

## Trophic polymorphism in a terrestrial salamander

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### ABSTRACT

**Question:** Does habitat heterogeneity promote trophic polymorphism in a terrestrial salamander?

**Hypothesis:** Eastern red-backed salamanders (*Plethodon cinereus*) in upland and lowland habitats differ morphologically because their prey's size differs between those habitats.

**Field site:** Five mature hardwood forests in central New York and northern Pennsylvania, USA, with known differences in diet between upland and lowland habitats.

**Methods:** We collected animals and examined their stomach contents and their cranial morphology, the latter with digital stereomicroscope images and morphometric methods.

**Results:** We found morphological differences between upland and lowland salamanders, although there was a considerable phenotypic range for both habitats. Lowland salamanders generally had relatively shorter heads and a lower jaw/head ratio, and upland salamanders generally had the converse. Within and among habitats, cranial morphology was associated with diet, where salamanders with lowland-like morphology consumed more large prey and fewer small prey, and salamanders with upland-like morphology consumed the converse.

**Conclusions:** The observed trophic polymorphism and association with food use within populations suggests that this variation may accentuate variation at larger scales, and may play an important role in diversification within the genus.

*Keywords:* geometric morphometrics, *Plethodon cinereus*, resource use, salamander, trophic polymorphism.

### INTRODUCTION

There is a growing awareness of the ecological and evolutionary importance of resource or trophic polymorphisms (see reviews by Skúlason and Smith, 1995; Smith and Skúlason, 1996; Wilson, 1998; Bolnick *et al.*, 2003). Trophic polymorphism is an association between morphological or behavioural phenotype and diet among members of a single phenotypically variable population (Robinson, 2000). Most biologists recognize cases of discrete trophic polymorphisms

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where morphs are easily distinguished, and readily accept that those polymorphisms are adaptive (Skúlason and Smith, 1995; Smith and Skúlason, 1996). Less appreciated but potentially more common are cases of trophic polymorphism where phenotypes cannot easily be distinguished and show a continuous, unimodal distribution (Wilson, 1998; Svanbäck and Eklöv, 2002). Historically, such variation was often assumed to be ‘noise’ around a locally adaptive mean. The realization that such variation is functional and may evolve among individuals in sympatry has revealed important ecological constraints on species (Skúlason and Smith, 1995; Robinson, 2000; Svanbäck and Eklöv, 2003), informed theories of evolutionary divergence within populations (Skúlason and Smith, 1995; Wilson, 1998) and improved our understanding of species’ influences on ecosystem processes (Persson, 1999). Despite their informative value and potential commonness, examinations of resource polymorphisms remain limited for many taxa (reviewed by Skúlason and Smith, 1995; Smith and Skúlason, 1996; Bolnick *et al.*, 2003).

There are several reasons why trophic polymorphisms are probably common among animals. Species have access to diverse food resources, but there are often trade-offs between efficient use of different resources (Bolnick *et al.*, 2003). Trade-offs in resource use efficiency create multiple potential trophic niches. When competition for resources is high, negative density dependence creates frequency-dependent selection to specialize on those resource niches, resulting in adaptive diversification among individuals within a population (Wilson, 1998; Bolnick *et al.*, 2003). Many animal populations are distributed among various habitats where resource availability or the strategies necessary to secure resources may change dramatically between habitats; therefore, resource polymorphisms may be particularly common within populations distributed across a range of habitats. For example, studies of fish show morphological diversification between individuals in pelagic habitats that feed primarily on zooplankton and individuals from littoral habitats that feed primarily on macroinvertebrates (Wilson, 1998; Robinson, 2000; Svanbäck and Eklöv, 2002, 2003; Svanbäck and Persson, 2004).

