Oecologia (2004) 138: 532–538
DOI 10.1007/s00442-003-1466-2

POPULATION ECOLOGY

**William J. Resetarits Jr. · Josef F. Rieger ·
Christopher A. Binckley**

Threat of predation negates density effects in larval gray treefrogs

Received: 24 March 2003 / Accepted: 12 November 2003 / Published online: 13 January 2004

Abstract While density-dependence is central to most theory regarding population regulation and community structure, specific mechanisms that modify its effects in the absence of changes in consumer-resources ratios (e.g., thinning) are not well understood. To determine if the threat of predation alters effects of density, we investigated the interaction between density of larval treefrogs (*Hyla chrysoscelis*) and the non-lethal presence of a predatory fish (*Enneacanthus obesus*). A significant density by fish interaction was consistent for all response variables (e.g., larval survivorship, mass, and time to metamorphosis) driven by a complete lack of density effects in the presence of predators, while predator-free tanks showed classic density-dependent responses. Given that female *H. chrysoscelis* strongly avoid ovipositing in ponds containing fish, certain larval adaptations are apparently not constrained by maternal behavior and suggest redundancy in response to predators. Our data suggest that non-lethal effects of predators can determine larval performance irrespective of larval density, and that the non-lethal effects of predators can be strong whether lethal effects are strong or weak.

Keywords Competition · Density-dependence · Non-lethal effects · Predator induction · Predator-prey interactions

Introduction

Density-dependence is central to most theories of population regulation, species interactions, and community structure (e.g., Pearl and Reed 1920; Pearl 1925; Volterra 1926; Lotka 1932; Gause 1934, 1935; Nicholson and Bailey 1935; and subsequent derivations thereof, e.g., see Cappuccino and Price 1995; Chesson 1996; Turchin 1999) and is a readily observed phenomenon in both natural and experimental systems involving a broad range of organisms (e.g., Park 1948; de Wit 1960; Harper 1967; Brockelman 1969; Vandermeer 1969; Le Cren 1973; Wilbur 1987). Models of population regulation assume density-dependence at some stage in any population persisting over multiple generations, unless affected by density-independent factors preventing expression of density-dependence (e.g., Nicholson 1933; Nicholson and Bailey 1935; Haldane 1953; Royama 1977; Murdoch 1994; Chesson 1996). The longstanding debate is not whether density-dependence is characteristic of natural populations, but whether they are typically regulated by density-dependence (Andrewartha and Birch 1954; Nicholson 1957; Royama 1977; Turchin 1999). Whether a given population is regulated in a density-dependent or density-independent fashion depends on a variety of intrinsic and extrinsic factors, as well as their interactions. As such, ecologists have spent considerable effort documenting the role of density-dependence and examining factors that can override its effects. Disturbance and predation have been repeatedly demonstrated to ameliorate the effects of density-dependent competition in both natural and experimental systems by modifying density itself (e.g., Paine 1966; Lubchenco 1978; Morin 1983; Wilbur 1987). Less well understood are factors that modify density-dependence in the absence of mortality. This is analogous to the distinction between interaction chain indirect effects (density-mediated indirect effects), where interactions are affected by changes in number, and interaction modification indirect effects (trait-mediated indirect effects), where the nature of species interactions changes with changes in behavior (Wootton 1993; Abrams 1995).

One of the most consistent patterns in community ecology has been the observation of density-dependent competition in larval amphibians (e.g., Brockelman 1969; DeBenedictis 1974; Wilbur 1977a, 1977b; Woodward 1982; Smith 1983, 1987; Petranka 1989; Berven 1990; Scott 1990; Altwegg 2003), which have been an important

---

W. J. Resetarits Jr. (✉) · J. F. Rieger · C. A. Binckley
Department of Biological Sciences, Old Dominion University,
Norfolk, VA 23529, USA
e-mail: wresetar@odu.edu
Tel.: +1-757-6833763
Fax: +1-757-6835283

model system for the study of density-dependence. Whether in mesocosms, enclosures, or whole-pond experiments, the responses of larval amphibians to increasing density in the absence of predation or disturbance are both predictable and dramatic. Resulting largely from exploitative competition for limited resources (Dickman 1968; Steinwascher 1978; Seale 1980), size and time to metamorphosis, along with survival, respond consistently to changes in density (Wilbur 1987). However, both increases in limiting resources and thinning (lethal direct effect) via predation (or disturbance) can reduce negative effects of density by reducing consumer-resource ratios (e.g., Wilbur 1972; Morin 1983; Smith 1983; Relyea 2002a). Perceived predation risk itself (non-lethal direct effect) can alter prey activity (e.g., Lawler 1989; Skelly and Werner 1990; Anholt et al. 2000), growth rate (e.g., Van Buskirk and Yurewicz 1998; Relyea and Werner 1999), development rate and time to metamorphosis (Wilbur 1987), and morphology (e.g., McCollum and Van Buskirk 1996; Van Buskirk et al. 1997; Relyea 2001, 2002a), and may affect the outcome of interspecific competition by differentially altering the activity levels of competing species (e.g., Werner 1991; Werner and Anholt 1996; Relyea 2000). Thus, the induced non-lethal effects of predators might be expected to interact with intraspecific competition to affect larval survival and performance.

