



## Research

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# In a warmer Arctic, mosquitoes avoid increased mortality from predators by growing faster

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Climate change is altering environmental temperature, a factor that influences ectothermic organisms by controlling rates of physiological processes. Demographic effects of warming, however, are determined by the expression of these physiological effects through predator–prey and other species interactions. Using field observations and controlled experiments, we measured how increasing temperatures in the Arctic affected development rates and mortality rates (from predation) of immature Arctic mosquitoes in western Greenland. We then developed and parameterized a demographic model to evaluate how temperature affects survival of mosquitoes from the immature to the adult stage. Our studies showed that warming increased development rate of immature mosquitoes ( $Q_{10} = 2.8$ ) but also increased daily mortality from increased predation rates by a dytiscid beetle ( $Q_{10} = 1.2–1.5$ ). Despite increased daily mortality, the model indicated that faster development and fewer days exposed to predators resulted in an increased probability of mosquito survival to the adult stage. Warming also advanced mosquito phenology, bringing mosquitoes into phenological synchrony with caribou. Increases in biting pests will have negative consequences for caribou and their role as a subsistence resource for local communities. Generalizable frameworks that account for multiple effects of temperature are needed to understand how climate change impacts coupled human–natural systems.

## 1. Introduction

The ability of individuals in a population to survive to the adult reproductive stage is a critical factor shaping population dynamics. Individuals must acquire the necessary nutrition for growth while avoiding mortality risks from natural enemies. Factors that slow growth rate, such as low food quality [1,2] and the threat of predation [3], can lead to a decrease in survival because individuals remain in a vulnerable juvenile stage for a greater amount of time [4].

Most of the biomass and biodiversity on Earth is ectothermic. Thus, temperature is a globally important driver of physiology, growth rates and potentially survival. Recent interest in the consequences of climate warming on ecological systems has generated numerous theoretical and empirical studies that demonstrate how warming increases metabolic rates in diverse ectothermic taxa [5,6]. Consequently, consumption rates of food resources also increase with warming. If food intake rate is greater than the rate of energy expenditure for body maintenance and survival, growth rates will also increase with warming [7].

Demographic responses to environmental temperature, however, are ultimately determined by the expression of these physiological effects through food webs and species interactions [8–10]. Assuming abundant resources, an organism can complete development in fewer days under warmer conditions,

consequently with less exposure to natural enemies before reaching the reproductive life stage. Top-down control by predators, however, will also be temperature dependent [10]. Mortality risks could be elevated if predators also experience an increase in metabolic and consumption rates [6,7,10]. Thus, depending on the relative strength of temperature effects on growth rate versus mortality rates, warming will lead to positive or negative demographic outcomes for the prey population.

We studied an aquatic insect predator–prey system in the Arctic to measure the effects of increasing temperature on prey survival to the adult reproductive stage. Average temperatures in the Arctic have increased at twice the global rate in the past 100 years [11,12] and the low biodiversity of Arctic ecosystems provided a natural but relatively simple predator–prey interaction for this study. Our focal prey population was the Arctic mosquito, *Aedes nigripes* Zett (Kalaallisut: ippernaq; Diptera: Culicidae), a univoltine insect that can be a significant pest to humans, caribou and other wildlife [13]. First, we integrated field observations with laboratory experiments to quantify the effects of temperature on immature mosquito development rate and the rate of mortality from predation. Second, we developed a model to estimate the probability of mosquito survival to the reproductive (adult) stage across a range of temperatures that represent future climate change scenarios for the Arctic.

## 2. Material and methods

### (a) Study system and observations

We conducted this study in the tundra ecosystem located between the town of Kangerlussuaq, Greenland (67°0'33.1" N, 50°41'19.1" W) and the margin of the Greenland Ice Sheet. This area is dominated by low elevation mountain ridges and temporary and permanent ponds that cover approximately 14% of the landscape [14] and are mostly fishless. Vegetation consists of grasses, sedges and dwarf shrubs (*Salix* spp., *Betula nana*, [15]). Caribou (*Rangifer tarandus*) and muskoxen (*Ovibos moschatus*) are common large herbivores in this system [15].

