

TEMPERATURE DEPENDENCY OF PREDATOR-PREY INTERACTIONS:
INCREASED FEEDING RATES AND MACRONUTRIENT INTAKE BY
PREDATORS

By

RYAN WALKER

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Dr. Angélica González

And approved by

Dr. Angélica González

Dr. Amy Savage

Dr. Daniel Shain

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THESIS ABSTRACT

Temperature dependency of predator-prey interactions: increased feeding rates and
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By

RYAN WALKER

Thesis Director:

Dr. Angélica González

Temperature dependency of consumer–resource interactions is of fundamental importance for understanding and predicting the responses of food webs to climate change. Previous studies have shown temperature-driven shifts in herbivore consumption rates and resource preference resulting from differences in resource nutrient content, but little is known about the role of nutrition in temperature-driven shifts in predator-prey interactions. I performed a laboratory experiment to study the effects of increased temperatures and prey macronutrient content (lipid dense or protein dense) on interaction strengths and predator nutrition using wolf spiders (*Pardosa* sp) as study model. Additionally, I tested the effects of local thermal adaptation or acclimatization on predator nutritional demands using a field reciprocal transplant experiment between low (26°C) and high (15°C) elevations using two common spider species (*Leucauge* sp and *Cyclosa* sp) present along the elevation gradient. Spider feeding rates increased with warmer temperatures, but feeding responses differed depending on prey macronutrient content. Spiders fed lipid dense prey showed a sharp, rapidly saturating increase in

feeding rates while those fed protein dense prey showed more gradual increases with increasing temperature. My transplant experiment revealed that populations from *Leucauge* sp and *Cyclosa* sp consistently showed higher prey mass consumption at the low elevation/warmer site than their counterparts from a high elevation/cooler site. The strong elevation differences on prey mass consumption are consistent with acclimatization responses to contrasting thermal environments. Overall, rising temperatures affected predator-prey interactions by increasing the strength of interactions and the demands of both, energy and protein by predators. Further, my findings suggest that spiders are able to increase their feeding rates and prey mass consumption in response to temperature changes over a short time period, which might represent important buffers against climate change.

INTRODUCTION

Consumer-resource interactions (e.g., herbivore-plant, predator-prey) are central to the structure and function of ecological communities (Paine 1980, Tilman 1986). The strength of consumer-resource interactions plays a fundamental role in shaping the stability of food webs (Pimm, 1979, Pimm 1984, Rooney & McCann 2012). Many approaches to estimating interaction strengths have done so by quantifying consumer consumption rates on a given prey (Wootton & Emmerson 2005). As the strength of consumer-resource interactions can vary in response to changes in environmental factors such as temperature and nutrient availability (Rall et al. 2010, Mas-Martí et al. 2015), a better understanding of how temperature and resource nutrient content affects the strength of interactions is fundamentally important in order to predict the consequences of climate change on food web structure and stability.

Ectothermic consumers, organisms whose physiology is temperature-dependent, are expected to show the greatest responses to changes in environmental temperature due to increases in their metabolic rates (Schmalhofer 2011, Schulte 2015). To compensate for this increase in their metabolism, consumers must regulate their diet by increasing their food intake or risk starvation (Rall et al. 2010, Lemoine & Burkepile 2012). Studies of ectothermic consumers across trophic guilds have shown that increases in feeding rates correlate with increased temperatures (Dreisig 1980, Sanchez-Salazar et al. 1987, Dangles et al. 2013, Lemoine et al. 2014, Mas-Martí et al. 2015). However, increases in consumption rates as a result of increased temperatures often do not fully compensate for elevated metabolic rates, especially at high temperatures (Rall et al. 2010, Lemoine & Burkepile 2012). Studies have shown that herbivores change their diet in response to

rising temperatures by increasing carbon intake to fuel increased metabolic demands (Lee et al. 2015) or nitrogen intake to fuel faster development (Schmitz et al. 2016). However, the effects of increasing temperatures on the nutritional needs of ectothermic predators remains poorly understood, as are the potential impact of these temperature-dependent responses on predator-prey interactions under climate change.

Climatic gradients have been widely used as natural experiments in which spatial differences in climate are used to infer species responses to temporal changes in temperature and climate (Körner 2007, Read et al. 2014). Local thermal adaptation to varying climates across spatial gradients has been widely observed in terrestrial ectotherms (Angilletta et al. 2002, Hodkinson 2005, Barton 2011). In tropical areas, where seasonal variations in temperature are low, the thermal adaptation hypothesis predicts that species will be adapted to living within a very narrow thermal range (Janzen 1967, Kaspari et al. 2015). Although tropical areas experience fairly constant year-round environmental temperature, this changes with altitude, decreasing $\sim 6.5^{\circ}\text{C}$ for 1 km of elevation (Barry 2008). Species along these elevation gradients are predicted to vary in their thermal tolerance range, with higher thermal tolerances occurring at lower elevations (Kaspari et al. 2015, Garcia-Robledo et al. 2016). The degree of thermal adaptation and acclimatization to variations in environmental temperature is of vital importance for understanding species responses to climate change (Buckley et al. 2013, Buckley et al. 2014). Thus, elevation gradients are good systems for conducting natural experiments on the effects of temperature on consumer nutritional demands and trophic interactions (Rasmann et al. 2014).