We have previously demonstrated that female *Hyla chrysoscelis* selectively oviposit in fish-free habitats (Resetarits and Wilbur 1989; Rieger 2002; Binckley and Resetarits 2003; W.J. Resetarits, unpublished work). Because females strongly prefer fishless habitats, fish may not generate strong responses in larval *H. chrysoscelis* since selection has limited opportunity to mold larval responses to fish. We conducted an experiment in which different densities of larval *H. chrysoscelis* were introduced into habitats with and without caged predators, and examined the effects of perceived predation risk on standard larval life-history parameters (Morin 1983; Wilbur 1987). Both within and among species, activity level and larval growth rates are positively correlated (Morin 1983; Woodward 1983; Lawler 1989; Relyea and Werner 1999), and thus we could focus on measures of larval performance that reflect changes in activity. Our goal was to examine the response of larval *H. chrysoscelis* to the non-lethal presence of a predatory fish, *Enneacanthus obesus*, and to examine how the non-lethal effects of fish interact with intraspecific density-dependence, specifically asking "What is the relative importance of competitor density versus predator induction in determination of per capita rates?"

Materials and methods

H. chrysoscelis is the southern, diploid member of the *H. versicolor* complex and breeds in a variety of ponds and ephemeral pools after heavy rains during late spring and summer. Larval development is rapid and metamorphosis can occur in as little as 4–5 weeks under favorable conditions. Larval *H. chrysoscelis* have not been reported to overwinter and so must reach metamorphic size before either the pond dries or temperatures fall to the point where metamorphosis is precluded. It is a common species in the Coastal Plain of Virginia and one of the most abundant anurans at Naval Security Group Activity Northwest (NSGANW), our field site on the eastern edge of the Great Dismal Swamp in southeastern Virginia.

We evaluated the influence of density and the non-lethal presence of fish predators on size at, time to, and survival to metamorphosis in the gray tree frog (*H. chrysoscelis*). We established 16 experimental cattle watering tanks (0.61 m deep×1.65 m diameter) in an open field at NSGANW (Morin 1983). Tanks were ≈1 m from one another and formed four spatial blocks each containing four tanks. On 18 July 2000, all tanks were filled to a depth of 50 cm (≈1,000 l total volume) with water pumped from a nearby borrow pit. A screen filter (mesh diameter: 2 mm) was placed over the pump intake to prevent transport of larval anurans or insects into the tanks. Zooplankton and phytoplankton were capable of passing through the filter and served as prey for the caged fish predators and food for the larval anurans. We added 2 kg forest-raked pine straw to each pool to add nutrients and additional structural complexity. Tanks were covered with fiberglass mesh lids (mesh size 2 mm) to prevent colonization by aquatic insects (Morin 1983), and allowed to age for 1 week. Fish cages constructed from 115-l plastic trashcans with two 25×50 cm side sections replaced with fiberglass screening were placed in each of the 16 tanks (Resetarits 2001).

Experimental design

We manipulated the presence of predators (0 or 7 fish) and tadpoles (density of 100 or 200 hatchings) using a full factorial, randomized complete block design. All treatments were randomly assigned to tanks in each block.

We collected small *E. obesus* from ponds at NSGA, and on 20 July sets of seven fish (10–20 g total mass) were randomly selected and assigned to appropriate tanks within each block. This density fell within the natural range encountered at our field site (personal observation) and mirrored the density used in a previous study of oviposition-site choice in a related species, *H. squirella* (Binckley and Resetarits 2002). Densities of *H. chrysoscelis* were low but within the range of natural densities (personal observation). Use of enclosures eliminated all physical interactions between predators and tadpoles but allowed for non-lethal communication (chemosensory, auditory, and/or mechanical); this level of stimulus had been previously shown to elicit a response in both adult *H. squirella* and *H. chrysoscelis* (Binckley and Resetarits 2002, 2003). Fish were held in open tanks with zooplankton and larval insects as food sources, prior to random assignment to experimental units. Zooplankton, phytoplankton, and periphyton were abundant both inside and outside the enclosures within the experimental tanks. Adult female *H. chrysoscelis* respond to the presence of fish without the need for consumption of conspecifics (Resetarits and Wilbur 1989; Rieger 2002; unpublished data); therefore, we did not feed larval *H. chrysoscelis* to caged fish before or during the experiment, which is required for inducing morphological responses to other caged predators (McCollum and Van Buskirk 1996). Since the adult response to fish appears to be general (Binckley and Resetarits 2003) and induced at very low densities (Rieger 2002), tadpoles may encounter fish that are not a serious predation threat or occur at very low densities, but which may nonetheless induce larval responses. Thus, directly induced responses are more general than responses requiring consumption of conspecifics. Three fish from different pools died during the experiment; these fish were removed but not replaced because use of multiple individuals per pool provided sufficient strength and redundancy in stimulus levels.