In this study, we evaluate whether eastern red-backed salamander (*Plethodon cinereus* Green) populations exhibit shifts in cranial morphology associated with a shift in diet between two common habitats within deciduous forests. Furthermore, we assess whether patterns of trophic polymorphism observed between habitats occurred within habitats, and discuss the potential contributions of within- and between-habitat processes to diversification within salamander populations. *Plethodon* provide a good opportunity to examine patterns of trophic polymorphism because they are the most abundant vertebrates in deciduous forests (Burton and Likens, 1975b; Hairston, 1996), and within forests utilize a broad range of habitats and microhabitats that vary in invertebrate composition (salamander prey) and physical factors that regulate salamander foraging (Feder, 1983; Feder and Londos, 1984; Maerz *et al.*, 2005). Maerz *et al.* (2005) show that within forests, *P. cinereus* in lowland habitats consume greater numbers of moderate to large prey, while conspecifics in upland habitats consume greater numbers of small microarthropods. It should be noted that some of the prey that drive temporal and spatial resource variation within these habitats are non-native species (Maerz *et al.*, 2005). Interspecific and inter-population comparisons show that *P. cinereus* populations that feed on smaller prey have relatively long heads with an expanded front of the jaw, depression in the main jaw articulation, and compression in the posterior region compared with populations or species that feed on larger prey (Adams and Rohlf, 2000). By extension, we hypothesized that *P. cinereus* would exhibit similar within-populations shifts in morphology between upland and lowland habitats associated with shifts in prey size.

## MATERIALS AND METHODS

### Study sites

Salamanders were collected from five mature forests in central New York and northern Pennsylvania, USA. Previous research has already established that salamander diets across the sites are similar, and within each site differ significantly between lowland and upland habitats (Maerz *et al.*, 2005). Salamanders in lowland habitats consume greater numbers of moderate to large prey and salamanders in upland habitats consume greater numbers of microarthropods.

At three of the sites, Binghamton University Nature Preserve (BUNP) in Broome Co., NY, and Forest 1 (HPF1) and Forest 3 (HPF3) at the Edmund Niles Huyck Preserve, Albany Co., NY, salamanders were collected from lowland and upland habitats only 300–400 m apart. At Mason Road (MRBC) in Broome Co., NY and Taylor Farm (TFSC) in Susquehanna Co., PA, we could only collect salamanders from lowland or upland habitat respectively, because the opposing habitats had been cleared for agriculture. Lowland habitats were dominated by sugar maple (*Acer saccharum*) with sweet birch (*Betula lenta*), red oak (*Quercus rubra*), American beech (*Fagus grandifolia*) and white oak (*Q. alba*) as subordinate species. Lowland soils had a pH of 5.5–6.0 and sparse leaf litter layers with frequent patches of bare soil and no humus horizon. Upland habitats were dominated by American beech or white oak with red oak, red maple and sugar maple the subordinates. Upland soils had a soil pH of 4.0–5.0 and a continuous layer of leaves and distinct humus horizon.

Although not evaluated for all sites, mark–recapture analysis suggests *P. cinereus* densities are similar between upland and lowland habitats (Maerz and Madison, 2000), and potential competitor communities are similar between sites. The northern slimy salamander (*P. glutinosus*), which is significantly larger than *P. cinereus*, was captured at similar densities at all sites except HPF1 and HPF2. Historic collections show *P. glutinosus* was present at HPF1 and HPF2 as recently as the 1940s, although the species appears to have been extirpated (R. Wyman, personal communication). Mountain dusky salamanders (*Desmognathus ochrophaeus*), efts of the red-spotted newt (*Notophthalmus viridescens*), and yellow-spotted salamanders (*Ambystoma maculatum*) occur in low abundance at all sites (J.C. Maerz, unpublished data).

### Salamander sampling

Within each habitat at each site, a 50 × 50 m sampling plot was established and salamanders were collected between 24 and 28 May and again between 28 September and 20 October 1999. Salamanders were found by turning over rocks and logs, and sifting through leaf litter. Salamanders were euthanized immediately in a chloretone bath and kept on ice until preserved in 10% buffered formalin within a few hours of capture. We measured the snout–vent length of each animal, and then dissected its stomach to collect prey.

### Measurement and identification of prey

Each prey was measured for its length and maximum width and its volume was estimated as a cylinder using the width as the diameter and the length as the axis. Prey were identified to the highest taxonomic resolution possible, generally to family, and then sorted by family