Spiders are an ideal model for studying predator nutrition and predator-prey interactions due to their abundance, diversity, impact on their communities, and feeding behavior. Spiders can be major controllers of arthropod density in ecosystems, and have been shown to influence plant diversity both by controlling herbivore populations and altering herbivore-feeding behavior (Schmitz 2003, Rosenheim et al. 2004, Barton 2011). Spiders typically use extraoral digestion when consuming prey, which allows spiders to maximize nutrient intake while also minimizing the consumption of inedible portions of the prey item that would require additional energy to process and excrete (Foelix 2011). Additionally, spiders are able to regulate their nutrient intake during extraoral digestion, preferentially absorbing specific nutrients such as lipids and proteins depending on their current body condition and needs (Mayntz et al. 2005, Salomon et al. 2008, Wilder 2011).

To determine how predator-prey interactions and predator macronutrient intake respond to increased temperatures, I combined laboratory and field experiments, including a field reciprocal transplant experiment between low- and high- elevation sites that differ in environmental temperature. Specifically, I asked: (i) How do feeding rates (number of prey consumed per unit time) and prey mass consumption (proportion of prey mass consumed) of predators change in response to shifts in temperature and prey nutrient content and (ii) How do differences in local thermal adaptation affect temperature mediated changes in prey mass consumption by predators? I hypothesized that spider feeding rates and prey mass consumption would both increase at higher temperatures due to their increased nutritional needs. Additionally, I hypothesized that prey nutrient content would affect both predator feeding rates and prey mass

consumption, with spiders feeding on a higher number of protein-dense prey, but extracting a lower amount of nutrients compared to those feeding on lipid-dense prey. This prediction derives from the observation that spiders fed prey low in limiting nutrients consume a greater number of prey but consume a smaller proportion of each individual prey consumed (Mayntz et al. 2005), and the assumption that spiders would increase lipid intake over proteins at higher temperatures to compensate for an increased metabolism (Schmalhofer 2011). I also hypothesized that if spider populations are locally adapted to their thermal environment, they should display similar prey mass consumption across elevations. Alternatively, if thermal tolerances of spiders do not reflect local thermal adaptation but instead are a result of acclimatization, spiders should show a greater prey mass consumption at warmer, low elevations regardless of their home climate due to increased metabolic demands.

Overall, the reciprocal transplant experiments allowed me to test (i) whether prey mass consumption differed between spiders that originated from the low elevation (high temperature) or high elevation (low temperature) sites, which may indicate adaptation to the temperature in the local environment (i.e., main effect of elevation of “origin”); (ii) whether prey mass consumption were determined by their local temperature, comparing the responses of spiders between their origin and transplant sites to test whether these temperature responses are due to acclimatization or adaptation; and (iii) whether the temperature dependency of prey mass consumption differed between the spiders from the low and high elevations (i.e., origin x transplant elevations).

MATERIAL AND METHODS

Feeding rates and prey consumption experiment

I performed a full-factorial experiment to test the effects of temperature and prey macronutrient composition on the feeding rates (i.e., a proxy for interaction strengths) and prey mass consumption of wolf spiders (*Pardosa* sp). The spiders (purchased from Carolina Biological Suppliers) were placed individually into plastic containers and supplied with water *ad libitum*. Before the experiment, spiders were starved for one week to ensure full gut clearance, during which the individuals were maintained in incubators at 20°C, 25°C, 30°C, or 35°C. These temperatures were selected based on average spring and summer temperatures in North Carolina where spiders were collected, and on lab experiments assessing the maximum critical temperatures of a group of wolf spiders (results not shown). Following the starvation period, spiders were fed *ad libitum* on either lipid-dense (34% lipid/51% protein by dry mass) or protein-dense (24% lipid/69% protein by dry mass) house crickets (*Acheta domesticus*). Crickets were raised on specialized dietary media (Table S1) for one week to ensure proper nutrient content (following Wiggins et al 2018). The spiders were randomly assigned to one of eight treatments: 20°C /lipid-dense prey, 20°C /protein-dense prey, 25°C /lipid-dense prey, 25°C /protein-dense prey, 30°C /lipid-dense prey, 30°C /protein-dense prey and 35°C /lipid-dense prey, and 35°C /protein-dense prey.

