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Foraging strategy mediates ectotherm predator–prey responses to climate warming

LAURA A. TWARDOCHLEB,[1,2,5] TYLER C. TREAKLE,[3] AND PHOEBE L. ZARNETSKE[2,4]

[1]*Department of Fisheries and Wildlife, Michigan State University, East Lansing, Michigan 48824 USA*
[2]*Program in Ecology, Evolutionary Biology and Behavior, Michigan State University, East Lansing, Michigan 48824 USA*
[3]*Department of Biology, College of William and Mary, Williamsburg, Virginia 23187 USA*
[4]*Department of Integrative Biology, Michigan State University, East Lansing, Michigan 48824 USA*

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Abstract. Climate warming and species traits interact to influence predator performance, including individual feeding and growth rates. However, the effects of an important trait—predator foraging strategy—are largely unknown. We investigated the interactions between predator foraging strategy and temperature on two ectotherm predators: an active predator, the backswimmer *Notonecta undulata*, and a sit-and-wait predator, the damselfly *Enallagma annexum*. In a series of predator–prey experiments across a temperature gradient, we measured predator feeding rates on an active prey species, zooplankton *Daphnia pulex*, predator growth rates, and mechanisms that influence predator feeding: body speed of predators and prey (here measured as swimming speed), prey encounter rates, capture success, attack rates, and handling time. Overall, warming led to increased feeding rates for both predators through changes to each component of the predator's functional response. We found that prey swimming speed strongly increased with temperature. The active predator's swimming speed also increased with temperature, and together, the increase in predator and prey swimming speed resulted in twofold higher prey encounter rates for the active predator at warmer temperatures. By contrast, prey encounter rates of the sit-and-wait predator increased fourfold with rising temperatures as a result of increased prey swimming speed. Concurrently, increased prey swimming speed was associated with a decline in the active predator's capture success at high temperatures, whereas the sit-and-wait predator's capture success slightly increased with temperature. We provide some of the first evidence that foraging traits mediate the indirect effects of warming on predator performance. Understanding how traits influence species' responses to warming could clarify how climate change will affect entire functional groups of species.

Key words: climate change; freshwater food web; functional traits; Holling Type 2 functional response; hunting mode; metabolic theory of ecology; predation.

INTRODUCTION

Ecologists are challenged with predicting the consequences of climate change on ecological communities. This effort requires understanding how warming affects predators, because changes to predator populations can lead to large consequences across communities through trophic interactions (Zarnetske et al. 2012, Urban et al. 2017). In particular, we require knowledge of how temperature affects individual predator feeding and growth rates (hereafter, *predator performance*) that in turn influence individual predator survival and populations (Vasseur and McCann 2005, Lang et al. 2017). Species traits, such as predator and prey body speed and predator foraging strategy, that modify the effects of temperature on predator performance (Barton and Schmitz 2009, Vucic-Pestic et al. 2011, Öhlund et al. 2014) can help us predict the performance of different predators under climate warming.

Despite recent research into the effects of climate warming on predator foraging (Vucic-Pestic et al. 2011, Öhlund et al. 2014, Culler et al. 2014, Frances and McCauley 2018, Uiterwaal and DeLong 2020), the relationship between predator foraging strategy and temperature remains poorly understood (Dell et al. 2014). Predator foraging strategies include active pursuit whereby predators patrol for prey and sit-and-pursue or sit-and-wait, where predators remain in a fixed location and attack prey that move within their pursuit distance (Preisser et al. 2007). Predators can be especially sensitive to climate change and can amplify its effects on ecological communities (Zarnetske et al. 2012, Urban et al. 2017) by influencing predator–prey population dynamics (Vasseur and McCann 2005), community stability (Paine 1980), and trophic cascades (Shurin et al. 2002). Thus, understanding how predator foraging strategy interacts with temperature to alter predator performance

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[5] E-mail: laura.twardochleb@water.ca.gov

will improve our ability to predict the direct and indirect effects of climate change on ecological communities.

Ectotherms experience especially strong effects of climate warming because rising temperatures alter their metabolism, which in turn influences other biological rates critical to survival, including body speed, feeding, and growth (Gillooly et al. 2001, Brown et al. 2004, Dell et al. 2011, Rall et al. 2012). Over sufficiently large temperature ranges, metabolism and feeding show unimodal responses to temperature, rising with temperature up to a thermal optimum, and declining at very high temperatures (Englund et al. 2011). Metabolic theory suggests that within the rising portion of the unimodal response, ectotherm rates of feeding and growth should scale exponentially with temperature as a result of increasing metabolism, with activation energies (strength of increase with temperature) between 0.60 to 0.70 eV (Brown et al. 2004). However, there is substantial deviation from this expectation in observed rates of predator feeding (Englund et al. 2011, Rall et al. 2012), which suggests that other components of predator–prey interactions, in addition to metabolism, are mediating the effects of temperature (Uiterwaal and DeLong 2020).

