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Global change biology

Cannibalism by damselflies increases with rising temperature

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Trophic interactions are likely to change under climate warming. These interactions can be altered directly by changing consumption rates, or indirectly by altering growth rates and size asymmetries among individuals that in turn affect feeding. Understanding these processes is particularly important for intraspecific interactions, as direct and indirect changes may exacerbate antagonistic interactions. We examined the effect of temperature on activity rate, growth and intraspecific size asymmetries, and how these temperature dependencies affected cannibalism in *Lestes congener*, a damselfly with marked intraspecific variation in size. Temperature increased activity rates and exacerbated differences in body size by increasing growth rates. Increased activity and changes in body size interacted to increase cannibalism at higher temperatures. We argue that our results are likely to be general to species with life-history stages that vary in their temperature dependencies, and that the effects of climate change on communities may depend on the temperature dependencies of intraspecific interactions.

1. Introduction

One of the most pressing challenges for ecologists is to predict the effects of global climate change on species interactions [1]. Temperature has been shown to alter species interactions [2], and theoretical research has attempted to link these shifts in interactions with temperature dependencies of vital rates (e.g. [3]). While species' temperature sensitivities have been useful for understanding shifts in interspecific interactions, they have rarely been used to account for shifts in intraspecific dynamics [4]. However, early studies on intraspecific interactions suggest that temperature can have profound impacts on population dynamics [4,5].

Cannibalism is an important intraspecific interaction common to many size-structured populations [6]. Cannibalism can have strong impacts on population dynamics because it introduces trophic structure within a single population [6,7], which can have dramatic effects on prey communities [8]. Research suggests that cannibalism rates may be influenced by temperature [9]; however, despite the importance of cannibalism for both population- and community-level processes, the mechanisms through which temperature alters cannibalism have not been thoroughly assessed.

Temperature can alter cannibalism rates via several mechanisms. Behavioural changes are common when temperature increases, and can have important implications for trophic interactions. For example, Barton & Schmitz [10] demonstrated that warming altered spider foraging behaviour and intraguild predation, and ultimately caused the extinction of one spider species. More generally, activity rate often increases with temperature [11], which can increase encounter rates and intensify trophic interactions [1]. Analogously, an increase in encounter rate mediated by elevated temperatures is likely to increase cannibalism [5].

Temperature can also alter cannibalism through its effect on growth and size asymmetries among individuals within a population. Cannibalism is often associated with size-structured populations created by differences in hatching time [6], with large individuals feeding on small individuals [6,7]. Variation in

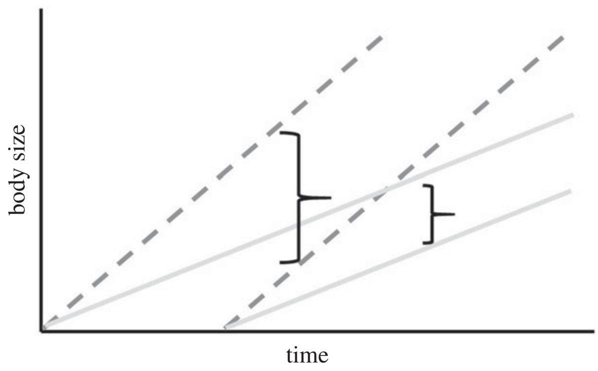

Figure 1. Temperature increasing growth rates and differences in body size when emergence time is temperature-independent. Individuals grow more quickly at high (dark-grey) than low (light-grey) temperatures. Increased growth rate exacerbates existing differences in body size (shown by parentheses) stemming from differences in birth/hatching time.

hatching or emergence time frequently creates cohorts independently of temperature, as is the case for obligately biennial and multi-annual populations, or if emergence time is temperature-independent (e.g. [12,13]). However, growth rates following hatching are accelerated at higher temperatures when species are below their thermal maxima [14], allowing greater growth between cohorts. As a result, coupling temperature-independent hatching or emergence with temperature-dependent growth rates should exacerbate size differences among cohorts (figure 1) and set the stage for increased cannibalism.

