

The Evolution of Foraging Rate across Local and Geographic Gradients in Predation Risk and Competition

Mark C. Urban* and Jonathan L. Richardson†

Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut 06269

Submitted May 9, 2014; Accepted March 17, 2015; Electronically published May 8, 2015

Online enhancement: appendix. Dryad data: <http://dx.doi.org/10.5061/dryad.222h3>.

ABSTRACT: Multiple theories predict the evolution of foraging rates in response to environmental variation in predation risk, intraspecific competition, time constraints, and temperature. We tested six hypotheses for the evolution of foraging rate in 24 spotted salamander (*Ambystoma maculatum*) populations from three latitudinally divergent sites using structural equation models derived from theory and applied to our system. We raised salamander larvae in a common-garden experiment and then assayed foraging rate under controlled conditions. Gape-limited predation risk from marbled salamanders solely explained foraging rate variation among populations at the southern site, which was dominated by this form of selection. However, at the middle and northern sites, populations evolved different foraging rates depending on their unique responses to local intraspecific density. The coupling of gape-limited predation risk from marbled salamanders and high intraspecific density at the middle site jointly contributed to selection for rapid foraging rate. At the northernmost site, intraspecific density alone explained 97% of the interpopulation variation in foraging rate. These results suggest that foraging rate has evolved multiple times in response to varying contributions from predation risk and intraspecific competition. Predation risk often varies along environmental gradients, and, thus, organisms might often shift evolutionary responses from minimizing predation risk to maximizing intraspecific competitive performance.

Keywords: optimal foraging, local adaptation, trophic interactions, common-garden experiments, geographic gradients.

Introduction

Foraging behavior can strongly affect individual fitness, trophic interactions, and ecosystem dynamics (Case 1978; Peters 1983; Werner 1986; Conover and Present 1990; Gotthard et al. 1994; Arendt 1997; Schmitz 1998; Blanckenhorn 2000). Foraging rate is expected to evolve in response to heterogeneous selective environments, including predation risk, resource levels, time constraints, and temperature

(table 1; Case 1978; Ricklefs 1984; Lima and Dill 1990; Conover and Schultz 1995; Abrams et al. 1996).

Biologists frequently highlight predation as a factor determining optimal foraging behaviors. Predation can select for rapid growth to escape early vulnerable stages if higher foraging rate is not associated with increased mortality (Williams 1966; Lack 1968). However, higher foraging rates usually increase predation risk by making individuals more easily detected by predators, less vigilant, or more likely to enter risky habitats. This relationship creates the well-known trade-off between maximizing growth rate and minimizing predation risk (Sih 1982; Lima 1985; Gilliam and Fraser 1987; Lima and Dill 1990; Skelly and Werner 1990; Werner and Anholt 1993; Schmitz 2008). As a consequence, prey frequently decrease foraging rate in response to increased predation risk (Skelly and Werner 1990; Werner and Anholt 1993; Abrams and Rowe 1996; Dmitriew 2011). Therefore, hypothesis 1a is that higher predation risk could lead to the evolution of lower foraging rates (table 1).

However, not all predators are alike. Many predators cannot consume the largest prey individuals because of gape limitation or handling constraints (Wilson 1975; Peters 1983; Hambright 1991; de Roos et al. 2003). Prey can grow into a size refuge from these size-limited predators and thereby overcome the costs of early predation risk through rapid growth into a size refuge (Reznick 1983; Spitze 1991; Day et al. 2002; Urban 2007a). Prey are expected to forage actively despite risks from gape-limited predators in order to reach a size refuge (hypothesis 1b, table 1). In contrast, prey can never enter a size refuge from size-unconstrained predators, which by definition can feed on all sizes of prey individuals. Therefore, size-unconstrained predators should select for reduced foraging rate.

Evolution by natural selection also can optimize a population's foraging rate in response to local resource levels (MacArthur and Pianka 1966; Schoener 1971). These hypotheses sometimes are developed for growth rate, and,

* Corresponding author; e-mail: mark.urban@uconn.edu.

† Present address: Department of Biology, Providence College, Providence, Rhode Island 02918.

Table 1: Hypotheses of foraging strategies that form the basis of a priori models of spotted salamander foraging rate evolution

Explanation	Hypothesis	References
1. Predation:		
a. Gape unconstrained	More gape-unconstrained predators → decreased foraging rate	Williams 1966; Urban 2007a
b. Gape limited	More gape-limited predators → increased foraging rate	Williams 1966; Urban 2007a
2. Resources:		
a. Low overall resource environment	Low resources → decreased foraging rate High resources → increased foraging rate	Grime and Hunt 1975; Sih 1984
b. High overall resource environment	Low resources → increased foraging rate High resources → decreased foraging rate	Sih 1984; Ferguson and Talent 1993; Arendt 1997
3. Time constraints	Less time → increased foraging rate	Houston et al. 1993; Abrams et al. 1996
4. Temperature	Countergradient selection for increased foraging rate under colder natural conditions	Levinton 1983

thus, to apply them, we assume that foraging rate correlates positively with growth rate, as is often the case (e.g., Laurila et al. 2006). Most models include the assumption of a diminishing return in energy obtained as foraging rates increase (Ware 1975; Hirvonen 1999). Therefore, when saturation is reached in high-resource habitats, the costs of foraging continue to increase, which results in an intermediate optimum for foraging rate. The evolution of foraging rates depends on what aspects of foraging performance are optimized, absolute resource levels, and absolute costs associated with foraging. In low-resource environments and assuming high absolute costs to foraging and for organisms that maximize net benefits, an increase in resources shifts the benefit curve higher and thus increases the advantage for more foraging (hypothesis 2a, table 1; Sih 1984). The food-limitation or stress-tolerant hypothesis also predicts that low foraging and growth rates should evolve in low-resource environments (Clutton-Brock et al. 1985; Gotthard et al. 1994; Blanckenhorn 2000). The stress-tolerant strategy is to grow slowly, make efficient use of the limited resources, and thereby survive periods of low resources that would otherwise starve fast growers or retard their development (Grime and Hunt 1975; Arendt 1997; Blanckenhorn et al. 2011). The mechanism underlying this hypothesis usually is thought to be that high metabolic rates are required to fuel rapid growth, but these same high metabolic rates starve fast growers when resources become depleted (Case 1978; Conover and Present 1990; Gotthard et al. 1994; Sinervo and Adolph 1994). In contrast, foraging rate should evolve in opposite directions in response to resource differences when resources are high and close to the saturation point. Consumers that optimize net benefits can reach the saturation point of energy gained per effort more quickly if they are close to that saturation point in high-resource environments and thus

should decrease foraging rate as resources increase (hypothesis 2b, table 1; Sih 1984). Minimizing costs or foraging area covered also leads to decreases in foraging rate with higher resources across the entire gradient (Sih 1984). Hence, depending on the relative costs and benefits of foraging and growth in a particular environment, high intraspecific density and low resources could select for either higher or lower foraging rates.

Besides predation risk and resources, time constraints or performance optimization at local temperatures also might explain variation in foraging or growth rates. Time constraints generally select for more rapid growth to maturity or development into stages that allow persistence during altered conditions (hypothesis 3, table 1; Grime and Hunt 1975; Newman 1992; Houston et al. 1993; Abrams et al. 1996). For instance, aquatic organisms inhabiting temporary ponds often must grow to a minimum size in order to undergo metamorphosis before ponds dry (Werner 1986; Richter-Boix et al. 2011). Also, high-latitude populations that experience shorter growing seasons might grow or develop faster to reach resistant stages before the growing season ends (Berven 1982; Conover and Present 1990; Gotthard 2004; Laurila et al. 2006; Lindgren and Laurila 2009). The environmental-compensation and countergradient-selection hypotheses (Conover and Schultz 1995) suggest that populations evolve to maximize growth under the environmental conditions they typically experience (Krogh 1916; Levinton 1983). For instance, high-latitude or high-altitude populations often grow faster than low-latitude or low-altitude populations at the low temperatures that they typically experience (Berven et al. 1979; Levinton 1983; Conover and Present 1990), and similar responses occur at more local scales between cold and warm habitats (Skelly 2004). Hence, hypothesis 4 is that populations from cold environments will forage more than popula-

tions from warm environments when tested at cooler temperatures.

Here, we evaluate whether the hypotheses in table 1 explain variation in foraging rate among 24 populations of the spotted salamander (*Ambystoma maculatum*) distributed equally among three geographically divergent sites (fig. 1). We codify our expectations in a series of a priori structural equation models, find the best-fitting models, and explore multivariate explanations for the genetically based patterns of foraging rate that we observe among natural populations of spotted salamanders. Adaptive evolution finds a compromise among selective agents that are often correlated and confounded across natural landscapes (Jones et al. 1977; Reznick et al. 2001). Understanding evolution at sites that vary in key selective factors can help unravel the independent effects of correlated selection regimes (Reznick et al. 2001). Prior research at one site in southern New England suggested that natural selection from predatory marbled salamanders led to the evolution of higher foraging rates in spotted salamander populations that face high marbled salamander predation risk (Urban 2007c, 2013). However, other selection regimes correlated with marbled salamander predation risk, such as resource

heterogeneity, also could explain genetic divergence in foraging rate. We explore alternative hypotheses for the evolution of foraging rate at our original southern site and expand the geographic extent of our inquiry to two sites 80 and 160 km north of the original site. Corresponding to the northern range margin (fig. 1), the marbled salamander becomes rare at the middle site and does not occur at the northern site. We explore whether gape-unconstrained predation risks, zooplankton resources, pond permanence, and pond temperature differ among sites, allowing us to assess contributions from these alternative selection regimes. We then assess the relationship between these selection regimes and foraging rate measured in common-garden experiments in order to separate contributions from genetics and the environment.