On 24 July, we randomly allocated *H. chrysoscelis* hatchlings to all tanks within a block. Tadpoles were taken from 10 separate clutches of eggs obtained from captured amplectant pairs on the same night, and were randomized in subsets of 10 from each clutch into 24 sets of 100 tadpoles each. This ensured that genetic diversity did not differ between tanks and any minor variation among clutches were equalized among tanks. Sets were then randomly assigned to the appropriate tanks. Tanks were searched every other day for metamorphs, which were returned to the laboratory and weighed to the nearest 0.001 g upon tail resorption. This protocol was carried out until 30 October, when the experiment was terminated after 2 weeks of no additional metamorphs. *H. chrysoscelis* cannot successfully overwinter, so those tadpoles that did not metamorphose by 30 October failed to survive and were not quantified. We left the tanks in place with the remaining tadpoles to confirm the inability of *H. chrysoscelis* to overwinter; no additional metamorphs emerged, and no tadpole survived the mild winter at our field site.

Data analysis

The experiment crossed two densities of larval *H. chrysoscelis* with the presence/absence of *E. obesus*. We analyzed the effects of block, density, presence/absence of fish, and the interaction between density and fish presence on the response variables of survival, mass at metamorphosis, and time to metamorphosis. Blocking did not increase the efficiency of the design, so the block term was rolled into the error term for all analyses. We used univariate analysis of variance (ANOVA) on arcsine square-root transformed values of survival (proportion surviving to metamorphosis), and multivariate analysis of variance (MANOVA), along with separate univariate ANOVAs, on log transformed values of mass at metamorphosis and time to metamorphosis. Since insufficient data exist in most studies to effectively test assumptions regarding normality and heteroscedascity of residuals, we rely on common transformations to improve the behavior of the data, the Central Limit Theorem, and the robustness of ANOVA to any remaining deviations from the assumptions (Steele and Torrie 1980; Morin 1983; Johnson 1995). Survival could not be included in a MANOVA because zero values produce undefined values of mass and time to metamorphosis. Only cells with four or more metamorphs were included in the MANOVA, eliminating three tanks with values of 0 (Low-Fish),1, and 2 (both Hi-Nofish) metamorphs, respectively. Survival values were relatively low because they exclude individuals that did not reach metamorphosis before further growth and development were truncated by the onset of cooler weather, which is precisely what occurs in natural ponds with drying and/or cold. Data were analyzed using PROC GLM within SAS for Windows version 8.0 (SAS Institute 1998) using type III sums of squares and α=0.05. PROC GLM is specifically designed to deal with unbalanced data in both ANOVA and MANOVA.

Results

For survival to metamorphosis, the significant density-by-fish interaction dominated (Table 1, Fig. 1a) due to a lack of density effect with fish and a strong density effect without fish. Density was significant in the ANOVA of survival, while the main effect of fish was not; however, main effects may be meaningless in the presence of strong interactions (Nelder 1977; Sahai and Ageel 2000). In our case interpretation is rather simple; more metamorphs are produced at low density only in the absence of fish.

The MANOVA revealed a marginal effect of density, no effect of fish, but once again a highly significant density by fish interaction (Table 2, Fig. 1b,c). No effects were close to significant in the individual univariate ANOVAs (Table 2). The density by fish interaction again derives from lack of a density response for mass at metamorphosis with fish and a counterintuitive decrease in time to metamorphosis at high density with fish (Fig. 1b,c). Responses in the absence of fish are precisely as expected; high density results in smaller mass at metamorphosis and a longer time to metamorphosis (Fig. 1b,c).

The significant density by fish interaction forms a highly consistent pattern in the data (Tables 1, 2; Fig. 1). At high density, treatments with fish produced more metamorphs that were larger and emerged sooner, while at low density, fishless tanks produced more and larger metamorphs that emerged sooner. The presence of fish completely obviates the typical density-dependent pattern seen in fishless tanks and in most previous studies of larval anurans.