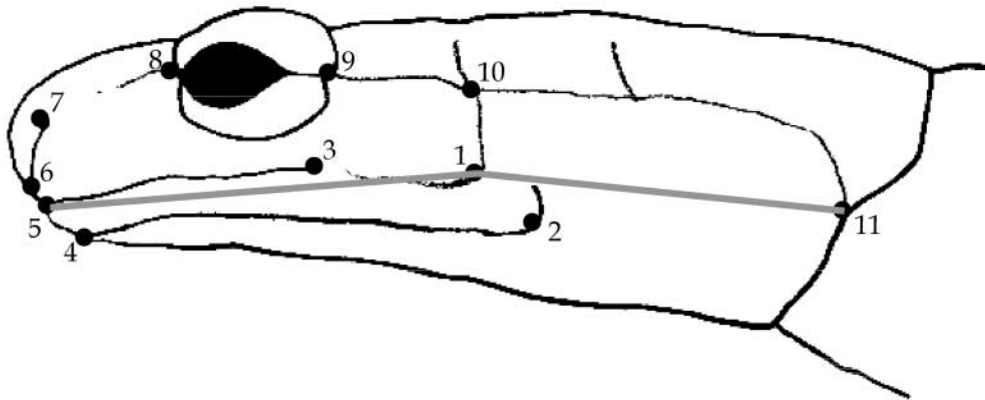
into distinct morphotypes. Morphotype reference specimens were identified to species at the Cornell University Insect Collection. For this study, the size of the largest prey in a salamander's stomach, and the numbers of prey in each of three size classes (small:  $< 1 \text{ mm}^3$ ; medium:  $1\text{--}10 \text{ mm}^3$ ; large:  $> 10 \text{ mm}^3$ ) were used as variables in the analyses.

### Measurement of salamander cranial morphology

To quantify head morphology (shape), we used geometric morphometrics. With this approach, morphology is first quantified using a set of homologous landmarks, and shape variables are generated from these after the effects of non-shape information (position, orientation and scale) have been held mathematically constant (for descriptions, see Rohlf and Marcus, 1993; Adams *et al.*, 2004). First, digital images of the left lateral side of the head were obtained for each specimen (Fig. 1a) using a Nikon DXM-1200 high-resolution digital camera mounted on a Nikon SMZ-1500 stereomicroscope. From each image, the x,y-coordinates of 11 anatomical skull and jaw landmarks were measured from each image (Fig. 1b) using TPSDIGIT (Rohlf, 2001). Then generalized Procrustes analysis (GPA) was performed to remove the effects of non-shape information and superimpose all specimens on a common coordinate system (Rohlf and Slice, 1990). Shape variables were obtained using thin-plate spline and standard uniform equations (Bookstein, 1991, 1996; Rohlf and Bookstein, 2003). Because landmarks were quantified from both the jaw and skull of each salamander, we used the separate subset method to allow for simultaneous analysis of the skull and mandible (Adams, 1999, 2004). The resulting shape variables were used to test ecological and evolutionary hypotheses using standard multivariate analyses (e.g. Adams and Rohlf, 2000).

### Statistical analyses

A three-factor nested analysis of variance (ANOVA) was used to assess the effects of habitat, site and season on the size of the largest prey. Because two of our sites lack corresponding upland or lowland habitats, we could not conduct a full-factorial analysis, so we nested site as a factor within each habitat type. This at least enabled us to evaluate



**Fig. 1.** Locations of *Plethodon cinereus* cranial landmarks used in this study (redrawn from Adams, 2004). Linear distances for jaw length and back of the head length are indicated.

whether prey size varied in similar habitats across sites. A habitat-by-season interaction term was included in our model. An identical model was used for our multivariate analysis of variance (MANOVA) of habitat, site, and season effects on numbers of small, medium and large prey. When the site or interaction terms were significant, planned contrasts were used to compare groups. We used JMP 5.1 (© 1989–2003, SAS Institute Inc.) to conduct both analyses.

To compare morphology among sites and habitats, a two-factor MANOVA was performed on the shape variables with habitat and site as factors, followed by pair-wise analyses using generalized Mahalanobis distances. For the pair-wise comparisons, groups were separated by upper versus lower, as well as by site. To better understand patterns of morphological variation between habitats, an ordination plot from a principal components analysis (PCA) was generated, and thin-plate spline deformation grids for the group means were obtained (see Bookstein, 1991).

To examine relationships between cranial morphology and numbers of different sized prey, a two-block partial least squares analysis [TPSPLS (Rohlf, 2002)] was performed on both the whole group and each subgroup (e.g. location  $\times$  site grouping). The significance of the multivariate correlation was determined with a permutation test.

