

The direct and indirect effects of temperature on a predator–prey relationship

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Abstract: Abiotic factors may directly influence community structure by influencing biotic interactions. In aquatic systems, where gape-limited predators are common, abiotic factors that influence organisms' growth rates potentially mediate predator–prey interactions indirectly through effects on prey size. We tested the hypothesis that temperature influences interactions between aquatic size-limited insect predators (*Notonecta kirbyi*) and their larval anuran prey (*Hyla regilla*) beyond its indirect effect on prey size. *Notonecta kirbyi* and *H. regilla* were raised and tested in predator–prey trials at one of three experimentally maintained temperatures, 9.9, 20.7, or 25.7°C. Temperature strongly influenced anuran growth and predator success; mean tadpole mass over time was positively related to temperature, while the number of prey caught was negatively related. At higher temperatures tadpoles attained greater mass more quickly, allowing them to avoid capture by notonectids. However, the probability of capture is a function of both mass and temperature; temperature was a significant explanatory variable in a logistic regression equation predicting prey capture. For a given prey mass, tadpoles raised in warmer water experienced a higher probability of capture by notonectids. Thus, rather than being static, prey size refugia are influenced directly by abiotic factors, in this case temperature. This suggests that temperature exerts differential effects on notonectid and larval anurans, leading to differences in the probability of prey capture for a given prey mass. Therefore, temperature can influence predator–prey interactions via indirect effects on prey size and direct effects on prey.

Résumé : Des facteurs abiotiques peuvent influencer directement la structure d'une communauté en agissant sur les interactions biotiques. Dans les systèmes aquatiques, où l'ouverture de la gueule est souvent limitée chez les prédateurs, les facteurs qui influencent les taux de croissance peuvent potentiellement modifier les interactions prédateur–proie indirectement, en affectant la taille des proies. Nous avons éprouvé l'hypothèse selon laquelle la température influence les interactions entre des insectes aquatiques prédateurs de taille limitée (*Notonecta kirbyi*) et leurs proies, les larves de la rainette (*Hyla regilla*) en plus d'influencer indirectement la taille des proies. Des prédateurs *N. kirbyi* et des proies *H. regilla* ont été élevés et testés au cours d'expériences prédateurs–proies à l'une de trois températures expérimentales, 9,9, 20,7 et 25,7°C. La température influence fortement la croissance des anoues et le succès des prédateurs; la masse moyenne des têtards est en corrélation positive avec la température, alors que le nombre de proies capturées est en corrélation négative avec la température. Aux températures plus élevées, les têtards atteignent une plus grande masse plus rapidement, ce qui leur évite d'être capturés par les notonectes. Cependant, la probabilité de capture des têtards est fonction de la température aussi bien que de leur masse; la température est une variable explicative significative dans l'équation de régression logistique qui prédit la capture des proies. Pour une masse donnée de proie, les têtards élevés à température plus élevée ont une probabilité plus forte d'être capturés par des notonectes. Donc, loin d'être statiques, les refuges des proies en fonction de leur taille, sont influencés directement par des facteurs abiotiques, dans ce cas-ci la température. Ces résultats indiquent que la température agit différemment sur les notonectes et sur les larves d'anoues, ce qui résulte en des différences dans les probabilités de capture des proies pour une masse donnée. La température peut donc influencer les interactions prédateurs–proies, d'une part par ses effets indirects sur la taille des proies et, d'autre part, par action directe sur les proies.

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Introduction

Abiotic effects have been called the least appreciated mechanism in community ecology (Dunson and Travis 1991). In an attempt to integrate the roles of biotic and

abiotic factors in structuring communities, some ecologists have emphasized the compound effects that both factors can have on species interactions (Resh and Barney 1987; Streams 1987; Warner et al. 1991). For example, studies of temporary-pond communities have revealed complex inter-

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actions between biotic factors, such as competition, predation, and parasitism, and abiotic factors, such as hydroperiod (Wilbur 1987; Kiesecker and Skelly 2001). Likewise, anthropogenic influences on abiotic factors, such as pH, can influence species interactions between larval amphibians (e.g., Freda and Dunson 1986; Sadinski and Dunson 1992; Warner et al. 1993; Kiesecker 1996).

In the presence of fluctuating abiotic conditions, interactions among species will be influenced if the species are affected differentially. For example, one can imagine a shift in an abiotic factor favoring the mean physiological optimum of one species over another, translating into differential predation, competition, parasitism, etc. Unless the physiological optima of the species are known for a particular abiotic factor, it is difficult to predict which species will be favored in biotic interactions. In addition, throughout ontogeny, species will likely experience different effects of abiotic factors, depending on their developmental stage. The effects of abiotic factors on species interactions have been demonstrated for several systems. For example, temperature influences species interactions by mediating competition (Park 1962; Streams 1987), determining spatial segregation of habitats (Baltz et al. 1982; Streams 1987; Martin 1988), and affecting rates of immigration and establishment (Gaines and Roughgarden 1985). Thermal conditions are especially important in predator-prey interactions that involve ectothermic organisms (Thomson 1978; Gresens et al. 1982; Cockrell 1984; Bailey 1989) and, potentially, those that involve ectotherms involved in size-dependent predation (Brodie and Formanowicz 1983; Travis et al. 1985; Formanowicz 1986). While much research has quantified the physiological effects of temperature on organisms, few studies have involved experimental manipulation of temperature in an attempt to assess its role in species interactions. However, aquatic systems allow for the spatial randomization and precise thermal control of experimental units, thus reducing experimental error. Furthermore, aquatic macroorganisms such as insects, fish, and amphibians lend themselves to experiments on the effects of temperature on species interactions because they are ectothermic and experience a range of different biotic interactions throughout ontogeny. Amphibians are especially well suited because their larval stage is strongly influenced by size-structured interactions, such as gape-limited predation (Brodie and Formanowicz 1983).

