = 0.037).

We found significant differences between the numbers of ants consumed and the number found in territories for four ant species (Fig. 2; Table 1). Resident salamanders appear to avoid preying on *M. punctiventris, M. americana, L. alienus* while selectively preferring *A. picea. Myrmica punctiventris* accounted for 20.2% of ants collected within territories but made up only 4.7% of the formicid diet of territory residents. *Myrmecina americana* accounted for 14.5% of the ants collected in territories but accounted for only 2.3% of ants in stomach contents. *Lasius alienus* accounted for 42.8% of ants in litter samples, but accounted for only 5.8% of ants in the diet. In contrast *A. picea* made up 37.2% of ants in resident stomachs but only accounted for 6.0% of ants collected in salamander territories.

<center>DISCUSSION</center>

Our results suggest individuals of *Plethodon cinereus* exhibit selective foraging behavior within their territories and this behavior varies temporally. Ant community composition
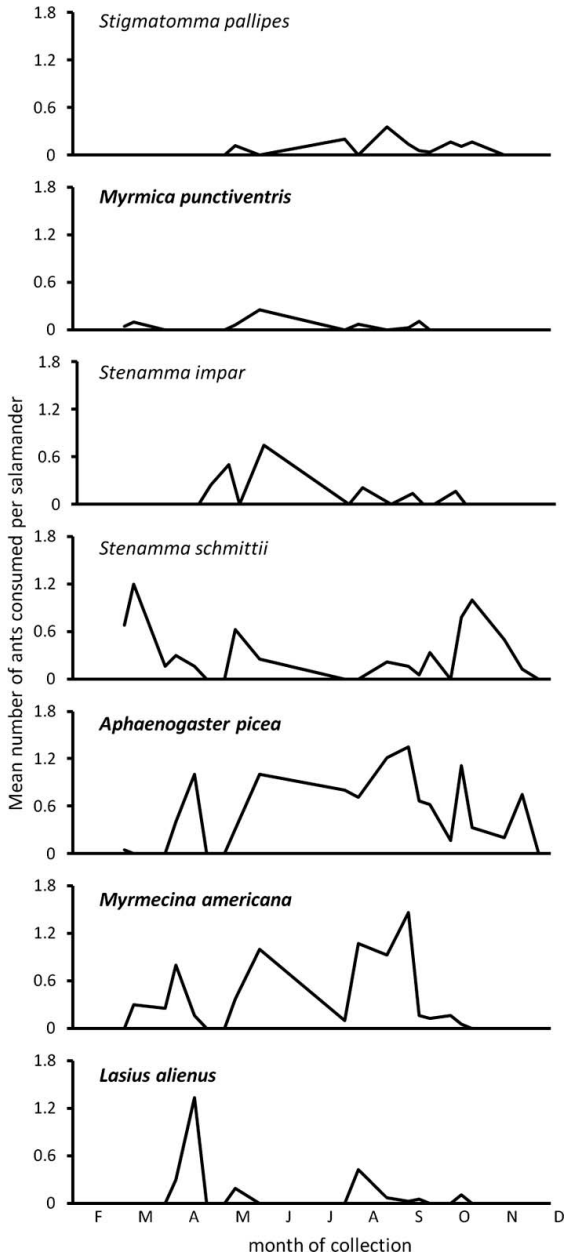
FIG. 1.—Mean number of ants found in stomachs of red-backed salamanders (n = 256) collected November 2006 through November 2007. The seven most common taxa of 13 found are graphed. Ant taxa in bold are those species that were either avoided or preferred by salamanders in the fall of 2013
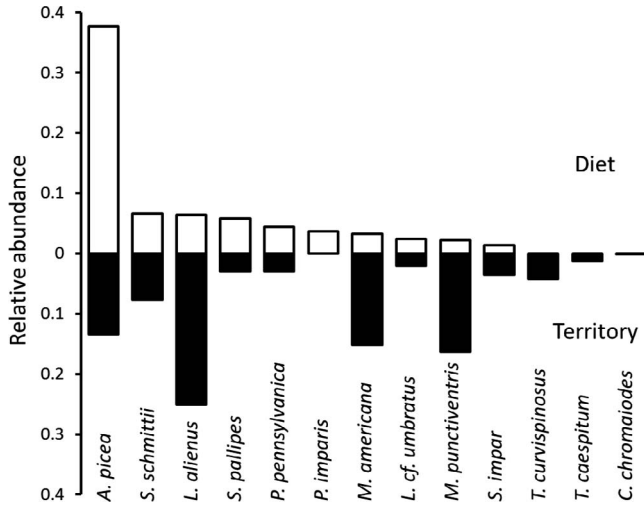
Fig. 2.—Relative abundances of ants found in the diet (open bars) and the territories (closed bars) of red-backed salamanders collected in the fall of 2013. Stomach contents and territory samples were collected simultaneously