Following a 48-hour feeding period, consumed crickets were removed, counted, dried at 60°C for 72 hours and weighed to the nearest 0.0001 mg (Mettler Toledo micro mass balance; XP6U). The lipid content of the crickets was measured gravimetrically using chloroform as a solvent (Wilder & Rypstra 2009). Twelve crickets (six lipid dense,

six protein dense) were randomly selected to provide an initial wet to dry mass equation ($\text{Dry mass} = \text{wet mass} \times 0.215 + 0.015$) to be used in the estimation of initial body mass, protein content, and lipid content. These individuals were sacrificed and dried at 60 °C for 72 h, and their total dry mass, protein, and lipid contents were measured using same approaches used for eaten crickets. Protein content was estimated using the Bradford assay (following Wiggins et al 2018). Dried samples were crushed and sonicated in 0.1 M NaOH before being centrifuged. Bradford reagent was mixed with the supernatant and measured for absorbance at 595 nm. Prey mass consumption by spiders was estimated by subtracting the total dry mass all consumed crickets from the estimated initial dry mass of the consumed crickets. Feeding rates were estimated based on the number of consumed crickets (dead with signs of predation).

Reciprocal transplant experiment

In order to test the effects of temperature on the total prey mass consumption of spiders in tropical systems, I conducted a reciprocal transplant field experiment between low (420 masl) and high elevation (2200 masl) sites in the Napo region of Ecuador. The low elevation site, Jatun Sacha Biological Reserve, is located in the Amazon River Basin and has an average temperature of 26 ± 2.1 °C. The high elevation site, Yanayacu Biological Station, is located in the Andean Cloud Forest and has an average temperature of 15 ± 2.3 °C. At each sampling site, I collected individuals of two orb weaver spiders (*Leucauge* sp and *Cyclosa* sp), which are the most common species across the elevation gradient within the Napo region of Ecuador.

Individuals of each species were transplanted from the low-elevation (Jatun Sacha) to the high-elevation (Yanayacu) site: *Leucauge* n=12 and *Cyclosa* n=12, and from the high-elevation to the low-elevation site: *Leucauge* n=12 and *Cyclosa* n=10. An additional group of individuals of each species were collected and transferred in situ to act as controls (low elevation: *Leucauge* n=13 and *Cyclosa* n=15, high elevation *Leucauge* n=10 and *Cyclosa* n=10). Therefore, each site (low elevation and high elevation) acted as both a origin (where spiders were collected from) and a transplant site (to which spiders were transplanted). Spiders were kept in open air laboratories, which ensured climatic variables were maintained but prevented spiders from escaping. Spider were maintained in large plastic containers with perforated lids, given water by lightly misting the web every few days, and allowed to acclimatize to the laboratory setting over a five-day period, during which spiders were starved to ensure full gut clearance. After this period, spiders were subsequently fed a single worker termite every other day for 6 days (3 prey per spider). Termites were collected from a single nest at the low elevation site in order to ensure all prey would be similar in nutrient content. Additional termites were collected to act as standards for estimating initial prey mass. Consumed prey were removed from each spider container after one day, dried, and stored until chemical analysis. At the end of the experiment, prey (termites) and spiders were dried in a lab oven at 60°C for 72 hours and measured for dry body weight.

I was able to estimate initial body mass of termites fed to spiders using a mass to length equation ($\text{Dry mass} = \text{length} \times 1.77 - 0.030$) developed by measuring the body length of each termite to the nearest 0.001 cm using ImageJ. In addition, twenty termites were randomly selected to provide an initial length-dry mass equation (not fed to spiders).

These 20 termites were sacrificed and dried at 60 °C for 72 h, and their total dry mass was measured using same approaches used for eaten termites. I then estimated termite consumption by subtracting the body mass remaining in each consumed prey item from the estimated initial body mass of a similarly sized unconsumed prey.

Statistical analyses

To compare feeding rates and prey mass consumption by spiders, we used two separate type III analyses of covariance (ANCOVA) with spider feeding rates or prey mass consumption as dependent variables, temperature and diet (lipid dense or protein dense) as main factors, and spider body mass as a covariate. Type III ANCOVAs were selected due to spider mortality resulting in an unbalanced experimental design.

To examine total prey mass consumption by spiders in natural conditions, I used Linear Mixed Models (LMMs) with either total prey mass consumption as response variables, origin site (low or high elevation) and transplant site (low or high elevation) as main factors and their interactions, spider body mass as a covariate, and feeding trial as a random effect. Independent LMMs were performed for each species (*Leucauge* sp and *Cyclosa* sp). All analyses were performed with the lme4 package in R version 3.3.3 (Bates et al. 2015; R Core Team, 2017).