Arctic mosquitoes develop in shallow temporary ponds. The beginning of ice melt in May triggers the hatch of mosquito eggs that have been in diapause since the previous summer. After hatching, larvae graze on vegetation and develop in three to four weeks. Adults emerge between late May and mid June and are present for four to six weeks, during which mating and blood-feeding occurs. Females oviposit in the drying margins of the shallow ponds [16] and by late July most adult activity has ceased. During the larval and pupal stage, predation by larvae of the predaceous diving beetle, *Colymbetes dolabratus* Paykull (Kalaallisut: minngup qullugai; Coleoptera: Dytiscidae), is a primary source of mortality (L. Culler 2011, personal observation). *Colymbetes dolabratus* is by far the most abundant top predator in these fishless snowmelt ponds throughout the summer. Adult *C. dolabratus* overwinter and mate below 1–2 m of ice in deeper ponds and disperse for oviposition as the lakes begin to thaw [17]. Because lakes on the landscape thaw at different rates, adult *C. dolabratus* are emerging and ovipositing throughout early summer. Therefore, the lakes contain larval *C. dolabratus* from May through to August (L. Culler 2010–2011, personal observation). At ambient temperatures during early summer, beetle larvae develop in 10–20 days on a diet of mosquito larvae and pupae.

We installed iButton data loggers (Maxim iButton® model DS1921G) in four snowmelt ponds in 2011 and 2012 (electronic

supplementary material, table S1) that recorded hourly temperatures for the approximate duration of mosquito development. We sampled the mosquito and predator populations in these four ponds every 2–4 days from 24 May–20 June in 2011 and 8 May–12 June in 2012. At each pond on each sampling date, we took 15 samples that were haphazardly collected from around the perimeter of the pond. Each sample consisted of five scoops of water with a 350 ml collecting cup mounted on a 1 m wooden dowel. The five scoops were combined in a pan and we counted and recorded the numbers of prey (larval and pupal mosquitoes) and predators (larval beetles). We also collected 50 individual mosquitoes from each pond on the initial sampling date in each year. We dried and weighed each individual and compared initial mosquito sizes between years. Once mosquito pupae were present, we anchored emergence traps to steel posts at the pond margins to measure dates of mosquito emergence.

### (b) Temperature effects on development time

We conducted a laboratory experiment to measure how temperature affected mosquito development time and thus the number of days that mosquitoes were exposed to mortality from beetle predators. On 9 May 2012, we collected 240 first-instar mosquito larvae from Black Pond (electronic supplementary material, table S1) and randomly allocated 40 individuals each to six chambers (Danby Maitre'D® DWC620PL-SC countertop coolers). Each chamber was set to a constant temperature within the range of temperatures measured in the ponds during mosquito development: 4, 7, 10, 13, 16 and 19°C. Mosquitoes were reared in groups of eight (five groups per temperature) in 200 ml plastic cups containing 150 ml of pond water and gently rinsed vegetation from the pond as food. We were unable to use an individual cup for each larva due to space constraints but we regularly moved larvae among different cups and also randomly reassigned temperatures to chambers every few days to avoid cup and chamber effects. The densities of mosquito larvae in each cup were less than what was measured in the field and we added fresh pond water and vegetation every 2 days to ensure larvae were not food-limited.

Individuals that pupated were moved into a cup with pond water that was covered by an inverted funnel and collecting jar to capture emerging adults (Bioquip, Mini Mosquito Breeder 1425DG). We recorded the date of emergence and sex for each individual. Development time ( $D$ ) was calculated as the number of days from the start of the experiment until emergence. We logged hourly temperatures in each chamber and used those to calculate the mean temperature ( $T$ ) that each individual experienced between the beginning of the experiment and the day it emerged. We then fit a nonlinear model that described development time ( $D$ ) as a function of temperature ( $T$ ):

$$D = \beta_1 \times e^{(\beta_2 \times T)}, \quad (2.1)$$

where development time decreases exponentially with increasing temperature [1], but we also fit a linear model (constant decrease) and an intercept-only model (no effect of temperature) as alternatives and used Akaike information criteria to compare goodness of fit (AICc; [18]). We validated the final model by using it to predict development times in each of the four ponds in 2011 and 2012 based on the water temperatures recorded by the loggers. Starting with the hourly temperature recorded in each pond at hour 00.00 on the day immediately after mosquito hatch, we calculated the proportion of development that would be completed during that hour and then each subsequent hour. Then we cumulatively summed these values until a value of 1 was reached, indicating complete development. We then tested for a correlation between the modelled number of days until complete development for each pond (in 2011 and

2012) and the observed number of days until emergence for each pond (in 2011 and 2012) from our emergence trap data.