By increasing metabolism, prey handling time, the length of time required for a predator to subdue and ingest an individual prey, declines with temperature below the thermal optimum (Englund et al. 2011). Handling time determines the maximum feeding rate for predators with a saturating, Type 2 functional response, and all else being equal, a decrease in prey handling time with temperature increases the predator's functional response (Holling 1959). Through metabolic increases, rising temperatures also increase predator and prey body speed, for example, the swimming speed of aquatic animals (Dell et al. 2011, Grady et al. 2019). Foraging theory indicates that predator and prey body speed mediate a predator's feeding rate by influencing components of its functional response (Holling 1959), including its encounter rate, capture success (the number of successful attacks per encounter), and the attack rate parameter (Holling 1966, McGill and Mittelbach 2006). Specifically, encounter rates increase with predator or prey body speed (Holling 1966, McGill and Mittelbach 2006, Dell et al. 2014). In turn, a predator's attack rate increases with rates of prey encounter and capture success (Holling 1966). All else being equal, the higher the attack rate, the higher the predator's functional response (Holling 1959). Thus, by increasing body speed, warming results in higher encounter rates between predators and prey (Vucic-Pestic et al. 2011, Öhlund et al. 2014), which leads to higher attack rates (given constant capture success), and higher feeding rates (Rall et al. 2012). Little is known from contemporary theory about how warming should influence capture success. However, capture success should increase if the body speed of predators increases more with warming than the escape speed of their prey, whereas capture success should decrease if warming increases prey escape speed more than predator attack speed (Grady et al. 2019).

The effects of temperature on predator metabolism and feeding can either increase or decrease predator individual growth rates. Higher feeding rates can result in faster individual growth rates if prey ingestion exceeds metabolism. However, predator growth rates can decrease at very high temperatures if metabolism exceeds ingestion (Culler et al. 2014, Lang et al. 2017). This process is referred to as a decline in energetic efficiency, whereby the biomass losses from metabolism exceed the biomass gains from feeding, resulting in predator starvation (Lang et al. 2017). Therefore, metabolism and predator and prey body speed mediate the effects of temperature on predator feeding and growth rates.

Ecological theory predicts that foraging strategy is another species trait that should interact with temperature to mediate the effects of climate warming on ectotherm predator feeding and its components of body speed, prey encounter, and attack rates (Dell et al. 2014). This is because actively foraging predators have higher body speeds, rates of prey capture, consumption, and metabolism relative to sit-and-wait predators (Huey and Pianka 1981, Taigen and Pough 1983). Theory predicts that the temperature scaling of active predator encounter and attack rates will depend on the relative temperature scaling of predator and prey body speed (Dell et al. 2014). Theory also predicts that because the body speed of sit-and-wait predators will not vary with temperature, the temperature scaling of sit-and-wait predator encounter and attack rates will depend on the temperature scaling of prey body speed. Therefore, if body speed of active predators and prey increase under warming (Dell et al. 2011), prey encounter rates will also increase, resulting in higher feeding rates for active predators (Dell et al. 2014). Further, warming will increase feeding rates for sit-and-wait predators only if prey body speed (and thus encounter rate) increases with warming (Dell et al. 2014). Although theory also predicts that prey handling time will decrease with warming, the magnitude of decrease is not expected to differ systematically between active and sit-and-wait predators (Dell et al. 2014).

We expect that predator foraging strategy mediates the effects of temperature on ectotherm predator feeding rates through its effects on predator body speed and encounter rate (Dell et al. 2014). All else being equal, we predict that climate warming could be more advantageous for performance of active predators because of their increased body speed and feeding rates. In addition, we propose that foraging strategy mediates the effects of temperature on predator growth rates through its effects on predator metabolism, whereby active predators have higher metabolic rates than sit-and-wait predators because of the metabolic demands of movement during feeding (Huey and Pianka 1981, Taigen and Pough 1983). Therefore, we suggest that metabolism will increase more with temperature for active compared to sit-and-wait predators. If metabolic rates of active predators increase more with warming than feeding rates, this would result in lower energetic efficiencies that reduce individual growth rates and could result in starvation (Lang et al. 2017). Thus, even if feeding rates of active predators are higher relative to sit-and-wait predators, their individual growth rates may be lower because of higher metabolic rates (Huey and Pianka 1981, Taigen and Pough 1983), potentially leading to smaller population sizes or local extinction in warmed conditions (Vasseur and McCann 2005).

Here, we examine the relationships between foraging strategy and temperature on ectotherms using pairwise interactions from a three-species aquatic community module (sensu Paine 1980), consisting of an active prey species, the water flea *Daphnia pulex*, an active predator, the backswimmer *Notonecta undulata*, and a sit-and-wait predator, the damselfly *Enallagma annexum*. Our work provides one of the first tests of recent theory (Dell et al. 2014) predicting how foraging strategy mediates the effects of temperature on predator feeding. We test the following hypotheses with a series of predator–prey experiments across a temperature gradient where we measure each predator's individual growth rate and functional response to prey. As temperature increases, we expect:

> H1: Swimming speed of the active predator and prey will increase as a result of increasing metabolism.
> H2: Prey encounter rates and capture success will increase more strongly for the active predator than for the sit-and-wait predator as a result of the active predator's faster swimming speed.
> H3: Prey attack rates will increase more for the active predator than the sit-and-wait predator as result of the active predator's higher prey encounter rate and capture success.
> H4: Prey handling time will decrease by a similar magnitude for the active and sit-and-wait predator.
> H5: Individual growth rates of the active predator will increase less than growth rates of the sit-and-wait predator as a result of the active predator's higher metabolism.

