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EFFECTS OF WATER TEMPERATURE ON LARVAL AMPHIBIAN PREDATOR-PREY DYNAMICS

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***Abstract*.—Predation represents an important driver of species persistence and community structure. Climate change can influence predation through changes in the distribution and abundance of predatory species. Furthermore, predator-prey dynamics may be influenced by climate-induced shifts in the behavior of predators and/or prey. Our research employed a model system consisting of larval amphibians (*Lithobates clamitans*) as prey, and three species of predatory dragonfly larvae, *Ladona julia*, *Aeshna interrupta*, and *Didymops transversa*. Our goal was to assess whether simulated climate-induced changes in predator assemblages and abiotic conditions may influence predator-prey dynamics. The study was conducted in replicated aquatic microcosms, with water temperature manipulated across a range of temperatures. Predation studies involved a single dragonfly of a focal species and 10 larval *L. clamitans*. Our best-fitting model included dragonfly species, water temperature, and the interaction between the two factors. Survival of anuran larvae decreased for both *Aeshna interrupta* and *Didymops transversa,* but remained constant with increasing water temperature for *Ladona julia*. Our study demonstrates the potential for climate-induced changes in the composition of predator species to interact with altered abiotic conditions in shaping predator-prey dynamics.**

Key Words.—Anisoptera; Green Frog; *Lithobates clamitans*; mesocosm; Odonata

INTRODUCTION

Global climate change is one of the most significant threats to biodiversity worldwide (Thomas et al. 2004). Amphibians are particularly vulnerable to the direct effects of warming temperatures and altered levels of precipitation due to their limited vagility, permeable skin leading to a high risk of desiccation, and the reliance of many species on suitable aquatic and terrestrial conditions for completion of their life history cycle (Corn 2005). Climate change can also influence amphibian species persistence and community structure through a wide array of indirect effects at the species level, and interactions among species across trophic levels (Blaustein et al. 2010). Changes in susceptibility to predation may represent one of the most significant indirect pathways by which climate change may influence amphibian populations and there is a need for research that focuses at the ecosystem rather than species level to understand the complex pathways by which climate change effects may affect amphibians (Walther et al. 2002; McLachlan et al. 2007; Yang and Rudolf 2010).

Climate-induced increases in water temperature in temperate wetlands (Rouse et al. 1997; Stefan et al. 1998) represent a likely mechanism by which interactions between amphibians and their predators may be altered. This is particularly true for larval anurans whose morphology (McCollum and Leimberger 1997), growth (Morin 1986, 1987; Lawler 1989; Skelly and Werner 1990), behavior (Relyea and Werner 1999; Relyea 2001), and survival (Morin 1986; Lawler 1989; Semlitsch 1990; Werner and McPeek 1994) have all been shown to be affected by predators. Aquatic invertebrates, particularly dragonfly (Anisoptera) naiads represent significant predators of larval amphibians (Caldwell et al. 1980; Alford 1999). Warmer water temperatures may influence dragonfly predation of larval amphibians by altering interactions among existing co-occurring species of the two taxa. As prey capture rates (hereafter termed predatory efficiency) by invertebrates typically increase at higher water temperatures (Thompson 1978; Jamieson and Scudder 1979), changes in temperature clearly have the potential to influence the survival of amphibian larvae.

Climate change has also been linked to shifts in the distribution of dragonfly species (Paulson 2001). Adult dragonflies are considerably more vagile than amphibians (Wikelski et al. 2006) and less likely to be limited by terrestrial habitat heterogeneity including barriers to dispersal. This suggests that the distribution of currently co-occurring dragonfly naiads and amphibian may become decoupled under altered climate regimes as has been seen with other taxa (Van der Putten 2010). These changes in the distribution and abundance of dragonfly species may be important for amphibian populations if predatory efficiency varies among dragonfly naiad species and/or if there are interspecific differences in the responses of individual dragonfly species to changes in water temperature. The role of

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temperature in driving predator-prey dynamics is dependent on the behavior of both predator and prey (Dell et al. 2013); thus, the variation in foraging strategies known to exist among species of dragonfly naiads (Pritchard 1964; Peckarsky 1982; Corbet 1999) may be important in governing temperature-dependent depredation of larval amphibians by different species of naiads.