Larval anurans are preyed upon heavily by both aquatic and terrestrial predators (Calef 1973; Smith 1983). Ephemeral ponds are important breeding habitats for amphibians because they are devoid of permanent aquatic predators, such as fish, which may have a profound effect on amphibian larvae (Grubb 1972; Semlitsch and Gibbons 1988; Kiesecker and Blaustein 1998). Mobile aquatic predators such as insects, which exploit temporary ponds, also have a significant effect on amphibian larvae (Pritchard 1964; Calef 1973; Heyer et al. 1975; Travis 1983b; Smith 1983). However, because of the smaller size of these predators, amphibian larvae may grow too large to be captured (Heyer et al. 1975; Caldwell et al. 1980; Travis et al. 1985). For example, the ability of notonectids to feed on larval anurans is greatly reduced as tadpole size increases (Cronin and Travis 1986). This results in strong selective pressures from environmental conditions that favor larger tadpole body size (Travis 1983a,

1983b; Travis et al. 1985). Many inferences have been made about the relationship between abiotic factors and traits that affect predation, such as growth rate, yet few data exist. Several studies have conclusively shown that the degree of success of prey escape is positively correlated with body size in amphibian larvae (Heyer et al. 1975; Caldwell et al. 1980; Brodie and Formanowicz 1983; Crump 1984; Travis et al. 1985; Formanowicz 1986). From these data it was inferred that abiotic effects which modulate growth would in turn affect predation via indirect effects on prey size (Semlitsch and Gibbons 1988). One recent study confirmed this by demonstrating that pH affected the growth rates of ambystomatid salamanders and anuran prey items differentially, which in turn affected the ability of the predator to capture the prey (Kiesecker 1996). As discussed, the relevance of temperature to ectotherms suffering size-dependent predation makes temperature a logical factor for use in investigating abiotic effects on biotic interactions. However, whether or not direct effects of temperature work concomitantly with its effects on prey growth rates has not been considered.

We investigated the effect of temperature on interactions between *Notonecta kirbyi* and *Hyla regilla* larvae. It was concluded from previous research that notonectids may act as agents of selection on anurans because of size-limited predation (Cronin and Travis 1986). *Notonecta kirbyi* are found in sympatry with *H. regilla* throughout Oregon and prey on *H. regilla* tadpoles in both the field and the laboratory (personal observation). The tendency of *H. regilla* to exploit breeding sites devoid of large permanent aquatic predators, and its sympatry with *N. kirbyi*, makes this an excellent system of study to address questions about how temperature affects a size-limited predator-prey relationship. Our study addressed the relative contribution of direct versus indirect effects of temperature on the predation of *H. regilla* by *N. kirbyi*. For example, when both species are raised under the same thermal conditions, does temperature influence the ability of adult notonectids to capture *H. regilla* tadpoles beyond its indirect effects on prey growth rates during tadpole ontogeny? In other words, does higher temperature favor escape by *H. regilla* because of greater mass, favor increased predation by *N. kirbyi* because of increased metabolic demands (Bailey 1988), or have no effect because effects on prey growth rates are offset equally by effects on the predator? If temperature influences the probability of a tadpole being captured in addition to its indirect effects on mass, then prey size refugia, often considered to be subject to a strictly physical limit, may be more plastic than was previously thought.

Materials and methods

More than 100 *H. regilla* egg packets containing circa 25 eggs each were collected from Todd Lake (Deschutes County, Oregon) on 2 July 1996. Clutches were housed in aerated glass aquaria filled with 38 L of dechlorinated tap water at 15°C. Larvae were allowed to attain stage 21 (Gosner 1960), a free-swimming, feeding stage, before being tested. Tadpoles were fed Purina Rabbit Chow food pellets ground in a mortar and pestle. Food was measured volumetrically to ensure that the quantity was constant among larvae.

Adult *N. kirbyi* were collected from E.E. Wilson wildlife refuge (Benton County, Oregon) on 7 July 1996 and maintained under laboratory conditions until tested. *Notonecta kirbyi* are sympatric with *H. regilla* at both sites and throughout much of Oregon and were collected at a different site from predators strictly out of convenience. Notonectids were fed a variety of vertebrates (larvae of *Ambystoma macrodactylum*, *Rana cascadae*, and *H. regilla*) and invertebrates (cladocerans, copepods, and corixids) ad libitum. Organisms used in this study were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care.