METHODS

Aquatic community module

Notonecta (Hemiptera: Notonectidae) are piercing-sucking predators that actively hunt by swimming toward and grasping prey (Fox 1975). *Enallagma* (Odonata: Coenagrionidae) are engulfing predators that hunt from aquatic plants by waiting for prey to move within striking distance of their labium, a prehensile mouthpart for grasping (Merritt and Cummins 1996). *Daphnia* (Cladocera: Daphniidae) are actively swimming prey that compose a large proportion of the diet of nymphal *Notonecta* and *Enallagma* (Lawton 1970, Scott and Murdoch 1983). Our community module is well suited to address the interactions between foraging strategy and temperature, because all three species coexist in shallow ponds (Hanly 2017, Twardochleb, *unpublished data*) where predators share prey resources, and are of similar body sizes (McPeek and Crowley 1987, Gergs and Ratte 2009). Therefore, this community module can provide insight into how temperature influences measures of predator performance among species that differ in foraging strategy, but otherwise share similar ecological requirements and local adaptation to temperature.

Predator functional response experiments

We conducted functional response experiments to quantify relationships between predator feeding rates and temperature (H3 and H4), and we analyzed video recordings of these experiments to assess how temperature affects predator and prey swimming speed (H1), and encounter rates and capture success (H2). Experiments were conducted from July to October 2017 at Kellogg Biological Station in southwestern Michigan, USA. We collected predators and prey from fishless ponds in Lux Arbor Reserve, Barry County, Michigan and acclimated them to laboratory conditions at 20°C until their first molt (several days to 2 weeks), then placed them inside an environmental growth chamber (I36LLVL, Percival Scientific, Perry, Iowa, USA) set to 10, 15, 20, 25, 30, or 35°C, which encompassed the mean (24°C) and range (10–31°C) of ambient pond temperatures during spring to fall, and one temperature (35°C) above ambient. We monitored chamber temperature using HOBO pendant temperature loggers (UA-001-64, Onset Corporation, Bourne, Massachusetts, USA). We fed predators pond zooplankton and allowed them to acclimate to a given temperature for 24 h (Thompson 1978), and we then deprived them of food to standardize hunger levels. We acclimated *Daphnia* to a given temperature for 2 h prior to trials (Thompson 1978).

For *Notonecta* trials, we used densities of 10, 20, 50, and 100 *Daphnia* per liter. For *Enallagma* trials, we used densities of 5, 10, 20, 50, and 100 *Daphnia* per 100 milliliter for 10–20°C, and 5, 10, 20, 50, 100, and 150 *Daphnia* per 100 milliliter for 25–35°C. Prey densities were determined from preliminary trials in 2016 and 2017 in order to capture the shape of the functional response curve. For each trial, we placed an individual predator into an experimental arena with *Daphnia* for 1 h inside an environmental chamber. We quantified the number consumed as the difference between initial and final prey densities, including a correction for errors in enumerating *Daphnia*. We replicated each prey density at every temperature at least four times for a total of 100 trials for *Notonecta* and 158 trials for *Enallagma*. Methods followed those commonly used in functional response experiments (e.g., Thompson 1978, Vucic-Pestic et al. 2011).

Testing H1: Video analysis of predator and prey swimming speed

We video recorded functional response experiments at each temperature for *Notonecta* (29 total) and *Enallagma* (30 total) to test H1 and H2. Speed (cm/s) for *Notonecta* (28 total) and *Daphnia* (24 total) was quantified using Tracker Video Analysis software.[6] We calculated *Daphnia* speed over 20-s intervals three times during each trial by tracking the *Daphnia* closest to the center of the experimental arena. We averaged these three speeds by trial. *Notonecta* speed was calculated by accounting for two distinct swimming patterns; short bursts lasting 1–2 s each that were associated with attacks, and longer "patrolling" movements lasting 3–5 s each that occurred between bouts of attacking and consuming prey. We analyzed the relationship between *Notonecta* speed and temperature individually for "burst" and "patrolling" movements but found no effect of temperature on "burst" swimming speed (see Appendix S1: Tables S2 and S3).

Testing H2: Video analysis of encounter rates and capture success

We quantified encounters as the number of reactive plus nonreactive encounters. A reactive encounter was any instance when a predator visibly reacted to prey, and a nonreactive encounter was when prey moved within the predator's reactive distance, but the predator did not react visibly. We used a reactive distance of a 4 * 1 cm rectangle around *Notonecta* (Giller and McNeill 1981), and a 0.5-cm-radius circle around *Enallagma* (Johansson 1993). We quantified capture success as the number of successful attacks per encounter (reactive and nonreactive) (Holling 1966).

Testing H3 and H4: Prey attack rates and handling time from functional response experiments

We fit separate, Type 2 functional response curves (Holling 1959) to feeding data for each predator species and each temperature using Rogers' random predator equation to account for prey depletion (Rogers 1972):

$$N_c = N\left(1 - e^{-a(t - hN_c)}\right). \tag{1}$$

here, N_c is the number of prey consumed (per hour), N is prey abundance, a is the attack, or search rate (L/h), and h is handling time. We used the 'frair' R package (Pritchard et al. 2017) to fit the lambert w version of Eq. 1 using maximum-likelihood estimation (Bolker 2008). See Appendix S1: Table S1 for fits of Eq. 1 to feeding data.

We used estimates of a and h (Eq. 1) to test H3 and H4. We fit three models to describe the temperature dependence of a and h for each predator: an intercept (Eq. 2), an exponential (Eq. 3), and a quadratic model (Eq. 4). The intercept model describes no effect of temperature on the biological rate of interest Y (in this case, a or h):

$$Y = c. \tag{2}$$

here, c is the model intercept.