We evaluated three hypotheses in order to examine the potential mechanisms by which changes in the distribution of dragonfly species coupled with changes in water temperature may influence larval amphibian survival: (1) predatory efficiency of dragonfly naiads will increase as water temperature increases (hence tadpole survival will decrease); (2) predatory efficiency will differ among dragonfly genera; and (3) dragonfly predation efficiency will differ among genera along a water-temperature gradient. To evaluate these hypotheses, we used Green Frogs, *Lithobates clamitans*, as a model species for Ranids (including *L. catesbeiana* and *L. septentrionalis*) that share similar habitats and life-history characteristics in the temperate northeastern United States (Gibbs et al. 2007).

MATERIALS AND METHODS

Our study was conducted in the Adirondack Park in upstate New York (44.434462°N, 74.257375°W). *Lithobates clamitans* and dragonfly larvae were collected from a mesotrophic pond surrounded by mixed northern hardwood forest (Black Pond: 44.43535°N, 74.298756°W, datum WGS 84; elevation = 497 m). *Lithobates clamitans* is a highly abundant Ranid species that is ubiquitous in ponds across the northeastern USA. To obtain *L. clamitans* larvae, we collected adult *L. clamitans* and placed them in 56 L containers in male-female pairs to allow breeding to occur. Oviposition occurred on 11 June 2012. Eggs and subsequent larvae were kept in aerated containers in the lab, with larvae fed commercial fish food *ad libitum* until the onset of the study. The larvae used in this experiment were 4−5 weeks old (~Gosner stage 30; mean total length ± SD = 11.81 mm ± 0.86).

We collected dragonfly larvae by dip-netting and sifting through the substrate on the bottom of the focal wetland. We then separated larvae, choosing species with sufficient individuals of similar size for experiments. Dragonfly larvae were fed mosquito larvae *ad libitum* until 24 h before the onset of experiments. We used three dragonfly species from three different families as anuran predators: *Aeshna interrupta* (Variable Darner; Family Aeshnidae; mean total length ± SD = 13.01 mm ± 1.19), *Ladona julia* (Chalk-fronted Corporal; Family Libellulidae; mean ± SD = 22.07 mm ± 1.77), and *Didymops transversa* (Stream Cruiser; Family Macromiidae; mean ± SD = 20.06 mm ± 4.28). The three families and genera were chosen as they are all abundant in the region and differ in their predation strategies. Aeshnidae are active predators that move through the water-body in search of suitable prey (Pritchard 1964; Corbet 1999). Libellulidae and Macromiidae are ambush predators typically found in the leaf litter that adopt a fixed position and wait for prey to come within striking range (Pritchard 1964; Corbet 1999).

We conducted our experiments under laboratory conditions in polyethylene microcosms (32 cm × 18 cm × 12 cm) filled with 3 L of strained lake water and 30 ml of suspended algae as a food source for *L. clamitans* larvae. We also added five American Beech (*Fagus grandifolia*) leaves and five Paper Birch (*Betula papyrifera*) leaves to each container as cover to help simulate more natural conditions for predator/prey behavior. Overhead fluorescent lighting was used to provide a standardized regime of 12 hours of simulated daylight. To test the effects of water temperature on predation by each of our three dragonfly species, we established five water baths. Each bath was assigned one of five temperature treatments: (1) cool (mean temperature [°C] ± SE; 16.6 ± 0.1); (2) ambient temperature in the laboratory (20 ± 0.6); (3) low heat (22.4 ± 0.6); (4) medium heat (24.5 ± 0.1); and (5) high heat (28 ± 0.5). This temperature range encompassed and extended beyond the upper range of July temperatures measured at 1-m depth in 67 permanent wetlands in the study area in 2010 (mean 20.2 °C, range 12.9–23.9; David Patrick, unpubl. data). We maintained water temperature in the cool treatment using frozen ice-packs that were rotated on a regular interval. Water temperatures in the heated treatments were maintained using submersible aquarium heaters. We checked the temperature of each water bath daily using an EC500 Waterproof Exstik II pH/Conductivity Meter (Extech Instruments, Nashua, New Hampshire, USA). We placed four microcosms into each water bath (Fig. 1), allowing the water temperature to stabilize for 24-hours before beginning our experiments.