We tested the effects of temperature on both growth and development of *H. regilla* larvae and on predation of *H. regilla* by *N. kirbyi*. Three temperature treatments were tested in a randomized block design and replicated five times. Each block consisted of three 66 × 45 × 15 cm Rubbermaid containers (boxes), in each of which circulated water maintained at one of the three temperatures (3 treatments × 5 replicate blocks = 15 boxes in total). We used utility pumps (21.96 L/min) to pump water from three 190-L reservoirs to boxes that were at the same temperature in all blocks. Water was returned to the reservoirs by drainpipes inserted in the center of each box. Standpipes maintained a constant water level while allowing the flow of water through each box. Reservoirs were either left at room temperature, heated with a Polyscience supertemp 200D water heater, or cooled with a thermal expansion chamber cooling core. Water temperatures were maintained at 9.9°C (±1.25°C, SD = 0.50°C), 20.7°C (±1.0°C, SD = 0.48°C), and 25.7°C (±0.75°C, SD = 0.31°C); these treatments will be referred to as cool, ambient, and warm, respectively. Experimental temperatures were chosen to reflect within- and among-pond variation experienced by *N. kirbyi* and *H. regilla* during a single day or growing season throughout Oregon; temperatures within ponds commonly range from 6 to 30°C in midsummer, when tadpoles are developing (Wollmuth et al. 1987; Watkins 2000). While the same water was pumped to all the boxes within a temperature treatment, the water flowing through the box was used only to maintain the experimental temperature. This provided a spatially non-confounded experimental design in which there was minimal variation between the temperatures of the five replicates.

Both predators and prey were held in 600 mL of dechlorinated tap water in opaque polyethylene containers (cups) that held only one animal each. Twenty-four cups were simultaneously submerged in each box, of which 4 were *N. kirbyi* holding cups (4 × 15 boxes = 60 total; 12 per block; 20 per treatment) and 20 were *H. regilla* holding cups (20 × 15 boxes = 300 total; 60 per block; 100 per treatment). The cups were submerged in the boxes for the entire experiment. Tadpoles and notonectids were haphazardly selected for the experiment from glass aquaria and then randomly assigned to treatments. The 24 animals held in each box were completely isolated from each other by the barrier created by the plastic cups. At no time did the animals share resources (water, food, etc.).

All water in contact with organisms was changed every 3 days, i.e., five times during the experiment. Neither dissolved oxygen nor microorganism levels were measured but visual assessment of containers suggested that no food spoilage occurred during the experiment. Animals were fed immediately after the cups were cleaned, so food was never a limiting factor. Temperatures in the boxes were measured daily by randomly sampling the temperatures of four cups within each box at random times. A 12 h light : 12 h dark photoperiod was used throughout the experiment.

Predator-prey trials were conducted every 3 days for 15 days. For each trial we randomly selected four tadpoles per box (4 × 5 = 20 tadpoles per treatment, 20 tadpoles × 3 treatments = 60 tadpoles) and combined each with a single notonectid from the same box. Trials were conducted in the box in which the animals were raised and in the cup that housed the notonectid during the experiment. The same 60 notonectids were tested five times (i.e., five tri-

Table 1. Results of a repeated-measures ANOVA comparing the mean mass of *Hyla regilla* tadpoles measured every 3 days for 15 days among three temperature treatments.

Source	df	Mean square	F	P
Between treatments				
Treatment	2	0.278	48.677	<0.0001
Error	12	0.006		
Within treatments				
Time	4	0.425	269.470	<0.0001
Time × treatment	8	0.038	23.978	<0.0001
Error	48	0.002		

als over 15 days) throughout the experiment. As suggested by pilot studies, larvae were combined with notonectids for 2 h. On completion of the testing period we calculated the proportion of tadpoles eaten per box (0.0, 0.25, 0.5, 0.75, or 1.0). We measured the blotted wet mass of each larva being tested to the nearest 0.01 g prior to exposure to a notonectid. Larvae that were tested with notonectids and not consumed were not used in subsequent trials. Both notonectids and tadpoles were fed ad libitum until just prior to each predation trial. Previous studies instituted a starvation period prior to testing a single predator (Cronin and Travis 1986). However, our pilot studies indicated that this led to mortality of notonectids that were used in subsequent tests, consequently we tested the notonectids without a prior starvation period.

