

# Red flour beetles balance thermoregulation and food acquisition via density-dependent habitat selection

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## Keywords

fitness; ideal free distribution; isodar; thermal preference; *Tribolium castaneum*.

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## Abstract

Theories of habitat selection assume that habitat selection patterns are based on the fitness consequences of selecting a particular habitat, and predict that individuals should be distributed between habitats so that each individual obtains the same fitness. The predictions are relatively simple when habitat suitability is based upon the quantity of depletable resources, such as food, in a habitat: individuals should be distributed between habitats in proportion to the depletable resources in those habitats. Yet, non-depletable resources can also be important in habitat selection. For example, ectotherms must obtain heat from the environment, which causes them to select habitats based, at least partly, upon thermal quality. Non-depletable resources can cause habitat selection that is independent of density and may modify the value of depletable resources. We used red flour beetles *Tribolium castaneum* to test the hypothesis that habitat selection by ectotherms depends upon both food abundance and temperature. We determined the thermal preference of red flour beetles. We then conducted habitat selection experiments with beetles when habitats were set at their preferred temperature and 10°C below their preferred temperature. We simultaneously manipulated food abundance in both habitats, and varied population density. We also examined the fitness effects of habitat selection by measuring oviposition rates of beetles. Beetles selected the habitat within their preferred temperature when food was equal between habitats and when food was higher in that habitat across all population densities. Beetles showed equal preference for high- and low-temperature habitats when food was higher in the low-temperature habitat across all population densities. Fecundity was always higher at the preferred temperature of beetles, regardless of food abundance or population density. Temperature is clearly an important factor in habitat selection of ectotherms and should be considered whenever thermal differences exist between habitats.

## Introduction

Theories of habitat selection assume that individuals select habitats in a manner that allows each individual to obtain the same expectation of fitness (Fretwell & Lucas, 1969; Rosenzweig, 1981; Rosenzweig & Abramsky, 1986; Morris, 1988). This starting point is known as the ideal free distribution (Fretwell & Lucas, 1969). Because all animals must obtain food, food is often considered to be one of the most important factors in habitat selection. In a simple scenario, individuals should distribute themselves between habitats in proportion to food availability in those habitats (see review in Kennedy & Gray, 1993). The underlying mechanism for this habitat selection pattern is negative density dependence (Fretwell & Lucas, 1969; Rosenzweig, 1981; Morris, 1988): as population density increases, individual fitness decreases because per capita food availability decreases.

Although most theories of habitat selection go beyond food availability and often include factors such as interference competition (the ideal despotic distribution: Fretwell & Lucas, 1969; Fretwell, 1972; Morris, 1988), interspecific competition (Rosenzweig & Abramsky, 1986; Morris, 1988) and predation risk (Moody, Houston & McNamara, 1996; Grand & Dill, 1999), theories of habitat selection typically do not account for factors such as moisture or temperature (Huey, 1991), which do not decline with density. This general lack of consideration for environmental density-independent factors is likely a result of most theories of habitat selection being originally applied to endotherms such as birds (Fretwell, 1969; Fretwell & Calver, 1969) and mammals (Rosenzweig & Abramsky, 1986; Morris, 1988), and only later applied to ectotherms (e.g. Rodríguez, 1995; Haugen *et al.*, 2006; Knight, Morris & Haedrich, 2008). Although theories of habitat selection can still be applied to ectotherms, they

should incorporate environmental temperature, a density-independent factor, as an important driver of habitat selection because temperature profoundly affects the performance of ectotherms (Huey, 1991; Blouin-Demers & Weatherhead, 2001; Buckley, Hurlbert & Jetz, 2012). Furthermore, a theory of habitat selection that incorporates temperature would also be important for endotherms because endotherms are also affected by temperature (e.g. Schwab & Pitt, 1991; Humphries, Thomas & Speakman, 2002), albeit less dramatically than ectotherms.

Habitat suitability for ectotherms depends upon environmental temperature (Huey, 1991; Blouin-Demers & Weatherhead, 2001, 2002, 2008; Row & Blouin-Demers, 2006) because temperature has a marked effect on performance (Blouin-Demers & Weatherhead, 2008) and, ultimately, on fitness (Gilchrist, 1995). Thus, thermal quality (how far, on average, environmental temperature is from the optimal temperature for performance) of a habitat is a key driver of habitat selection in ectotherms. It has even been suggested that some ectotherms, such as snakes, select habitats independently of density because temperature is more important than food availability to fitness (Harvey & Weatherhead, 2006); thus, some ectotherms may trade-off temperature for food in habitat selection.