### (c) Temperature effects on mosquito mortality rates

We estimated daily *per capita* mortality rates ( $m$ , units of larval deaths  $\cdot$  larva $^{-1} \cdot$  d $^{-1}$ ) using our field data. First, we calculated the average number of prey (mosquito larvae and pupae) per sample (mean of 15 samples) in each pond in 2011 and 2012, at two time points, (a) after beetle predators were present and no new larvae were hatching,  $N_o$ , and (b) before adults began to emerge,  $N_f$ . Daily *per capita* mortality rate was calculated as

$$m = - \left[ \frac{\ln(N_f/N_o)}{d} \right], \quad (2.2)$$

where  $d$  was the number of days between the two time points [19].

We conducted laboratory experiments to test for effects of temperature on mortality from predation. Second-instar beetle larvae were collected from East Pond (electronic supplementary material, table S1) on 6 June 2011 and 28 May 2012. Each larva was placed in a 50 ml vial with pond water and vegetation and fed two mosquito larvae per day until moulting. After moulting, individuals were randomly assigned to one of three (2011) or six (2012) temperature chambers set to environmentally relevant temperatures (see above) and held for 24 h without food to allow hardening of the exoskeleton, standardization of hunger levels and adjustment to temperature. During the same 24 h period, we established foraging arenas for each predator: 200 ml plastic cups with 150 ml pond water, four to six pieces of vegetation (*Hippurus vulgaris*) and 10 late-instar mosquito larvae (collected from East Pond). We placed cups in the chambers to allow mosquito prey to acclimate for 24 h. Then, each beetle larva was added to its arena and the number of mosquito larvae consumed after 15 h was recorded. Dytiscid larvae are piercing-sucking predators with falcate mandibles [20] and leave behind digested prey that are easy to distinguish from undigested prey [21,22]. We did not replace prey as they were consumed. Non-predator mosquito mortality was negligible.

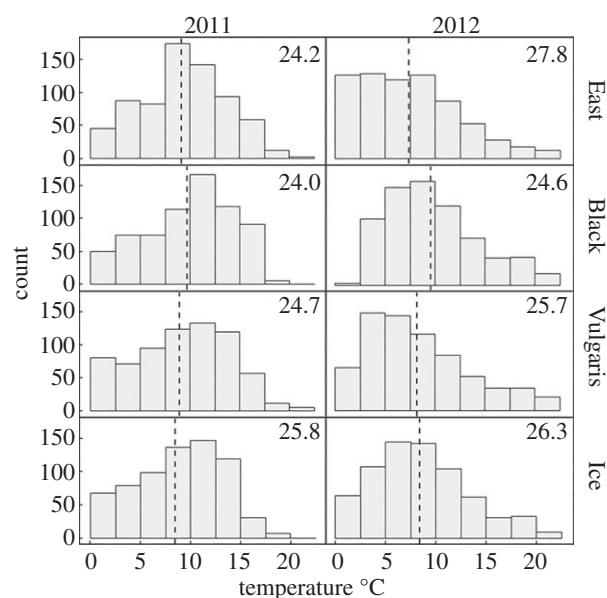
In 2011, we ran a total of 49 beetle predators in three trials (moulted on 7, 9 or 10 June) and in 2012 a total of 54 beetles in two trials (moulted on 31 May or 1 June). For the trials in 2011, experimental temperatures were 4, 10 and 16°C; trials in 2012 were at 4, 7, 10, 13, 16 and 19°C. We logged hourly temperatures (Maxim iButton model DS1921G) during each trial and used those to calculate a mean temperature to use as the independent variable in our analysis since actual chamber temperatures varied slightly during each trial. For the dependent variable, we calculated the mean number of mosquito larvae consumed per predator per day (adjusted from the 15 h trial), hereafter termed predation rate, as the average of the four to six arenas at each temperature (total  $n = 9$  for 2011, 10 for 2012). We calculated  $Q_{10}$ , the factor by which predation rate changed over 10°C, from two-parameter exponential nonlinear models [10] fit to the relationship between predation rate and temperature for each year independently (PROC NLIN, SAS v.9.4).