The Arrhenius equation (Gillooly et al. 2001) describes the temperature dependence of biological reaction rates for temperatures below thermal optima (Englund et al. 2011):

$$Y = ce^{E_a\left(-\frac{1}{kT}\right)} \tag{3}$$

where c is a fitted constant, E_a is the activation energy (eV) describing the strength of the temperature response, k is Boltzmann's constant (8.617×10^{-5} eV), and T is temperature (K). We also fit the Arrhenius–quadratic model describing the temperature dependence of biological rates for temperatures below and above thermal optima (Englund et al. 2011):

$$Y = ce^{b\left(-\frac{1}{kT}\right)+q\left(\frac{-1}{kT}\right)^2}. \tag{4}$$

Here, c, b (eV), and q (eV^2) are fitted parameters. Models were fit using linear regression in R, and regression fits were weighted by the inverse of the standard error around each estimate of a and h (n = 6 estimates of a and h per predator, n = 1 estimate per temperature, per predator).

Testing H5: Predator growth experiments

We ran experiments to quantify relationships between temperature and predator individual growth rates, from July to September 2018. Our temperature gradient included 10, 15, 20, 25, 30, or 35°C. Predators were collected and acclimated the same way as above (see Testing H1: Predator functional response experiments). We measured initial wet mass by gently blotting predators dry on a paper towel and weighing them (±0.01 mg) on a microbalance (Sartorius XM1000P, Goettingen, Germany). We then fed each predator *Daphnia* for 3 (*Notonecta*) or 4 (*Enallagma*) d. Each predator was fed ad libidum by ensuring that we fed enough *Daphnia* to recover at least two individual *Daphnia* the following day (5–50 *Daphnia*/d; Culler et al. 2014). After 3 or 4 d of feeding, we deprived predators of food to allow for gut evacuation, blotted them dry, and then weighed them for final wet mass. We then dried predators for 24 h at 60°C and weighed them again for final dry mass. We calculated the relationship between wet and dry mass using linear regression (*Notonecta*: final dry mass =

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[6] https://physlets.org/tracker/.

0.0033 + 0.94 * final wet mass, $R^2 = 0.98$; *Enallagma*: final dry mass = −0.61 + 0.22 * final wet mass, $R^2 = 0.75$), and used this relationship to calculate initial and final dry mass for the trials (McPeek and Anholt 2004). We then calculated daily relative growth rate (RGR) as

$$\mathrm{RGR} = \frac{[(\text{final dry mass}) - (\text{initial dry mass})]}{[(\text{trial length(days)}) * (W_e^m)]} \tag{5}$$

where W_e is the exponential mean dry mass and m is an allometric scaling exponent that accounts for the effect of body size on growth rate (Gordon 1968). The exponential dry mass accounts for the fact that insect growth rates are exponential rather than linear. Rather than dividing the mass change by the mean dry mass of the organism, we divide by the exponential dry mass to obtain mass-specific growth rates. We set m equal to −0.34 (Niven and Scharlemann 2005). We replicated each temperature treatment six times for *Notonecta* (36 trials) and seven times for *Enallagma* (42 trials). We used estimates of *RGR* (Eq. 5) to test H5.

Statistical analyses

We used analysis of variance (ANOVA) to test whether biological rates varied with temperature and between predator species. We tested whether *Notonecta* or *Daphnia* speed varied with temperature using one-way ANOVA with temperature as the predictor. We used two-way ANOVA with temperature and predator species as predictors, and encounter rate, capture success, or *RGR* as responses. Data were log transformed as needed to meet assumptions of normality and homoscedasticity. For significant ANOVA models, we ran Tukey's HSD to test pairwise differences between temperature and predator species. We also assessed temperature effects by fitting intercept (Eq. 2), Arrhenius (Eq. 3), and Arrhenius–quadratic (Eq. 4) models for encounters, capture success, attack rates, handling time, and growth rates. We also fit intercept and Arrhenius models for *Notonecta* and *Daphnia* swimming speed, and a segmented Arrhenius model for *Daphnia* swimming speed. We fit the segmented model using maximum likelihood estimation (MLE) with the 'Segmented' R package (Muggeo 2008). We used Akaike's information criterion corrected ($\mathrm{AIC_c}$) for small sample sizes to select the best-fitting model (see Appendix S1: Table S2), except in the case of the segmented Arrhenius model. To compare models fit using ordinary least squares (intercept and Arrhenius) and MLE (segmented), we selected the model with the lowest residual variation and $\mathrm{AIC_c}$ value, and the highest R^2 (Appendix S1: Table S4). When the Arrhenius equation was selected as the best model, we based inference on whether 95% confidence intervals for E_a (Eq. 3) overlapped zero or overlapped between predators. All analyses were implemented in R Version 3.5.1 (R Development Core Team 2018). Significance levels for all models were set to 0.05.

For more details on the experimental methods described above, see Appendix S1.

RESULTS

Testing H1: Video analysis of predator and prey swimming speed

Prey *Daphnia* swimming speed (cm/s) increased with temperature (ANOVA, $F_{5,18} = 16.73$, $P < 0.01$; Tukey's HSD; Appendix S1: Table S5). A segmented Arrhenius model with a breakpoint of 28.36 ± 1.46 (°C ± 1 SE) provided the best fit to the relationship between *Daphnia* speed and temperature (Fig. 1; Appendix S1: Table S3, S4). We found an activation energy $E_a = 0.11 \pm 0.06$ (eV ± 1 SE) at temperatures below the breakpoint, and $E_a = 1.04 \pm 0.23$ (eV ± 1 SE) above the breakpoint. The Arrhenius equation was the best fit to the relationship between temperature and "patrolling" speed of the active predator *Notonecta* (Fig. 1; Appendix S1: Table S2, S3), but ANOVA indicated no strong differences in speed among temperatures ($F_{5,22} = 0.83$, $P = 0.55$).