## RESULTS

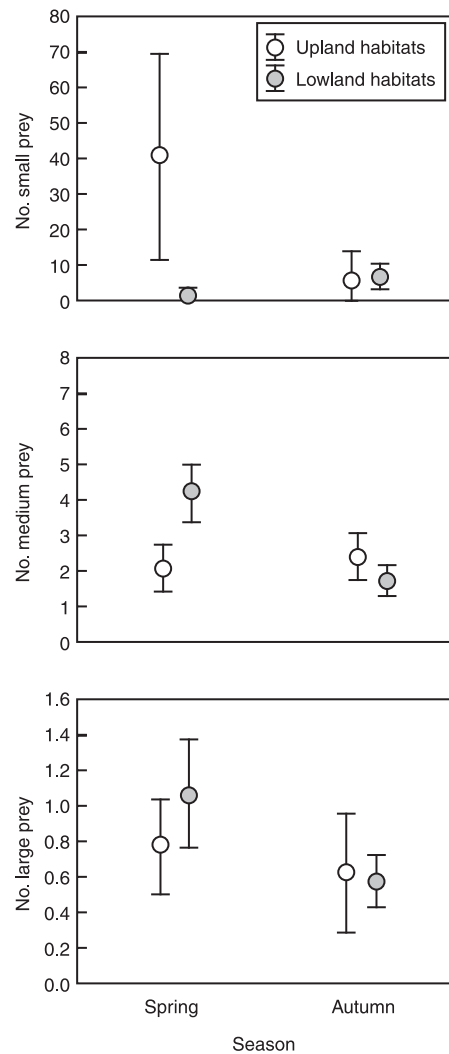
We collected 475 salamanders, 413 (87%) of which had prey in their stomachs. Common prey were Acarina (mites), Araneida (spiders), Collembola (springtails), adult Coleoptera (beetles, primarily Curculionidae), larval Coleoptera, adult Diptera (flies), larval Diptera, formicid Hymenoptera (ants), non-formicid Hymenoptera (wasps), larval Lepidoptera (moths), shelled Gastropoda (snails) and non-shelled Gastropoda (slugs). Some taxa fell consistently into prey size groups (e.g. mites, springtails and snails were always small prey and larval Lepidoptera were always large prey), but most taxa, particularly larvae, varied considerably in size.

Maximum prey size was significantly larger for salamanders from lowland habitats (mean  $\pm$  1 standard error:  $27.35 \pm 3.36$  mm<sup>3</sup>) than those from upland habitats ( $12.33 \pm 1.40$  mm<sup>3</sup>; MS = 14014,  $F_{1,403} = 6.890$ ,  $P = 0.009$ ), but within habitats did not vary significantly among sites (MS = 2584,  $F_{6,403} = 1.271$ ,  $P = 0.270$ ). Maximum prey size was also similar between salamanders caught in spring or autumn samples (MS = 178,  $F_{1,403} = 0.088$ ,  $P = 0.768$ ), and there was no interaction between habitat and season on maximum prey size (MS = 554,  $F_{1,403} = 0.272$ ,  $P = 0.602$ ).

Mean numbers of small, medium and large prey also differed significantly between sites (Roy's Maximum Root [RMR] = 0.438,  $F_{3,402} = 24.736$ ,  $P < 0.001$ ), as well as among sites (RMR = 0.438,  $F_{6,404} = 29.466$ ,  $P < 0.001$ ). Planned contrasts showed no significant differences among sites in lowland salamander diets, but significant diet differences between TFSC salamanders and salamanders from the other three upland habitats. Some salamanders collected at TFSC had large Lepidoptera larvae in their stomachs, which distinguished TFSC diets from salamander diets in other upland habitats. No significant diet differences were found among the BUNP, HPF1 and HPF3 upland habitats. There was also a significant interaction between habitat and season (RMR = 0.279,  $F_{3,402} = 31.434$ ,  $P < 0.001$ ). Contrasts showed significant differences between habitats in salamander prey sizes during both seasons. During spring, salamanders in upland habitats consumed greater numbers of small prey while lowland salamanders consumed greater numbers of medium to

large prey (Fig. 2). During autumn, prey size distributions were similar between habitats because of lower microarthropod numbers in upland salamander diets, the occurrence of large Lepidoptera larvae in one upland habitat (TFSC), and the failure to find earthworms in any lowland salamander diets.