We develop specific predictions for our system based on each of the six hypotheses reviewed above. We predicted that high gape-unconstrained predation risk would lead to the evolution of reduced foraging rate and that gape-unconstrained predation risk would depend on pond area and permanence (prediction 1a, table 1; fig. 2) based on previous research (Urban 2004, 2007b). We expect that gape-limited predation risk from the most important gape-limited

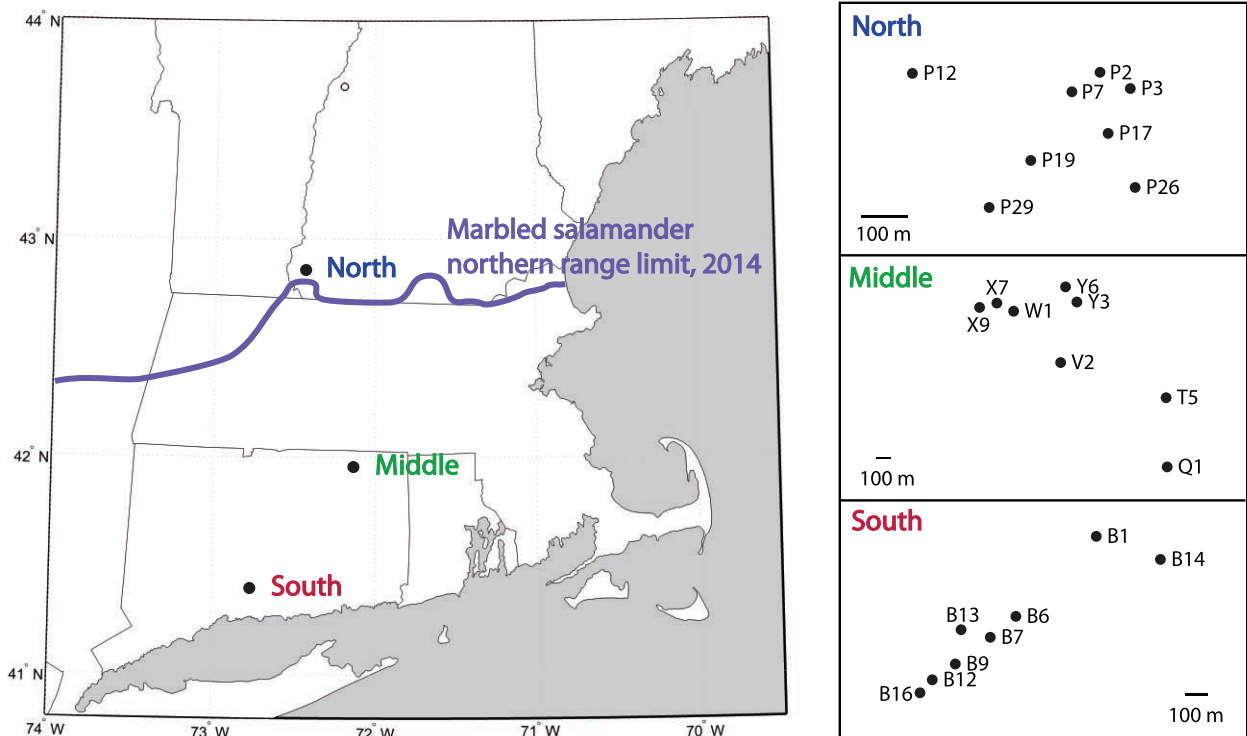
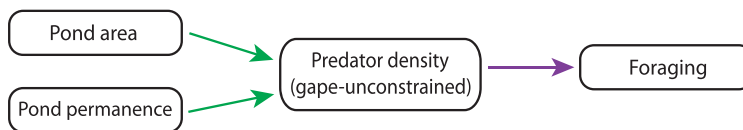


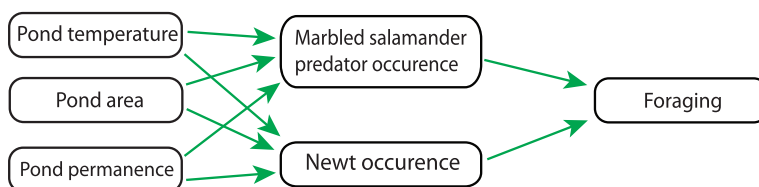
Figure 1: We studied populations from three sites separated by approximately 80 km: the southern (Northford, CT), middle (Union, CT), and northern (Chesterfield, NH) sites. At each regional site, we studied eight spotted salamander populations, indicated on the right by alphanumeric identifiers in their regional spatial configuration. We also display the northern range limit of marbled salamanders in New England, modified from Petranka (1998) and updated with new sightings.

- predicted positive associations between two factors
- predicted negative associations between two factors

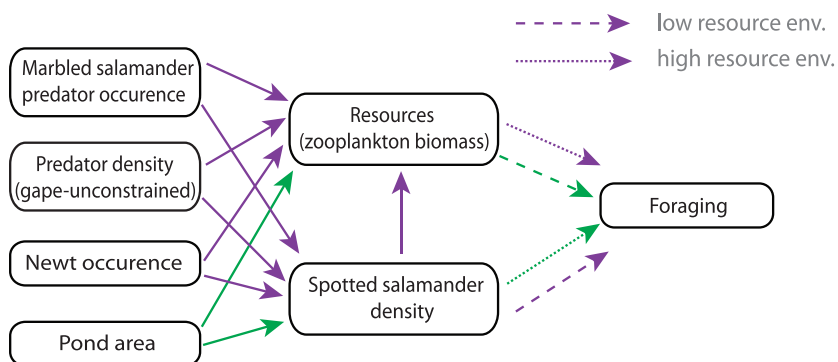
Prediction 1a (gape-unconstrained predation):



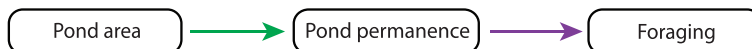
Prediction 1b (gape-limited predation):



Prediction 2a/2b (low vs. high resource environment):



Prediction 3 (time constraints):



Prediction 4 (countergradient selection based on temperature):

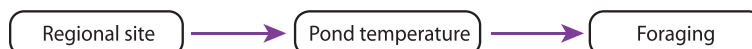


Figure 2: Specific predictions for the evolution of spotted salamander foraging evolution based on the hypotheses presented in table 1. These predictions were then used to develop structural equation models. We also include specific predictions about how environmental variation is expected to be associated with drivers of foraging evolution. Green arrows indicate positive associations, and purple arrows indicate negative associations.

predators in our system, marbled salamander larvae and red-spotted newt adults (*Notophthalmus viridescens*), would select for rapid foraging into a size refuge (prediction 1b, table 1; fig. 2). Recently hatched spotted salamander larvae mostly feed on zooplankton. Lower zooplankton resources might result from environmental conditions such as pond area and high densities of consumers. Multiple species eat zooplankton, including spotted salamanders, marbled salamanders, and newts. Lower zooplankton resources, in turn, might lead to either lower (prediction 2a) or higher (prediction 2b) foraging rates, depending on absolute resource levels, costs to foraging, and the performance metric optimized. Assuming high costs to high foraging rate (Urban 2007c) and low absolute resources in our system, we predict the evolution of higher foraging rate in low-resource environments (prediction 2b). We test the time constraints hypothesis (prediction 3) by evaluating if more temporary ponds select for more rapid foraging rate. Last, we evaluate countergradient selection for temperature (prediction 4) by testing whether local pond temperature correlates with variation in foraging rate among ponds as a consequence of performance optimization under different regional temperature regimes at each site.

Methods

Study Sites and Natural History

We studied 24 spotted salamander populations distributed evenly among three sites in New England (fig. 1). Each site encompasses a 2-km² area of undisturbed, mixed deciduous forest at altitudes <300 m. Marbled salamanders occur in 66%, 36%, and 0% of ponds at the southern (Northford, CT), middle (Union, CT), and northern (Chesterfield, NH) sites, respectively (fig. 1). We consider each pond to constitute a separate population based on prior evidence of significant neutral and quantitative genetic variation among ponds (Urban 2007c; Richardson and Urban 2013).

The spotted salamander is a large terrestrial mole salamander that inhabits eastern North America. Each spring, adults migrate from upland terrestrial habitat into temporary ponds to mate and to lay eggs. Small (~15 mg) aquatic larvae hatch after 4–7 weeks. Spotted salamander larvae must survive a gauntlet of predators, including marbled salamander larvae, adult newts, and diving beetles before metamorphosing into terrestrial juveniles by late summer when most temporary ponds dry.

The marbled salamander is an apex predator in temporary ponds in this region (Urban 2013). The marbled salamander range extends to 43°N latitude in southern New Hampshire (fig. 1), whereas the spotted salamander range extends as far north as 52° latitude in Quebec, Canada. The more restricted northern range of marbled salamanders has

been linked to their sensitivity to cold winter temperatures (Herstoff and Urban 2014). Unlike spotted salamanders, marbled salamanders breed in the autumn rather than spring. Their larvae must survive the winter under the ice, and cold winter pond temperatures decrease overwinter survival (Herstoff and Urban 2014).