Testing H2: Video analysis of encounter rates and capture success

Prey encounters, quantified as an hourly rate at a density of 20 *Daphnia* per liter ($\mathrm{h^{-1}}$ 20 *Daphnia* $\mathrm{L^{-1}}$), differed across the temperature range ($F_{5,44} = 12.19$,

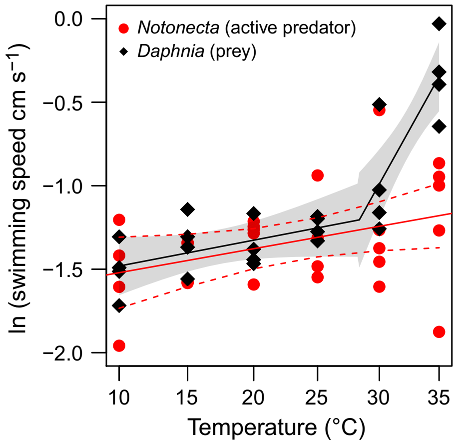

FIG. 1. The Arrhenius equation provided the best fit for the relationship between temperature and swimming speed (cm/s) of *Notonecta*, with slope E_a (activation energy, eV ± 1 SE) = 0.10 (±0.05). A segmented model provided the best fit for *Daphnia*, with a breakpoint near 28°C, $E_a = 0.11$ (± 0.06) at temperatures below the breakpoint, and $E_a = 1.04$ (± 0.23) above the breakpoint. The 95% confidence intervals around the best-fit line are represented by gray bands for *Daphnia* and broken red lines for *Notonecta*.

$P < 0.01$; Appendix S1: Table S6), between the active predator *Notonecta* and sit-and-wait predator *Enallagma* ($F_{1,44} = 971.52$, $P < 0.01$), and there was an interaction between temperature and predator species on encounter rates ($F_{5,44} = 2.92$, $P = 0.02$). *Notonecta* had more prey encounters than *Enallagma* at all temperatures, and *Enallagma* had more encounters at higher than lower temperatures (Fig. 2a; Appendix S1: Table S7). *Enallagma* had a fourfold increase in prey encounters between 10 and 35°C, compared to a twofold increase for *Notonecta* (Fig. 2). The fit of the Arrhenius equation revealed that E_a for encounters was greater for *Enallagma* than *Notonecta* (Fig. 2a; Appendix S1: Table S3). There were nonoverlapping 95% confidence intervals for E_a (*Notonecta*: 0.06–0.23, *Enallagma*: 0.30–0.66), indicating a stronger increase in *Enallagma*'s encounter rate with warming.

Capture success (number of successful attacks per encounter) varied between predators ($F_{1,44} = 49.64$, $P < 0.01$) and was higher overall for *Enallagma* than *Notonecta* (Fig. 2b). Although there was not an overall effect of temperature on capture success ($F_{5,44} = 0.60$, $P = 0.70$), the Arrhenius–quadratic model (Eq. 3) provided the best fit to the relationship between capture success and temperature for *Notonecta*, and the Arrhenius equation provided the best fit for *Enallagma* (Fig. 2 b; Appendix S1: Table S2, S3). This indicates that *Enallagma* capture success increased slightly with temperature, but *Notonecta* capture success increased up to a thermal optimum of 22.64 ± 0.01 (°C ± 1 SE), and then declined. There was no strong interactive effect of temperature and predator species on capture success ($F_{5,44} = 0.99$, $P = 0.43$).