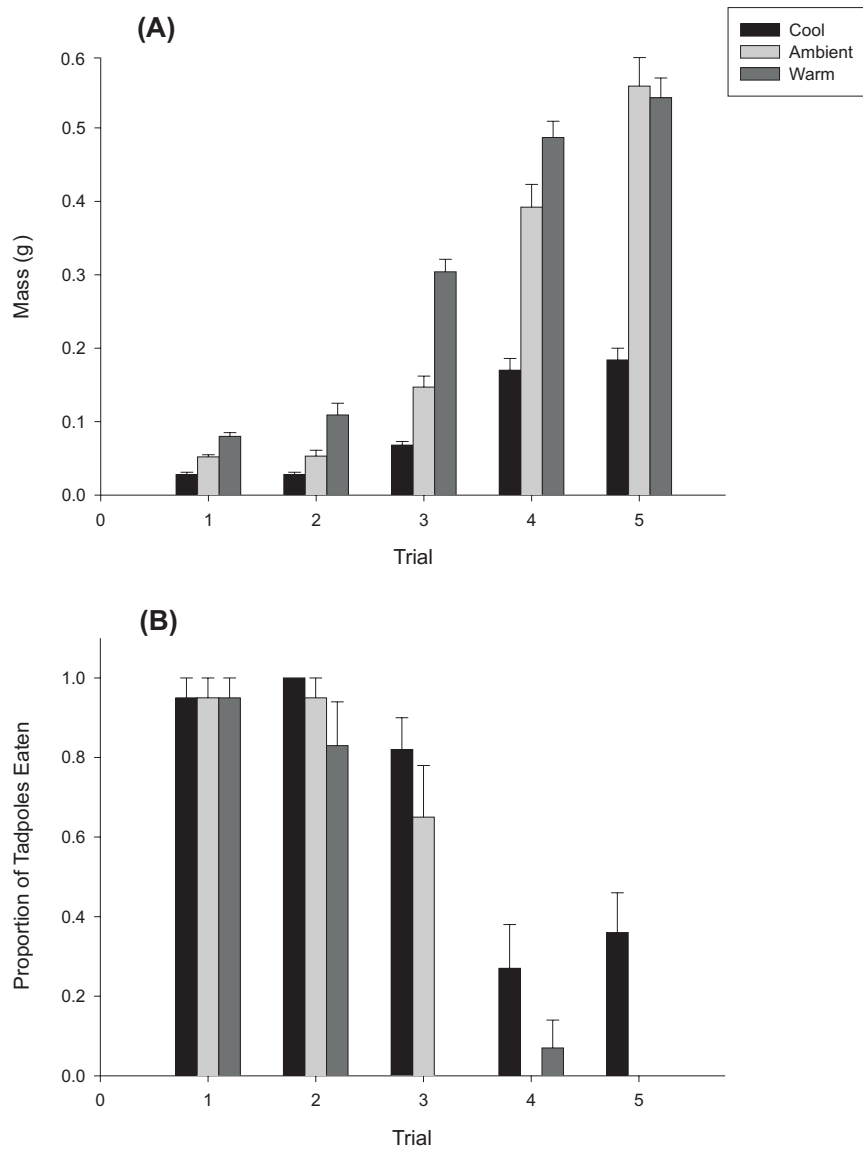
At each time interval we calculated the mean mass of four tadpoles from each box and analyzed differences among treatments using a repeated-measures ANOVA with treatment and time as fixed effects. Preliminary analysis indicated no significant block effect, therefore block and error terms were combined for the remaining tests. We estimated the probability of prey capture using SAS Proc Logistic (SAS Institute Inc. 2000), with mass and temperature as predictors in a multiple logistic regression. The model fit was assessed using the deviance statistic with a χ^2 distribution, the maximum rescaled r^2 statistic, and Hosmer and Lemeshow's goodness-of-fit test (Allison 1999).

Results

The mean mass of *H. regilla* tadpoles increased in each treatment over the five trials (Fig. 1A). The mean mass of *H. regilla* over the five time trials was strongly linearly related to temperature (mass = 0.013(temperature) - 0.032; $r^2 = 0.999$, $P = 0.0078$). A significant effect of treatment and time by treatment on tadpole mass was detected over the five trials ($F_{[8,48]} = 23.978$, $P < 0.0001$ from a repeated-measures ANOVA; Table 1). Tadpoles in the warm treatment had the highest mean mass and those in the cool treatment had the lowest, except for trial 5 in which the tadpoles in the ambient treatment exhibited a mean mass not significantly different from that of tadpoles in the warm treatment. While no specific data are reported for development, we observed warm-treatment tadpoles in the final trial to be at later Gosner (1960) stages than those the remaining treatments.

The proportion of tadpoles eaten decreased in each treatment over the course of the experiment (Fig. 1B). Temperature was negatively correlated with the total number of prey caught per treatment over the five trials (number of prey captured = -0.935(temperature) + 64.52; $r^2 = 0.99$, $P = 0.063$). The proportion of tadpoles eaten in the warm treatment decreased to zero after trial 2, except for a slight increase in trial 4. In the ambient treatment the proportion eaten was intermediate in trial 3, dropped to zero in trial 4, and remained

Fig. 1. (A) Mass (mean \pm SE) of *Hyla regilla* tadpoles in cool, ambient, and warm treatments over five predation trials. (B) Proportion (mean \pm SE) of tadpoles eaten in cool, ambient, and warm treatments by the predator *Notonecta kirbyi* over five predation trials. Trials were conducted every 3 days.



at zero for trial 5. The proportion of tadpoles eaten in the cool treatments decreased more gradually than in either the ambient or the warm treatment and never reached zero as it did for the other treatments.