differed between stomach contents and litter samples and the ant diversity observed in the diet represented a subset of that available in the surrounding litter habitat. Therefore, *P. cinereus* preyed on a subset of the available ants present within their territories. Our seasonal data suggest one ant species (*picea*) commonly consumed in the spring and summer became rare in the environment in the fall but was preferentially sought out by salamanders and therefore remained abundant in the diet. Additionally, two of the ant

TABLE 1.—Number of ants obtained from litter of *Plethodon cinereus* territories and from the stomachs of territorial residents. Numbers following species names indicate number of salamanders that consumed that ant species. Numbers in parentheses show corrected values for Winkler extractors (see text). Tests were only run if at least six territories or guts contained ants of focal taxa. Paired Wilcoxon signed-ranks test, two tailed. Bold denotes significant differences at alpha = 0.05

|	Winkler litter extraction	Stomach contents	Z	P
Stigmatomma pallipes – 5	9	6	—	—
Ponera pennsylvanica – 2	16	5	—	—
Myrmica punctiventris – 2	67 (14)	4	2.55	**0.011**
Stenamma impar – 1	5	1	—	—
Stenamma schmittii – 3	10 (2.1)	6	0.84	0.41
Aphaenogaster picea – 18	20 (4.3)	32	2.99	**0.003**
Temnothorax curvispinosus – 0	7	0	—	—
Tetramorium caespitum – 0	1	0	—	—
Myrmecina americana – 2	48 (10)	2	3.21	**0.001**
Prenolepis imparis – 2	0	11	—	—
Lasius alienus – 5	142 (30)	5	3.25	**0.001**
Lasius cf. *umbratus* – 1	6	14	—	—
Camponotus chromaiodes – 0	1	0	—	—
Total	332	86		
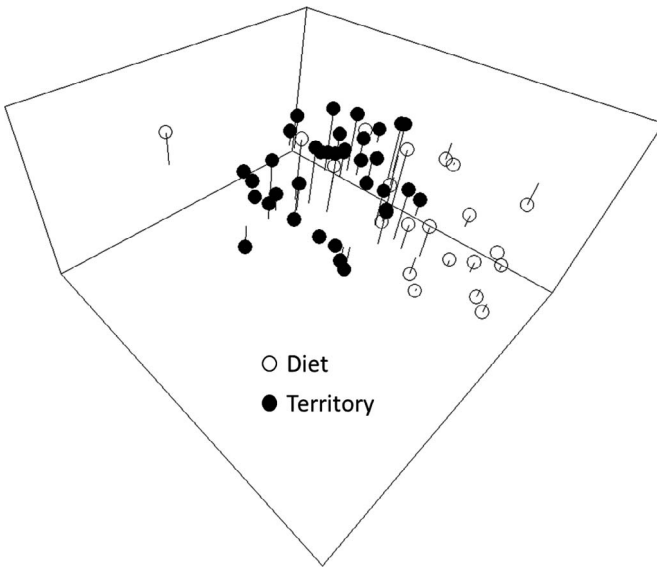
Fig. 3.—Nonmetric multidimensional scaling (nMDS) plot depicting variation between ant species composition found in stomach contents of territory residents versus that found in the territory. Each symbol represents an individual stomach sample (open symbols) or leaf litter sample from a resident's territory (filled symbols). The distance between symbols represents the difference in ant community composition