Table 1 Analysis of variance for survival. Data were arcsine square-root transformed

Source	*df*	SS	MS	*F*	Pr>*F*
Density	1	0.363	0.363	8.84	0.0116
Fish	1	0.086	0.086	2.09	0.1740
Density*Fish	1	0.233	0.233	5.68	0.0346
Error	12	0.493	0.041		

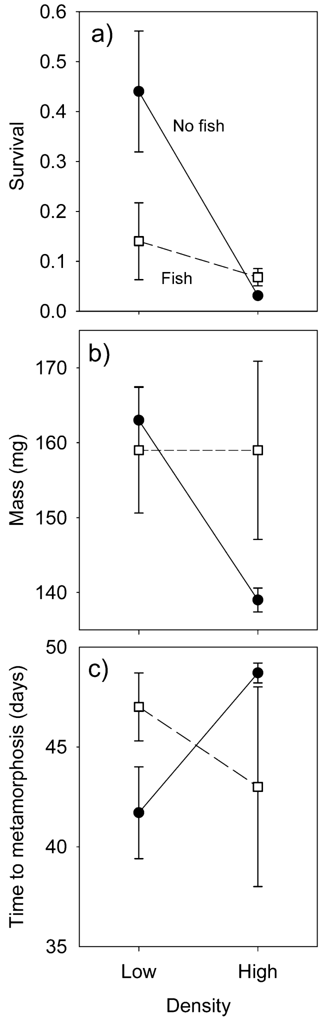

Fig. 1a–c Interaction diagrams illustrating the effects of Low versus High density and Fish versus No Fish treatments for **a** survival, **b** mass at metamorphosis, and **c** time to metamorphosis

Table 2 Multivariate analysis of variance of size at metamorphosis and time to metamorphosis, and component univariate ANOVAs. Both response variables were log transformed

Source	Wilks' λ	*F*	Num *df*/Den *df*	Pr>*F*
Density	0.5058	3.91	2, 8	0.0654
Fish	0.7546	1.30	2, 8	0.3242
Density*Fish	0.2701	10.81	2, 8	0.0053

Source	*df*	SS	MS	*F*	Pr>*F*
Density	1	0.0033	0.0033	1.82	0.2103
Fish	1	0.0014	0.0014	0.76	0.4061
Density*Fish	1	0.0031	0.0031	1.72	0.2222
Error	9	0.016	0.0018		

Source	*df*	SS	MS	*F*	Pr>*F*
Density	1	0.00049	0.00049	0.11	0.7428
Fish	1	0.00003	0.00003	0.01	0.9310
Density*Fish	1	0.00984	0.00984	2.37	0.1581
Error	9	0.03736	0.00415		

Discussion

Density-dependent competition is critical to any discussion of population regulation (Murdoch 1994; Chesson 1996; Turchin 1999) and particularly germane to any discussion of anuran larval ecology (reviews: Wilbur 1997; Alford 1999), as density affects survival, growth, development rate, and timing and size at metamorphosis (e.g., Wilbur and Collins 1973; Werner 1986; Smith 1987; Berven 1990; Altwegg 2003). Density interacts with predation and disturbance to produce complex landscapes of variation in performance and reproductive success (Morin 1983; Smith 1983, 1987; Werner 1986; Wilbur 1987; Resetarits and Fauth 1998). While density-mediated (lethal) effects have received considerable attention, mechanisms affecting density-dependent competition in the absence of changes in consumer-resource ratios (trait-mediated effects) are only beginning to be explored. Predation and disturbance are known to alter aspects of anuran larval life-history independent of changes in density (e.g., by accelerating development in the presence of predators or threat of desiccation; Wilbur 1987); however, dominant impacts are viewed as deriving from reduced density and competitive release (Morin 1983; Wilbur 1987; Fauth and Resetarits 1991). Growing evidence suggests non-lethal effects of predators can have important effects on larval behavior, performance, and morphology (e.g., Werner 1991; McCollum and Van Buskirk 1996; Van Buskirk and Yurewicz 1998; Anholt et al. 2000; Peacor and Werner 2001; Peacor 2002; Relyea 2002a; Bolker et al. 2003; Werner and Peacor 2003), and thus may impact density-dependence sans mortality. Under what conditions might density-dependence be obviated in favor of other processes that ultimately determine larval performance?

Predatory fish play an especially important role in the distributional dynamics of aquatic organisms (e.g., Werner and McPeek 1994; Hecnar and M'Closkey 1996; Wellborn et al. 1996; Babbitt and Tanner 2000; Snodgrass et al. 2000; Eason and Fauth 2001); for many temporary pond amphibians (including *H. chrysoscelis*), fish often indicate complete (or nearly complete) reproductive failure. Fish also generate strong behavioral responses in both adult (Resetarits and Wilbur 1989; Rieger 2002; Binckley and Resetarits 2003) and larval (Petranka et al. 1987; Kats et al. 1988) *H. chrysoscelis*. While ovipositing *H. chrysoscelis* strongly avoid predatory fish, avoidance is seldom complete (e.g., Resetarits and Wilbur 1989; Rieger 2002; Binckley and Resetarits 2003), so a percentage of larvae ultimately find themselves faced with these predators. Do larval *H. chrysoscelis* possess induced behaviors that facilitate survival when maternal habitat selection fails? Or do they rely on maternal choice to place them in the appropriate habitat (Woodward 1983; Resetarits and Wilbur 1989; Resetarits 1996)? Habitat selection can limit opportunities for adaptive evolution by limiting exposure to specific aspects of the selective landscape (Holt 1985; Rosenzweig 1987), or providing plasticity that obviates selection for specific characters (Brandon 1988; Huey et al. 2003). We might expect larvae to lack specialized morphological/physiological adaptations to fish (typically unpalatability) since maternal behavior limits exposure and, in fact, we do not see such specializations in *H. chrysoscelis* (or its cryptic sister species *H. versicolor*). However, they do respond to predators such as larval dragonflies and salamanders with induced morphological changes and/or reduced activity that presumably reduces susceptibility to predation (e.g., Skelly 1992; McCollum and Van Buskirk 1996; Van Buskirk and McCollum 2000a, 2000b).