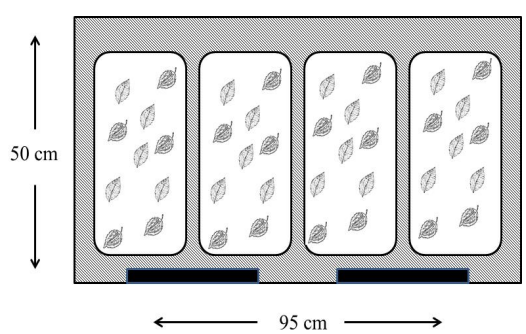

FIGURE 1. Schematic representation of experimental setup consisting of water baths containing four plastic microcosms. Aquarium heaters are shown as solid rectangles.

TABLE 1. Candidate models predicting the survival of Green Frog, *Lithobates clamitans*, tadpoles in relation to species of dragonfly larvae, size of dragonfly larvae, and water temperature in 60 artificial microcosms. K is the number of parameters in the model, ΔAIC_C is the difference between the model with the lowest AIC_C and any given model, AICwt is the AIC_C weight, and -2LL is -2 times × log likelihood.

Model	K	ΔAIC_C[a]	AICwt	-2LL
Odonate species + Average water temperature + Odonate species × Average water temperature	6	0	0.82	224.62
Odonate species + Average water temperature	4	3.08	0.18	231.70
Odonate species	3	10.64	0	241.26
Odonate species + Odonate species × Odonate size	6	14.15	0	238.77
Average water temperature	2	29.78	0	262.40

[a] The AIC_c for the best fitting model was 236.62

Each combination of water temperature treatment and dragonfly naiad species was replicated 5 times (n = 60 microcosms in total). To allow us to include odonate size as a covariate potentially influencing predation, we initially measured the length of each dragonfly larva digitizing individual photographs using the ImageJ software (*http://rsbweb.nih.gov*), then grouped individuals into four size classes for each species (size classes denoted as small "S," medium "M," large "L," and extra-large "XL"). Size classes ([mean total length [mm] ± SE) for each species were as follows *Aeshna interrupta* (S = 11.7 ± 0.4 ; M = 12.8 ± 0.2; L = 13.1 ± 0.1; XL = 14.5 ± 1.2), *Ladona julia* (S = 20.1 ± 0.3; M = 21.1 ± 0.3; L = 22.7 ± 0.8; XL = 24.4 ± 0.5), and *Didymops transversa* (S = 16.1 ± 0.3; M = 17.3 ± 0.3; L = 20.5 ± 2.7; XL = 26.3 ± 1.0). We then randomly assigned one individual from each size class to a temperature treatment. We randomly assigned 10 *L. clamitans* larvae to each experimental container. Prior research using the same microcosms and tadpole densities as this study demonstrated that the range of water temperatures we employed does not significantly influence mortality of larval *L. clamitans*, and that background mortality (the probability of a tadpole dying in the absence of predation during a 24-hr period) is extremely low (<1%; David Patrick, unpubl. data). We therefore attributed mortality during the study period to predation. The larval amphibians and dragonfly assigned to each container were placed in separate plastic cups and allowed to acclimatize for two hours at the experimental temperature, and then released into the microcosm. After 24 h we removed the dragonfly larvae and counted the surviving *L. clamitans* larvae. The duration chosen for the study was based on preliminary observational studies which indicated the potential for rapid predation, with a single dragonfly larvae (*Aeshna interrupta*) consuming 6 *L. clamitans* larvae within a 5-min period.

To assess the drivers of larval survival in relation to water temperature and dragonfly presence, we employed generalized linear models (GLMs) with the proportion of surviving tadpoles as the dependent variable, dragonfly species, dragonfly larval size, and temperature as independent variables, and a binomial distribution of errors. We tested simple models (single variable and additive models), as well as models including two-way interaction, and used Akaike's Information Criterion corrected for small sample size (AICc) and likelihood ratio tests to identify the best model. We used Program R version 2.15.2. for all analyses (R Development Core Team, Vienna, Austria).