Marbled salamander larvae are gape-limited predators that feed on prey with a maximum body width <37% of their gape width (Urban 2008b), which includes small spotted salamander larvae (Stenhouse et al. 1983; Petranka 1998). Spotted salamander larvae can enter a size refuge from marbled salamander predation ~4 weeks after hatching by growing too large for efficient capture (Urban 2013). Consequently, marbled salamander larvae induce selection in spotted salamander larvae for rapid growth into a size refuge (Urban 2008b). At the same time, marbled salamanders are three times more likely to eat rapidly foraging individuals, setting up a trade-off between early- and late-mortality risk that is mediated by foraging behavior (Urban 2007c). Larval marbled and spotted salamanders also compete for the same zooplankton prey (Urban 2013). Marbled salamanders decrease the density and biomass of zooplankton in experiments and in the field (Urban 2013). Hence, marbled salamanders also potentially induce selection on spotted salamander foraging rate by decreasing shared resources.

Red-spotted newt adults are another gape-limited predator in temporary ponds that prey on spotted salamander larvae (Petranka 1998) but for a more limited time window than marbled salamanders because newt adults have smaller overall gapes and grow more slowly than marbled salamander larvae (Urban 2008b). Newts most effectively capture prey items 37% or less the width of their gape width (Urban 2008b). Spotted salamander larvae can grow into a size refuge from newts within several weeks of hatching, and research shows that newt cues can induce rapid early growth into this size refuge for populations sampled across our geographic extent (Urban 2008b). Newts also consume shared zooplankton resources and thus could influence resource dynamics in ponds.

Gape-unconstrained predators in the system include large dragonflies (e.g., *Aeshna* spp.) and diving beetles (*Dytiscus verticalis*). We detail the full list of gape-unconstrained predators in previous work (Urban 2007b, 2008b). Diving beetles, in particular, are important and abundant predators at all three sites (Urban 2008b) that induce selection for small body size and large relative tail muscle size in spotted salamander larvae (Urban 2010).

Besides predation, intraspecific competition might also play an important role in selecting for divergent foraging rates. Prior research provides substantial evidence for density dependence in spotted salamander survival and growth in the wild and in experiments. In experiments, spotted sal-

amanders face high mortality and grow slowly in high densities (Brodman 1996; Walls 1998). In the field, Shoop (1974) observed stable larval abundances through time despite high variation in the number of eggs laid and greater larval survival to metamorphosis in years when fewer eggs were laid.

Abiotic and Biotic Variables

We next evaluated how selection regimes varied among sites and differed in their correlations within and across sites. We used our full data set of abiotic and biotic variables measured at 12–14 ponds over multiple years (see table A1 for details; tables A1, A2 available online) at each site up to 2010, when we conducted the common-garden experiment. Data are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.222h3> (Urban and Richardson 2015). Based on prior research (Schneider and Frost 1996; Wellborn et al. 1996; Urban 2004, 2007b) and considering the six hypotheses of adaptive foraging rate in table 1, we expected the following pond characteristics to determine foraging rate directly or indirectly by influencing other variables: marbled salamander and newt prevalence, gape-unconstrained predation risk, zooplankton biomass, intraspecific egg and larval density, pond permanence, and water temperature.

We estimated pond permanence as the mean number of days that ponds held water, beginning with spotted salamander breeding and ending when we observed no water during weekly surveys across 3 years (table A1). Mean temperature data were recorded at each of the 24 ponds in the study in 2013 using Hobo Pendant temperature loggers (Onset, Bourne, MA) placed at the point of maximum depth and 10 cm below the surface of the water. Two temperature loggers were removed from the water by beavers. We calculated the mean temperature of ponds at each site for a period offset by the average difference in median breeding date among the sites. On average, spotted salamanders bred 9 days later at the middle site compared to the southern site and 15 days later at the northern site compared to the middle site. By offsetting temperature data, we calculated the mean temperature that the salamanders experience given climate-based differences in their breeding phenology. Because spotted salamanders breed successively later in northern populations, they experience relatively similar water temperatures despite the climatic differences among sites.

We estimated intraspecific density in spotted salamanders at the egg stage and 2–3 weeks after hatching. Although the two measures are correlated with varying degrees within sites ($\rho = 0.73, 0.17, \text{ and } 0.61$, at southern, middle, and northern sites, respectively), egg density provides an estimate of the initial density of hatchlings, whereas

larval density incorporates changes owing to predation, pathogens, and changes in pond area. We estimated egg densities by conducting visual censuses of each pond and averaging these numbers across years (table A1; 5 years for multisite comparisons and 5–8 years for analyses at individual sites). We divided the number of egg masses by pond area and multiplied by 81, the mean number of eggs per egg mass at the southern site (Urban et al. 2015). We estimated pond area at its maximum water depth in early spring as the area of an ellipse defined by the maximum dimension and perpendicular width (Batzler et al. 2004). We conducted annual dip net surveys for spotted salamander larvae at 2–3 weeks after hatching at all three sites in 4 years (2002–2005).

We performed annual area-standardized dip net surveys for 4–7 years (see table A1 for details) to estimate predator risk using the same methods as above. We preserved field samples and identified them to the lowest taxonomic level possible using standard keys (Merritt et al. 2008) under a $\times 8$ –100 Leica M125 stereoscope. We classified predators as gape limited and gape unconstrained based on prior research (Urban 2007b). We measured marbled salamander and newt prevalence as the proportion of years in which these species were observed during annual surveys. We used interannual prevalence rather than density because we have a longer data set on occurrence for these two species and because density estimates require standardization by pond area, which varies greatly within and among years depending on recent rainfall. We used total density to characterize gape-unconstrained predation because at least one gape-unconstrained predator inhabited every pond, resulting in no variation in prevalence but strong variation in density.

We collected zooplankton samples with a 15.6-cm-diameter vertical tube zooplankton sampler (Paggi et al. 2001) before spotted salamanders hatched at each site in 2010 (southern and middle sites) and 2011 (northern site). We sampled at the maximum pond depth and at each cardinal direction midway between maximum depth and the shoreline in order to sample both deep and shallow habitats. We recorded water depth at each sampling point to adjust for differences in volume. Zooplankton were filtered through 80- μm mesh, pooled, and preserved in 70% ethanol (Williamson and Reid 2001). We identified samples to species using standard texts and a region-specific reference (Smith 2001; Thorp and Covich 2001; Haney 2010) using a $\times 8$ –100 Leica M125 stereoscope and $\times 40$ –1,000 Olympus CHBS compound microscope. Immature and male copepods could be identified only to taxonomic order (Williamson and Reid 2001). In each sample, we measured the length of a maximum of 100 individuals in each identifiable taxonomic group and then used published length-mass regressions (McCauley 1984) to estimate the total zooplankton biomass per liter of water sampled.

Common-Garden Experiment

We chose populations for the common-garden experiment from a set of 12–14 ponds under long-term study at each site by stratifying across marbled salamander predation risk (southern and middle sites) and overall predation risk at the northern site, where marbled salamanders are absent. We collected five egg masses from the field after fertilization and raised them in a common garden to limit environmental trait induction. Divergent breeding dates among ponds meant that egg masses were collected over a period of two and a half weeks. Egg masses were held in an incubator (Percival Scientific model I-41; Perry, IA) at 6.0°C, a temperature that slows further development, such that all eggs were raised at the same outdoor temperatures at similar stages. Once all egg masses were collected, two sections of 12 eggs were separated from each egg mass with a sterilized scalpel. Each site was represented by eight ponds, each pond by five families, and each family by two replicates (3 sites \times 8 ponds \times 5 families \times 2 replicates = 240 experimental units). Each egg mass section was placed in 18 cm of aged well water in a 19-L container under 50% shade cloth. The mean stage (Harrison 1969) and hatching proportion of egg masses were not significantly related to site of origin (Markov chain Monte Carlo randomization test, $P > .18$) in mixed-effects models with site as a fixed factor and population as a random effect. We used binomial errors for proportion hatching and included an individual-level term to account for detected overdispersion (Warton and Hui 2011). Stage did not differ significantly among sites ($P = 0.502$). However, we detected significant variation among populations in both stage and hatching proportion using likelihood ratio tests ($LR_1 = 52.8$ and 28.2 , respectively, $P < .001$), but this variation was not linked significantly to foraging rate ($F_{1,22} = 0.3$ and 0.2 , respectively, $P > .5$). Therefore, we did not include these traits as additional covariates in analyses. After hatching, we provided homogenized wild zooplankton ad lib.

Foraging Trials

We measured foraging rate in laboratory common-garden experiments as the biomass of prey consumed. Biomass consumed correlates well ($\rho = +0.58$) with foraging behavior measured in previous experiments (Urban 2007c). We measured biomass consumption when larvae were 2–3 weeks old, which corresponds to the period of highest mortality for spotted salamander larvae and maximal foraging rate differences in previous work (Urban 2007c). We haphazardly chose one larva from each outdoor container, representing two individuals from each family. We evaluated foraging rate in populations from the three sites in

random order under the same conditions. The order of the tests among sites was not a significant factor in the observed trait variation ($LR_1 = 0.00$, $P = .998$), and, therefore, this temporal block was excluded from further analyses. Each larva was placed in an individual $7 \times 7 \times 18$ -cm (900-mL-volume) glass container. Each family was split between two blocks located on two sets of shelves in a temperature-controlled incubator (Percival Scientific, model I-41). Block also was not significant ($LR_1 = 0.00$, $P = .993$) and was removed from further analysis. We set lighting to the natural outdoor day length and temperature to 13.2°C, the mean average temperature from each site for this developmental stage. We added 120 mL of water containing marbled salamander kairomones to each container because spotted salamanders decrease their activity and growth in response to marbled salamander kairomones (Urban 2007c, 2008a). In previous work, we found no evidence for a site \times predator cue treatment interaction (Urban 2008a). To increase replication of populations within sites and enhance our power to find genetic differences in response to local environmental gradients, we concentrated on responses to marbled salamander cues and did not evaluate noncue responses. Marbled salamander kairomones were created by feeding spotted salamander larvae to marbled salamanders, filtering the surrounding water with 80- μ m mesh to remove zooplankton, and adding the filtered water immediately to spotted salamander containers.