species avoided by *P. cinereus* in the fall season (*Myrmecina* and *Lasius alienus*) were prevalent in the diets during spring and summer. We found no evidence the two color morphs of red-backed salamanders differentially prey on ant taxa, but striped salamanders consumed significantly more ants and were found in territories with significantly higher ant abundance than were unstriped salamanders.

The relative abundance of ants between stomach contents and resident territories differed significantly for four species; the remaining nine species were not significantly different or were too rare to compare statistically (Table 1). Our data suggest *A. picea* is a preferred prey species, making up the largest portion of the formicid diet of salamanders (37.2%), despite being relatively rare in our Winkler samples. This fact is reflected in the seasonal data in which red-backed salamanders preyed on *Aphaenogaster* throughout the active foraging season. In northeastern Ohio, *A. picea* is an abundant species, accounting for 22% of the ants sampled from litter in the summer months (Ivanov and Keiper, 2009), but by fall, its abundance appears to decline, accounting for only 6% of all ants in our litter samples (Table 1). *Aphaenogaster picea* is a cold tolerant species that prefers moist forest habitat and nests in damp areas, such as within or under rotten logs, bark, and tree limbs (Ellison *et al.*, 2012; King *et al.*, 2013). These climatic and habitat preferences are similar to those of *P. cinereus* (Petranka, 1998). Therefore, we suggest *P. cinereus* forages on this species extensively as a result of shared microhabitat specialization, especially in the summer months. Species within the genus *Aphaenogaster* are classified as medium-sized ants, ranging from 4-6 mm long (Ellison *et al.*, 2012), and may represent more profitable prey as compared to smaller-bodied prey, maximizing the net energy gained by predators while foraging (Jaeger *et al.*, 1981; Jaeger, 1990). A recent study by Lewis *et al.* (2014) corroborates

the notion that *Aphaenogaster* might be preferred prey of woodland salamanders. They found ants of this genus made up a majority of ant prey and 27% of all prey taken by Red-legged Salamanders (*P. shermani*) in the Appalachian Mountains of North Carolina. Because *Aphaenogaster* is considered a dominant ant species, especially in cooler temperate habitats (Fellers, 1989; King *et al.*, 2013), it is not surprising these ants are important components of terrestrial salamander diets.

Myrmica punctiventris, M. americana, and *L. alienus* were significantly more abundant in litter extractions than in stomach samples, suggesting *P. cinereus* selectively avoids these ant species while foraging. Ivanov and Keiper (2009) found these species to be very abundant in northeast Ohio, and in their study, *M. punctiventris, M. americana*, and *L. alienus* accounted for 14%, 13%, and 14% of all individuals captured, respectively. In the current study, *M. punctiventris, M. americana*, and *L. alienus* accounted for over 77% (20.2%, 14.5%, and 42.8% respectively) of all ants captured in resident salamander territories (Table 1). Conversely, these species accounted for only ~13% (4.7%, 2.3%, and 5.8% respectively) of all ants within salamander stomachs (Table 1). These results suggest *M. punctiventris, M. americana*, and *L. alienus* are avoided by *P. cinereus* in resident territories in the fall. Interestingly, two of these taxa (*M. americana*, and *L. alienus*) are prevalent in the guts of salamanders during other times of the year. These seasonal differences in diet might result from foraging decisions made by salamanders related to the costs of tolerating prey defenses. For example we found *M. americana* was prevalent in salamander guts during the drier summer months when food becomes a limited resource (Jaeger, 1972). Alternatively, diet variation might emerge from seasonal differences in the chemical defenses of ants or in their aggressive behavior.