Larval *H. chrysoscelis* do respond to fish, and three important measures of performance (survival, mass, and time to metamorphosis) were strongly affected by threat of predation. The effectiveness for reducing actual predation rates remains debatable however, but it is interesting both that this response exists and that it involves fish cues themselves, rather than more general cues related to conspecific mortality ("the scent of death" sensu McCollum and Van Buskirk 1996; Kats and Dill 1998). *H. chrysoscelis* thus possesses a degree of redundancy in its specific response to fish, with one layer involving maternal oviposition behavior, and the second involving larval behavior.

The most striking aspect of the observed responses is the complete insensitivity to density exhibited by larval *H. chrysoscelis* in the presence of fish, attesting to the strong impact of perceived predation risk. In a short-term experiment, Van Buskirk and Yurewicz (1998) found that both competition and predation risk (caged dragonflies) determined growth rates for *Rana sylvatica*; predation risk predominated early in larval development, and competition dominated later. In our case, since performance in both high- and low-density tanks with fish did not differ and was reduced relative to low-density fishless pools, performance was determined solely by responses to fish when viewed over the entire larval period. Rather than the expected additive response, density effects were instead completely obviated with fish. Predators impact larval anurans via both mortality and non-lethal effects (Peacor and Werner 2001). For survivors, these effects are typically in opposite directions. Mortality relaxes pressures on resources and generates competitive release, while threat of predation reduces foraging rate, can cause habitat shifts, and may generate morphological changes, all of which have significant costs. In Fauth's (1990) study of predation by newts and crayfish on larval *H. chrysoscelis*, negative effects of the cost of predator avoidance were offset by positive effects of thinning. Skelly (1992) suggested predators should have a net negative effect on survivors where competitive release cannot compensate for costs of predator avoidance, as when predators are relatively ineffective or performance (e.g., growth) is not density-dependent. Our data suggest that even if *E. obesus* were allowed to reduce larval densities of *H. chrysoscelis*, as simulated by our LOW density treatment, the strong negative effects generated by predator avoidance would still obviate any competitive release.

Because we manipulated density directly, it serves as a metric of cost of predator avoidance, in this case roughly equivalent to a doubling of density (from 100 to 200), or conversely, no competitive release at a simulated 50% predation rate. This contrasts starkly with expectations. At high densities, the potential does exist for competitive release, not via reduction in numbers, but via reduced activity. While we did not quantify activity levels or resources, fish tanks were easily recognized by lack of larval activity and abundance of accumulated periphyton. Reduced activity results in reduced grazing pressure on phytoplankton and periphyton resources, increasing the quantity (and perhaps quality) of resources available. By reducing per-capita foraging rates, surviving individuals at high densities achieve higher per-capita growth rates and metamorphose sooner with than without fish. This fits certain theoretical predictions (e.g., Abrams 1987, 1992) and parallels results obtained by Peacor (2002) for bullfrogs faced with predation threat from dragonflies, though our observed positive effect is small relative to negative impacts derived from lack of competitive release at low densities.

Non-lethal effects of a predator in our study obviate competitive release and solely determine performance irrespective of larval densities. This supports the idea that non-lethal effects of predators can be strong whether lethal effects are strong or weak (Peacor and Werner 2001). The subversion of density effects is an unexpected result, especially in an organism so carefully tuned to variation in density. Understanding the multiple roles of predators in natural systems and identifying their effects on a variety of prey is a critical task in understanding the dynamics of natural communities (Chalcraft and Resetarits 2003a, 2003b). Increasingly, the non-lethal impacts of predators on the distribution and abundance of prey species rather than simply on behavior, performance, and morphology have moved to the fore in our attempts to understand assembly of natural communities (e.g., Resetarits and Wilbur 1989; Blaustein 1999; Peacor and Werner 2001; Resetarits 2001; Binckley and Resetarits 2002, 2003; Murphy 2003). The strength of non-lethal effects we observed and their interaction with density further support the idea that predators impact individuals and species well beyond those fated for conversion to predator biomass (Resetarits and Wilbur 1989; Lima and Dill 1990; Lima 1998; Blaustein 1999; Peacor and Werner 2001; Relyea 2002b; Werner and Peacor 2003). In a specific sense, the strength of non-lethal effects observed here may both reflect and help explain the dramatic effects of fish (as contrasted with other groups of predators) on amphibian distribution and abundance.