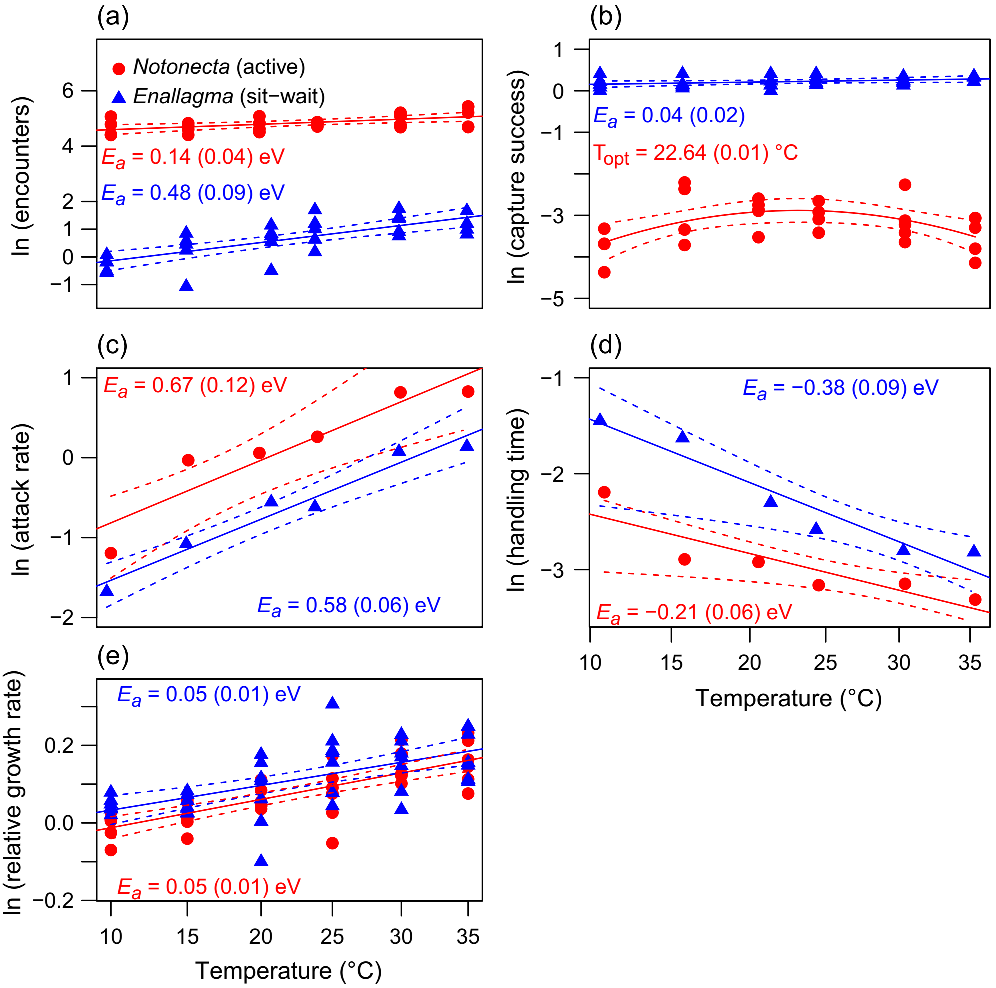

FIG. 2. Relationships between temperature, functional response components, and growth rates. (a) Best fit lines of the Arrhenius equation for encounters (per h 20 *Daphnia* per L ± 1 SE); (b) fit of the Arrhenius equation for capture success (number of successful attacks per encounter) of *Enallagma*, and the Arrhenius–quadratic equation for *Notonecta*; (c) Arrhenius fit for attack rates (L/h), (d) handling time (h), and (e) relative growth rates (mg mg$^{0.34}$/d). E_a (eV ± 1 SE) is the activation energy, and T_{opt} (°C ± 1 SE) is the thermal optimum. Broken lines represent 95% confidence intervals.

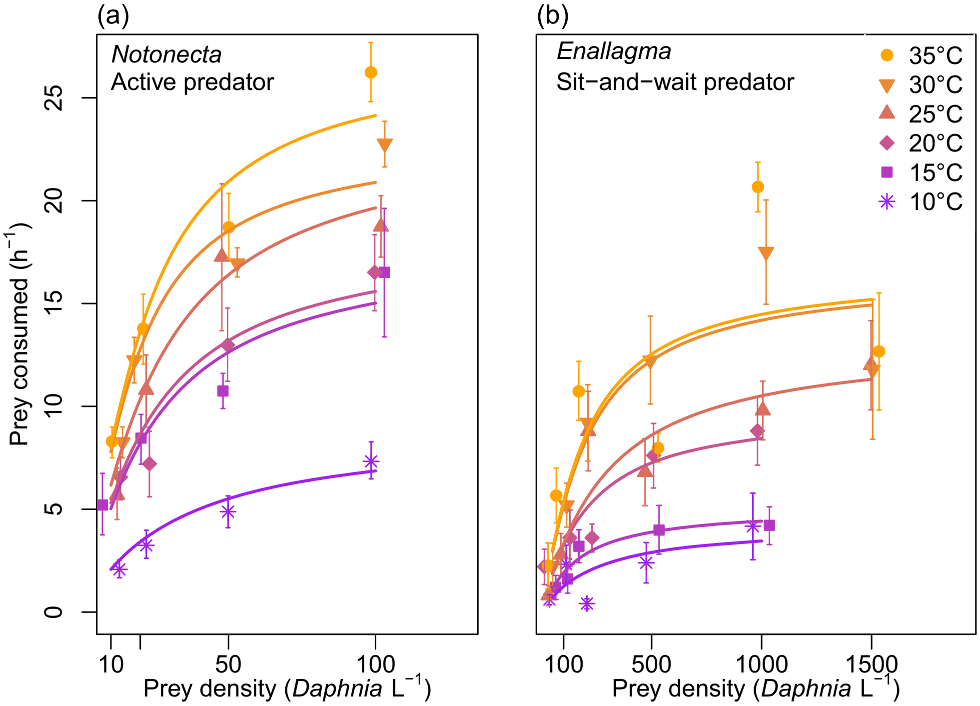

FIG. 3. Functional responses at each temperature for (a) *Notonecta* and (b) *Enallagma.*

Testing H3: Prey attack rates from functional response experiments

Predator functional responses (Eq. 1) increased with temperature for both predators (Fig. 3). However, functional responses of *Notonecta* saturated at tenfold lower prey densities than functional responses of *Enallagma* (Fig. 3). Attack rates were higher for *Notonecta* than *Enallagma*, but their attack rates increased by a similar magnitude with warming (Fig. 2c; Appendix S1: Table S3). The 95% confidence intervals for E_a (Eq. 2) overlapped between predator species (*Notonecta*: 0.33 to 1.01, *Enallagma*: 0.42 to 0.73). Attack rates from video observations supported these results (Appendix S1: Tables S2, S3).