The probability of a tadpole being eaten was evaluated by a best fit multiple logistic regression. Both mass and temperature were significant predictors of tadpole capture in the model, but mass had a much stronger effect than did temperature (Table 2). The estimates of maximum rescaled r^2 , the deviance χ^2 statistic, and Hosmer and Lemeshow's statistic all suggest that the logistic regression model based on mass and temperature provides a suitable fit to the data (Table 2). The model predicts that for a given mass, tadpoles raised in warm water have a greater probability of capture than do those raised under ambient temperature, which have a greater probability of capture than those raised in the cool treatment (Fig. 2). The maximum divergence of the three probability functions occurs when *H. regilla* larvae reach a

mass of 0.15 g; a warm-treatment tadpole has a 64.4% chance of being captured, while tadpoles raised in ambient and cool temperatures have a 54.5 and 33.0% chance of being captured, respectively (Fig. 2).

While both *H. regilla* and *N. kirbyi* incurred some mortality prior to predation trials, it was unrelated to temperature for either species (*H. regilla*: one-way ANOVA F test, $F_{[2,12]} = 0.88$, $P = 0.44$; *N. kirbyi*: one-way ANOVA, $F_{[2,12]} = 1.73$, $P = 0.22$).

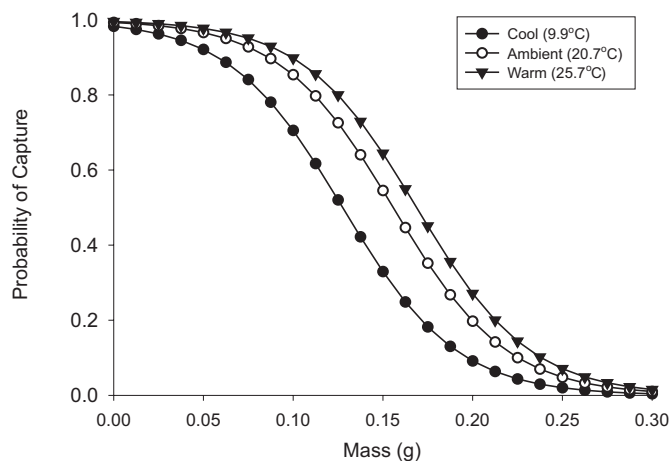
Discussion

The effect of temperature on the growth and development of anurans is well established; tadpole growth is positively correlated with temperature over species-specific ranges (Lillie and Knowlton 1897; Moore 1939; Smith-Gill and Berven 1979; Harkey and Semlitsch 1988). Although larvae reared at lower temperatures take longer to metamorphose,

Table 2. Parameter estimates and goodness-of-fit statistics for the multiple logistic regression equation predicting the probability of *H. regilla* being captured by *Notonecta kirbyi* in five predation trials over 15 days.

(A) Model parameters.					
Variable	df	Parameter estimate	SE of estimate	Wald's χ^2	P
Intercept	1	3.222	0.761	17.914	<0.0001
Mass	1	-31.669	4.44	50.868	<0.0001
Temperature	1	0.083	0.042	3.941	0.0471
(B) Estimates of model fit.					
Goodness-of-fit statistic	df	Value	$P > \chi^2$		
Deviance	95	61.042	0.9974		
Hosmer and Leseshow	8	2.0869	0.9782		
Maximum rescaled r^2	na	0.7971	na		

Fig. 2. Best fit lines for the multiple logistic regression predicting the probability of capture of *H. regilla* tadpoles during predation trials as a function of tadpole mass for three temperature treatments. The best fit logistic regression equation is $\text{prob}(\text{capture}) = \exp(3.222 - 31.669 \times \text{mass} + 0.083 \times \text{temperature}) / (1 + \exp(3.222 - 31.669 \times \text{mass} + 0.083 \times \text{temperature}))$.



they often attain larger body sizes (Wilbur and Collins 1973; Harkey and Semlitsch 1988). Temporal or geographic variation in temperature in nature may produce differences in the phenotypes of larvae of the same species. Berven et al. (1979) concluded that phenotypic variation among populations of *Rana clamitans* from different elevations was largely attributable to differences in temperature.

Our experimental manipulations of temperature produced results that are consistent with a positive correlation between temperature and growth, and qualitatively in the final trial, a positive correlation between growth and length of the larval period. Tadpoles from the warm treatment in trial 5 were beginning to metamorphose but were similar in mass to tadpoles in the ambient treatment. This is likely an artifact of late-stage metamorphosis, when tadpoles begin to reabsorb their tail and lose mass (Wilbur and Collins 1973).

The thermal ecology of insects is also well understood (Ward and Stanford 1982). Higher temperatures increase the functional response of many aquatic insect predators by increasing metabolic demands, increasing attack rate, and decreasing handling time (Thomson 1978; Gresens et al. 1982;

Baily 1989). Bailey (1988) found that notonectid swimming activity increased as a function of temperature. From this he inferred that temperature would directly influence notonectid predatory behavior. Likewise, energetic characteristics of aquatic insect predators, such as food consumption, assimilation, and metabolism, increase at higher temperatures (Heiman and Knight 1975; Jayakumar and Mathavan 1991). Data that demonstrate an inverse relationship between temperature and gut clearance for notonectids (Giller 1984) are typical of the response of insect metabolism to temperature. Consequently, at higher temperatures insects are likely to feed more often to meet the increased metabolic demands.