RESULTS

Survival of anuran larvae varied among our microcosms (mean % survival ± SE: 54.8 ± 2.7; range 10–100). Our best-fitting model included dragonfly species, the average water temperature during the course of the study, and the interaction between the two factors (Table 1). All the other models including those incorporating variation in dragonfly naiad size had overall low support (low AICc weights; Table 1). Overall, survival of anuran larvae remained constant with increasing water temperature for *Ladona julia* (% survival ± SE: cool temperature treatment [17 °C] = 62.5 ± 2.5; warmest treatment [28 °C] = 70.0 ± 12.2), and decreased for *Aeshna interrupta* (% survival ± SE: cool temperature treatment [17 °C] = 65.0 ± 0.5; warmest treatment [28 °C] = 27.5 ± 6.3). Survival of anuran larvae initially increased with rising water temperature for *Didymops transversa*, but the two highest temperatures demonstrated lower survival (% survival ±

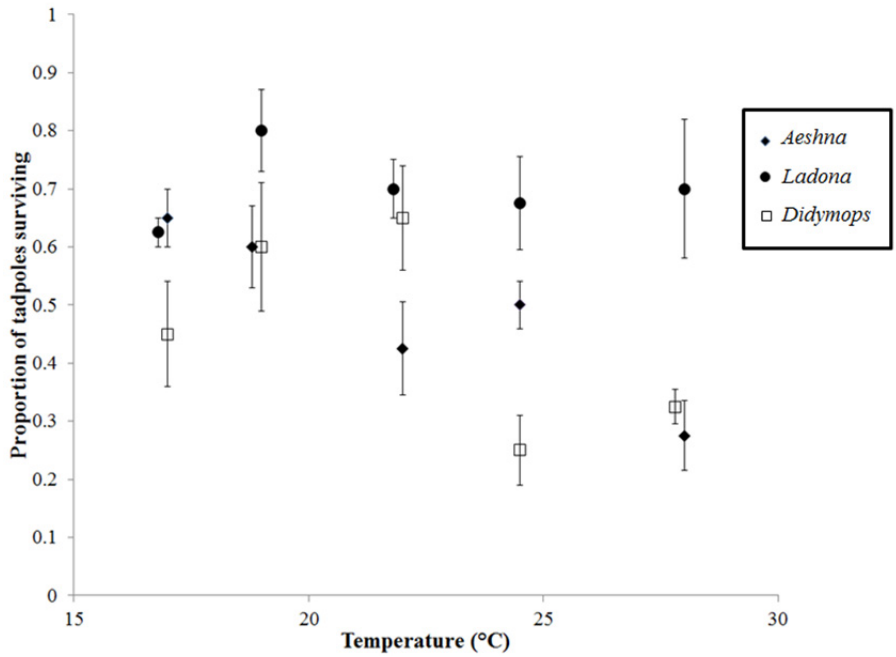

FIGURE 2. Survival (± SE) of *Lithobates clamitans* tadpoles in relation to species of dragonfly larvae and water temperature. Dragonfly species were *Aeshna interrupta* ("*Aeshna*"), *Ladona julia* ("*Ladona*") and *Didymops transversa* ("*Didymops*"). Where error bars overlapped, observations were offset (-0.2 °C) to allow comparison of variation.

SE: cool temperature treatment [17 °C] = 45.0 ± 9.6; warmest treatment [28 °C] = 32.5 ± 2.5; Fig. 2).