Acknowledgments We would like to thank D. Chalcraft, J. Loman, D. Skelly, and C. Resetarits for providing valuable comments on the manuscript. This project benefitted from logistical support from R. Turner and the Commanding Officers, Naval Security Group Activity Northwest. Funding was provided by NSF (DEB-0096051) and EPA-STAR (R825795-01-0) grants to W.J.R.

References

Abrams PA (1987) Indirect interactions between species that share a predator: variations on a theme. In: Kerfoot WC, Sih A (eds) Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, pp 38–54

Abrams PA (1992) Why don't predators have positive effects on prey populations? Evol Ecol 6:449–457

Abrams PA (1995) Implications of dynamically variable traits for identifying, classifying, and measuring direct and indirect effects in ecological communities. Am Nat 146:112–134

Alford RA (1999) Ecology: resource use, competition, and predation. In: McDiarmid RW, Altig R (eds) Tadpoles. University of Chicago Press, Chicago, Ill, pp 240–278

Altwegg R (2003) Multistage density dependence in an amphibian. Oecologia 136:46–50

Andrewartha HG, Birch LC (1954) The distribution and abundance of animals. University of Chicago Press, Chicago, Ill

Anholt BR, WernerEE, Skelly DK (2000) Effects of food and predators on the activity of four larval ranid frogs. Ecology 81:3509–3521

Babbitt KJ, Tanner GW (2000) Use of temporary wetlands by anurans in a hydrologically modified landscape. Wetlands 20:313–322

Berven KA (1990) Factors affecting population fluctuations in the larval and adult stages of the wood frog (*Rana sylvatica*). Ecology 71:1599–1608

Binckley CA, Resetarits WJ Jr (2002) Reproductive decisions under threat of predation: squirrel treefrog (*Hyla squirella*) responses to banded sunfish (*Enneacanthus obesus*). Oecologia 130:157–161

Binckley CA, Resetarits WJ Jr (2003) Functional equivalence of non-lethal effects: generalized fish avoidance determines distribution of gray treefrog (*Hyla chrysoscelis*) larvae. Oikos 102:623–629

Blaustein L (1999) Oviposition site selection in response to risk of predation: evidence from aquatic habitats and consequences for population dynamics and community structure. In: Wasser SP (ed) Evolutionary theory and processes: modern perspectives. Kluwer, Netherlands, pp 441–456

Bolker B, Holyoak M, Klivan V, Rowe L, Schmitz O (2003) Connecting theoretical and empirical studies of trait-mediated interactions. Ecology 84:1101–1114

Brandon RN (1988) The levels of selection: a hierarchy of interactors. In: Plotkin HC (ed) The role of behavior in evolution. MIT, Cambridge, Mass, pp 51–71

Brockelman WY (1969) An analysis of density effects and predation in *Bufo americanus* tadpoles. Ecology 50:632–644

Cappuccino N, Price PW (1995) Population dynamics: new approaches and synthesis. Academic, New York

Chalcraft DR, Resetarits WJ Jr (2003a) Predator identity and ecological impacts: functional redundancy or functional diversity? Ecology 84:2407–2418

Chalcraft DR, Resetarits WJ Jr (2003b) Mapping functional similarity on the basis of trait similarities. Am Nat 162:390–402

Chesson P (1996) Matters of scale in the dynamics of populations and communities. In: Floyd RB, Sheppard AW, De Barro PJ (eds) Frontiers of population ecology. CSIRO, Melbourne, pp 353–368

DeBenedictis PA (1974) Interspecific competition between tadpoles of *Rana pipiens* and *Rana sylvatica*: an experimental field study. Ecol Monogr 44:129–151

Dickman M (1968) The effect of grazing by tadpoles on the structure of a periphyton community. Ecology 49:1188–1190

Eason GW, Fauth JE (2001) Ecological correlates of anuran species richness in temporary pools: a field study in South Carolina, USA. Isr J Zool 47:347–365

Fauth JE (1990) Interactive effects of predators and early larval dynamics of the treefrog *Hyla chrysoscelis*. Ecology 71:1609–1616

Fauth JE, Resetarits WJ Jr (1991) Interactions between the salamander *Siren intermedia* and the keystone predator *Notophthalmus viridescens*. Ecology 72:827–838

Gause GF (1934) The struggle for existence. Williams and Wilkins, Baltimore, Md

Gause GF (1935) Experimental demonstration of Volterra's periodic oscillation in the numbers of animals. J Exp Biol 12:44–48