RESULTS

Feeding rates and prey mass consumption experiment

Feeding rates (Figure 1) and prey mass consumption (Figure 2) increased significantly with temperature but not with macronutrient diet (Table 1). While not significant, spiders

fed protein-dense prey showed a steady, gradual increase in both feeding rates and prey mass consumption with increasing temperatures, whereas those fed lipid-dense prey showed a sharp increase and saturated response (i.e., maximum predation rate and prey consumption). There was no significant interaction between temperature and prey macronutrient composition on the feeding rates or prey mass consumption of spiders (Table 1).

Reciprocal transplant experiment

Prey mass consumption was consistently higher for both populations of *Cyclosa* sp at the low elevation/warmer site (Figure 3a). Although *Cyclosa* spiders transplanted from the high elevation site to the low elevation site and viceversa converged to similar prey mass consumption as those transplanted *in situ*, I found no significant effect of origin, transplant, or their interaction on the consumption of prey by this spider (Figure 3a, Table 2). The population of *Leucauge* sp from high elevations consumed less prey mass when transplanted *in situ* than when compared to those individuals transplanted to low elevations (Figure 3b; Table 2 main effect "transplant"). However, those individuals from low elevation when transplanted to high elevation showed no significant change in their prey mass consumption, (Figure 3b; Table 2). The origin x transplant site interaction for the prey consumption was statistically significant for *Leucauge* sp, with transplants having a greater effect on spiders originating from high elevations than on those originating in low elevations (Table 2).

DISCUSSION

In this study I investigated the effects of temperature and prey macronutrient composition on the feeding behavior of predators. I found that increases in temperature caused significant increases in spiders feeding rates and prey mass consumption. These results are consistent with previous studies that show increases in the strength of consumer-resource interactions with rising temperatures, mediated by rises in ectotherm metabolism (Dreisig 1980, Sanchez-Salazar et al. 1987, Dangles et al. 2013, Lemoine et al. 2014, Mas-Martí et al. 2015). The overall increase in the consumption of lipid-dense and protein-dense prey by predators in response to temperature corresponds well with a general increase in resource consumption to support higher metabolic demands (Dreisig 1980, Lemoine et al 2014). However, the shape of these responses may be constrained by the nutritional composition of the food resources available to consumers, as has been shown for herbivores and detritivores (Lee et al. 2015, Mas-Martí et al. 2015, Schmitz et al. 2016).

While nonsignificant, there were slight differences in the pattern of feeding rates and prey mass consumption between the two diets in response to rising temperatures. Spiders fed protein-dense prey had a gradual, linear increase in feeding rates and prey mass consumption, whereas those fed lipid-dense prey increased their consumption more rapidly until reaching a saturation point. These results do not support my prediction that protein-fed spiders would consume more prey than lipid-fed spiders while lipid-fed spiders would consume a greater proportion of each individual prey than protein-fed spiders. When looking at the highest temperature group, predator responses resulted in a nonsignificant trend in total prey mass consumption, with lipid-fed spiders consuming

more biomass than the protein-fed spiders (T-test = 2.1814, $p=0.076$). This suggests that a protein-dense diet may be more nutritionally beneficial at higher temperatures as spiders did not maximize their biomass consumption to maintain their body condition. Further, these results do not support my prediction that lipids would be a limiting macronutrient at higher temperatures due to their importance as a source of metabolic energy (Wilder 2011). It is possible that increasing temperatures may increase metabolic demands for nitrogen due to the increased rate of protein denaturing at higher temperatures, or that increased temperatures reduced spiders' ability to absorb nitrogen postingestion (Lemoine & Shantz 2016). Additionally, spiders have been shown to utilize excess protein as an alternative source of metabolic energy (Jensen et al 2011), which may lessen the metabolic demand for increased lipid consumption. Overall, temperature-dependent shifts in interaction strengths and increased demands for nutrient-dense prey at higher temperatures can have major implications for the stability of food webs. Several lines of evidence suggest that increasing temperatures may result in reduced overall protein content in a wide range of organisms (Woods et al. 2003) and lower nitrogen digestion efficiencies (Lemoine & Shantz 2016). Therefore, the macronutrient content of prey may influence changes in predator-prey interactions, at least at extreme temperatures.

My reciprocal transplant experiment suggested that both local thermal adaptation and acclimatization may significantly affect predator-prey interactions in response to warming, with effects varying between species. While populations of *Cyclosa* spiders transplanted to or originating from the low elevation/warm site showed slightly greater prey consumption, these responses were not significantly different. These results suggest

that for *Cyclosa* spiders, there was little effect of thermal adaptation or acclimatization on interaction strengths. In contrast, *Leucauge* spiders showed contrasting patterns of prey mass consumption when originating from or transplanted to the high elevation/cold site. Spiders from high elevations showed a marked increase in prey mass consumption at the warmer low elevation site, while those from the low elevation site showed no change in prey mass consumption at the high elevation site. Additionally, *in situ* prey mass consumption of low elevation *Leucauge* spiders was significantly greater than that of high elevation spiders. This suggests that populations of *Leucauge* spiders differ in the plasticity of their response to changes in local thermal environment. The high elevation population is highly plastic and adjusted their prey consumption to track expected changes in metabolic rate, while the low elevation population displayed no plasticity in their feeding responses to decreased temperatures. While differences in thermal plasticity have been shown to occur between populations (e.g. Liefting & Ellers 2008), the degree of variation in thermal responses between low and high elevation *Leucauge* populations is much larger than that previously observed in other studies. Predator responses to changing temperatures appear to be not only species specific, but can even vary between populations within a species.