We tested for the effects of temperature and size-structure on cannibalism using larval *Lestes congener*, damselflies that have variable hatching dates determined by location of oviposition on grasses surrounding ponds, rather than temperature [13]. Our study tested the aforementioned ideas by hypothesizing that (i) activity rates will be elevated at high temperatures, (ii) differences in body size among individuals will be larger at higher temperatures and (iii) cannibalism will increase at higher temperatures owing both to increased activity rates and larger differences in body size.

2. Material and methods

We tested for the effects of temperature and age-structure on cannibalism using the damselfly *L. congener*. Eggs are laid on grasses surrounding ponds, and hatching is controlled by rising water in spring rather than temperature, causing variation in hatching date to occur when eggs are different distances above the pond [13]. By staggering when eggs are wetted, we can produce cohorts with the same history from the same conditions [13].

We collected eggs in November 2015 from a pond at Koffler Scientific Reserve, Canada, by sampling grass stems onto which females had oviposited. Stems were kept outside until the beginning of the experiment. Beginning on 14 January 2016, we created four age-cohorts of damselflies spaced 5 days apart by placing vegetation with eggs into pools of artificial *Daphnia* medium (ADaM; [13]). Pools were kept in a growth chamber at 18°C with a 16 L : 8 D cycle. After the first hatching (approx. 12 days), we transferred damselflies into the experiment described below. We consider the hatching of the first damselfly from the first cohort as day 0 of the experiment.

(a) Experimental design

We tested for the effects of temperature and size-structure on cannibalism. Two damselflies were introduced to cylindrical plastic containers (14 cm high × 11.5 cm diameter; large nymphs are less than 3 cm long) filled with 850 ml of ADaM and one strip of mesh to provide habitat structure (5 × 10 cm, 0.66 mm mesh; [13]). To create variation in size-structure, we introduced one damselfly hatched on day 0, and another hatched on day 0, 5, 10 or 15. Each size-structure treatment was replicated 30 times, then divided equally between two temperatures (18°C and 24°C). These temperatures are realistic water temperatures during the summer when nymphs are in ponds (S. McCauley 2017, personal communication). Nymphs were fed approximately 25 brine shrimp three times per week [13].

We checked the replicates bi-weekly for dead or cannibalized nymphs. We recorded cannibalism if there were clear signs of chewing, as nymphs do not feed on dead prey [13]. To quantify the effect of our treatments on body size, we measured head width (the standard measure of size in gape-limited odonates; [13]) of all individuals on days 0 and 44 using ImageJ software. We estimated larval activity rate using an open field test that quantifies movement [13]. We removed focal individuals from mesocosms, then placed them in 9 cm Petri dishes filled with ADaM from the focal mesocosm on day 45 of the experiment. We then checked the position of each individual every 20 min for 3 h (10 observations), counting the number of times the focal individual moved between squares in a 2 × 2 cm grid drawn on the bottom of the dish [8] before returning all individuals to the cannibalism experiment. We ended the experiment after 97 days when all replicates had either zero or one individual remaining.

(b) Statistical methods

We used a series of generalized linear mixed-effects models (GLMM) to test for the effects of temperature and hatch date (timing) on activity, growth rates and cannibalism. Because all replicates had at most one individual at the end of the experiment, we calculated cannibalism rate as 1/(weeks until cannibalism), and replicates without cannibalism recorded were assigned a rate of zero. We then tested whether cannibalism rate was predicted by temperature and timing using a LM.

We then aimed to elucidate the proximate mechanisms driving differences in cannibalism across treatments. We estimated activity rate using a GLMM with a Poisson distribution (count data of number of times an individual moved between 2 × 2 cm^2) and a log-link function, including temperature and timing as main effects and replicate as a random effect. We tested for differences in growth rate by estimating differences in body size (head width) among treatments. We used a LMM including temperature and timing as main effects, and replicate as a random effect.