Haldane JBS (1953) Animal populations and their regulation. New Biol 15:9–24

Harper JL (1967) A Darwinian approach to plant ecology. J Ecol 55:247–270

Hecnar SJ, M'Closkey RT (1996) The effects of predatory fish on amphibian species richness and distribution. Biol Conserv 79:123–131

Holt RD (1985) Population dynamics in two-patch environments: some anomalous consequences of optimal habitat distribution. Theor Popul Biol 28:181–208

Huey RB, Hertz PE, Sinervo B (2003) Behavioral drive versus behavioral inertia in evolution: a null model approach. Am Nat 161:357–366

Johnson DH (1995) Statistical sirens: the allure of nonparametrics. Ecology 76:1998–2000

Kats LB, Dill LM (1998) The scent of death: chemosensory assessment of predation risk by prey animals. Ecoscience 5:361–394

Kats LB, Petranka JW, Sih A (1988) Antipredator defenses and the persistence of amphibian larvae with fishes. Ecology 69:1820–1865

Lawler SP (1989) Behavioral responses to predators and predation risk in four species of larval anurans. Anim Behav 38:1039–1047

Le Cren ED (1973) The population dynamics of young trout (*Salmon trutta*) in relation to density and territorial behavior. Rapp PV Reun Int Explor Mer 164:241–246

Lima SL (1998) Nonlethal effects in the ecology of predator-prey interactions. Bioscience 48:25–34

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619–640

Lotka AJ (1932) The growth of mixed populations: two species competing for a common food supply. J Wash Acad Sci 22:461–469

Lubchenco J (1978) Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. Am Nat 112:23–39

McCollum SA, Van Buskirk J (1996) Costs and benefits of a predator-induced polyphenism in the gray treefrog *Hyla chrysoscelis*. Evolution 50:583–593

Morin PJ (1983) Predation, competition and the composition of larval anuran guilds. Ecol Monogr 53:119–138

Murdoch WW (1994) Population regulation in theory and practice. Ecology 75:271–287

Murphy PJ (2003) Does reproductive site choice in a neotropical frog mirror variable risks facing offspring? Ecol Monogr 73:45–67

Nelder JA (1977) A reformulation of linear models. J R Statist Soc A. 140:48–77

Nicholson AJ (1933) The balance of animal populations. J Anim Ecol 2:131–178

Nicholson AJ (1957) The self adjustment of populations to change. Cold Spring Harbor Symp Quant Biol 22:153–172

Nicholson AJ, Bailey VA (1935) The balance of animal populations. Proc Zool Soc Lond Part 3 551–598

Paine RT (1966) Food web complexity and species diversity. Am Nat 100:65–75

Park T (1948) Experimental studies of interspecies competition. I. Competition between populations of the four beetles, *Tribolium confusum* Duvall and *Tribolium castaneum* Herbst. Ecol Monogr 18:267–307

Peacor SD (2002) Positive effect of predators on prey growth rate through induced modifications of prey behavior. Ecol Lett 5:77–85

Peacor SD, Werner EE (2001) The contribution of trait-mediated indirect effects to the net effects of a predator. Proc Natl Acad Sci 98:3904–3908

Pearl R (1925) The growth of populations. Q Rev Biol 2:532–548

Pearl R, Reed LJ (1920) On the rate of growth of the population of the United States since 1790 and its mathematical representation. Proc Natl Acad Sci USA 6:275–288

Petranka JW (1989) Density-dependent growth and survival of larval *Ambystoma*: evidence from whole-pond manipulations. Ecology 70:1752–1767

Petranka JW, Kats LB, Sih A (1987) Predator-prey interactions among fish and larval amphibians: use of chemical cues to detect predatory fish. Anim Behav 35:426–434

Relyea RA (2000) Trait-mediated indirect effects in larval anurans: reversing competitive outcomes with the threat of predation. Ecology 81:2278–2289

Relyea RA (2001) The relationship between predation risk and antipredator responses in larval anurans. Ecology 82:541–554

Relyea RA (2002a) The many faces of predation: How induction, selection, and thinning combine to alter prey phenotypes. Ecology 83:1953–1964

Relyea RA (2002b) Competitor-induced plasticity in tadpoles: consequences, cues, and connections to predator-induced plasticity. Ecol Monogr 72:523–540

Relyea RA, Werner EE (1999) Quantifying the relation between predator-induced behavior and growth performance in larval anurans. Ecology 80:2117–2124

Resetarits WJ Jr (1996) Oviposition site choice and life history evolution. Am Zool 36:205–215

Resetarits WJ Jr (2001) Experimental evidence that past predation affects community assembly: fish avoidance in a colonizing/ovipositing aquatic beetle. Oecologia 129:155–160

Resetarits WJ Jr, Fauth JE (1998) From cattle tanks to Carolina bays: the utility of model systems for understanding natural communities. In: Resetarits WJ Jr, Bernardo J (eds) Experimental ecology: issues and perspectives. Oxford University Press, New York, pp 133–151

Resetarits WJ Jr, Wilbur HM (1989) Choice of oviposition site by *Hyla chrysoscelis*: role of predators and competitors. Ecology 70:220–228

Rieger JF (2002) The effect of a predator gradient on female oviposition site selection and larval performance. Thesis, Old Dominion University, Norfolk

Rosenzweig ML (1987) Habitat selection as a source of biological diversity. Evol Ecol 1:15–30

Royama T (1977) Population persistence and density dependence. Ecol Monogr 47:1–35

Sahai H, Ageel M I (2000) The analysis of variance: fixed, random and mixed models. Birkhauser, Boston

SAS Institute (1998) SAS/STAT User's Guide, Release 8.0. SAS Institute, Cary, N.C.