Overall, my findings suggest that rising temperatures increase predator-prey interaction strengths, and that this increase may be only slightly affected by differences in prey macronutrient content. Additionally, these temperature-dependent responses vary between species and populations, and seem to be influenced by local thermal adaptation and acclimatization. While not explicitly tested, one major difference between the different spider species used in these experiments is their hunting behavior. Wolf spiders

are typically ambush hunters that regularly move between different foraging patches, while both *Leucauge* and *Cyclosa* spiders are orbweavers which must wait for prey to become entangled within their web (Foelix 2011). Rising temperatures are likely to have differing effects on species depending on their hunting behavior (Wilmers et al. 2007). Although it was beyond the scope of this study, thermal sensitivity differences between predators and prey can potentially alter trophic interactions in a larger degree (Schmitz & Trussell 2016, Lemoine 2017). My laboratory and reciprocal transplant experiments only tested the effects of rising temperatures and prey macronutrient content on predator feeding responses. Additional experiments combining the responses of both prey and predators with varying hunting strategies from cold and warm environments will give further insight into how local thermal adaptation or acclimatization may affect trophic interactions and food web structure under climate change.

CONCLUSIONS

An important issue in ecological theory is to understand how increased temperatures will affect trophic interactions and food web dynamics (Petchey et al., 1999, Tylianakis et al. 2008, Rall et al. 2010, Dell et al. 2014). Increased temperature affects ectotherm behavior and physiology not only via increases in their feeding rates and changes in consumer resource interactions, but also alters the nutritional needs of the consumers. The observed short-term responses in feeding behavior and physiology suggest that predators may buffer rising temperatures via plastic responses. However, rising temperatures may exceed the capacity of an organism to display physiological and behavioral responses to maintain its energetic demands and performance (Sinclair et al. 2016). Additionally,

warming effects on trophic interactions may differ depending on the hunting behavior of predators (Wilmers et al. 2007). Mismatches between consumer requirements and resource availability and/or quality could have significant effects on predator performance, especially for sit-and-wait predators (Sinclair et al. 2016). Further, the role of plasticity in species-level and predator-prey responses to climate change will depend on whether plasticity confers a fitness advantage and enhances the ability of adaptive evolution to climate change (Price 2003). These behavioral and physiological responses to rising temperatures are likely to have major effects on food web dynamics.

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TABLES

Table 1. Results for two-way analysis of covariance (ANCOVA) testing the influence of temperature, prey macronutrient composition (i.e., diet) and their interactions on the feeding rates and prey mass consumption of spiders, with spider body mass as the covariate. Significant effects ($P < 0.05$) are highlighted in bold.

Feeding rate	Sum Sq	Df	F	P-value
Temperature	78.498	3	6.538	<0.001
Diet	3.034	1	0.7580	0.388
Spider body mass	41.712	1	10.423	0.002
Temperature x diet	12.227	3	1.018	0.393
Prey mass consumption				
Temperature	7543	3	7.487	<0.001
Diet	122.7	1	0.365	0.548
Spider body mass	29.9	1	0.089	0.767
Temperature x diet	850.6	3	0.844	0.477

Table 2. Results of the linear mixed effect models (LMMs) analyses testing origin and transplant site effects and their interactions on prey mass consumption of spiders with feeding trial as a random effect and spider body mass as a covariate. Significant effects ($P < 0.05$) are highlighted in bold.

<i>Cyclosa</i> nutrient intake	Sum Sq	Std.Error	Df	t-value	P-value
Origin site	-0.084	2.155	108	-0.039	0.969
Transplant site	2.862	2.378	108	1.204	0.231
Spider body mass	1.069	1.305	108	0.819	0.415
Origin x transplant	-0.886	3.243	108	-0.273	0.785
<i>Leucauge</i> nutrient intake					
Origin site	6.728	2.333	114	2.884	0.005
Transplant site	6.505	2.347	114	2.772	0.007
Spider body mass	-0.189	1.372	114	-0.138	0.891
Origin x transplant	-8.109	3.290	114	-2.465	0.015

FIGURE LEGENDS

Figure 1. Effect of temperature and prey macronutrient composition on feeding rates of *Pardosa* spiders. Increased temperatures resulted in a significant increase in spider feeding rates. 20°C /lipid-dense prey (n=8), 20°C /protein-dense prey (n=7), 25°C /lipid-dense prey (n=11), 25°C /protein-dense prey (n=10), 30°C /lipid-dense prey (n=6), 30°C /protein-dense prey (n=5) and 35°C /lipid-dense prey (n=4), and 35°C /protein-dense prey (n = 4).