The avoidance of certain ant species by salamanders may be the result of defenses utilized to deter predators. Species within the genus *Myrmica* are known to exhibit intraspecific and interspecfic aggression towards other ants (Cammaerts-Tricot, 1975; Garnas *et al.*, 2007), as well as defensive stinging behavior towards potential predators (Sturtevant, 1931). Therefore, it is likely that *P. cinereus* avoids foraging on *M. punctiventris* due to its aggressive/defensive behavior. It is unknown whether *M. americana* emits defensive chemicals, but other myrmicine ants do contain chemicals (Daly *et al.*, 2000). Therefore, it is possible that *P. cinereus* avoids preying on *M. americana* due to chemical defenses. The formicine, *L. alienus,* utilizes volatile organic compounds (*i.e.*, formic acid) as a chemical defense mechanism. Regnier and Wilson (1969) established that *L. alienus* contains at least 12 volatile compounds used for alarm communication and combat defense. While *P. cinereus* preferentially avoided preying on *L. alienus* at our study site, Maerz *et al.* (2005) found that *L. alienus* was the fourth most common ant and a volumetrically important ant species (mean of 10% of ant volume) in the diet of *P. cinereus* from New York and Pennsylvania. Geographic differences in salamander diet could emerge from a variety of factors including variation in the toxins produced by *L. alienus* and variation in the susceptibility of salamanders to toxin. Alternatively, avoidance of common prey might not be energetically feasible, despite their defenses.

Previous studies have shown the two color morphs of *P. cinereus* are differentiated on a number of niche axes including thermal optima (Moreno, 1989), seasonal activity (Lotter and Scott, 1977), mate choice (Acord *et al.*, 2013), territorial behavior (Reiter *et al.*, 2014), response to predators (Venesky and Anthony, 2007), and diet (Anthony *et al.*, 2008). In general the striped morph is thought to be a superior territory holder, reaping benefits such as higher quality mates and prey. Indeed, the diet of striped morphs has been shown to be dominated by softer-bodied, presumably higher quality prey, while the unstriped morph

consumes more chitinous prey, such as ants (Anthony *et al.*, 2008). Contrary to our prediction, we found no evidence the striped morph gains access to and consumes more profitable ant prey. Ants consumed by both morphs were dominated by *Aphaenogaster*, which appears to be a preferred ant prey. We did, however, detect significant differences in the total number of ants eaten by the two morphs and the total number of ants found in territories of the two morphs. In our territory-to-diet comparisons, striped morphs consumed 2.5 times more ants than their unstriped counterparts. This difference was reflected in striped territories containing 40% more ants than unstriped territories. It may be that because ants are an important part of the diet of red-backed salamanders, striped salamanders maintain territories that offer them foraging opportunities on this prey group.

Trophic polymorphisms have been defined as an association between the morphological or behavioral phenotype and diet that differs among individuals (Robinson, 2000). Trophic polymorphisms have been described across many diverse taxa (Smith and Skúlason, 1996; Bolnick *et al.*, 2003) and they have attracted the attention of evolutionary biologists because of their importance to the process of speciation (Adams *et al.*, 2007). Numerous studies have shown that, in *Plethodon*, diet and cranial morphology are linked and vary across populations (Adams and Rohlf, 2000; Swart and Adams, 2004; Deitloff *et al.*, 2013), but fewer studies have examined variation within populations (*e.g.,* Maerz *et al.*, 2006). Our study provides additional evidence of a within-population trophic polymorphism in *P. cinereus*. Striped morphs at our study site are more aggressive than their unstriped competitors, and this difference enhances their ability to maintain territories (Reiter, 2014). This behavioral polymorphism presumably allows striped salamanders to access additional prey in their territories. An interesting avenue of future study would be to examine cranial variation within color polymorphic populations of *P. cinereus* to determine if diet differences correlate with morphology.