Testing H4: Handling time from functional response experiments

Although handling time was lower for *Notonecta* than *Enallagma* across all temperatures (Fig. 2d), handling time of *Enallagma* decreased more with warming (Appendix S1: Table S3). However, predators had overlapping 95% confidence intervals for E_a (Eq. 3) of handling time (*Notonecta*: −0.05 to −0.36, *Enallagma*: −0.13 to −0.62), which indicates that the rate of change in handling time with warming did not differ significantly between the two predators.

Testing H5: Predator growth experiments

Predator *RGR* (Eq. 4; mg mg$^{0.34}$/d) increased with temperature (Fig. 2e; $F_{5,67} = 15.88$, $P < 0.01$; Appendix S1: Table S7) and differed between predator species ($F_{1,67} = 475.60$, $P < 0.01$), but there was no interaction between temperature and predator species ($F_{5,67} = 1.02$, $P = 0.4$). *Enallagma* had an overall higher *RGR* than *Notonecta* (Fig. 2e). The Arrhenius equation provided the best fit to the relationship between *RGR* and temperature for *Notonecta* and *Enallagma* (Fig. 2e; Appendix S1: Table S2, S3). Overlapping 95% confidence intervals for E_a (*Notonecta*: 0.04–0.07, *Enallagma*: 0.02–0.06) indicate that *Notonecta* and *Enallagma* experienced a similar magnitude of increase in *RGR*.

DISCUSSION

We found that both predators—*Notonecta* and *Enallagma*—increased their feeding rates with temperature (Fig. 3) as a result of changes to each component of the functional response, including predator and prey swimming speed, encounter rates, capture success, attack rates, and handling time. Prey swimming speed increased with warming according to a segmented Arrhenius function (Fig. 1), which is consistent with other studies demonstrating that body speed can show biphasic responses to increasing temperature (Gibert et al. 2016). This overall increase in prey swimming speed increased encounter rates with both predators (Fig. 2). The active predator also increased its swimming speed (Fig. 1), which further contributed to increases in its prey encounter rate (Fig. 2). However, the increase in prey swimming speed more strongly influenced the encounter rate with the sit-and-wait predator; whereas the encounter rate with the active predator increased twofold with warming, the encounter rate with the sit-and-wait predator increased fourfold (Fig. 2). In addition, increasing prey speed may have contributed to a decline in capture success for the active predator at high temperatures, whereas the sit-and-wait predator experienced a slight increase in capture success. The predators experienced similar increases in attack rates and individual growth rates and decreases in handling time with increasing temperatures (Fig. 2).

Foraging strategy and prey body speed mediate the effects of warming

Feeding rates of sit-and-wait predators have been found to increase with warming when they forage for active prey (Culler et al. 2014, Frances and McCauley 2018) but not inactive prey (Novich et al. 2014). Thus, if prey speed remains constant or declines in warm climates, sit-and-wait strategies could be less energetically efficient because their encounter and feeding rates may not increase enough to offset their higher metabolism. By contrast, active predators are affected by their own body speed as well as prey speed. Therefore, when temperatures rise, active predators may be able to increase their encounter and feeding rates whether they are foraging for mobile or immobile prey (e.g., Vucic-Pestic et al. 2011, Öhlund et al. 2014) by increasing their own body speed. If prey speed does not increase with temperature, active predators could gain a relative performance advantage over sit-and-wait predators at high temperatures.

Foraging strategy and prey body speed also mediated capture success. Whereas the active predator's capture success declined at high temperatures, the sit-and-wait predator was successful at all temperatures, and its success increased somewhat with warming. This increase may have been because of unmeasured changes in predator movement that could influence capture success, such as faster protrusion of the labium, the raptorial appendage that damselflies use to capture prey. Overall, our observations suggest that the sit-and-wait predator may have had higher capture success because it was less detectable than the active predator. We observed that *Daphnia* moved away from the active predator as it approached but moved away from the sit-and-wait predator only after an unsuccessful attack, as prey were apparently unaware of the predator's location prior to the attack. Studies in aquatic environments have shown that prey rely on visual cues to assess predator location and risk. Prey respond to these visual cues through reduced activity and escape responses (Hall and Clark 2016, Fischer et al. 2017).

Given that prey detect predator movement as a predation risk, capture success may have decreased with warming for the active predator by two mechanisms: (1) active predators are more likely to be detected by prey because they are moving, and (2) prey's escape ability was enhanced because of their faster body speed. This is supported by the fact that the active predator's "burst" swimming speed (associated with prey attacks) remained constant, whereas the prey's swimming speed increased with warming (Appendix S1: Tables S2, S3). Our results are consistent with previous research showing that warming increases swimming speed of *Daphnia* (Ziarek et al. 2011) but contrast with other findings of predator body speed increasing more with temperature than prey speed (Dell et al. 2011). Our results are also consistent with studies showing that capture success decreases when prey relative speed increases with warming (Grigaltchik et al. 2012, Grady et al. 2019). Knowledge of the thermal responses of prey body speed is thus necessary to predict the outcomes of warming on predator–-prey interactions.