Figure 2. Effect of temperature and prey nutrient composition on prey mass consumption (% dry mass) of *Pardosa* spiders. Increased temperature resulted in a significant increase in the prey mass consumed by spiders.

Figure 3. Responses of spiders' prey mass consumption to reciprocal transplants to different elevations at Ecuador. Interaction plots of the differences between *Cyclosa* individuals (a) and *Leucauge* individuals (b) in overall prey mass consumption. Means and standard errors are estimates from GLMMs. Origin and transplant groups: Lo, Low elevation origin site; Lt, Low elevation spiders transplanted to high elevation site; Ho, High elevation origin site; and Ht, High elevation spiders transplanted to low elevation site. The colour of the arrows (from red to blue) indicates the decrease in air temperature from the low to the high elevation site.

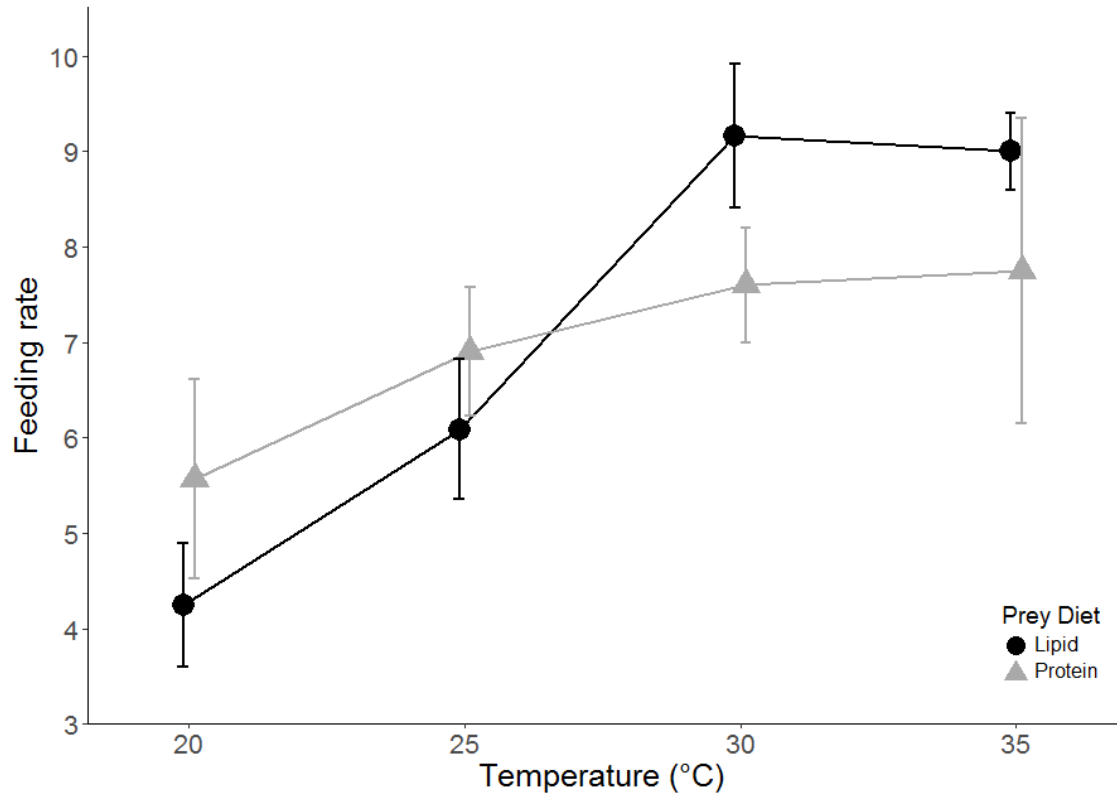


Figure 1.