We hand-counted 240 sets of the four numerically dominant zooplankton taxa in natural ponds: 10 cyclopoid copepods, 10 large cladocerans (mostly *Scapholeberis mucronata*), and 80 small cladocerans (*Bosmina longostiris* and *Chydorus sphaericus*). The zooplankton were collected from natural ponds. The zooplankton sets were randomized, and one set was added to each container. Randomly selected samples were preserved to estimate initial zooplankton biomass.

After 24 hours, uneaten zooplankton were collected with 80- μ m mesh and preserved for enumeration and identification. We calculated biomass by measuring the length of each zooplankton and then applying published length-mass regressions (McCauley 1984). We used biomass rather than density because biomass better reflects the energy gained per time unit and the zooplankton differed greatly in size. Biomass eaten was calculated as the mean biomass from samples of initial zooplankton minus the biomass in each container after 24 hours of salamander feeding.

Evidence suggests that foraging rates are underlain by genetic differences. We raised larvae in a common garden from eggs to minimize environmental induction. Previous research has shown that foraging rates remain constant across years and thus do not change if a particular selective agent is absent in a given year (Urban 2007c, 2013). We can also reject four of the most common sources of

maternal effects that can produce nongenetic trait variation (Lynch and Walsh 1998; Mousseau and Fox 1998): habitat choice, maternal care, egg provisioning, and environmental conditioning of females or eggs (Urban 2013).

Statistical Analyses

We first evaluated environmental differences among sites in a multivariate ANOVA. Finding a significant effect, we performed univariate analyses with respect to site of origin both as an unordered categorical factor and with latitude, and we corrected P values using the Holm-Bonferroni method. Prevalence data were analyzed with a generalized linear model with quasi-binomial errors to account for detected overdispersion, and results were analyzed using a χ^2 test. We evaluated multiple comparisons using Tukey contrasts. We also performed a linear discriminant analysis in the *lda* function in R (ver. 3.0) to determine whether potential selective factors distinguished significantly among the three sites. We first used leave-one-out cross validation to determine the accuracy of linear functions in categorizing ponds by selection regime and then calculated discriminant functions for the full data set. We also tested for significant correlations among factors using Spearman's rank correlations after correcting for multiple tests using the Holm-Bonferroni method.

We tested structural equation models with the *semPLS* package in R. We used a partial least squares approach to structural equation modeling, which chooses weightings for variables that maximize the linear relationships among composite variables (Lohmöller 1989). This approach is robust to small sample size, nonnormal distributions, and nonlinear and colinear relationships among variables (Chin 1998). We estimated path coefficients and determined their significance by bootstrapping model results 10,000 times and evaluating whether bias-corrected ninety-fifth-percentile confidence intervals overlapped with 0. We evaluated model performance using the goodness-of-fit metric.

We performed a second analysis to understand whether potential selective factors, including marbled salamander and newt prevalence, gape-unconstrained predation risk, zooplankton biomass, intraspecific egg and larval density, and pond permanence and temperature, explained significant variation in foraging rate within each of the three sites. We used multiple regression without interactions among factors rather than structural equation models at this stage because within-site sample size (eight populations) was limited. We used the Akaike information criterion corrected for small sample size (AICc) to characterize the fit of all subsets of selective factors and calculated model-averaged regression coefficients, weighted by AICc, along with associated confidence intervals with the *dredge* and *model.avg* functions in the *MuMIn* library in R. We

used the AICc weight to determine the relative support for models (Burnham and Anderson 2002).

Results

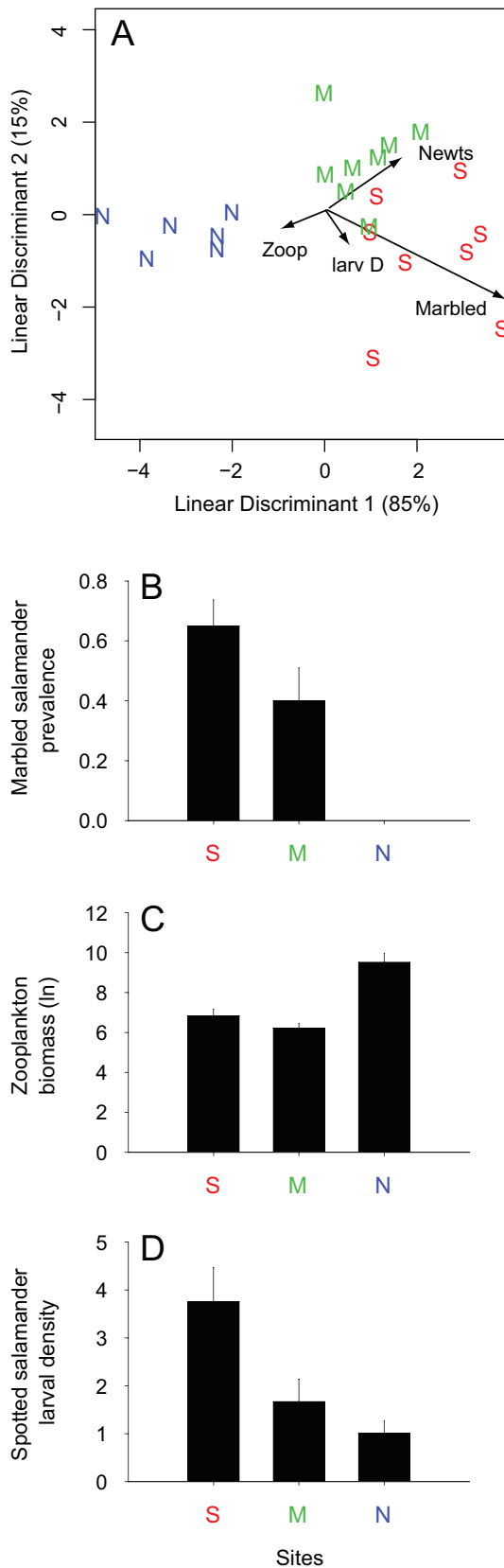
Selection Regimes

Sites significantly differed in eight environmental variables in a multivariate ANOVA (Wilks's $\lambda = 0.08$; $F_{16,24} = 3.7$, $P = .002$). We categorized sites with 55% accuracy based on environmental features using linear discriminant function analysis (fig. 3A). The most uncertainty occurred in discriminating between the southern and the middle sites. The first discriminant function explained 85% of the variation. This axis was associated with higher marbled salamander prevalence and lower zooplankton biomass. The second axis explained 15% of the variance and was associated mainly with higher newt prevalence. Given the significant multivariate differences among sites, we next tested each factor individually. After correcting P values for multiple tests, we found that marbled salamander prevalence, zooplankton biomass, and spotted salamander larval density varied significantly among sites and with latitude (table A2; $P < .005$). Marbled salamander prevalence significantly differed among sites, with the highest prevalence at the southern site, intermediate prevalence at the middle site, and no marbled salamanders at the northern site (fig. 3B). Zooplankton biomass was highest at the northern site (fig. 3C) compared to the middle and southern sites. Spotted salamander larval density was highest at the southern site compared to the middle and northern sites (fig. 3D).

Of the eight factors analyzed across all three sites, only one set was significantly correlated after adjusting for multiple tests: newts were more prevalent in more permanent ponds (Spearman's $\rho = +0.62$). The structure of environmental correlations differed substantially among sites (fig. 4). At the southern site, permanent ponds were associated with higher newt prevalence ($\rho = +0.86$). At the middle site, spotted salamander eggs reached higher densities in ponds with high marbled salamander prevalence ($\rho = +0.87$), and newt prevalence again increased with pond permanence ($\rho = +0.90$). At the northern site, we detected no significant correlations after correction for multiple tests.

Models of Variation in Foraging Rate among Populations

The two structural equation models with highest goodness of fit were modeled on predictions 1b and 2: gape-limited predation from both newts and marbled salamanders and resource limitation (fig. 5). Gape-limited predation from



marbled salamanders, but not newts, significantly explained foraging rate differences ($R^2 = 0.41$; fig. 5, prediction 1b). Whereas gape-limited predation from marbled salamanders significantly explained variation in foraging rate among populations in model 1b, factors related to resource limitation did not explain significant variation in foraging rate among populations in model 2.

The selection of a structural equation model emphasizing marbled salamander prevalence was influenced by the southern site, where marbled salamander prevalence strongly explains variation in foraging rates among populations (fig. 6C; $F_{1,6} = 4.1$, $P < .001$, $R^2 = 0.90$). We performed a post hoc exploration of all subsets of selective factors for each site and found that the minimum-AIC_c model at the southern site included only marbled salamander prevalence (AIC_c weight = 0.95) and not newt prevalence or other selective factors. In addition, marbled salamander prevalence was the only model-averaged coefficient that did not overlap with 0.