### (d) Model development

We developed a demographic model to quantify how temperature effects on prey mortality rate ( $m_t$ , units of larval deaths  $\cdot$  larva $^{-1} \cdot$  d $^{-1}$ ) and development time ( $D_t$ , units of days) influenced the probability that a mosquito survived to the adult stage across a range of temperatures ( $t$ , 7–22°C) as

$$P(\text{survival}_t) = (1 - m_t)^{D_t}, \quad (2.3)$$

$m_t$  was determined by taking the average value for  $m$  (across all ponds and years) from equation (2.2) at mean pond temperatures



**Figure 1.** Distribution of hourly temperatures and mean pond temperature (dashed line) in each pond for the first 28 days after mosquitoes hatched, 24 May–21 June in 2011 and 9 May–6 June in 2012. Also shown is the predicted number of days for mosquito development to the adult stage based on our laboratory model (figure 2).

( $t = 8.3^\circ\text{C}$ ) and scaling it according to the measured  $Q_{10}$  values for predation rate.  $D_t$  was the number of days of development at temperature ( $t$ ) from our laboratory experiment.

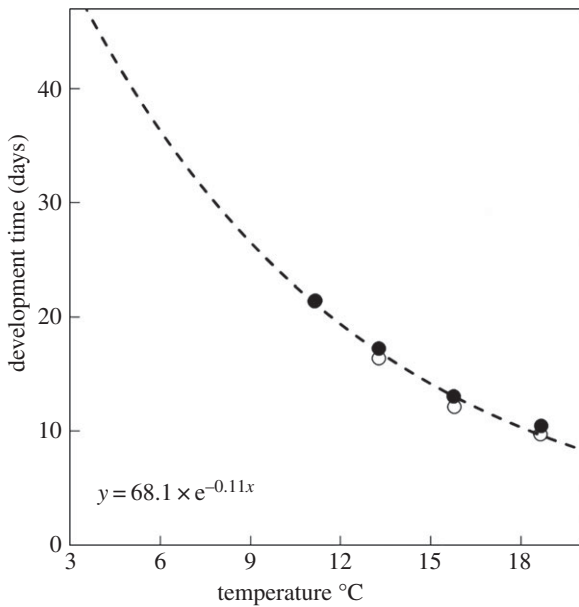
## 3. Results

In 2012, ponds thawed approximately two weeks earlier than in 2011. Consequently, the phenology of mosquitoes and beetles was advanced in 2012 relative to 2011. We started studies 15 days earlier in 2012 than in 2011 (8 versus 23 May) when mean larval mosquito mass ( $\pm$  s.e.) was about  $0.15 \pm 0.004$  mg in both years. In each year, beetles hatched approximately 7 days after mosquitoes hatched, and average dates of first mosquito emergence were 1 June and 15 June in 2012 and 2011, respectively. In spite of the differences in dates between years, water temperatures were about the same during the time of mosquito development (average =  $8.4$  versus  $9.1^\circ\text{C}$  in 2011 versus 2012). However, the distribution of hourly temperatures (range:  $0$ – $22.5^\circ\text{C}$ ) indicated a right skew in 2012 relative to 2011 (figure 1).

In the laboratory at constant temperatures, development times decreased from 21 days at  $11^\circ\text{C}$  to 10 days at  $19^\circ\text{C}$  (figure 2). Development time clearly continued to increase at lower temperatures because all of the mosquitoes at  $3.9$  and  $6.7^\circ\text{C}$  were still larvae after 30 days. Males emerged 0.1–0.9 days ahead of females. The response was well fit with a negative exponential model (figure 2). Development times predicted for each pond by the laboratory-generated model applied to the hourly temperature measurements (figure 1) were positively correlated with time until first emergence as recorded by the emergence traps ( $r = 0.92$ ,  $p = 0.01$ ; figure 3).

Daily *per capita* mortality rate ( $m$ ) in the ponds averaged  $0.014$  larval deaths  $\cdot$  larva $^{-1} \cdot$  d $^{-1}$  (table 1). In the laboratory at constant temperatures, predation rates (larvae consumed  $\cdot$  predator $^{-1} \cdot$  d $^{-1}$ ) increased with warming (figure 4). Over a