Salamander cranial morphology varied significantly among sites (Wilks'  $\lambda = 0.519$ ,  $F_{45,1174.2} = 6.437$ ,  $P < 0.001$ ) and between habitats (Wilks'  $\lambda = 0.149$ ,  $F_{15,395.0} = 3.814$ ,  $P < 0.001$ ). There was also a significant interaction between site and habitat (Wilks'  $\lambda = 0.725$ ,  $F_{45,1174.2} = 2.998$ ,  $P < 0.001$ ). Average generalized Mahalanobis distance between upland and lowland habitats within sites was greater (2.00) than the distance between

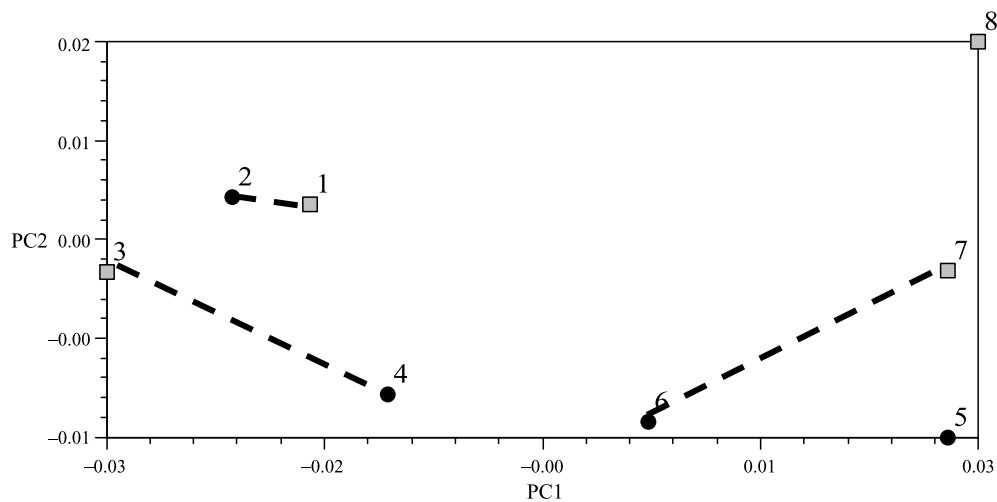


**Fig. 2.** Weighted mean ( $\pm 2$  standard errors) numbers of small ( $< 1 \text{ mm}^3$ ), medium ( $1\text{--}10 \text{ mm}^3$ ) and large ( $> 10 \text{ mm}^3$ ) prey in adult *P. cinereus* diets from upland and lowland forest habitats during spring and autumn. Within habitats and seasons, means are weighted by site to correct for unequal sample sizes.

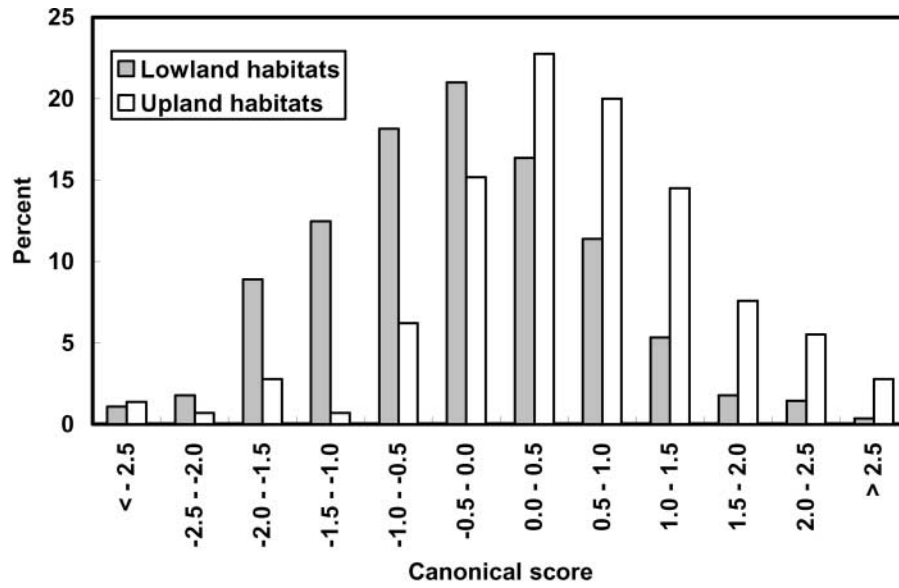
geographic locations (1.78), indicating habitat explained more of the variation in head shape than did site. A principal components analysis of individual group means confirmed a consistent morphological pattern within habitats across sites and that one site, BUNP, accounted for the interaction between site and habitat (Fig. 3). At all sites except BUNP, salamanders showed a consistent change in morphology between lowland (low CV2 scores) and upland habitats (high CV2 scores; Fig. 3). Compared with other sites, the difference between BUNP lowland and upland mean canonical variate (CV) scores was small and indicated salamanders from both habitats were more typical of upland morphs (Fig. 3).