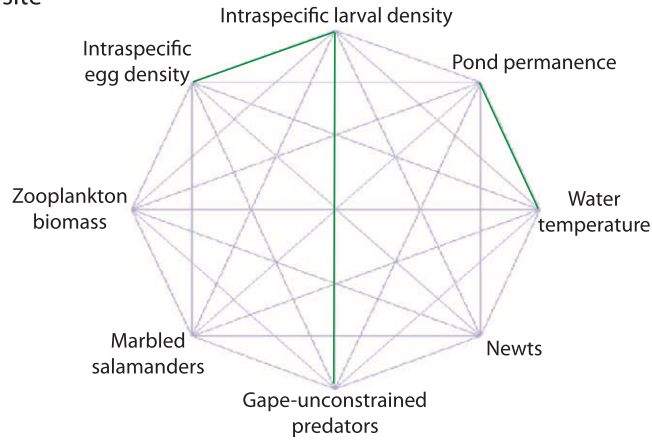
In contrast, marbled salamander prevalence did not significantly explain foraging rates at the middle site (fig. 6B; $F_{1,6} = 2.6$, $P = .16$, $R^2 = 0.30$). Instead, the minimum-AIC model included only spotted salamander egg density (AIC_c weight = 0.63), and this factor was the only model-averaged estimate that did not overlap with 0. Spotted salamanders facing high intraspecific egg densities at the middle site foraged more intensely (fig. 6E; $F_{1,6} = 9.8$, $P = .020$, $R^2 = 0.62$). The next-highest-weighted models included no factors (AIC_c weight = 0.22) and marbled salamander prevalence (AIC_c weight = 0.06).

At the northern site, the minimum-AIC_c model included larval density alone (AIC_c weight = 0.99). At this site, foraging rate was lower for populations originating from ponds with higher intraspecific larval densities (fig. 6G; $F_{1,5} = 141.5$, $P < .001$, $R^2 = 0.97$).

Figure 3: Geographic variation in environments among sites. A, Plot of the southern (S), middle (M), and northern (N) sites with respect to the two linear discriminant functions. The first linear discriminant function explained 85% of the variation and was correlated with higher marbled salamander prevalence and lower zooplankton biomass. The second linear discriminant function explained 15% of the variance and was correlated with higher newt prevalence and lower spotted salamander larval density. The top relative contributions to the two linear discriminant functions are shown, including zooplankton biomass (zoop), spotted salamander larval density (larv D), newt prevalence (newts), and marbled salamander prevalence (marbled). Univariate analyses further suggested significant mean (\pm SEM) differences among sites in marbled salamander prevalence (B), zooplankton (ln-transformed) biomass (C), and spotted salamander larval density (D).

Within-site environmental correlations

Northern site

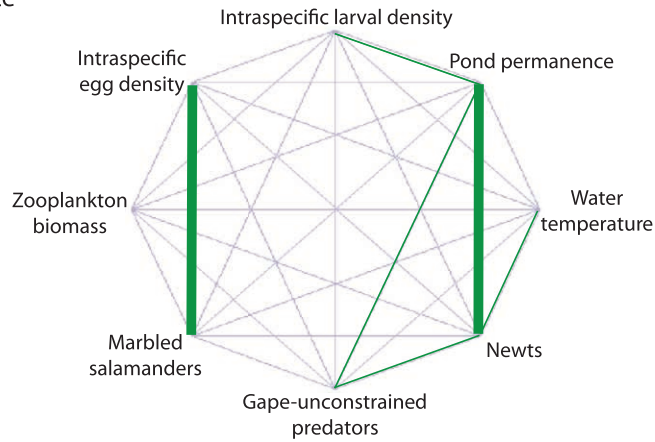


Key

Positive correlation

Negative correlation

Middle site



Southern site

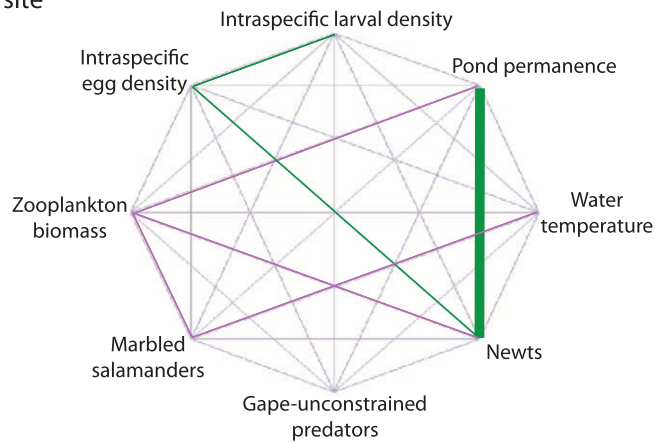


Figure 4: Within-site correlations of environmental characteristics of ponds. Correlations that were significant after correction for multiple tests are indicated with thick lines. Correlations that are significant without this correction are indicated with thin lines. Green lines indicate positive correlations, and purple lines indicate negative correlations.

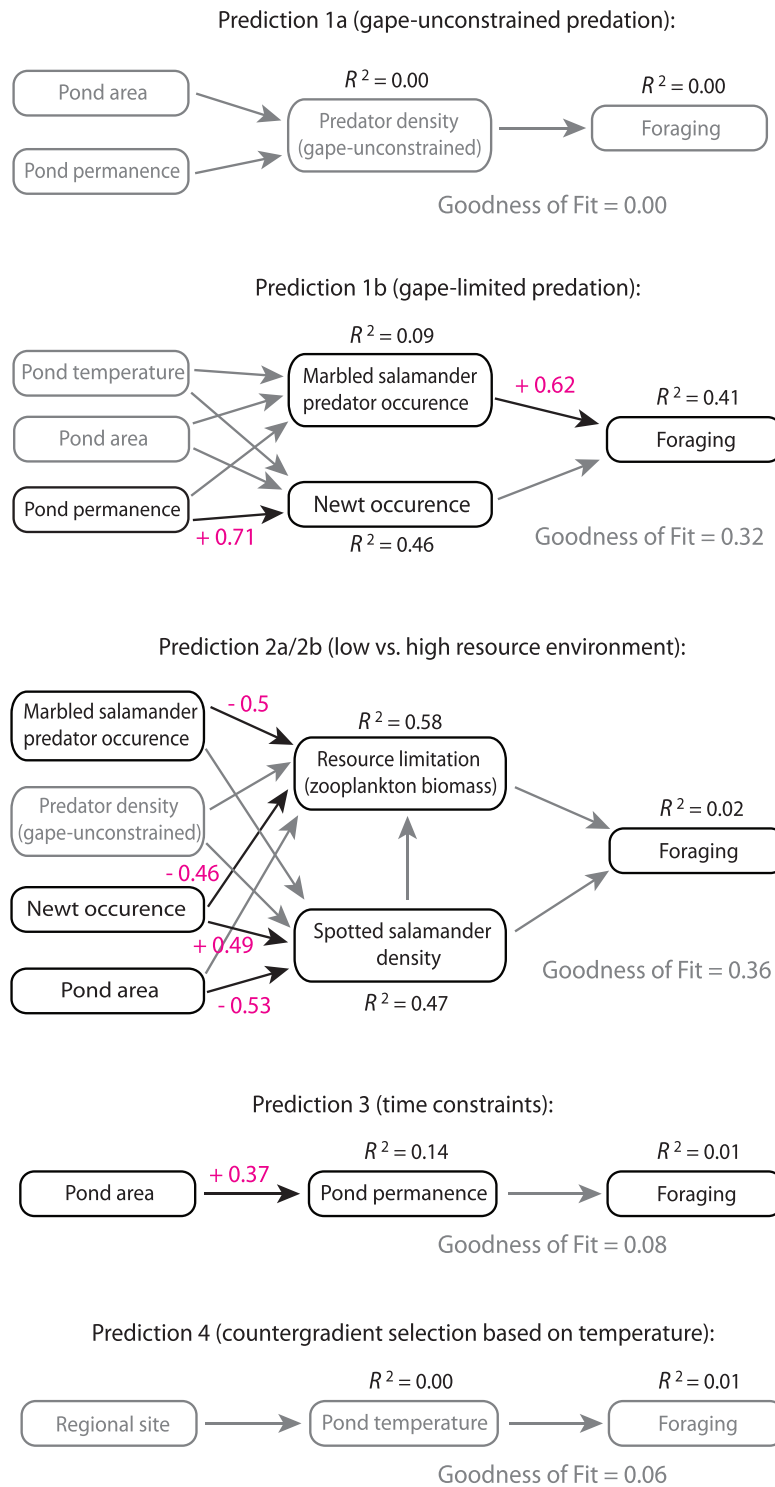


Figure 5: A priori structural equation models and their parameterization. Prediction numbers refer to those found in table 1. We provide the variance explained (R^2) by factors above each predicted response and the goodness of fit next to each model. Standardized path coefficients are found associated with arrows. Only those coefficients found to be significant are included. Factors and relationships that are significant are indicated in black, and nonsignificant ones are indicated in gray.