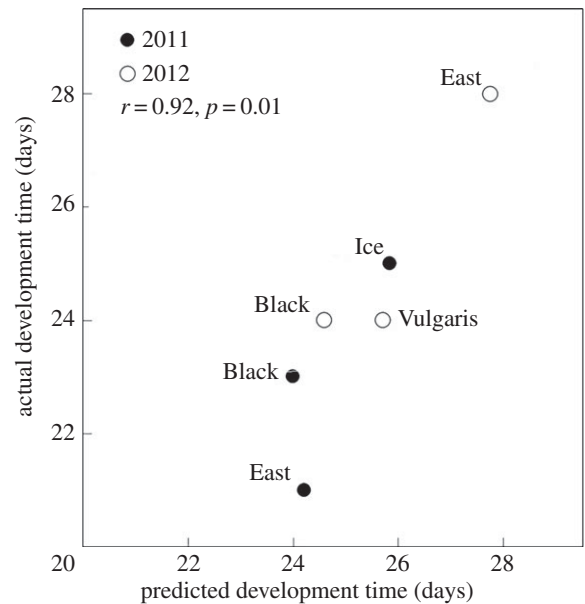


**Figure 2.** Development time of immature mosquitoes to the adult reproductive stage decreased with warming. Mosquitoes at 4 and 7°C were still larvae at the end of the 30 day experiment. Number of females (filled circles) and males (open circles) at 10, 13, 16 and 19°C were 7 and 3, 16 and 6, 8 and 10, and 9 and 16, respectively. Dashed line is the best-fit exponential model fit to our data.

10°C range, predation rate increased by 20% in 2011 ( $Q_{10} = 1.2$ ) and 50% in 2012 ( $Q_{10} = 1.5$ ). Multiplying  $m$  by the average number of mosquito prey for every predator in each pond resulted in an average predation rate of 3.0 larvae consumed  $\cdot$  predator $^{-1} \cdot$  d $^{-1}$ , similar to what we measured in the laboratory (table 1 and figure 4).

In 2011 and 2012, mosquitoes completed approximately 20% of their development by the time the predators hatched. Thus, regardless of temperature, daily *per capita* mortality rate from predation was 0 for the first 20% of mosquito development. We incorporated this into our model. During the time when predators hatched and before mosquitoes began to emerge, daily *per capita* mortality rate ranged from 0.04 to 0.24 larval deaths  $\cdot$  larva $^{-1} \cdot$  d $^{-1}$  (table 1). In addition to scaling, this with temperature according to the measured  $Q_{10}$  values for predation (1.2 and 1.5), we also used a  $Q_{10}$  of 2, a frequently reported value for the temperature sensitivity of biological processes [23].

Despite an increase in daily mortality from predation with warming, the faster development of mosquitoes through the larval stage improved their survival probability considerably (53% and 160% increase with warming scenarios of 2 and 5°C, respectively; figure 5). The qualitative conclusion was robust across the measured  $Q_{10}$  values (1.2–1.5) and even held with a simulated  $Q_{10}$  for predation as high as 2.0 (figure 5). Furthermore, survival probability still increased with warming in a scenario representing a higher abundance of predators relative to prey (75% quantile value from field data,  $m = 0.17$  larval deaths  $\cdot$  larva $^{-1} \cdot$  d $^{-1}$ ; figure 5). We also simulated the probability of survival in each of the four ponds in 2011 and 2012 by using the measured hourly temperatures and the temperature models for development time and mortality. With a 2°C and 5°C warming scenario applied to pond temperatures, probability of survival across all ponds would increase by 18% and 53%, respectively.



**Figure 3.** Actual development time as indicated by collection of adult mosquitoes in emergence traps was strongly and positively correlated with development times predicted for each pond from the laboratory model (figure 2) across 2011 and 2012. In 2011, *Vulgaris* died before mosquitoes emerged and no mosquitoes emerged from Ice in 2012.

## 4. Discussion

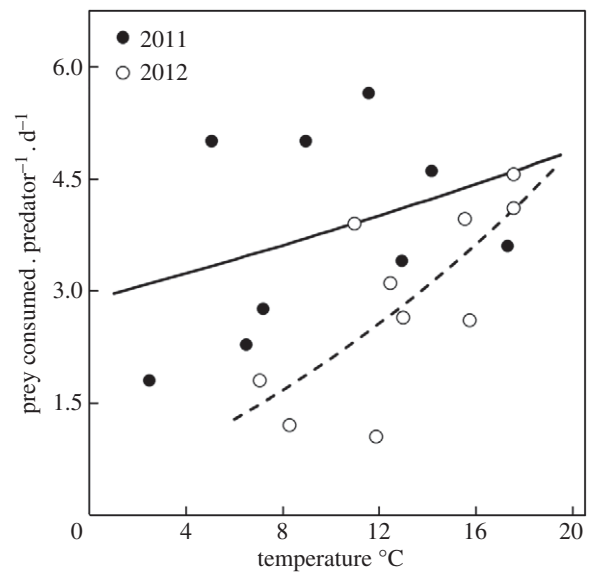
Mosquitoes were highly responsive to changes in environmental temperature. A warmer spring and earlier pond thaw in 2012 resulted in mosquito phenology that was advanced by two weeks relative to 2011. Furthermore, development times decreased by about 10% for every 1°C increase in temperature (figure 2), which decreases time spent exposed to predators in the vulnerable juvenile stage. However, daily mortality of mosquito larvae and pupae from predation by *C. dolabratus* also increased with temperature (figure 4). Adding temperature into a simple predator–prey model allowed us to assess whether the demographic effects of decreased exposure time were more or less than the effects of increased daily risks (figure 5). The tendency of warming temperatures to accelerate development rate, but also increase daily mortality risks, is probably quite general in mid- to high-latitude systems (e.g. [1,10,24]). Our approach offers a general tactic for evaluating when opposing effects from warming temperatures lead to increased or decreased top-down control on prey populations.