A plot of CV2 scores for all salamanders shows clearly the biased distribution of high CV2 scores in upland habitats (Fig. 4). Shape differences between upland and lowland habitats were most evident in the back of the jaw and in jaw length (Fig. 4). Consistent with our hypothesis, salamanders from lowland habitats had relatively shorter heads with compression of the front of the jaw, and an expansion in the posterior region of the skull. Salamanders from upland habitats had relatively longer heads, an expanded front of the jaw, depression in the main jaw articulation, and compression in the posterior region of the skull. This finding was confirmed using the ratio of jaw length to the length of the back of the head (see Fig. 1). Using a *t*-test we found a significantly larger jaw/head ratio in upland sites relative to lowland sites ( $t_{363} = 3.83$ ,  $P < 0.0001$ ). Furthermore, this pattern was consistent across sites where upland habitats attained a significantly larger jaw/head ratio than lowland habitats (Fig. 5). It is notable that even among lowland and upland BUNP salamanders, which principal components analysis indicated had similar overall skull morphologies, there was a large difference in the jaw length to back of the head ratio consistent with patterns at other sites.

There was a significant correlation between prey size and head shape ( $r = 0.23$ ,  $P_{\text{rand}} = 0.041$ ). Loadings of small and large prey were of the same magnitude but in opposite directions. Combined with the head shape data, this supports our hypothesis that



**Fig. 3.** PCA plot of group means from cranial shape analysis. Sites are connected by the dotted line. Labels 1 and 2 refer to HPF1, 3 and 4 to HPF3, 5 to MRBC, 6 and 7 to BUNP, and 8 to TFSC. Upland (squares) and lowland habitats (circles) are distinguished and different habitats within sites are connected by dashed lines.

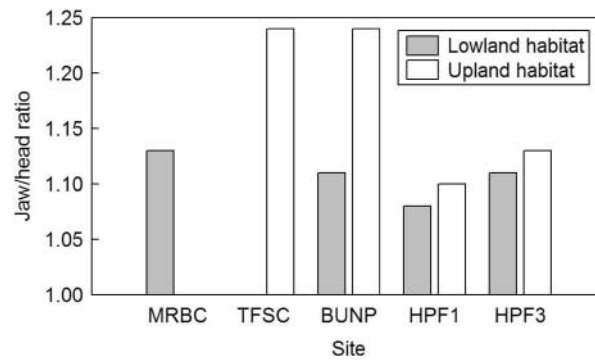


Mean lowland morph



Mean upland morph

**Fig. 4.** Distributions of canonical variate scores and thin-plate spline deformation grids showing differences in *Plethodon cinereus* cranial morphology between lowland and upland habitats. Bars show percentages of individuals to correct for differences in sample size between habitats. Deformations in the grids indicate regions of shape change.



**Fig. 5.** Mean ratio of jaw length to back of head length for *P. cinereus* from upland and lowland habitats.



salamanders with compression in the front and mid portions of the jaw ('lowland habitat' morphology) consumed more large prey and fewer small prey, while salamanders with expansion in the front and mid portions of the jaw ('upland habitat' morphology) consumed more small prey and fewer large prey.

Within habitats within sites, there were no statistically significant correlations between head shape and use of prey size classes or taxonomic groups. This was most likely an artifact of reduced sample sizes in subgroups limiting the power of multivariate tests. An examination of the correlation coefficients from each analysis showed all coefficients were positive, ranging from 0.30 to 0.59 (mean  $r = 0.47$ ).