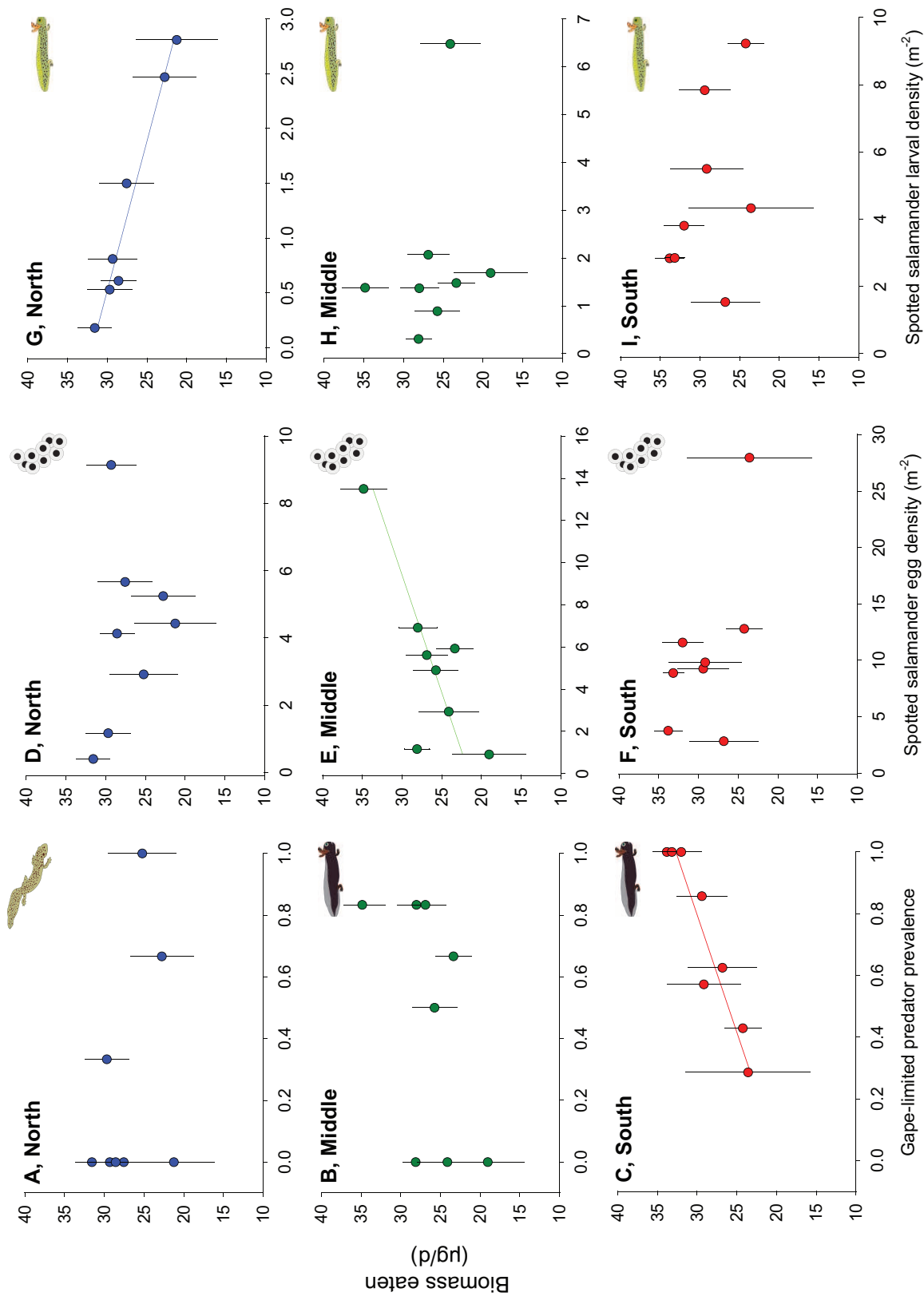


Figure 6: Mean biomass eaten per day (\pm SEM) for each population in relation to gape-limited predator prevalence (A–C), spotted salamander egg density in eggs per square meter (D–F), and spotted salamander larval density in larvae per square meter (G–I). The gape-limited predators are the adult red-spotted newt at the northern site and the marbled salamander larva at the middle and southern sites, as indicated by pictures in each subpanel’s upper right corner. Only significant regression relationships are indicated with lines: C, foraging $\sim 19.5 + 13.1 \times$ gape-limited prevalence, $P < .001$; E, foraging $\sim 21.6 + 0.9 \times$ spotted salamander egg density, $P = .020$; G, foraging $\sim 31.9 - 3.7 \times$ spotted salamander larval density, $P < .001$.

Discussion

We tested six hypotheses commonly expected to explain the evolution of foraging rate. We found that foraging rates were best explained by differences in gape-limited predation from marbled salamanders but not newts (fig. 5, prediction 1b) and resource limitation via intraspecific density (predictions 2a, 2b). Critically, instead of finding support for one prediction across all sites, we found support for a different prediction at each site. Although we initially included adult newts as functionally equivalent to marbled salamanders in terms of their gape-limited predation risk (fig. 2, prediction 1b), the data did not support an effect of newts on foraging rate evolution. We also found little support for the evolution of foraging rates in response to gape-unconstrained predation, time constraints, or temperature (predictions 1a, 3, 4).

Marbled salamander prevalence explained substantial variation (90%) in mean foraging rates among populations at the southern site, where marbled salamanders are most common, providing support for prediction 1b and the evolution of increased foraging rate in response to gape-limited predation. We did not find a significant effect of newts, another gape-limited predator, on foraging rate evolution. Although marbled salamanders are similar to newts in their gape limitation, they feed on spotted salamander larvae for a shorter period than marbled salamanders because marbled salamander larvae have larger overall gapes and grow faster than newt adults (Urban 2008*b*). Newts also occur at lower densities than marbled salamanders at the southern and middle sites (Urban 2008*b*). Intraspecific density was uncorrelated with foraging rates at the southern site even though spotted salamander egg densities are highest here. One potential explanation is that marbled salamanders decrease shared zooplankton resources at the same time as they prey on spotted salamanders. Hence, competition for limited resources might depend at least partially on marbled, in addition to spotted, salamander density.

At the middle site, spotted salamanders did not significantly forage more when they originated from ponds with higher marbled salamander prevalence (fig. 6*B*). Instead, populations foraged significantly more when they came from ponds with high intraspecific egg density ($R^2 = 0.62$; fig. 6*E*), suggesting support for prediction 2b. Here, egg density acts as a proxy for the competitive environment experienced by newly hatched larvae. Larvae might evolve to forage more rapidly when faced with high intraspecific hatchling densities if individuals optimize net benefits and foraging more provides only marginal energetic returns because they are already close to their maximum foraging efficiency as theory predicts (Sih 1984). Under these conditions, higher hatchling density and subsequently

lower resources should lead to the evolution of increased foraging rate to reach the maximum resource benefit (Sih 1984). Another potential explanation is that selection from the gape-limited marbled salamander, which was correlated with spotted salamander egg density at the middle site (Spearman's $\rho = +0.90$), provides an additional benefit to foraging by lowering costs to foraging relative to gape-unconstrained predators and supporting rapid growth into a size refuge even when food is limiting. This strong correlation could produce a common axis of selection for intense foraging rates (fig. 7): at one end of the axis are ponds with intense gape-limited predation from marbled salamanders and high intraspecific density, where joint selection favors increased foraging rate. At the other end, ponds are dominated by gape-unconstrained predators and low intraspecific density, where joint selection favors more cautious foraging.

We found no relationship between foraging rates and the prevalence of newts, the only predatory gape-limited salamander, at the northern site. Insights are limited, though, because larvae were exposed to marbled salamander cues instead of newt cues, and induced responses to newt cues might have shown different patterns. However, previous work showed no significant differences between growth rates among populations at the northern site in response to high versus low predation risk from newts (Herstoff and Urban 2014). Instead, we found that intraspecific larval density explained 97% of the variation in foraging rates among populations at the northernmost site (fig. 6*G*). Intraspecific density was associated with lower, not higher, foraging rates at the northern site. In contrast

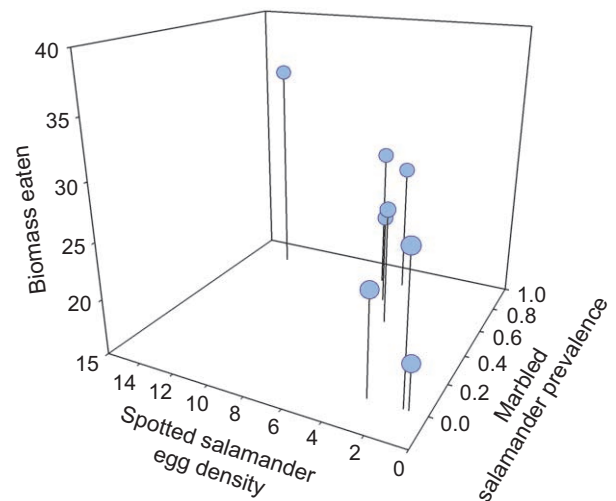


Figure 7: Biomass eaten at the middle site increases along an axis of correlated selection from higher gape-limited predation risk and spotted salamander egg density.

to what we observed at the middle site, this pattern matches prediction 2a. Theory suggests that lower resources should reduce foraging rates in a generally resource-poor environment where costs to foraging are high (Ware 1975; Sih 1984). Under these conditions, decreasing foraging rate minimizes costs associated with trying to find rare resources in a risky environment (Clutton-Brock et al. 1985; Gotthard et al. 1994; Blanckenhorn et al. 2011). Yet, the northern site had the highest resource densities of the three sites. What else might explain these contrasting effects of intraspecific density on foraging rate evolution at the middle and northern sites? The only study factors significantly correlated with larval density were egg density ($\rho = +0.61$, $P = .021$) and gape-unconstrained predator density ($\rho = +0.54$, $P = .044$), and neither of these factors was significantly associated with foraging rate at the northern site ($P > .5$). One potential answer originates from the shift in relative risk to spotted salamanders from marbled salamanders to gape-unconstrained predators. The evolution of foraging rates in response to intraspecific density might shift depending on relative threats from marbled salamanders versus other predator species and the different fitness costs of foraging associated with each predator type.