### (a) Phenology

Ice melt, egg hatch, larval development and the adult biting season will surely advance as air temperatures continue to warm in the Arctic. Warming of winter temperatures in particular may advance the mosquito season because of its effects on ice thickness and therefore duration of ice cover [25]. During our 2 years of study, the phenology of predators and prey remained coincident even though pond thaw was much earlier in 2012. This differs from cases of trophic mismatch (e.g. [26,27]). The ability of dytiscid predators to match further advances in the phenology of the prey population remains unknown, but might depend upon the timing of ice-out in larger lakes where *C. dolabratus*

**Table 1.** The average number of mosquito prey per sample (larvae and pupae combined, with standard errors of 15 samples in parentheses) on the date when no new mosquitoes were hatching and predators were initially present ( $N_o$ ) and on the last date before mosquitoes began to emerge ( $N_i$ ), the number of predators per sample (average of all samples between  $N_i$  and  $N_f$  with standard deviation in parentheses), mean pond temperature during the time interval, daily per capita mortality rate ( $m$ ), and predation rate in each pond in 2011 and 2012.

	no. prey/sample		date		avg. no. predators	mean		predation rate	
	$N_o$	$N_f$	$N_i$	$N_f$		temp (°C)	$m$		
2011	East	18.6 (3.2)	3.8 (0.7)	5/30	6/8	0.4 (0.2)	9.0	0.18	8.9
	Black	24.4 (5.3)	7.5 (1.2)	6/8	6/13	1.0 (1.1)	12.0	0.24	5.8
	Vulgaris	32.3 (4.7)	17.2 (6.6)	5/30	6/10	1.1 (0.7)	8.3	0.06	1.7
2012	Ice	5.2 (1.2)	1.2 (0.4)	5/30	6/10	1.4 (1.7)	8.2	0.13	0.5
	East	2.9 (0.5)	2.1 (0.6)	5/23	5/31	0.2 (0.1)	7.7	0.04	0.5
	Black	14.7 (2.4)	5.2 (1.3)	5/21	5/28	0.5 (0.5)	7.9	0.15	4.5
	Vulgaris	13.5 (2.7)	6.3 (1.5)	5/18	5/23	1.0 (1.0)	5.8	0.15	2.1
	Ice	0.3 (0.2)	0.1 (0.1)	5/28	6/4	1.5 (0.4)	7.2	0.16	0.0
					average		8.3	0.14	3.0