## DISCUSSION

A number of reviews suggest that within-population trophic polymorphisms are probably common among diverse taxa (Skulason and Smith, 1995; Smith and Skulason, 1996; Wilson, 1998; Bolnick *et al.*, 2003). While examples of trophic polymorphisms are relatively rich for fishes, examples for birds, mammals, reptiles and amphibians remain limited (Smith and Skulason, 1996; Bolnick *et al.*, 2003). Our study shows red-backed salamander populations exhibit a mean shift in morphology between upland and lowland habitats that is associated with diet differences between habitats. Admittedly, we have not demonstrated a functional relationship between morphology and diet, as could be found experimentally through a functional morphological analysis. Nevertheless, the pattern we observed is consistent with a hypothesized biomechanical model, and directly parallels correlated shifts in morphology and diet seen between *P. cinereus* populations and between *P. cinereus* and sympatric *P. hoffmani* (Adams and Rohlf, 2000; Swart and Adams, 2004). Collectively, these studies reveal a common association between salamander cranial morphology and diet, suggesting that the morphological variation is functional and possibly a product of natural selection.

Our study also shows considerable morphological overlap between salamanders captured in the different habitats, and that the mean difference in morphology between habitats was small relative to the variation in morphology within habitats. Phenotypic differences between habitats that are small relative to variation within habitats appear common in studies of trophic polymorphisms (Ehlinger and Wilson, 1988; Robinson *et al.*, 1993; Wilson, 1998; Svanbäck and Eklöv, 2002), and raises questions about the processes regulating diversification within populations. For example, broad phenotypic overlap between habitats may indicate constraints on phenotypic divergence between habitats due to high inter-habitat dispersal or hybridization. In fish, pelagic morphs move between pelagic and littoral habitats to breed, creating opportunities for sampling pelagic morphs in littoral habitats and hybridization among morphs (Svanbäck and Eklöv, 2002). Stable isotope and parasite data suggest that pelagic morphs captured in littoral habitats were long-term residents of those habitats, so incidental sampling of dispersing individuals is unlikely to explain phenotypic overlap between habitats (reviewed by Bolnick *et al.*, 2003). However, hybrids between pelagic and littoral morphs can compose the largest portion of fish populations, despite being maladaptive in both habitats, and therefore account for much of the overlap between habitats (Wilson, 1998). We are unclear of the role of dispersal and hybridization in promoting phenotypic variation within red-backed salamander populations. Adult *P. cinereus* exhibit long-term fidelity to small home ranges (Mathis *et al.*, 1995), but recent studies show long-distance dispersal among sub-adult *P. cinereus* does occur (Marsh *et al.*, 2004).

Opposing selective pressures may also constrain trophic diversification between habitats. We observed temporal convergence in prey size distributions between habitats, and Maerz *et al.* (2005) found convergence in *P. cinereus* diets between habitats during drier periods in between rains. Temporal or stochastic patterns of prey convergence may favour morphological convergence. However, other generalist species are known to maintain broad diets while achieving remarkable morphological trophic specialization for stochastic resources (Robinson and Wilson, 1998). Morphological specialization must significantly compromise exploitation of other important resources for it to constrain diversification (Robinson and Wilson, 1998). We must also consider the possibility that non-trophic selective pressures are constraining trophic specialization between habitats. For example, Adams (2004) found that individual *P. teyahalee* cranial morphology was correlated with levels of aggression, showing that cranial morphology is affected by factors besides resource use; however, a similar study of *P. cinereus* and *P. hoffmani* failed to find any correlation between cranial morphology and aggression (Jaeger *et al.*, 2002). Maerz and Madison (2000) found evidence of territoriality among upland TFSC *P. cinereus* but not lowland MRBC or BUNP, but observed high levels of aggression among captive male *P. cinereus* from all three populations (J.C. Maerz, personal observation). Importantly, prey availability may be linked to *Plethodon* social behaviour (Mathis *et al.*, 1995; Maerz and Madison, 2000). The indirect effects of prey availability on social behaviour might produce selective pressures that interact with the direct selective effects of prey availability on salamander morphology.