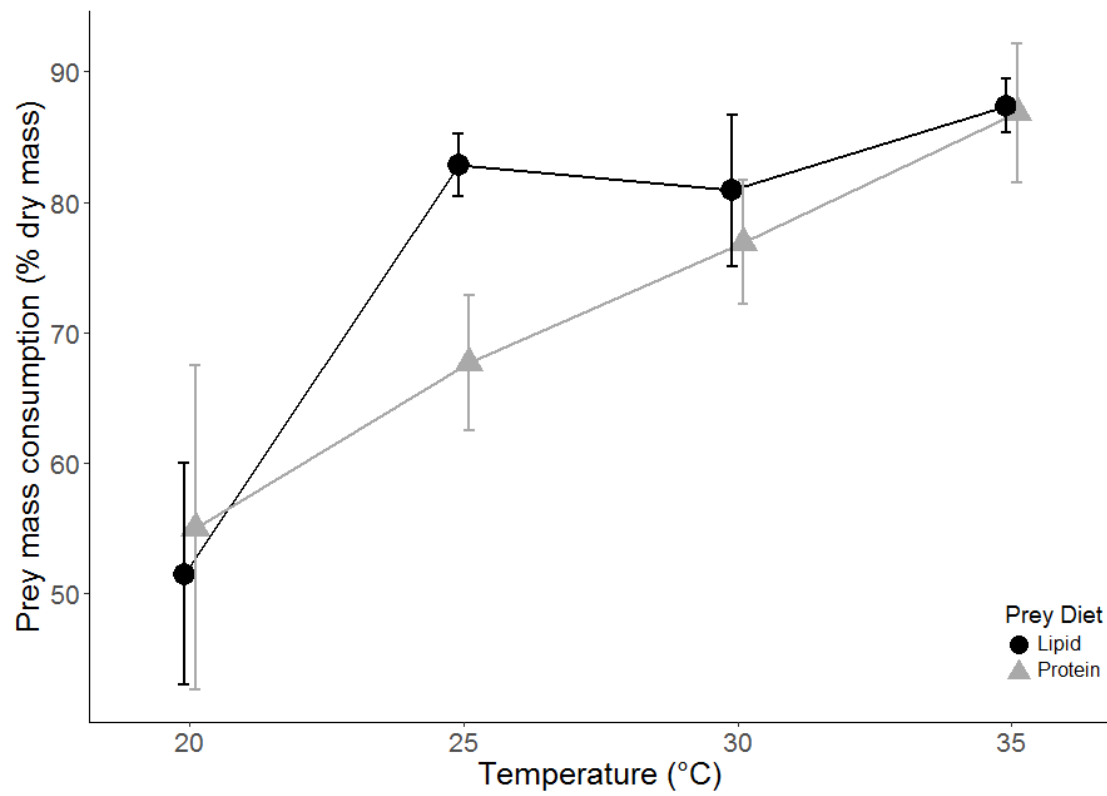


Figure 2.