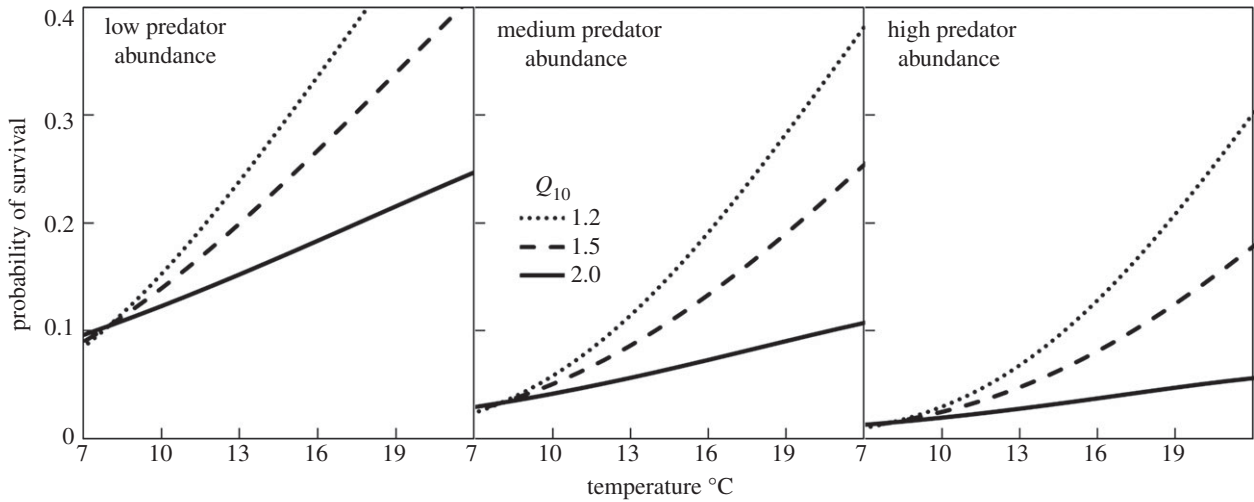


**Figure 4.** Predation rates by *C. dolabratus* beetles on mosquito prey, as measured in a laboratory experiment, increased with warming more strongly in 2012 ( $Q_{10} = 1.5$ , dashed line) versus 2011 ( $Q_{10} = 1.2$ , solid line). Points are means calculated from four to six arenas run at each temperature.

overwinter [17] compared to the shallow ponds where mosquitoes overwinter.

Presumably, average pond temperatures during the growing season will increase as air temperatures increase, but it is not certain that mosquitoes will experience warmer pond temperatures. Mosquito development season begins at the timing of ice melt when pond temperatures are very close to 0°C. When ponds melted later in 2011, reflecting the colder winter, water temperatures during mosquito development were in fact slightly warmer versus 2012 when the ponds melted earlier. In general, starting the season earlier moves the season towards dates when solar input is lower and the tendency is to be cooler, which opposes the effects of warming temperatures with solar day held constant. Predicting the effects of warming on northern ecosystems requires consideration of opposing effects from advancing springs versus warming summers.

For mosquito populations, changes in phenology may affect the biology of adults at least as much as immatures. Even for mosquitoes that complete larval development and emerge successfully as adults, their reproduction will be 0 or nearly so unless female adults get a blood meal [28,29]. Caribou are a source of blood for mosquitoes in a landscape where blood-meals are scarce [30,31]. In our study area, the proportion of female mosquitoes with mature eggs was about twice as high in the immediate area of the caribou herd (L. Culler 2012, unpublished data). Caribou populations may be particularly suitable for mosquitoes at the time of caribou calving because: there are more animals with the addition of the calves, the calves may be especially vulnerable, and the herds are less mobile [32,33]. Caribou phenology is linked with day length such that females calve around the same calendar day each year [27], therefore the timing of mosquito emergence dictates the overlap between the caribou and mosquitoes. In our study area, caribou calving tends to be about 3 June [27]. In 2012, the mosquitoes started emerging just a couple days prior to caribou calving, whereas in 2011, the mosquitoes began emerging about 10 days after caribou calving. Thus, the earlier spring produced more match between



**Figure 5.** Probability of prey survival to the adult stage increased with warming at all values of  $Q_{10}$  and under low, medium and high abundances of predators relative to prey.

adult mosquitoes and caribou calves. It is an interesting question whether warming in the Arctic will generally increase the overlap between adult mosquitoes and caribou calves or whether it will vary among locations. Increasing temporal overlap between mosquitoes and caribou calves should increase the abundance of mosquitoes on the landscape. Furthermore, locations of high mosquito abundance within the landscape probably reflect where the migratory caribou were last year during mosquito emergence. The locations of such mosquito hotspots would be expected to change with changes in mosquito phenology and caribou movements.

### (b) Survival

Predation rates on immature mosquitoes increased with increasing temperatures, as is expected for ectothermic animals where increases in food consumption are concomitant with increases in metabolic rates (e.g. [10]). However, the temperature sensitivity of predation was relatively modest ( $Q_{10}$  values = 1.2–1.5 versus more typical values of 2–3 for biological processes in poikilotherms; e.g. [23]). The low temperature sensitivity of *C. dolabratus* consumption rates is similar to that reported from the tadpole shrimp *Lepidurus arcticus*, a predaceous aquatic invertebrate common in some parts of Greenland [34]. The lack of a strong response of consumption rate could result from asymmetric thermal responses in consumer–resource dynamics [35] or other trait-related constraints [24]. For example, Arctic mosquito larvae may have been able to increase their predator escape velocity at warmer temperatures more than their predators increased their attack velocities. This hypothesis, and alternatives, could be tested with more detailed studies of temperature effects on predator–prey encounters (see methods in [36]). Regardless, the measured  $Q_{10}$  values for predation rate are less than the general  $Q_{10}$  for metabolic rate [5], indicating increasing energetic limitations for the predators at warming temperatures [7,10], and the possibility for a numerical response or declining predator abundance in subsequent years.