In a previous study that analyzed the number of tadpoles from three size classes captured by an insect predator at either 13 or 25°C, results were inconsistent across three species of anurans (Richards and Bull 1990). For two species, temperature had no effect on the number of same-sized tadpoles that were consumed. This suggests that the effects of temperature on predator metabolism were matched by proportional changes in prey activity (Richards and Bull 1990). For the third species, however, more tadpoles were captured in the 25°C treatment than in the 13°C treatment for all tadpole size classes that were tested. Thus, at least for one species, temperature had a greater impact on predator metabolism than on prey escape ability, which translated into more prey captured. Our experimental design reduced, if not eliminated, the possibility of changes in prey escape speed or escape distance, which were thought to increase the number of prey eaten in warmer treatments in the study by Richards and Bull (1990). The use of small cups and a 2-h testing period insured that predators had an ample chance to capture prey in our study. This is supported by our observations of repeated failure of capture attempts by notonectids in trials involving large tadpoles. However, reduced tadpole activity in cooler treatments, which has been associated with decreased predator-prey interactions and prey detectability (Moore and Townsend 1998), may have played a role in reducing predation even in our small cups.

In our experiment, the three treatments displayed little difference in the proportion of tadpoles eaten during the first two predation trials. By the third trial, the warm-treatment notonectids were virtually excluded from eating tadpoles for the remainder of the experiment, whereas the ambient-treatment notonectids were excluded in trial 4 until the end of the experiment. Within a treatment, our data strongly suggest

that temperature influenced tadpole growth, which in turn physically impeded prey capture by the size-limited predator. First, previous research unequivocally established the existence of size refugia for anuran tadpoles (Heyer et al. 1975; Caldwell et al. 1980; Brodie and Formanowicz 1983; Crump 1984; Travis et al. 1985; Formanowicz 1986). Additionally, a wealth of data has shown that functional response, metabolic digestion, and hunger level increase in insects at higher temperatures (discussed above). In light of this point, our results are supported by the strong possibility that notonectids in the warm treatment experienced the need to capture prey in order to meet increased metabolic demands, yet exhibited lower rates of predation. The repeated use of the same notonectid in predation trials leaves open the possibility that experience influenced predation rates. Our data suggest that this was not the case in our experiment: cool-treatment notonectids in trial 5 captured the same proportion of tadpoles of equal mass as in trial 4 (Fig. 1), suggesting that experience did not strongly influence our results.

While the inability of *N. kirbyi* to capture larger *H. regilla* within a temperature treatment is the result of changes in prey size, our logistic regression analysis suggests that among different temperatures, prey size refugia vary with abiotic conditions rather than being determined solely by the size of prey items. To our knowledge, mechanisms that might moderate the development of prey size refugia under different abiotic conditions during ontogeny have not been proposed or investigated. Larval *H. regilla* raised at 15°C develop greater muscle-enzyme activity and better locomotor skills than those raised at 25°C (Watkins 2000). This might provide a mechanism for the observed temperature-dependent size refugia because tadpoles of equal mass raised at different temperatures would differ in their capacity to physically break the grasp of a notonectid.

In nature, size-limited insect predators may switch to more abundant, vulnerable prey when tadpoles become too large to capture. Likewise, changes in prey characteristics, such as ease of capture, availability, and associated risks, may affect foraging behavior (Sih 1980, 1992). Cockrell (1984) found that variation in temperature caused notonectids to utilize their habitat differently, which led them to switch to more frequently encountered prey. On the other hand, prey species might also alter habitat use as a result of changes in their ontogenetic niche throughout development (Werner et al. 1983; Dupre and Petranka 1985). One might expect that individuals would distribute themselves throughout habitat patches so that they experience the highest relative payoff for a given phenotype. Thus, larval anurans might be expected to balance the conflicting selection pressures of metamorphosing in water of different temperatures. In cooler water the probability of capture by notonectids for a given tadpole size class is lower but development time is long, whereas in warmer water tadpoles experience higher probabilities of capture but develop rapidly to reach a size refuge more quickly. The combined effects of differential habitat use and prey size refugia may interact as important consequences of abiotic factors such as temperature.

Abiotic factors such as temperature produce a complex array of effects that may extend to population or community levels. How influences at the organism or species level may extrapolate to interactions among multiple species offers

interesting research opportunities for community ecologists. Moreover, directional changes in climate may lead to shifts in community structure because species differ in their response to abiotic influences (Davis 1986). Effects will most probably depend on the species involved (i.e., species-specific responses / abiotic tolerances) and will vary according to climatic factors (i.e., temperature, rainfall, etc.). The results of this experiment and others (e.g., Dunson and Travis 1991) suggest that abiotic variables should be regarded as factors in the mechanistic approach to community ecology (Schoener 1986; Wellborn et al. 1996).