We found that attack rates of the active predator increased with temperature with an activation energy of 0.67 eV (Fig. 3). However, encounter rate showed a weaker temperature scaling of 0.14 eV, and capture success decreased at high temperatures. These results suggest that unmeasured components of foraging, such as hunger, could have contributed to the increase in attack rates with warming. In addition, we did not test whether prey body speed responded differently to temperature between the two predators, which could have contributed to differences in the temperature scaling of their encounter rates. Unequal prey reaction distances may also have contributed to overall differences in encounter rate between the two predators (Holling 1966, Pawar et al. 2012). Further, we used different sizes of experimental venue for each predator species in order to achieve target prey densities and saturating functional responses (Appendix S1, Fig. 3). Because prey density is a primary determinant of encounter rate (Holling 1966, Pawar et al. 2012), the higher prey densities used for *Enallagma* (Fig. 3) could have increased its prey encounter rates relative to *Notonecta* and also affected its capture success. Despite this, we found that *Enallagma* had much lower prey encounter rates relative to *Notonecta* (Fig. 2). Other components of predator and prey biology may also influence how climate changes alter predator performance (Grady et al. 2019, Uiterwaal and DeLong 2020).

Our experiments used a single species of prey, and a single species of sit-and-wait and active predator. Therefore, our results may have been due to species-specific differences in temperature responses rather than differences in foraging strategy. We believe that additional research will reveal that foraging strategy affects species'

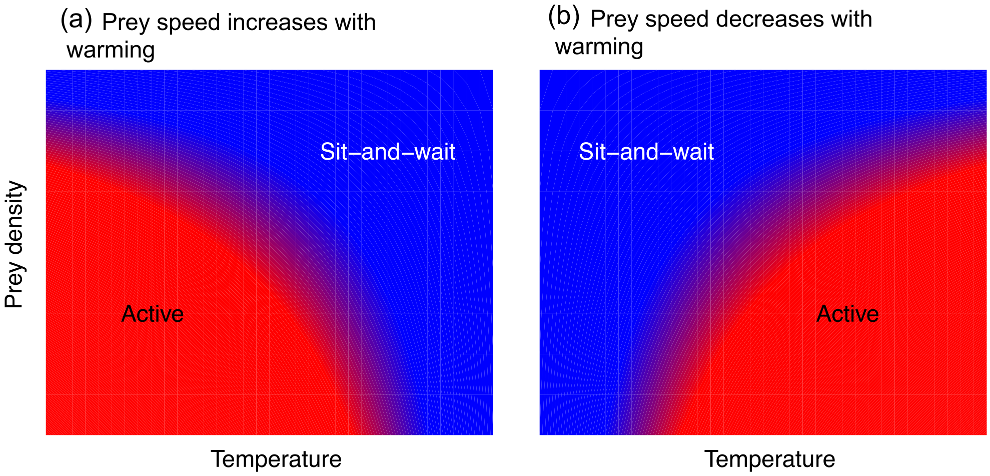

Fig. 4. Hypothesized combinations of temperature and prey density that should favor active or sit-and-wait strategies. (a) When prey speed increases with warming, active strategies could be advantageous at low temperatures when prey density is low. Sit-and-wait strategies could be advantageous at high temperatures when prey density is high. (b) When prey speed decreases with warming, active strategies could be favored at high temperatures when prey density is low. Sit-and-wait strategies could be favored at low temperatures when prey density is high.

responses to climate warming in predictable ways (e.g., Barton and Schmitz 2009, Archer et al. 2019). At present, more research using multiple species of active and sit-and-wait predator is needed to validate our results and predictions of theory (Dell et al. 2014). We outline below additional hypotheses that could be tested to reveal the influences of predator foraging strategy and prey body speed on predator performance at different temperatures and prey densities.

Conclusions

Foraging differences between active and sit-and-wait predators could scale up to influence their relative performance in environments that differ in prey density and temperature. We found that attack rates were higher overall for the active predator at 10-fold lower prey densities relative to the sit-and-wait predator (Figs. 2 and 3). In addition, encounter rates of the sit-and-wait predator were strongly affected by prey body speed, whereas encounter rates of the active predator were affected by predator and prey body speed. Our results support previous observations and theory predicting that active predators will gain a relative performance advantage when prey speed and density are low, and that sit-and-wait strategies will be advantageous when prey speed and density are high (Huey and Pianka 1981, Werner and Anholt 1993, Ross and Winterhalder 2015). In addition, we found that the sit-and-wait predator was more energetically efficient, because it had higher growth rates despite lower feeding rates (Fig. 2). This supports research showing that actively foraging species have higher metabolic rates than related sit-and-wait species (Huey and Pianka 1981, Taigen and Pough 1983). Taken together, this evidence suggests that sit-and-wait predators may be more efficient in high-prey-density environments, where their lower metabolism results in higher growth rates. Thus, we hypothesize that when prey speed increases with warming, active strategies should be relatively advantageous at low temperatures when prey density is low, whereas sit-and-wait strategies should be advantageous at high temperatures when prey density is high (Fig. 4a). If prey speed decreases with temperature, active strategies should be advantageous at high temperatures when prey density is low, and sit-and-wait strategies should be advantageous at low temperatures when prey density is high (Fig. 4b).

Tests of these hypotheses could improve trait-based assessments of predator performance under climate change. Indirect effects of warming on predator performance could influence predator persistence and population dynamics (Vasseur and McCann 2005), and food web structure and stability (Gilbert et al. 2014). Knowledge of trait-mediated effects of temperature on predators could also help predict ecosystem responses to climate change, because sit-and-wait and actively foraging predators have different effects on ecosystem functions that may strengthen with warming (Barton et al. 2009). Ultimately, knowledge of how foraging traits mediate the effects of temperature on predator performance can help clarify how climate change will affect entire functional groups of species.

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Supporting Information

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