Adaptive diversification within habitats is an alternative explanation to constraint for the broad overlap in salamander phenotypes between lowland and upland habitats. We found apparent correlations between morphology and diet within habitats that were similar to correlations based on all salamanders from lowland and upland habitats. To our knowledge, this is only the second description of such fine-scale trophic polymorphisms within populations (see Svanbäck and Eklöv, 2002). Negative density dependence is one force that will favour local diversification of resource use among individuals (Bolnick *et al.*, 2003). Local competition for prey resources can be high within *Plethodon* populations (Fraser, 1976), and may be promoting fine-scale trophic diversification within *P. cinereus* populations. Intraspecific competition for prey resources among neighbours is already recognized as a major force shaping *P. cinereus* socioecology (Mathis *et al.*, 1995; Maerz and Madison, 2000). Species-rich forest invertebrate communities offer a wide range of potential trophic niches within habitats. In addition, features such as pit-and-mound topography or the presence of springs can create microhabitat and associated invertebrate heterogeneity that may be comparable with larger-scale habitat differences. The availability of temporal trophic niches may also create opportunities for diversification within habitats (Smith and Skulason, 1996). When available, predation on large prey such as earthworms or Lepidoptera larvae and small, hyper-abundant prey such as collembola can dramatically increase salamander food intake; however, those prey may be much more stochastic resources than many moderate-sized prey such as ants (Maerz *et al.*, 2005). For example, earthworms are among the largest prey found in lowland salamander diets, but are generally not available on non-rainy nights, during warm seasons, or for extended periods following droughts.

We believe it is important to discuss the potential role of exotic species in the evolution of *P. cinereus* trophic polymorphisms. Invasions by non-native species can create novel selective regimes, and therefore may be important agents of modern evolutionary change in native taxa (Cox, 2004). As previously mentioned, many of the large and moderate-sized prey in salamander diets at our study sites are non-native species (Maerz *et al.*, 2005). While large and

moderate-sized native prey were also present, it is the non-native species that drive most of the temporal and spatial variation in food levels (Maerz *et al.*, 2005). We do not know whether resource gradients similar to the ones that exist today were present before the introduction of the native taxa, so at present we cannot evaluate whether the polymorphism we observe reflects a historic pattern or has recently evolved.

We believe that the discovery of resource polymorphisms within *P. cinereus* populations may be important for our understanding of several aspects of their ecology. First, the existence of resource polymorphisms among allopatric *P. cinereus* populations that are similar to the patterns of morphological and dietary character displacement between sympatric *P. cinereus* and *P. hoffmani* (Adams and Rohlf, 2000) suggests intraspecific trophic polymorphisms could play a role in the co-existence of competing species. A number of examples of trophic polymorphisms are associated with the loss of a competitor opening novel niches (Skulason and Smith, 1995; Bolnick *et al.*, 2003). *Plethodon* sp. richness is greater in the southern Appalachians, so one hypothesis is that ancestral *P. cinereus* was sympatric with other *Plethodon* sp., and therefore evolved with a compressed trophic niche. The loss of such competitors as *P. cinereus* radiated into the post-glacial forests of northeastern North America may have broadened the trophic niches available to *P. cinereus*. The alternative hypothesis is that trophic polymorphisms were an important precursor to character displacement between sympatric species (Skulason & Smith, 1995; Bolnick *et al.*, 2003). Second, *Plethodon* are noted for their remarkable densities compared with other vertebrates (Burton and Likens, 1975b; Hairston, 1996). While this may largely be explained by their extreme metabolic efficiency (Pough, 1980), the evolution of resource polymorphisms would reduce intraspecific competition, and therefore increase salamander carrying capacity. Finally, trophic polymorphisms may improve our understanding of species' influences on community and ecosystem dynamics (Persson, 1999). *Plethodon* influence ecosystem processes, including the decomposition of litter, nutrient dynamics and the flow of energy to higher trophic levels, primarily through their predation on soil invertebrates (Burton and Likens, 1975a; Hairston, 1996; Wyman, 1998). Whether resource polymorphisms affect salamander influences on those processes remains to be seen.

In conclusion, trophic polymorphisms are potentially common characteristics of populations that, when identified, can lead to a better understanding of important ecological constraints on a species and the processes that influence diversification. We have shown that trophic polymorphisms are found within red-backed populations between forest habitats, and provide evidence that they may also exist at finer scales. The polymorphism we describe is functionally similar to that observed between populations and sympatric species, suggesting it is probably common among *Plethodon* populations and potentially important to diversification within the genus. We hypothesize that trophic polymorphism is promoted at fine scales by high intraspecific competition, microhabitat heterogeneity and temporal stochasticity in the availability of high-value prey. Habitat heterogeneity may act upon and accentuate diversification at larger scales such as between habitats, populations and species.

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