Scott DE (1990) Effects of larval density in *Ambystoma opacum*: an experiment in large-scale field enclosures. Ecology 71:296–306

Seale DB (1980) Influence of amphibian larvae on primary production, nutrient flux, and competition in a pond ecosystem. Ecology 61:1531–1550

Skelly DK (1992) Field evidence for a cost of behavioral antipredator responses in a larval amphibian. Ecology 73:704–708

Skelly DK, Werner EE (1990) Behavioral and life-history responses of larval American toads to an odonate predator. Ecology 71:2313–2322

Smith DC (1983) Factors controlling tadpole populations of the chorus frog (*Pseudacris triseriata*) on Isle Royale, Michigan. Ecology 68:344–350

Smith DC (1987) Adult recruitment in chorus frogs: effects of size and date at metamorphosis. Ecology 68:344–350

Snodgrass JW, Bryan AL Jr, Burger J (2000) Development of expectations of larval amphibian assemblage structure in southeastern depression wetlands. Ecol Applic 10:1219–1229

Steele RGD, Torrie JH (1980) Principles and procedures of statistics: a biometrical approach. McGraw-Hill, New York

Steinwascher K (1978) Interference and exploitation competition among tadpoles of *Rana utricularia.* Ecology 59:1039–1046

Turchin P (1999) Population regulation: a synthetic view. Oikos 84:153–159

Van Buskirk J, McCollum SA (2000a) Influence of tail shape on tadpole swimming performance. J Exp Biol 203:2149–2158

Van Buskirk J, McCollum SA (2000b) Functional mechanisms of an inducible defence in tadpoles: morphology and behaviour influence mortality risk from predation. J Evol Biol 13:336–347

Van Buskirk J, Yurewicz KL (1998) Effects of predators on prey growth rate: relative contributions of thinning and reduced activity. Oikos 82:20–28

Van Buskirk J, McCollum SA, Werner EE (1997) Natural selection for environmentally induced phenotypes in tadpoles. Evolution 51:1983–1992

Vandermeer JH (1969) The competitive structure of communities: an experimental approach with protozoa. Ecology 50:362–371

Volterra V (1926) Fluctuations in the abundance of a species considered mathematically. Nature 118:558–560

Wellborn GA, Skelly DK, Werner EE (1996) Mechanisms creating structure across a freshwater habitat gradient. Annu Rev Ecol Syst 27:337–363

Werner EE (1986) Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. Am Nat 128:319–341

Werner EE (1991) Nonlethal effects of a predator on competitive interactions between two anuran larvae. Ecology 72:1709–1720

Werner EE, Anholt BR (1996) Predator-induced behavioral indirect effects: consequences to competitive interactions in anuran larvae. Ecology 77:157–169

Werner EE, McPeek MA (1994) Direct and indirect effects of predators on two anuran species along an environmental gradient. Ecology 75:197–213

Werner EE, Peacor SD (2003) A review of trait-mediated indirect interactions in ecological communities. Ecology 84:1083–1100

Wilbur HM (1972) Competition, predation, and the structure of the *Ambystoma-Rana sylvatica* community. Ecology 53:3–21

Wilbur HM (1977a) Density-dependent aspects of growth and metamorphosis in *Bufo americanus*. Ecology 58:196–200

Wilbur HM (1977b) Interactions of food level and population density in *Rana sylvatica*. Ecology 58:206–209

Wilbur HM (1987) Regulation of structure in complex systems: experimental temporary pond communities. Ecology 68:1437–1452

Wilbur HM (1997) Experimental ecology of food webs: complex systems in temporary ponds. Ecology 78:2279–2302

Wilbur HM, Collins JP (1973) Ecological aspects of amphibian metamorphosis. Science 182:1305–1314

Wit CT de (1960) On competition. Versl Landbouwkd Onderz Ned 66:1–82

Woodward BD (1982) Tadpole interactions in a desert anuran community. Oecologia 54:96–100

Woodward BD (1983) Predatory-prey interactions and breeding-pond species in a desert anuran community. Ecology 64:1549–1555

Wootton JT (1993) Indirect effects and habitat use in an intertidal community: interaction chains and interaction modifications. Am Nat 141:71–89