We then used a LMM to test if cannibalism rate was predicted by activity, body size differences, and their interaction, again including replicate as a random effect. We used log-likelihood ratios to test for significance of all models, with likelihoods determined from the maximum-likelihood solution. Statistical analyses were conducted in R (v. 3.1.1, 2014) using the base and the 'lme4' packages [15].

3. Results and discussion

Increased temperature elevated rates of intraspecific predation both directly and indirectly, causing sevenfold differences in cannibalism rates with 65% of all replicates experiencing cannibalism. Cannibalism increased with temperature ($p < 0.001$) and variation in hatching time ($p < 0.001$), particularly at high temperatures (timing × temperature: $p = 0.011$, figure 2*a*). These patterns were produced by two mechanisms. First, activity rates increased with temperature ($p = 0.002$, figure 2*b*), presumably increasing encounter rates and cannibalism ($p < 0.001$, figure 2*d*). High temperature increased

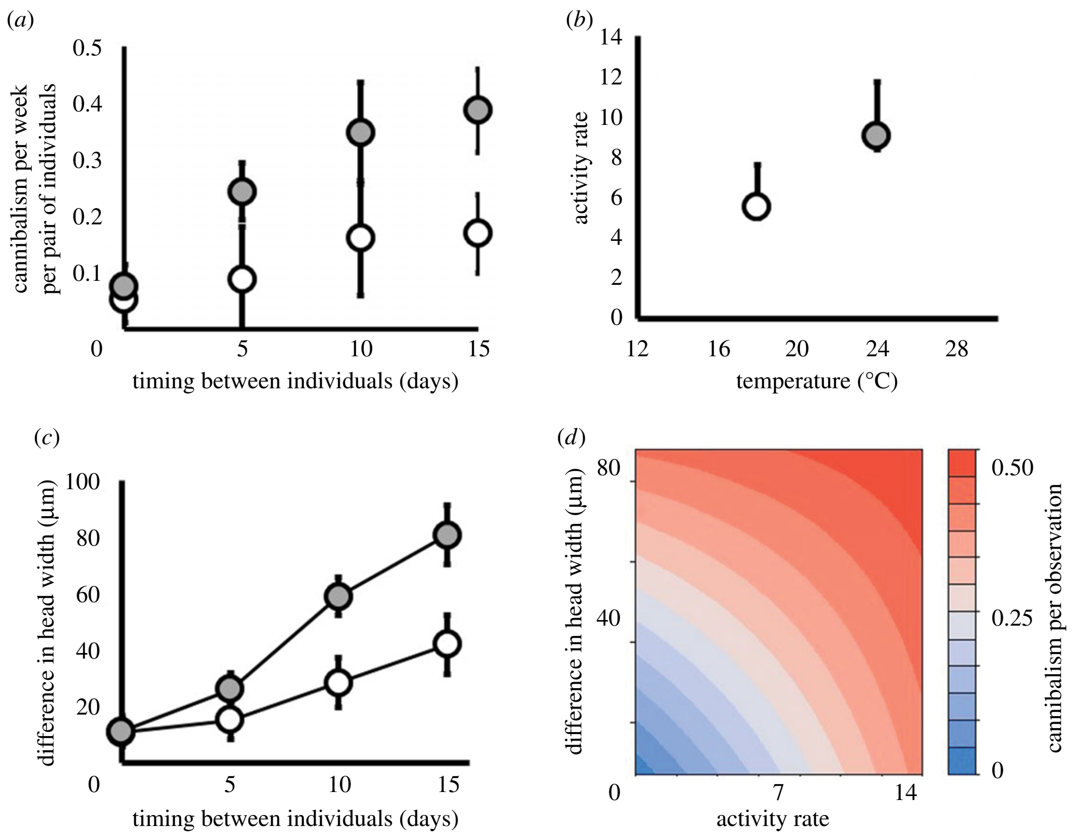

Figure 2. Patterns of activity, size and cannibalism across treatments. Cannibalism was greater in warmer treatments (darker grey) and with larger differences between individuals in hatching time (*a*). Cannibalism per week is the rate at which cannibalism occurred in replicates where there were two individuals remaining. Both activity rate (*b*; number of times an individual moved between $2 \times 2\ \mathrm{cm}^2$ in 3 h, $n = 94$ individuals) and body size differences (*c*) were greater at high temperature, with the size differences also increasing in treatments with more variation in hatching time. Timing differences had no effect on activity rate. Together, activity rate and body size differences predicted cannibalism (*d*). All error bars represent 1 s.d. (*d*) Estimated values from a LMM predicting cannibalism rate using body size differences and activity rate. Data in (*c*) are from the first measurement when sample size was largest (fewer individuals had died).

differences in body size (both $p < 0.001$, figure 2*c*), exacerbating size differences that resulted from variation in time of egg hatching (timing × temperature: $p < 0.001$, figure 2*c*) and further increasing cannibalism (figure 2*d*). The first mechanism is consistent with previous studies showing links between temperature and activity rate [5,11]; however, to our knowledge, the latter mechanism has never been demonstrated. We show that higher temperature can increase cannibalism and demonstrate a novel mechanism by which temperature can affect species interactions.