According to Fretwell & Lucas (1969), the suitability ( $S$ ) of habitat  $i$  can be described by

$$S_i = B_i - f(d_i)$$

where  $B_i$  is the basic suitability of a habitat and  $f(d_i)$  is some function describing the negative effects of density on suitability. Note that if habitat suitability is independent of depletable resources such as food, then  $f(d_i) = 0$  and habitat selection will be density-independent. The ideal free distribution starts with this equation and suggests that individuals will choose a habitat with the highest suitability, which leads to each individual obtaining the same fitness. Using the ideal free distribution as a starting point, Morris (1988) created isodars that predict the density of individuals in habitat A given their density in habitat B. Isodars use geometric mean regressions of the density of individuals in habitat A by the density of individuals in habitat B to estimate the density at which individuals will begin using habitat B (intercept), and the rate at which individuals will select between habitats as density increases (slope). Because differences in available resources between habitats are a function of conspecific density, of the quantity of depletable resources and of the ability of animals to extract those resources (which could be a function of thermal quality, for instance), isodars may be used successfully to predict habitat selection by ectotherms. Isodars are also able to detect effects of interference competition where dominant individuals exclude subordinates from preferred habitats (Morris, 1988; Knight *et al.*, 2008); isodars demonstrating interference competition are curvilinear (Morris, 1988).

In this paper, we use red flour beetles *Tribolium castaneum* to test the hypothesis that both thermal quality and food availability explain habitat selection patterns of ectotherms because thermal quality affects the ability of ectotherms to

extract resources (i.e. obtain, digest and assimilate resources). Specifically, we test the prediction that red flour beetles select habitats based upon food availability, which is a function of conspecific density, but that density-dependent habitat selection is strongly modulated by thermal quality, a density-independent factor. We determined the thermal preference of red flour beetles by allowing beetles to select their preferred body temperature in a thermal gradient. We created high thermal quality (within the preferred temperature range) and low thermal quality (below the preferred temperature range) habitats, and then created equal food and unequal food treatments between thermal habitats. We allowed beetles to select habitats under three treatment combinations at varying densities. Finally, we determined the fitness consequences of habitat selection by measuring oviposition rates in four food and temperature treatment combinations to determine if negative density dependence is modified by the thermal quality of a habitat.

## Materials and methods

We conducted all experiments with a colony of red flour beetles *T. castaneum* originally obtained from Carolina Biological Supply Company (Burlington, NC, USA). The starting colony consisted of 200 individuals, and we let the colony grow to *c.* 5000 individuals. We raised beetles in large cultures containing 95% all-purpose wheat flour and 5% brewer's yeast (all future mention of flour refers to this mixture). We maintained the cultures at 25°C and 70% humidity. We identified the sex of beetles at the pupal stage (Good, 1936) and separated males and females for experiments.

We conducted four experiments to determine if density-dependent habitat selection by red flour beetles is modified by thermal quality: (1) we determined the thermal preference of flour beetles; (2) we allowed beetles to select between one habitat set at their preferred temperature and a second habitat set at 10°C below their preferred temperature while varying food abundance and density; (3) we determined how much food was required to cause beetles to switch habitat preference to a lower thermal quality habitat; (4) we determined the fitness effects of habitat selection by examining oviposition rate under different temperature, food and density combinations, which allowed us to examine the assumptions of density-dependent habitat selection. Each of these four experiments is detailed below.

### Thermal preference

We determined the thermal preference of red flour beetles by placing beetles in a thermal gradient ranging from 25 to 40°C. We created the thermal gradient by placing a metal box (30 × 30 cm) with five runways (5 cm wide) in an environmental chamber set at 25°C and placing heating pads under one end of the gradient. We generated a thermal map of the gradient by measuring temperature every 1 cm. We placed 10 beetles in each lane, allowed them to acclimate to the gradient for 1 h and then took pictures of the beetles in the gradient every 5 min for 1 h using a digital camera. We assigned a

temperature to each beetle in each picture based upon its location on the thermal map. We used 100 male and 100 female beetles in this experiment, for a total of 10 replicates of 10 individuals for each sex. We estimated the thermal preference of all beetles as the interquartile range of all selected temperatures (Huey, 1991).