CONCLUSIONS

Our findings suggest *Plethodon cinereus*, a species that has been previously described as a broad generalist predator, selectively forages on ants. This behavior may be more common than previously considered and could have broad implications in our understanding of trophic interactions and foraging theory. *Plethodon cinereus* is considered to be one of the most abundant vertebrates in eastern North America (Burton and Likens, 1975), and its diet has been well studied; yet selective foraging with regard to preference and avoidance behavior has not been previously described. It is likely that, in addition to ants, *P. cinereus* selectively forages on other taxa (*e.g.,* Acari, Collembola), and it is possible that predators of high abundance, such as *P. cinereus*, could strongly influence food web dynamics and community structure of detrital forest-floor systems through selective foraging. We suggest the selective foraging behavior of *P. cinereus* on other prey taxa be further studied in both field and laboratory studies. Selective foraging behavior of other predators should also be investigated to further understand the occurrence and the effects of this behavior in natural systems.

Literature Cited

Abrams, P. A. 1996. Dynamics and interactions in food webs with adaptive foragers. *In:* G. Polis and K. Winemiller (eds.). Food webs: dynamics and structure. Chapman & Hall, New York. 8 p.

Acord, M. E., C. D. Anthony, and C. M. Hickerson. 2013. Assortative mating in a polymorphic salamander. *Copeia*, **2013**:676–683.

Adams, C. E., D. Fraser, A. J. Wilson, G. Alexander, M. M. Ferguson, and S. Skúlason. 2007. Patterns of phenotypic and genetic variability show hidden diversity in Scottish Arctic charr. *Ecol. Freshwater Fish*, **16**:78–86.

Adams, D. C. and J. F. Rohlf. 2000. Ecological character displacement in *Plethodon*: biomechanical differences found from a geometric morphometric study. *PNAS*, **97**:4106–4111.

Anthony, C. D. and R. A. Pfingsten. 2013. Eastern Red-Backed Salamander, *Plethodon cinereus*. p. 335–360. *In:* R. A. Pfingsten, J. G. Davis, T. O. Matson, G. Lipps, Jr., D. Wynn and B. J. Armitage (eds.). Amphibians of Ohio. Ohio Biological Survey Bulletin New Series, Vol 17, No 1.

———, M. D. Venesky, and C. M. Hickerson. 2008. Ecological separation in a polymorphic terrestrial salamander. *J. Anim. Ecol.*, **77**:646–653.

Bestelmeyer, B. T., D. Agosti, L. E. Alonso, C. R. F. Brandão, W. L. Brown, J. H. C. Delabie, and R. Silvestre. 2000. Field techniques for the study of ground-dwelling ants: an overview, description, and evaluation. Smithsonian Institution Press, Washington, D.C. 22 p.

Bolnick, D. I., R. Svanbäck, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey, and M. L. Forister. 2003. The ecology of individuals: incidence and implications of individual specialization. *Am. Nat.*, **161**:1–28.

Burton, T. M. 1976. An analysis of the feeding ecology of salamanders (Amphibia, Urodela) of the Hubbard Brook Experimental Forest, New Hampshire. *J. Herpetol.*, **10**:187–204.

——— and G. E. Likens. 1975. Salamander populations and biomass in the Hubbard Brook Experimental Forest, New Hampshire. *Copeia*, **1975**:541–546.

Cammaerts-Tricot, M. C. 1975. Ontogenesis of the defense reactions in the works of *Myrmica rubra* L. (Hymenoptera: Formicidae). *Anim. Behav.*, **23**:124–130.

Coovert, G. A. 2005. The ants of Ohio. *Bull. Ohio Biol. Survey New Ser.*, **15**:1–196.

Daly, D. W., H. M. Garraffo, P. Jain, T. F. Spande, R. R Snelling, C. Jaramillo, and A. S. Rand. 2000. Arthropod–frog connection: decahydroquinoline and pyrrolizidine alkaloids common to microsympatric myrmicine ants and dendrobatid frogs. *J. Chem. Ecol.*, **26**:73–85.