This work adds to a growing number of studies that suggest a prominent role for intraspecific density in the evolution of divergent life-history strategies (Bassar et al. 2013; Travis et al. 2013). Long-standing theory suggests that divergent foraging rates and competitive abilities can evolve in response to high intraspecific density (MacArthur and Wilson 1967; Pianka 1970; Arendt 1997; Mueller 1997). For instance, classic artificial selection experiments on *Drosophila* showed that high intraspecific competition could lead to the evolution of higher foraging rate (Mueller 1988; Sokolowski et al. 1997). In contrast, other studies suggest the evolution of slower growth in order to shunt resources to development or to prevent starvation during periods of low resources (Clutton-Brock et al. 1985; Gotthard et al. 1994; Blanckenhorn et al. 2011). The cost and benefit curves of foraging and the contributions of different factors to fitness determine the qualitative effect of resource density on optimal foraging (Schoener 1971; Sih 1984). Here, we show empirically that both increasing and decreasing foraging rate can evolve in response to intraspecific density within the same system depending on site-specific conditions.

The relative contributions from marbled salamander predation and intraspecific competition to foraging rate evolution shifted among sites in this study. The total density of predators, the prevalence and density of marbled salamanders, and the overall density of gape-limited predators decline at sites with colder temperatures in this system (Urban 2007b, 2008b). Winterkill similarly affects many large apex predators in freshwater habitats, often leading to reduced predation risk in shallow ponds at higher latitudes

(Greenbank 1945; Fang and Stefan 2000). This pattern of decreasing predation risk in colder regions holds more generally across a wide range of systems and taxa. For instance, marine algae, amphibians, birds, littoral gastropods, small mammals, and wasp larvae face declining predation risk at higher latitudes (Cody 1966; Vermeij 1978; Jeanne 1979; Gaines and Lubchenco 1982; Hanski et al. 2001; Laurila et al. 2008). We know less about changes in intraspecific density and competition across similar gradients, but we might expect higher contributions from intraspecific densities to selection in regions where predation risks are low. Further evidence indicates that traits related to intraspecific competition evolve at higher latitudes and antipredator traits evolve at lower latitudes (e.g., Laurila et al. 2008; Lindgren and Laurila 2010). Hence, we might commonly find the evolution of more defensive phenotypes at low latitudes or low elevations or in warmer habitats and the evolution of more competitive phenotypes at higher latitudes or higher elevations or in colder habitats.

Acknowledgments

Research was supported by National Science Foundation award DEB-1119877, the James S. McDonnell Foundation, and a University of Connecticut large faculty grant. Special thanks to the South Central Connecticut Regional Water Authority for access to field sites and to L. Didan and E. Herstoff for research assistance. We also thank E. Brodie III, N. Freidenfelds, and two anonymous reviewers for comments critical for improving earlier versions of the manuscript.

Literature Cited

- Abrams, P. A., O. Leimar, S. Nylin, and C. Wiklund. 1996. The effect of flexible growth rates on optimal sizes and developmental times in a seasonal environment. *American Naturalist* 147:381–385.
- Abrams, P. A., and L. Rowe. 1996. The effects of predation on the age and size of maturity of prey. *Evolution* 50:1052–1061.
- Arendt, J. D. 1997. Adaptive intrinsic growth rates: an integration across taxa. *Quarterly Review of Biology* 72:149–177.
- Bassar, R. D., A. Lopez-Sepulcre, D. N. Reznick, and J. Travis. 2013. Experimental evidence for density-dependent regulation and selection on Trinidadian guppy life histories. *American Naturalist* 181:25–38.
- Batzler, D. P., B. J. Palik, and R. Buech. 2004. Relationships between environmental characteristics and macroinvertebrate communities in seasonal woodland ponds of Minnesota. *Journal of the North American Benthological Society* 23:50–68.
- Berven, K. A. 1982. The genetic basis of altitudinal variation in the wood frog *Rana sylvatica*. II. An experimental analysis of larval development. *Oecologia (Berlin)* 52:360–369.
- Berven, K. A., D. E. Gill, and S. J. Smith-Gill. 1979. Countergradient selection in the green frog, *Rana clamitans*. *Evolution* 33:609–623.

- Blanckenhorn, W. U. 2000. The evolution of body size: what keeps organisms small? *Quarterly Review of Biology* 75:385–407.
- Blanckenhorn, W. U., P. A. Hoeck, C. Reim, and Y. Teuschl. 2011. A cost of being large: genetically large yellow dung flies lose out in intra-specific food competition. *Evolutionary Ecology* 25:875–884.
- Brodman, R. 1996. Effects of intraguild interactions on fitness and microhabitat use of larval *Ambystoma* salamanders. *Copeia* 1996: 372–378.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.
- Case, T. J. 1978. On the evolution and adaptive significance of post-natal growth rates in the terrestrial vertebrates. *Quarterly Review of Biology* 53:243–282.
- Chin, W. W. 1998. The partial least squares approach to structural equation modeling. Pages 295–336 in G. A. Marcoulides, ed. *Modern methods for business research*. Erlbaum, Mahwah, NJ.
- Clutton-Brock, T., S. Albon, and F. Guinness. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature* 313:131–133.
- Cody, M. L. 1966. A general theory of clutch size. *Evolution* 20:174–184.
- Conover, D., and T. C. Present. 1990. Countergradient variation in growth rate: compensation for length of the growing season among Atlantic silversides from different latitudes. *Oecologia (Berlin)* 83: 316–324.
- Conover, D. O., and E. T. Schultz. 1995. Phenotypic similarity and the evolutionary significance of countergradient variation. *Trends in Ecology and Evolution* 10:248–252.
- Day, T., P. A. Abrams, and J. M. Chase. 2002. The role of size-specific predation in the evolution and diversification of prey life histories. *Evolution* 56:877–887.
- de Roos, A. M., L. Persson, and E. McCauley. 2003. The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. *Ecology Letters* 6:473–487.
- Dmitriew, C. M. 2011. The evolution of growth trajectories: what limits growth rate? *Biological Reviews* 86:97–116.
- Fang, X., and H. G. Stefan. 2000. Projected climate change effects on winterkill in shallow lakes in the northern United States. *Environmental Management* 25:291–304.
- Ferguson, G. W., and L. G. Talent. 1993. Life-history traits of the lizard *Sceloporus undulatus* from two populations raised in a common laboratory environment. *Oecologia (Berlin)* 93:88–94.
- Gaines, S. D., and J. Lubchenco. 1982. A unified approach to marine plant-herbivore interactions. 2. *Biogeography*. *Annual Review of Ecology and Systematics* 13:111–138.
- Gilliam, J. F., and D. F. Fraser. 1987. Habitat selection under predation hazard: test of a model with foraging minnow. *Ecology* 68: 1856–1862.
- Gotthard, K. 2004. Growth strategies and optimal body size in temperate pararginiid butterflies. *Integrative and Comparative Biology* 44:471–479.
- Gotthard, K., S. Nylin, and C. Wiklund. 1994. Adaptive variation in growth rate: life history costs and consequences in the speckled wood butterfly, *Pararge aegeria*. *Oecologia (Berlin)* 99:281–289.
- Greenbank, J. 1945. Limnological conditions in ice-covered lakes, especially as related to winterkill of fish. *Ecological Monographs* 15:343–392.
- Grime, J. P., and R. Hunt. 1975. Relative growth-rate: its range and adaptive significance in a local flora. *Journal of Ecology* 63:393–422.
- Hambright, K. D. 1991. Experimental analysis of prey selection by largemouth bass: role of predator mouth width and prey body depth. *Transactions of the American Fisheries Society* 120:500–508.
- Haney, J. F. 2010. An image-based key to the zooplankton of the Northeast, USA. Version 4.0. University of New Hampshire Center for Freshwater Biology, Durham.
- Hanski, I., H. Henttonen, E. Korpimäki, L. Oksanen, and P. Turchin. 2001. Small-rodent dynamics and predation. *Ecology* 82:1505–1520.
- Harrison, R. G. 1969. Harrison stages and description of the normal development of the spotted salamander, *Amblystoma punctatum* (Linn.). Pages 44–66 in R. G. Harrison, ed. *Organization and development of the embryo*. Yale University Press, New Haven, CT.
- Herstoff, E., and M. C. Urban. 2014. Will pre-adaptation buffer the impacts of climate change on novel species interactions? *Ecography* 37:111–119.
- Hirvonen, H. 1999. Shifts in foraging tactics of larval damselflies: effects of prey density. *Oikos* 86:443–452.
- Houston, A. I., J. M. McNamara, and J. M. C. Hutchinson. 1993. General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions of the Royal Society B: Biological Sciences* 341:375–397.
- Jeanne, R. L. 1979. A latitudinal gradient in rates of ant predation. *Ecology* 60:1211–1224.
- Jones, J., B. Leith, and P. Rawlings. 1977. Polymorphism in *Cepaea*: a problem with too many solutions? *Annual Review of Ecology and Systematics* 8:109–143.
- Krogh, A. 1916. *Respiratory exchange of animals and man*. Longmans Green, London.
- Lack, D. A. 1968. *Ecological adaptations of breeding in birds*. Methuen, London.
- Laurila, A., B. Lindgren, and A. T. Laugen. 2008. Antipredator defenses along a latitudinal gradient in *Rana temporaria*. *Ecology* 89:1399–1413.
- Laurila, A., S. Pakkasmaa, and J. Merilä. 2006. Population divergence in growth rate and antipredator defences in *Rana arvalis*. *Oecologia (Berlin)* 147:585–595.
- Levinton, J. S. 1983. The latitudinal compensation hypothesis: growth data and a model of latitudinal growth differentiation based upon energy budgets. I. Interspecific comparison of *Ophryotrocha* (Polychaeta: Dorvilleidae). *Biological Bulletin* 165:686–698.
- Lima, S. L. 1985. Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the blackcapped chickadee. *Oecologia (Berlin)* 66:60–67.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- Lindgren, B., and A. Laurila. 2009. Physiological variation along a geographical gradient: is growth rate correlated with routine metabolic rate in *Rana temporaria* tadpoles? *Biological Journal of the Linnean Society* 98:217–224.
- . 2010. Are high-latitude individuals superior competitors? a test with *Rana temporaria* tadpoles. *Evolutionary Ecology* 24:115–131.
- Lohmöller, J.-B. 1989. Latent variable path modeling with partial least squares. *Physica*, Heidelberg.
- Lynch, M., and B. Walsh. 1998. *Genetics and analysis of quantitative traits*. Sinauer, Sunderland, MA.

- MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. *American Naturalist* 100:603–609.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, NJ.
- McCaughey, D. E. 1984. The estimation of the abundance and biomass of zooplankton in samples. Pages 228–265 in J. A. Downing and F. H. Rigler, eds. *A manual on methods for assessment of secondary productivity in fresh waters*. Blackwell, Oxford.
- Merritt, R. W., K. W. Cummins, and M. B. Berg. 2008. *An introduction to the aquatic insects of North America*. 4th ed. Hunt, Dubuque, IA.
- Mousseau, T. A., and C. W. Fox. 1998. The adaptive significance of maternal effects. *Trends in Ecology and Evolution* 13:403–407.
- Mueller, L. D. 1988. Evolution of competitive ability in *Drosophila* by density-dependent natural selection. *Proceedings of the National Academy of Sciences of the USA* 85:4383–4386.
- . 1997. Theoretical and empirical examination of density-dependent selection. *Annual Review of Ecology and Systematics* 28:269–288.
- Newman, R. A. 1992. Adaptive plasticity in amphibian metamorphosis. *BioScience* 42:671–678.
- Paggi, J. C., R. O. Mendoza, C. J. Debonis, and S. B. J. de Paggi. 2001. A simple and inexpensive trap-tube sampler for zooplankton collection in shallow waters. *Hydrobiologia* 464:45–49.
- Peters, R. H. 1983. *The ecological implications of body size*. Cambridge University Press, Cambridge.
- Petranka, J. W. 1998. *Salamanders of the US and Canada*. Smithsonian Institution, Washington, DC.
- Pianka, E. R. 1970. On *r*- and *K*-selection. *American Naturalist* 104:592–597.
- Reznick, D. 1983. The structure of guppy life histories: the trade-off between growth and reproduction. *Ecology* 64:862–873.
- Reznick, D., M. J. Butler IV, and H. Rodd. 2001. Life-history evolution in guppies. VII. The comparative ecology of high- and low-predation environments. *American Naturalist* 157:126–140.
- Richardson, J. L., and M. C. Urban. 2013. Strong selection barriers explain microgeographic adaptation in wild salamander populations. *Evolution* 67:1729–1740.
- Richter-Boix, A., M. Tejedo, and E. L. Rezende. 2011. Evolution and plasticity of anuran larval development in response to desiccation: a comparative analysis. *Ecology and Evolution* 1:15–25.
- Ricklefs, R. E. 1984. The optimization of growth rate in altricial birds. *Ecology* 65:1602–1616.
- Schmitz, O. J. 1998. Direct and indirect effects of predation and predation risk in old-field interaction webs. *American Naturalist* 151:327–342.
- . 2008. Effects of predator hunting mode on grassland ecosystem function. *Science* 319:952–954.
- Schneider, D. W., and T. M. Frost. 1996. Habitat duration and community structure in temporary ponds. *Journal of the American Benthological Society* 15:64–86.
- Schoener, T. W. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics* 2:369–404.
- Shoop, C. R. 1974. Yearly variation in larval survival of *Ambystoma maculatum*. *Ecology* 55:440–444.
- Sih, A. 1982. Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmani*. *Ecology* 63:786–796.
- . 1984. Optimal behavior and density-dependent predation. *American Naturalist* 123:314–326.
- Sinervo, B., and S. C. Adolph. 1994. Growth plasticity and thermal opportunity in *Sceloporus* lizards. *Ecology* 75:776–790.
- Skelly, D. K. 2004. Microgeographic countergradient variation in the wood frog, *Rana sylvatica*. *Evolution* 58:160–165.
- Skelly, D. K., and E. E. Werner. 1990. Behavioral and life-historical responses of larval American toads to an odonate predator. *Ecology* 71:2313–2322.
- Smith, D. G. 2001. *Pennak's freshwater invertebrates of the United States*. Wiley, New York.
- Sokolowski, M. B., H. S. Pereira, and K. Hughes. 1997. Evolution of foraging behavior in *Drosophila* by density-dependent selection. *Proceedings of the National Academy of Sciences of the USA* 94:7373–7377.
- Spitze, K. 1991. *Chaoborus* predation and life-history evolution in *Daphnia pulex*: temporal patterns of population diversity, fitness, and mean life history. *Evolution* 45:82–92.
- Stenhouse, S. L., N. G. Hairston, and A. E. Cobey. 1983. Predation and competition in *Ambystoma* larvae: field and laboratory experiments. *Journal of Herpetology* 17:210–220.
- Thorp, J. H., and A. P. Covich. 2001. *Ecology and classification of North American freshwater invertebrates*. Academic Press, Boston.
- Travis, J., J. Leips, and F. H. Rodd. 2013. Evolution in population parameters: density-dependent selection or density-dependent fitness? *American Naturalist* 181(suppl.):S9–S20.
- Urban, M. C. 2004. Disturbance heterogeneity determines freshwater metacommunity structure. *Ecology* 85:2971–2978.
- . 2007a. The growth-predation risk trade-off under a growing gape-limited predation threat. *Ecology* 88:2587–2597.
- . 2007b. Predator size and phenology shape prey survival in temporary ponds. *Oecologia (Berlin)* 154:571–580.
- . 2007c. Risky prey behavior evolves in risky habitats. *Proceedings of the National Academy of Sciences of the USA* 104:14377–14382.
- . 2008a. The evolution of prey body size reaction norms in diverse communities. *Journal of Animal Ecology* 77:346–355.
- . 2008b. Salamander evolution across a latitudinal cline in gape-limited predation risk. *Oikos* 117:1037–1049.
- . 2010. Microgeographic adaptations of spotted salamander morphological defenses in response to a predaceous salamander and beetle. *Oikos* 119:646–658.
- . 2013. Evolution mediates the effects of apex predation on aquatic food webs. *Proceedings of the Royal Society B: Biological Sciences* 280:1–9.
- Urban, M. C., L. A. Lewis, K. Fucikova, and A. Cordone. 2015. Population of origin and environment interact to determine oomycete infections in spotted salamander populations. *Oikos* 124:274–284.
- Urban, M. C., and J. L. Richardson. 2015. Data from: The evolution of foraging rate across local and geographic gradients in predation risk and competition. *American Naturalist*, Dryad Digital Repository. <http://dx.doi.org/10.5061/dryad.222h3>.
- Vermeij, G. J. 1978. *Biogeography and adaptation: patterns of marine life*. Harvard University Press, Cambridge, MA.
- Walls, S. C. 1998. Density dependence in a larval salamander: the effects of interference and food limitation. *Copeia* 1998:926–935.
- Ware, D. 1975. Growth, metabolism, and optimal swimming speed of a pelagic fish. *Journal of the Fisheries Board of Canada* 32:33–41.

Warton, D. I., and F. K. C. Hui. 2011. The arcsine is asinine: the analysis of proportions in ecology. *Ecology* 92:3–10.

Wellborn, G. A., D. K. Skelly, and E. E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics* 27:337–363.

Werner, E. E. 1986. Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. *American Naturalist* 128:319–341.

Werner, E. E., and B. R. Anholt. 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *American Naturalist* 142:242–272.

Williams, G. C. 1966. *Adaptation and natural selection*. Princeton University Press, Princeton, NJ.

Williamson, C. E., and J. W. Reid. 2001. Copepoda. Pages 915–953 in J. H. Thorp and A. P. Covich, eds. *Ecology and classification of North American freshwater invertebrates*. Academic Press, Boston.

Wilson, D. S. 1975. The adequacy of body size as a niche difference. *American Naturalist* 109:769–784.

Associate Editor: Edmund D. Brodie III
Editor: Judith L. Bronstein



Top left, a spotted salamander adult poses for a photograph in a temporary pond before it goes on to find a mate and breed. *Top right*, spotted salamander eggs develop in a shallow woodland pond in the spring sun. *Bottom right*, the last thing a salamander sees before being collected. Researcher Mark Urban uses a dip net to estimate the densities of spotted salamanders and their predators. Photo was taken from under the water surface. *Bottom left*, a marbled salamander larva patrols the leaf litter in a temporary pond. This top predator selects for spotted salamanders that have evolved to eat more. Photo credits: Mark Urban.