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References

- Allison, P.D. 1999. Logistic regression using the SAS system: theory and application. SAS Institute Inc., Cary, N.C.
- Bailey, P.C.E. 1988. The effect of density and temperature on the swimming and aggregating behavior of the backswimmer, *Anisops deanei* (Heteroptera: Notonectidae) and subsequent encounter rate with a sit-and-wait predator. *Ethology*, **77**: 44–57.
- Bailey, P.C.E. 1989. The effect of water temperature on the functional response of the water stick *Ranatra dispar* (Heteroptera: Nepidae). *Aust. J. Ecol.* **14**: 381–386.
- Baltz, D.M., Moyle, P.B., and Knight, N.J. 1982. Competitive interactions between benthic stream fishes, riffle sculpin, *Cottus gluosus*, and speckled dace, *Rhinichthys osculus*. *Can. J. Fish. Aquat. Sci.* **39**: 1502–1511.
- Berven, K.A., Gill, D.E., and Smith-Gill, S.J. 1979. Counter-gradient selection in the green frog, *Rana clamitans*. *Evolution*, **33**: 609–623.
- Brodie, E.D., Jr., and Formanowicz, D.R., Jr. 1983. Prey size of predators: differential vulnerability of larval anurans. *Herpetologica*, **39**: 67–75.
- Caldwell, J.P., Thorp, J.H., and Jervey, T.O. 1980. Predator-prey relationships among larval dragonflies, salamanders, and frogs. *Oecologia*, **46**: 285–289.
- Calef, G.W. 1973. Natural mortality of tadpoles in a population of *Rana aurora*. *Ecology*, **54**: 741–758.
- Cockrell, B.J. 1984. Effects of temperature and oxygenation on predator-prey overlap and prey choice of *Notonecta glauca*. *J. Anim. Ecol.* **53**: 519–532.
- Cronin, J.T., and Travis, J. 1986. Size limited predation on larval *Rana areolata* (Anura: Ranidae) by two species of backswimmer (Insecta: Hemiptera: Notonectidae). *Herpetologica*, **42**: 171–174.
- Crump, M.L. 1984. Ontogenetic changes in vulnerability to predation in tadpoles of *Hyla pseudopuma*. *Herpetologica*, **42**: 367–373.