Deitloff, J., J. O. Church, D. C. Adams, and R. G. Jaeger. 2009. Interspecific agonistic behaviors in a salamander community: implications for alpha selection. *Herpetologica*, **65**:174–182.

———, J. D. Peterson, and D. C. Adams. 2013. Complex species interactions and environmental conditions lead to unpredictable community outcomes in *Plethodon* salamanders. *Herpetologica*, **69**:1–10.

Ellison, A. E., N. J. Gotelli, E. J. Farnsworth, and G. D. Alpert. 2012. A Field Guide to the Ants of New England. Yale University Press, New Haven. 398 p.

Fellers, J. T. 1989. Daily and Seasonal Activity in Woodland Ants. *Oecologia*, **78**:69–76.

Folgarait, P. 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodivers. Conserv.*, **7**:1221–1244.

Fraser, D. F. 1976. Empirical evaluation of the hypothesis of food competition in salamanders of the genus *Plethodon*. *Ecol.*, **57**:458–471.

Gall, S. B., C. D. Anthony, and J. A. Wicknick. 2003. Behavioral interactions between salamanders and beetles indicate a guild relationship. *Am. Midl. Nat.*, **149**:363–374.

Garnas, G. R., F. A. Drummond, and E. Groden. 2007. Intercolony aggression within and among local populations of the invasive ant, *Myrmica rubra* (Hymenoptera: Formicidae), in Coastal Maine. *Environ. Entomol.*, **36**:105–113.

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.

HILEMAN, K. S., E. D. BRODIE JR., AND D. R. FORMANOWICZ. 1994. Avoidance of unpalatable prey by predaceous diving beetle larvae: the role of hunger level and experience (Coleoptera: Dytiscidae). *J. Insect Biol.*, **8**:241–249.

HÖLLDOBLER, B. AND E. O. WILSON. 1990. The ants. Belknap Press, Cambridge. 746 p.

HUGHES, R. N. 1997. Diet selection. Oxford University Press, Oxford. 28 p.

——— AND M. I. CROY. 1993. An experimental analysis of frequency-dependent predation (switching) in the 15-spined stickleback, *Spinachia spinachia*. *J. Anim. Ecol.*, **62**:341–352.

IVANOV, K. AND J. KEIPER. 2009. Effectiveness and biases of Winkler litter extraction and pitfall trapping for collecting ground-dwelling ants in northern temperate forests. *Environ. Entomol.*, **38**:1724–1736.

———, O. M. LOCKHART, J. KEIPER, AND B. M. WALTON. 2011. Status of the exotic ant *Nylanderia flavipes* (Hymenoptera: Formicidae) in northeastern Ohio. *Biol. Invasions*, **13**:1945–1950.

JAMESON, E. W., JR. 1944. Food of the red-backed salamander. *Copeia*, **1944**:145–147.

JAEGER, R. G. 1972. Food as a limited resource in competition between two species of terrestrial salamanders. *Ecology*, **53**:535–546.

———. 1990. Terrestrial salamanders evaluate size and chitinous content of arthropod prey. Spring-Verlag, Heidelberg. 15 p.

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

——— AND D. C. FORESTER. 1993. Social behaviour of plethodontid salamanders. *Herpetologica*, **49**:163–175.

———, R. G. JOSEPH, AND D. E. BARNARD. 1981. Foraging tactics of a terrestrial salamander: sustained yield in territories. *Anim. Behav.*, **29**:1100–1104.

KLEEBERGER, R. AND J. K. WERNER. 1982. Home range and homing behavior of *Plethodon cinereus* in northern Michigan. *Copeia*, **1982**:409–415.