In our system, the effects on survival of immatures from increases in predation with temperature were more than compensated for by the reduced exposure time to predators; i.e. development time was more temperature sensitive than

predation rate. Even when we simulated a  $Q_{10}$  of 2 for mortality rate and with a high abundance of predators relative to prey (but see above), the increasing top-down effects still did not compensate for the strong positive effects of temperature on mosquito development time (figure 5). The conclusion that warming temperatures will tend to increase mosquito survival in this system appears to be quite robust. In general, the effects of warming on top-down control are controlled by multiple mechanisms related to the duration and intensity of species interactions. Insect pest suppression may be enhanced by warming if predators consume more prey per day. However, if the pest phenology comes out of synchrony with predator phenology, the strength of top-down effects will increasingly depend upon the duration of overlap relative to the intensity of interactions during overlap.

### (c) Ecosystem consequences

Changes in the timing and intensity of mosquito emergence will affect the role of adult mosquitoes as pollinators of Arctic plants [37], food for other species, and pests of people and wildlife. For example, insects can be a substantial source of food for Arctic and migratory birds and asynchrony between insect emergence and bird reproduction can negatively affect chick growth [38]. In 2012, when the ponds melted earlier, mosquito emergence closely coincided with caribou calving. Insect harassment drives caribou movement [13,39,40], often to insect-free areas such as snow patches and wind-exposed sites at high elevations that offer less food [13,41,42]. Reduced food intake, caused by phenological mismatch with plants or increased time spent avoiding insect harassment, can decrease calf production and increase calf mortality [27]. Severe insect harassment, including direct loss of blood [43,44], is considered a critical factor affecting reindeer and caribou population ecology [45] that is in need of greater research, particularly as it relates to climate change [46,47].

In northern regions, caribou (and also managed reindeer in Fennoscandia) are an important subsistence resource for Arctic communities. In addition to mosquitoes, other notable pests of caribou are blackflies (Diptera: Simuliidae) and warble/bot flies (Diptera: Oestridae; [31]). We presently

lack comparable knowledge about how Arctic warming will influence the population dynamics of these pests. In addition, the appearance of new pests and vectors of disease via range expansions have been observed (e.g. [48]) and are expected to become more frequent [49]. Tactics for adaptive management of caribou and reindeer as subsistence resources in a rapidly changing Arctic include monitoring and surveillance of current and future pests [50,51] and application of local ecological knowledge [52] of animal movements in response to food availability and pest abundance [53].

#### (d) Temperature and consumer–resource dynamics

Warming influences important life-history traits such as survival probability via changes in physiology, phenology [54] and interaction rates with other species (e.g. [55–58]). For populations in highly seasonal environments, reproduction and death occur in pulses, the timing and intensity of which are controlled by temperature. The population model represented in figure 5 (equation (2.2)) for mosquitoes and dytiscids can be generalized to any system where survival to reproduction depends on mortality from consumers (predators, parasitoids and herbivores). The responses of such a system to warming will depend upon the relative thermal sensitivities of phenology, development times and predation intensity during the overlap between consumers and resources. Frameworks and models that can adequately account for multiple effects of temperature can elucidate

demographic consequences for populations (e.g. [59]) and how climate change will shape coupled human–natural systems.

**Ethics.** The study used the minimum number of animals necessary for scientific robustness and adhered to all local guidelines (Dartmouth Institutional Animal Care and Use Committee). Permission was obtained from the Government of Greenland.

**Data accessibility.** Data are available for download at <http://dx.doi.org/10.5061/dryad.bq21j>.

**Competing interests.** We have no competing interests.

**Authors' contributions.** L.E.C. conceived of the study, designed the study and collected field and laboratory data. L.E.C. and M.P.A. carried out statistical analyses and developed the model. L.E.C., M.P.A. and R.A.V. interpreted results. L.E.C. wrote early drafts of the manuscript and all authors contributed substantially to revisions.

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