DISCUSSION

Predation represents one of the most important drivers of species persistence and community structure (Hairston et al. 1960; Holt 1977; Knight et al. 2005). The rapid pace of recent anthropogenic climate change has been linked to disruption of predator-prey dynamics through both decoupled range shifts leading to novel interactions among species, and by influencing interactions among existing community assemblages (Walther et al. 2002; Parmesan and Yohe 2003; Gilman et al. 2010). These general trends have specific relevance for larval amphibian population processes: climate change has been linked to shifts in the distribution and abundance of both dragonflies and amphibians (Paulson 2001; Pounds 2001; Corn 2005; Popescu and Gibbs 2009). As dragonflies are far more vagile than amphibians (e.g., Common Green Darners, *Anax junius*, can move up to 150 km/day; Wikelski et al. 2006), it is likely that novel naiad predator assemblages will develop as climate change continues. The consequences of these shifts in predator species composition will depend on both inherent interspecific differences in predatory efficiency, and the potential mediating role of climate-induced shifts in water temperature. While interspecific differences in invertebrate predation of anuran larvae have been documented (Tarr and Babbitt 2002), the role of water temperature in these interactions is less well described. Our study clearly demonstrates that warmer water temperatures can dramatically increase susceptibility to dragonfly predators, but the effects are particular to the species of dragonfly and not necessarily the size of the predator. In our controlled experimental setup, we observed that average predation rates of larval Green Frogs by *Aeshna interrupta* doubled between the coldest and warmest treatments (17 to 28 °C). However, mean predation by *Didymops transversa* increased modestly by approximately 13%, while predation by *Ladona julia* remained relatively unchanged over the same temperature range. This variation in daily survival may have important implications for overall survival throughout the prolonged larval life-history stage of Ranid species breeding in permanent wetlands such as Green Frogs.

The interspecific differences in temperature-dependent larval amphibian survival we observed among dragonfly species reflects the importance of the behavioral responses of prey to the presence of predators and vice versa (Skelly and Werner 1990; Relyea 2001). Climate-induced changes in water temperature may modify the behavior of both larval dragonfly predators and larval amphibians, with warmer conditions leading to greater activity (Mellanby 1939; Duellman and Trueb 1986). However, any changes in activity levels as a result of warmer conditions will be modified by the behavioral plasticity of amphibian larvae, and by the foraging

strategy adopted by dragonfly species. Amphibian larvae typically respond to the presence of predators by reducing activity, but the magnitude of the response varies depending on the species of amphibian and predator (Skelly and Werner 1990; Relyea 2001). The positive effect on survival of reduced activity of larval amphibians in response to predators may be offset by increased activity of predators in warmer waters, particularly species that adopt an active hunting approach. Our results provide some support for this hypothesis, with the actively hunting *Aeshna interrupta* consuming far more tadpoles than the sedentary *Ladona julia* under warmer conditions. However, *Didymops transversa*, a species that should demonstrate a similar feeding ecology to *Ladona julia* also showed a modest increase in predation, particularly in the warmest temperature waters. This finding likely represents the scarcity of data relating to the feeding ecology of individual dragonfly species, and suggests that *Didymops transversa* may adopt a more active foraging mode despite the general tendency of species in this family towards ambush predation (Corbet 1999).

While our study provides clear evidence of variation in larval amphibian susceptibility to predation based on water temperature and species of dragonfly, there are a number of caveats when extending these findings to larval amphibians in general. We focused on a single amphibian species and a single size class of amphibian. As amphibian larvae tend to show a ubiquitous behavioral response to the presence of dragonfly larvae (Relyea 2001), we expect our results to extend to species other than the Green Frog; however, this hypothesis needs to be tested. Larger tadpoles demonstrate lower predation rates by dragonfly naiads; thus, we expect survival in our study would have been higher overall if we had used larger amphibian larvae (Semlitsch 1990; Jara 2008).

It is important to recognize that demonstrating decreased survival of larval amphibians in a short-term study does not necessarily lead to a change in population size. The vital rates of larval amphibians are a result of complex direct and indirect pathways influencing survival, growth, and time to metamorphosis (Morin 1983; Werner 1986; Werner and McPeek 1994). For example, a reduction in density due to predation may lead to an increase in growth rates and larger size at metamorphosis (Wilbur 1976), which would increase terrestrial survival. Understanding such carryover effects from the aquatic to the terrestrial stage (Chelgren et al. 2006), and partitioning the influence of aquatic versus terrestrial survival (Vonesh and De la Cruz 2002; Vonesh and Osenberg 2003) are critical for assessing population viability. Our results offer important insights into population viability analysis in two ways; first, strong temperature-dependent predation rates in the larval stage may be important to include in population viability analyses focusing on climate change, and second, it offers a direct way to assess spatial variation in mortality rates in relation to readily available bioclimatic variables. For example, air temperatures are known to be highly correlated to surface water temperatures (Livingstone and Lotter 1998), which can easily be incorporated into spatial population viability analyses.