### Habitat selection

We created three habitat selection treatments. All treatments had a habitat with high thermal quality (30°C, within the preferred temperature for red flour beetles – see the Results section; henceforth referred to as ‘warm’) and a habitat with low thermal quality (20°C; henceforth referred to as ‘cool’). We created habitats that varied in thermal quality by placing a clear plastic container ( $l \times w \times h = 31 \times 17 \times 10$  cm) with 1 cm of sand as substrate in a thermal chamber set to 20°C. We then placed one end of the plastic container on heat tape set to 30°C. To create variation in food availability, we placed flour on two glass slides (75 × 25 mm) 20 cm apart in the plastic container, one in each thermal habitat. The first treatment had equal food in the warm and cool habitats (2.5 mL of flour); the second treatment had high food in the warm habitat (2.5 mL of flour in warm, 0.625 mL of flour in cool); and the third treatment had high food in the cool habitat (2.5 mL of flour in cool, 0.625 mL of flour in warm). We placed five densities of female flour beetles in the middle of each container (10, 20, 30, 40 and 50 beetles) with 10 replicates of each density for each treatment. We used female beetles in this experiment because male red flour beetles emit aggregation pheromones (Suzuki, 1980) that could potentially change a beetle’s perception of habitat suitability. We counted the number of beetles in each habitat (defined as the total number of beetles found in each container half) after 24 h. We also counted the number of beetles in each habitat after 48 h, but we found no difference in distribution between 24 and 48 h and, therefore, we only present the data for 24 h for simplicity.

We used isodar analysis (Morris, 1988) to test for density-dependent habitat selection in each treatment. We analysed the abundance of beetles in the warm habitat as a function of the abundance of beetles in the cool habitat for each treatment using geometric mean regressions in R (package: lmodel2; function: lmodel2; Legendre, 2013). We tested for differences between isodars for each treatment by comparing the 95% confidence interval around the intercept and slope for each treatment isodar.

### Relative effects of thermal quality and of food abundance in habitat selection

We used the same habitats as in the previous experiment, but this time we used both unequal thermal quality (20 and 30°C) and equal thermal quality (30°C on both sides) treatments. We placed 0.625 mL of flour in the warm habitat (30°C). We then created eight treatments with increasing food in the cool habitat (equal increments from 0.625 to 5.0 mL). We placed 10 female red flour beetles at the centre of each container and then counted the number of beetles in each habitat after 24 h.

We replicated each treatment combination (eight food treatments in each of the two thermal quality treatments) 10 times.

We analysed the proportion of individuals in the low food habitat using analysis of covariance in R (package: stats; function: lm; R Core Team, 2012). We used thermal quality treatment, amount of food in the second habitat, the square of the amount of food in the second habitat and all two-way interactions as independent variables. We used bias-corrected Akaike’s information criteria (package: qpcR; function: AICc; Spiess, 2012) to select the best model. We considered the model with the lowest AICc to be the ‘best’ model as long as the difference in AICc ( $\Delta AICc$ ) between models was  $>2$ ; when  $\Delta AICc < 2$ , we chose the most parsimonious (fewest parameters) model (Akaike, 1973; Bozdogan, 1987). We also confirmed that statistical assumptions (i.e. normality, homogeneity of variance) were met.