KRELL, F. T., A. Y. C. CHUNG, E. DEBOISE, P. EGGLETON, A. GIUSTI, K. INWARD, AND S. KRELL-WESTERWALBESLOH. 2005. Quantitative extraction of macro-invertebrates from temperate and tropical leaf litter and soil: efficiency and time-dependent taxonomic biases of the Winkler extraction. *Pedobiologia*, **49**:175–186.

KRIVAN, V. AND O. J. SCHMITZ. 2003. Adaptive foraging and flexible food web topology. *Evol. Ecol. Res.*, **5**:623–652.

LEWIS, J. D., G. M. CONNETTE, M. A. DEYRUP, J. E. CARREL, AND R. D. SEMLITSCH. 2014. Relationship between diet and microhabitat use of Red-legged Salamanders (*Plethodon shermani*) in southwestern North Carolina. *Copeia*, **2014**:201–205.

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. 1977. Correlation between climate and distribution of the color morphs of the salamander *Plethodon cinereus*. *Copeia*, **1977**:681–690.

MAGLIA, A. M. 1996. Ontogeny and feeding ecology of the red-backed salamander, *Plethodon cinereus*. *Copeia*, **1996**:576–586.

MAERZ, J. C., J. M. KARUZAS, D. M. MADISON, AND B. BLOSSEY. 2005. Introduced invertebrates are important prey for a generalist predator. *Divers. Distrib.*, **11**:83–90.

———, E. M. MYERS, AND D. C. ADAMS. 2006. Trophic polymorphism in a terrestrial salamander. *Evol. Ecol. Res.*, **8**:23–35.

MATHIS, A. 1990. Territoriality in a terrestrial salamander: the influence of resource quality and body size. *Behaviour*, **112**:162–175.

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

MITCHELL, J. C. AND W. S. WOOLCOTT. 1985. Observations of the microdistribution, diet, and predator-prey relationships in the salamander *Plethodon cinereus* from the Virginia Piedmont. *VA J. Sci.*, **36**:281–287.

MORENO, G. 1989. Behavioral and physiological differentiation between the color morphs of the salamander, *Plethodon cinereus*. *J. Herpetol.*, **3**:335–341.

PETRANKA, J. W. 1998. Salamanders of the United States and Canada. Smithsonian Books, Washington, D.C. 592 p.

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

REGNIER, F. E. AND E. O. WILSON. 1969. The alarm-defence system of the ant *Lasius alienus. J. Insect Physiol.*, **15**:893–898.

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

ROBINSON, B. W. 2000. Trade offs in habitat-specific foraging efficiency and the nascent adaptive divergence of sticklebacks in lakes. *Behav.*, **137**:865–888.

SMITH, T. B. AND S. SKÚLASON. 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. *Annu. Rev. Ecol. Syst.*, **27**:111–133.

STEPHENS, D. W. AND J. R. KREBS. 1986. Foraging theory. Princeton University Press, Princeton. 238 p.

STURTEVANT, A. H. 1931. Ants collected on Cape Cod, Massachusetts. *Psyche.*, **38**:73–79.

SWART, C. C. AND D. C. ADAMS. 2004. The role of muscle mass and tooth number in ecological character displacement between *Plethodon cinereus* and *P. hoffmani* (Caudata: Plethodontidae). *Herpetologica* **60**:408–413.

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.

WALTON, B. M. 2005. Salamanders in forest-floor food webs: environmental heterogeneity affects the strength of top-down effects. *Pedobiologia*, **49**:381–393.

———. 2013. Top-down regulation of litter invertebrates by a terrestrial salamander. *Herpetologica*, **69**:127–146.

——— AND S. STECKLER. 2005. Contrasting effects of salamanders on forest-floor macro and mesofauna in laboratory microcosms. *Pedobiologia*, **49**:51–60.

———, D. TSATIRIS, AND M. RIVERA-SOSTRE. 2006. Salamanders in forest-floor food webs: invertebrate species composition influences top-down effects. *Pedobiologia*, **50**:313–321.