The results of our study represent an important first step in evaluating how warmer water temperatures may influence predator-prey dynamics for larval amphibians, but clearly more research is needed before the implications of this aspect of climate change for population persistence and community dynamics of Green Frogs can be assessed. We suggest a number of lines of enquiry for future studies that will help in building this understanding. These include specifically evaluating the role of variation in phenology and ontogeny of both predator and prey on predation; assessing inter-specific variation in the responses of different amphibian species to temperature-modified dragonfly predation; identifying the importance of habitat structure/complexity in modifying the interaction between climate change and predation; and assessing how thermally-induced changes in predation and growth rates (including density-dependent effects) influence larval vital rates and hence population dynamics.

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LITERATURE CITED

Alford, R.A. 1999. Ecology, resource use, competition, and predation. Pp. 240−278 *In* Tadpoles: The Biology of Anuran Larvae. McDiarmid, R.W., and R. Altig (Eds.). University of Chicago Press, Chicago, Illinois, USA.

Blaustein, A.R., S.C. Walls, B.A. Bancroft, J.J. Lawler, C.L. Searle, and S.S. Gervasi. 2010. Direct and indirect effects of climate change on amphibian populations. Diversity 2:281−313.

Caldwell, J.P., J.H. Thorp, and T.O. Jervey. 1980. Predator-prey relationships among larval dragonflies, salamanders, and frogs. Oecologia 46:285−289.

Chelgren, N.D., D.K. Rosenberg, S.S. Heppell, and A.I. Gitelman. 2006. Carryover aquatic effects on survival of metamorphic frogs during pond emigration. Ecological Applications 16:250−261.

Corbet, P.S. 1999. Dragonflies: Behavior and Ecology. Cornell University Press, New York, New York, USA.

Corn, P.S. 2005. Climate change and amphibians. Animal Biodiversity and Conservation 28:59−67.

Dell, A.I., S. Pawar, and V.M. Savage. 2013. Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. Journal of Animal Ecology 83:70−84.

Duellman, W.E., and L.Trueb. 1986. Biology of Amphibians. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Gibbs, J.P., A.R. Breisch, P.K. Ducey, G. Johnson, J. Behler, and R. Bothner. 2007. The Amphibians and Reptiles of New York State: Identification, Natural History, and Conservation. Oxford University Press, New York, New York, USA.

Gilman, S.E., M.C. Urban, J. Tewksbury, G.W. Gilchrist, and R.D. Holt. 2010. A framework for community interactions under climate change. Trends in Ecology and Evolution 25:325−331.

Hairston, N.G., F.E. Smith, and L.B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist 94:421−425.

Holt, R.D. 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology 12:197−229.

Jara, F.G. 2008. Tadpole-odonate larvae interactions: influence of body size and diel rhythm. Aquatic Ecology 42:503−509.

Jamieson, G.S., and G.G.E. Scudder. 1979. Food consumption in *Gerris* (Hemiptera). Oecologia 30:23−42.

Knight, T.M., M.W. McCoy, J.M. Chase, K.A. McCoy, and R.D. Holt. 2005. Trophic cascades across ecosystems. Nature 437:880−883.

Lawler, S.P. 1989. Behavioral responses to predators and predation risk in four species of larval anurans. Animal Behavior 38:1039−1047.

Livingstone, D.M., and A.F. Lotter. 1998. The relationship between air and water temperatures in lakes of the Swiss Plateau: a case study with paleolimnological implications. Journal of Paleolimnology 19:181−198.

McCollum, S.A., and J.D. Leimberger. 1997. Predator-induced morphological changes in amphibians: predation by dragonflies affects tadpole shape and color. Oecologia 109:615−621.

McLachlan, J.S., J.J. Hellmann, and M.W. Schwartz. 2007. A framework for debate of assisted migration in an era of climate change. Conservation Biology 21:297−302.

Mellanby, K. 1939. Low temperature and insect activity. Proceedings of the Royal Society of London B 127:473−487.

Morin, P.J. 1983. Predation, competition, and the composition of larval anuran guilds. Ecological Monographs 53:119−138.

Morin, P.J. 1986. Interactions between intraspecific competition and predation in an amphibian predator-prey system. Ecology 67:713−720.