### Fitness consequences of habitat selection

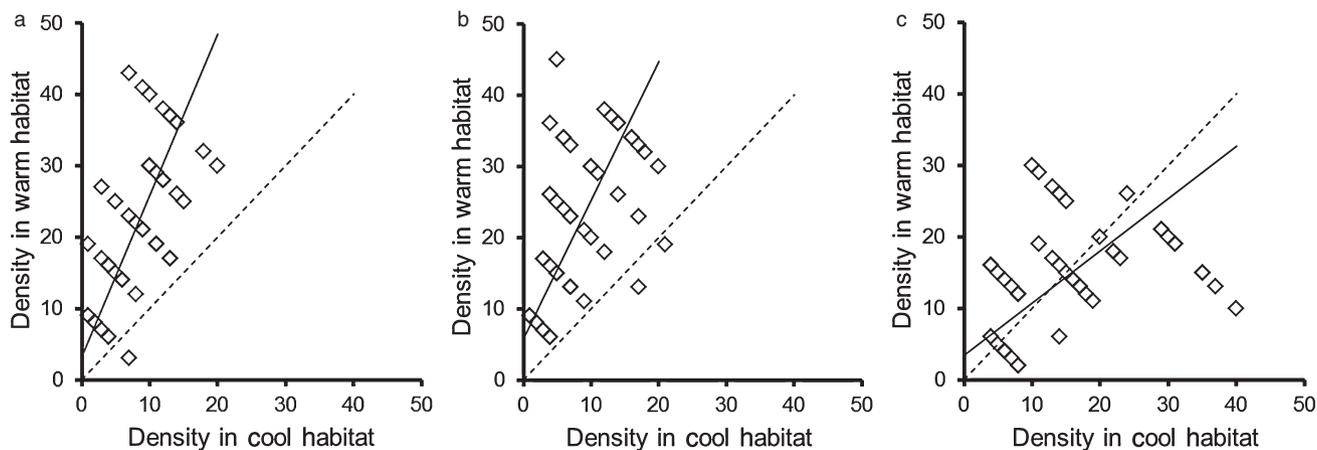
We tested the fitness consequences of habitat selection by measuring the fecundity (oviposition rate) of flour beetles. We placed five densities of beetles (10, 20, 30, 40 and 50) in 10 replicates of four habitat treatments: 30°C with 2.5 mL of flour, 30°C with 0.625 mL of flour, 20°C with 2.5 mL of flour and 20°C with 0.625 mL of flour. Prior to the experiment, flour was sifted through a 250- $\mu$ m sieve so that flour particles could not be confused with beetle eggs. We placed the flour in a plastic Petri dish (10-cm diameter) and then added beetles non-selectively obtained from a culture of ~5000 beetles. We assumed a 1:1 sex ratio in the culture based upon pilot studies, where the sex ratio of pupae in three different cultures was  $51.1 \pm 0.01\%$  female (three samples per culture per week over 12 weeks). Although the probability of obtaining an unequal sex ratio was higher for the low density than for the high density treatments, the probability was equal across a given density treatment, and the differences should have averaged out. We did not use beetles previously identified to sex as pupae due to the large number of beetles required for this experiment (1500 per sex). We placed each Petri dish in an incubator set to 20 or 30°C. After 4 days, we removed each Petri dish, sifted all eggs from the flour using a 250- $\mu$ m sieve and counted all eggs. We calculated per capita fecundity as the number of eggs laid divided by the density of individuals in the treatment.

We analysed per capita fecundity (square root-transformed) using multiple linear regression in R (package: stats; function: lm), with temperature (20 or 30°C), food (0.625 or 2.5 mL), density (10, 20, 30, 40 or 50), density<sup>2</sup>, and all two- and three-way interactions (excluding the three-way interaction with density and density<sup>2</sup>) as independent variables. Again, we used bias-corrected Akaike’s information criteria to select the best model.

## Results

### Thermal preference

Consistent with King & Dawson (1973), the thermal preference of red flour beetles was 28.8–33.8°C, with a mean selected



**Figure 1** Isodars for habitat selection experiments with red flour beetles *Tribolium castaneum*, where habitats were set at 20 and 30°C with food equal between habitats (a), food higher in the warm habitat (b) and food higher in the cool habitat (c). Density is the total number of beetles in a habitat. The solid line represents the isodar, calculated using geometric mean regression, and the dashed line represents equality between habitats.  $n = 10$  replicates for each density treatment, which are represented as diagonal rows of points. Bold outlines represent overlapping data points.

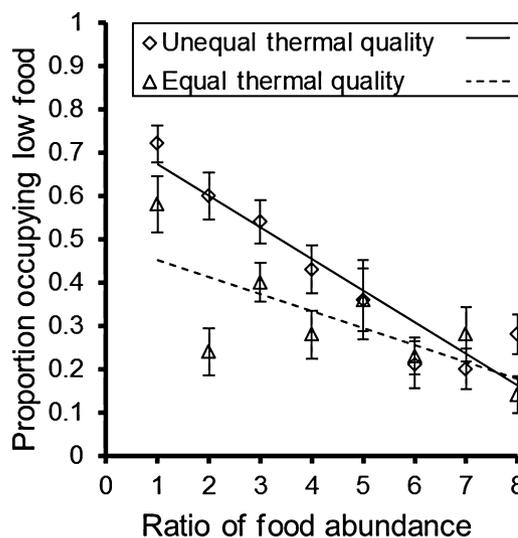
temperature of 31.8°C and a median selected temperature of 29.9°C (see Supporting Information Fig. S1). We used the median temperature (rounded to 30°C) as the high thermal quality habitat in the following experiments. Using the median selected temperature is a common method for determining the preferred temperature of a species (Hertz, Huey & Stevenson, 1993).