- Davis, M.B. 1986. Climatic instability, time lags, and community disequilibrium. In *Community ecology*. Edited by J. Diamond and T. Case. Harper and Row, New York. pp. 333–343.
- Dunson, W.A., and Travis, J. 1991. The role of abiotic factors in community organization. *Am. Nat.* **138**: 1067–1091.
- Dupre, R.K., and Petranka, J.W. 1985. Ontogeny of temperature selection in larval amphibians. *Copeia*, 1985: 462–467.
- Formanowicz, D.R. 1986. Anuran tadpole/aquatic insect predator–prey interactions: tadpole size and prey capture success. *Herpetologica*, **42**: 367–373.
- Freda, J., and Dunson, W.A. 1986. Effects of low pH and other chemical variables on the local distribution of amphibians. *Copeia*, 1986: 454–466.
- Gaines, S., and Roughgarden, J. 1985. Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. *Proc. Natl. Acad. Sci. U.S.A.* **82**: 3707–3711.
- Giller, P.S. 1984. Predator gut state and prey detectability using electrophoretic analysis of gut contents. *Ecol. Entomol.* **9**: 157–162.
- Gosner, K.L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica*, **16**: 183–190.
- Gresens, S.E., Cothran, M.L., and Thorp, J.H. 1982. The influence of temperature on the functional response of the dragonfly *Celithemis fasciata* (Odonata: Libellulidae). *Oecologia*, **53**: 281–284.
- Grubb, J.C. 1972. Differential predation by *Gambusia affinis* on the eggs of seven species of anuran amphibians. *Am. Midl. Nat.* **88**: 102–108.
- Harkey, G.A., and Semlitsch, R.D. 1988. Effects of temperature on growth, development and color polymorphism in the ornate chorus frog *Pseudacris ornata*. *Copeia*, 1988: 1001–1007.
- Heiman, D.R., and Knight, A.W. 1975. The influence of temperature on the bioenergetics of the carnivorous stonefly nymph, *Acroneuria californica* Banks (Plecoptera: Perlidae). *Ecology*, **56**: 105–116.
- Heyer, W.R., McDiarmid, R.W., and Weigmann, D.L. 1975. Tadpoles, predation and pond habitats in the tropics. *Biotropica*, **7**: 100–111.
- Jayakumar, E., and Mathavan, S. 1991. Effect of temperature on the growth and bioenergetics of *Laccotrephes griseus* (Hemiptera: Nepidae). *J. Therm. Biol.* **16**: 93–102.
- Kiesecker, J. 1996. pH-mediated predator–prey interactions between *Ambystoma tigrinum* and *Pseudacris triseriata*. *Ecol. Appl.* **6**: 1325–1331.
- Kiesecker, J.M., and Blaustein, A.R. 1998. Effects of introduced bullfrogs and smallmouth bass on the microhabitat use, growth and survival of native red-legged frogs. *Conserv. Biol.* **12**: 776–787.
- Kiesecker, J.M., and Skelly, D.K. 2001. Effects of disease and pond drying on gray tree frog growth, development, and survival. *Ecology*, **82**: 1956–1963.
- Lillie, F.R., and Knowlton, F.P. 1897. On the effect of temperature on the development of animals. *Zool. Bull.* **1**: 179–193.
- Martin, T.J. 1988. Interaction of salinity and temperature as a mechanism for spatial separation of three co-existing species of Ambassidae (Cuvier) (Teleostei) in estuaries on the south-east coast of Africa. *J. Fish. Biol.* **33**(Suppl.): 9–15.
- Moore, J.A. 1939. Temperature tolerance and rates of development in the eggs of Amphibia. *Ecology*, **20**: 459–478.
- Moore, M.K., and Townsend, V.R., Jr. 1998. The interaction of temperature, dissolved oxygen and predation pressure in an aquatic predator–prey system. *Oikos*, **81**: 329–336.
- Park, T.P. 1962. Beetles, competition, and populations. *Science* (Washington, D.C.), **138**: 1369–1375.
- Pritchard, G. 1964. The prey of dragonfly larvae (Odonata; Anisoptera) in ponds in northern Alberta. *Can. J. Zool.* **42**: 785–800.
- Resh, V.H., and Barney, M.A. 1987. Distribution of the Wilbur Springs shore bug. *Environ. Entomol.* **16**: 1087–1091.
- Richards, S.J., and Bull, C.M. 1990. Size-limited predation on tadpoles of three Australian frogs. *Copeia*, 1990: 1041–1046.
- Sadinski, W.J., and Dunson W.A. 1992. A multilevel study of the effects of low pH on amphibians of temporary ponds. *J. Herpetol.* **26**: 413–422.
- SAS Institute Inc. 2000. SAS version 8.01. SAS Institute Inc., Cary, N.C.
- Schoener, T.W. 1986. Mechanistic approaches to community ecology: a new reductionism? *Am. Zool.* **26**: 81–106.
- Semlitsch, R.D., and Gibbons, J.W. 1988. Fish predation in size-structured populations of treefrog tadpoles. *Oecologia*, **75**: 321–326.
- Smith, D.C. 1983. Factors controlling tadpole populations of the chorus frog (*Pseudacris triseriata*) on Isle Royale, Michigan. *Ecology*, **64**: 501–510.
- Smith-Gill, S.J., and Berven, K.A. 1979. Predicting amphibian metamorphosis. *Am. Nat.* **133**: 563–585.
- Sih, A. 1980. Optimal behavior: Can foragers balance two conflicting demands? *Science* (Washington, D.C.), **210**: 1041–1043.
- Sih, A. 1992. Prey uncertainty and the balancing of antipredator and feeding needs. *Am. Nat.* **139**: 1052–1069.
- Streams, F.A. 1987. Within-habitat spatial separation of two *Notonecta* species: interactive resource partitioning. *Ecology*, **68**: 935–945.
- Thomson, D.J. 1978. Towards a realistic predator–prey model: the effect of temperature on the functional response and life history of larvae of the damselfly, *Ischnura elegans*. *J. Anim. Ecol.* **47**: 757–767.
- Travis, J. 1983a. Variation in development patterns of larval anurans in temporary ponds. I. persistent variation within a *Hyla gratiosa* population. *Evolution*, **37**: 496–512.
- Travis, J. 1983b. Variation in growth and survival of *Hyla gratiosa* larvae in experimental enclosures. *Copeia*, 1983: 232–237.
- Travis, J., Keen, W.H., and Juilianna, J. 1985. The role of relative body size in a predator–prey relationship between dragonfly naiads and larval anurans. *Oikos*, **45**: 59–65.
- Ward, J.V., and Stanford, J.A. 1982. Thermal responses in the evolutionary ecology of aquatic insects. *Annu. Rev. Entomol.* **27**: 97–117.
- Warner, S.C., Dunson, W.A., and Travis, J. 1991. Interaction of pH, density, and priority effects on the survivorship and growth of two species ofhylid tadpoles. *Oecologia*, **88**: 331–339.
- Warner, S.C., Dunson, W.A., and Travis, J. 1993. Effect of pH variation on interspecific competition between two species of hylid tadpoles. *Ecology*, **74**: 183–194.
- Watkins, T.B. 2000. The effects of acute and developmental temperature on burst swimming speed and myofibrillar ATPase activity in tadpoles of the pacific tree frog, *Hyla regilla*. *Physiol. Biochem. Zool.* **73**: 356–364.
- Wellborn, G.A., Skelly, D.K., and Werner, E.E. 1996. Mechanisms creating community structure across a freshwater gradient. *Annu. Rev. Ecol. Syst.* **27**: 337–363.
- Werner, E.E., Mittelbach, G.G., Hall, D.J., and Gilliam, J.F. 1983. Experimental tests of optimal habitat use in fish: the role of relative habitat profitability. *Ecology*, **64**: 1525–1539.

- Wilbur, H.M. 1987. Regulation of structure in complex systems: experimental temporary pond communities: anuran responses. *Ecology*, **68**: 1437–1452.
- Wilbur, H.M., and Collins, J.P. 1973. Ecological aspects of amphibian metamorphosis. *Science* (Washington, D.C.), **182**: 1305–1314.
- Wollmuth, L.P., Crawshaw, L.I., Forbes, R.B., and Grahn, D.A. 1987. Temperature selection during development in a montane anuran species, *Rana cascadae*. *Physiol. Zool.* **60**: 472–480.