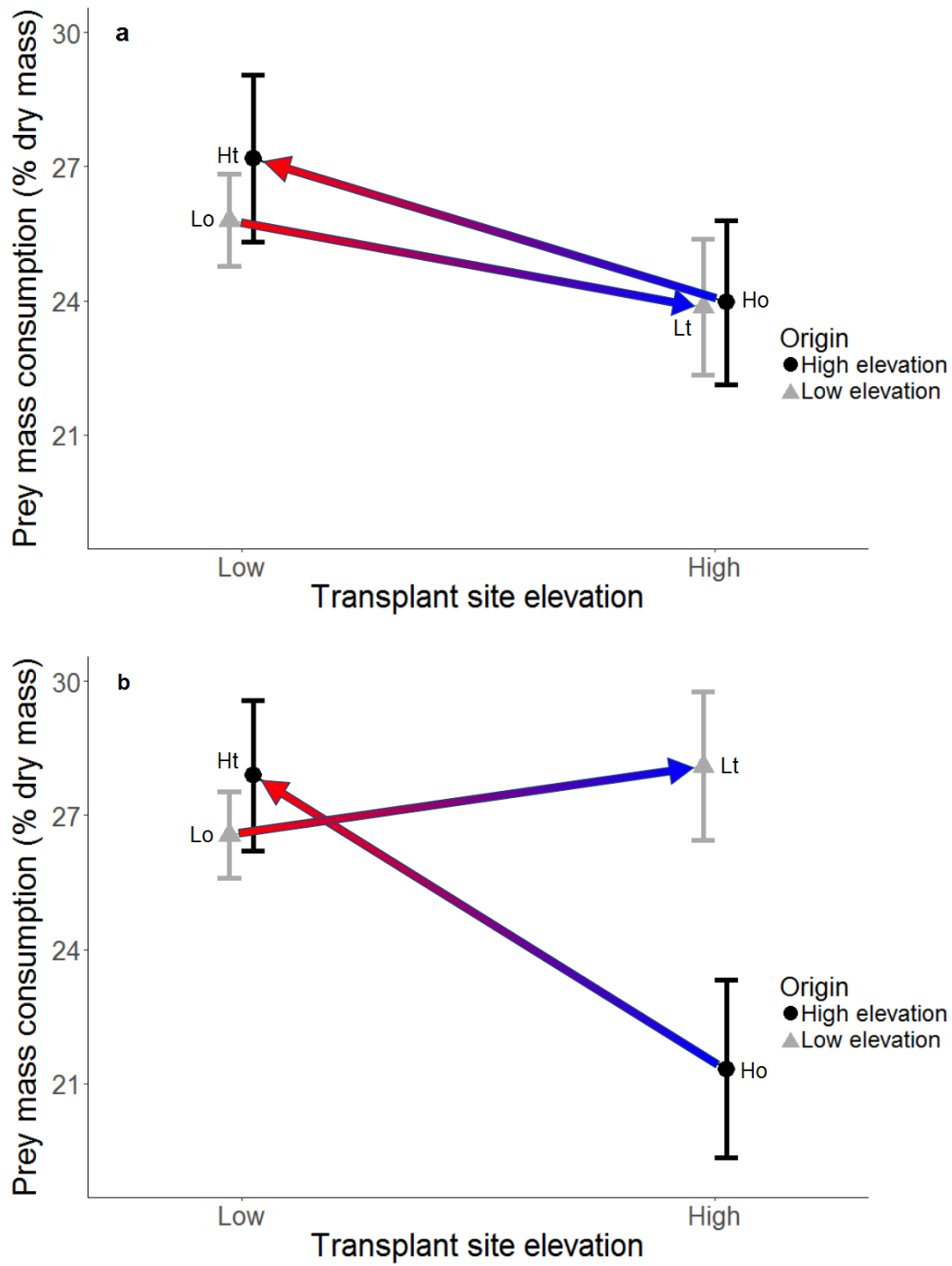


Figure 3.

SUPPLEMENTARY MATERIAL

Table S1. Ingredients in high fat and high protein dietary media fed to crickets (in grams).

	High fat (g)	High protein (g)
Egg white	11	120
Micellar casein	11	120
Sugar	55	7
Flour	85	14
Cellulose	94	33
Nipagin	1	1
Vitamin (capsule)	1	1
Cholesterol	0.5	0.5
Fish oil	3	3
Lard	22	3
Olive oil	22	3

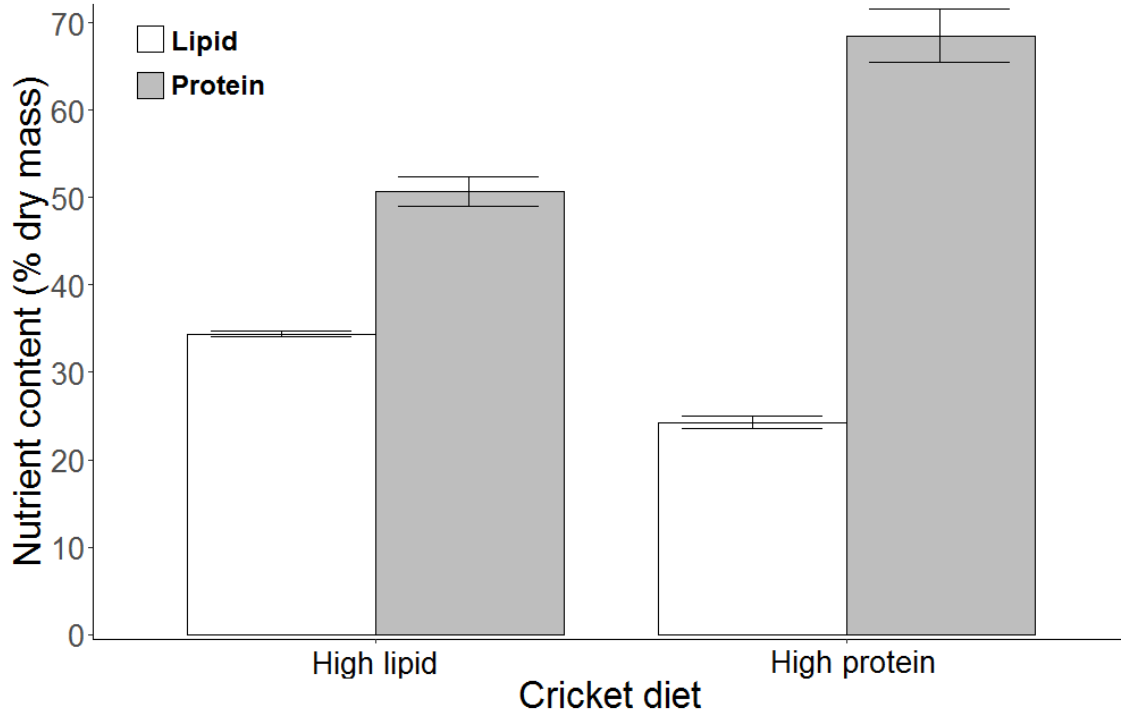


Figure S1. Mean nutrient content (% of dry mass, mean \pm SE n=12) of crickets raised on lipid dense or protein dense media (white = lipid content, grey = protein content). Lipid dense crickets contained 34% lipid and 51% protein by dry mass while protein dense crickets contained 24% lipid and 69% protein by dry mass. Diet resulted in a significant difference in protein ($t=-5.2103$, $p<0.001$) and lipid content ($t=12.95$, $p<0.001$).