Morin, P.J. 1987. Predation, breeding asynchrony, and the outcome of competition among treefrog tadpoles. Ecology 68:675−683.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37−42.

Paulson, D.R. 2001. Recent Odonata records from southern Florida - effects of global warming? International Journal of Odonatology 4:57−69.

Peckarsky, B. L. 1982. Aquatic insect predator-prey relations. BioScience 32:261−266.

Popescu, V.D., and J.P. Gibbs. 2009. Interactions between climate, beaver activity, and pond occupancy by the cold-adapted mink frog in New York State, USA. Biological Conservation 142:2059−2068.

Pounds, J.A. 2001. Climate and amphibian declines. Nature 410:639−640.

Pritchard, G. 1964. Prey capture by dragonfly larvae (Odonata; Anisoptera). Canadian Journal of Zoology 43:271−289.

Relyea, R.A. 2001. Morphological and behavioral plasticity of larval anurans in response to different predators. Ecology 82:523−540.

Relyea, R.A., and E.E. Werner. 1999. Quantifying the relation between predator-induced behavior and growth performance in larval anurans. Ecology 80:2117−2124.

Rouse, W.R., M.S.V. Douglas, R.E. Hecky, A.E. Hershey, G.W. Kling, L. Lesack, P. Marsh, M. McDonald, B.J. Nicholson, N.T. Roulet, et al. 1997. Effects of climate change on the freshwaters of arctic and subarctic North America. Hydrological Processes 11:873−902.

Semlitsch, R.D. 1990. Effects of body size, sibship, and tail injury on the susceptibility of tadpoles to dragonfly predation. Canadian Journal of Zoology 68:1027−1030.

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.

Stefan, H.G., X. Fang, and M. Hondzo. 1998. Simulated climate change effects on year-round water temperatures in temperate zone lakes. Climactic Change 40:547−576.

Tarr, T.L,. and K.J. Babbitt. 2002. Effects of habitat complexity and predator identity on predation of *Rana clamitans* larvae. Amphibia-Reptilia 23:13−20.

Thomas, C.D., A. Cameron, R.E. Green, M. Bekkenes, L.J. Beaumont, Y.C. Collingham, B.F.N. Erasmus, M. Ferreira de Siqueira, A. Grainger, L. Hannah, et al. 2004. Extinction risk from climate change. Nature 427:145−148.

Thompson, 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* (Odonata). Journal of Animal Ecology 47:757−785.

Van der Putten, W.H., M. Macel, and M.E. Visser. 2010. Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. Philosophical Transactions of the Royal Society of London B 365:2025−2034.

Vonesh, J.R., and O. De la Cruz. 2002. Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines. Oecologia 133:325−333.

Vonesh, J.R., and C. Osenberg. 2003. Multi-predator effects across life-history stages: non-additivity of egg and larval-stage predation in an African treefrog. Ecology Letters 6:503−508.

Walther, G., E. Post, P. Convey, A. Menzel, C. Parmesan, T.J.C. Beebee, J. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389−395.

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

Werner, E.E., and M.A. McPeek. 1994. Direct and indirect effects of predators on two anuran species along an environmental gradient. Ecology 75:1368−1382.

Wilbur, H.M. 1976. Density-dependent aspects of metamorphosis in *Ambystoma* and *Rana sylvatica*. Ecology 57:1289−1296.

Wikelski, M., D. Moskowitz, J.S. Adelman, J. Cochran, D.S. Wilcove, and M.L. May. 2006. Simple rules guide dragonfly migration. Biology Letters 2:325−329.

Yang, L.H., and V.H.W. Rudolf. 2010. Phenology, ontogeny and the effects of climate change on the timing of species interactions. Ecology Letters 2010:1−10.

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ELIZABETH HARPER'S research interests include using a combination of field data and ecological modeling to address conservation issues. She also studies the natural history of East African amphibians and recently co-authored a Field Guide to the Amphibians of the Eastern Arc and Coastal Mountains of Tanzania and Kenya. (Photographed by David Patrick).

DAVID PATRICK is a Conservation Biologist whose research focuses on population biology and the effects of habitat alteration on biodiversity. Much of his current research seeks to understand the effects of climate change for range-edge populations and communities. (Photographed by Elizabeth Harper).