Our work is consistent with other studies showing that predation tends to increase with temperature [1,14], although these patterns are rarely extended to include cannibalism [9]. Activity rate typically increases with temperature, increasing encounter rates and consequently predation [14]. Our experiment shows that this mechanism can be generalized to include cannibalism (figure 2*b*), as has been hypothesized [9], but not formally tested. We further show that increased growth rates can exacerbate existing size differences, increasing cannibalism (figure 2*a*,*b*). This mechanism is likely to increase size-structured population dynamics whenever emergence depends on a factor other than temperature (e.g. photo- or hydro-period), or when cohorts are evenly spaced regardless of temperature owing to seasonal constraints (e.g. in obligately biennial or multi-annual species where individuals must overwinter). While this mechanism has not been documented, phenological differences owing to differences in the temperature sensitivity of hatching time may have a similar effect among species [16]. Similarly, interspecific variation in the temperature-dependence of growth rate may reduce or exaggerate interspecific size differences [14], potentially altering interspecific interactions through the same mechanism by which cannibalism was altered in our study.

Cannibalism often has important impacts on community dynamics, and these consequences may be amplified by the effects of temperature on other species in the system. Increasing cannibalism is expected to weaken the effects of predators on prey [7], allowing prey to increase in abundance, while reducing the abundance of the basal resource (trophic release; [7,17]). Temperature can equally affect the population growth rates of prey species and basal resources and, in aquatic communities, increase the abundance of zooplankton and reduce the abundance of basal resources [17,18]. Increased cannibalism should exacerbate this pattern by reducing the effects of predators on zooplankton [7,8], suggesting that research on cannibalism would enrich our understanding of the temperature dependence of food web dynamics.

Our study shows that temperature alters cannibalism rates, and that these effects can stem from multiple mechanisms. Changes in growth rate in response to temperature may be important in altering both intra- and interspecific interactions [2] for suites of species with temperature-independent emergence times. Indeed, increased cannibalism among predators may be one mechanism causing trophic release when aquatic communities are warmed [18]. We suggest that the effects of temperature on intraspecific interactions can mediate the response of populations and communities to climate warming.

Data accessibility. Data are available at http://dx.doi.org/10.5061/dryad.7f0c4 [19].

Authors' contributions. All authors conceived/conducted the study. D. Start analysed data and wrote the manuscript. All authors edited and approved the final manuscript, and agree to be held accountable for the work in the manuscript.

Competing interests. We have no competing interests.

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