### Habitat selection

Red flour beetles preferred the warm habitat over the cool habitat across all densities when there was equal food in each habitat ( $n = 50$ ,  $R^2 = 0.44$ ,  $P < 0.0001$ ; Fig. 1a) and when there was more food in the warm habitat ( $n = 50$ ,  $R^2 = 0.26$ ,  $P < 0.001$ ; Fig. 1b). In the third treatment (high food in cool habitat), beetles preferred the warm habitat over the cool habitat at low population density, but started to prefer the cool habitat over the warm habitat as density increased ( $n = 50$ ,  $R^2 = 0.11$ ,  $P = 0.02$ ; Fig. 1c). The 95% confidence intervals around the intercepts for all three isodars overlapped, but the slopes for the equal and high food in warm habitat treatments were higher than the slope for the high food in cool habitat treatment (see Supporting Information Table S1).

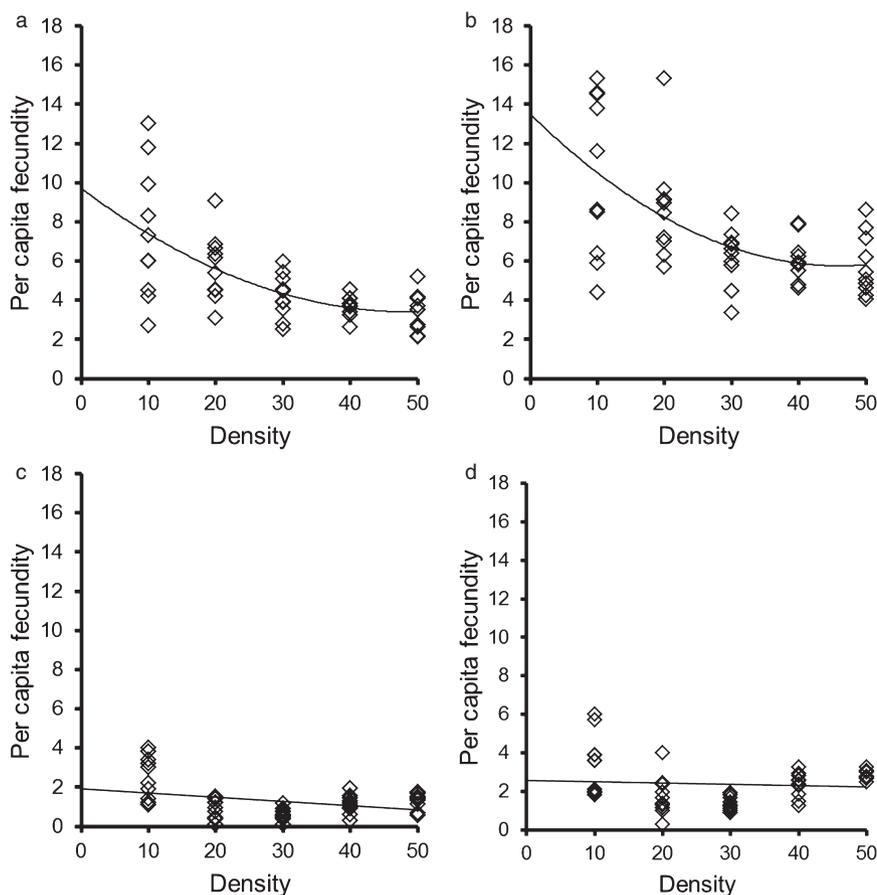
### Relative effects of thermal quality and of food abundance in habitat selection

The proportion of beetles in the low food habitat decreased as the amount of food increased in the high food habitat in both thermal quality treatments (d.f. = 156;  $R^2 = 0.38$ ,  $P < 0.0001$ ; Fig. 2, see Supporting Information Table S2). The proportion of beetles in the low food habitat was lower in the equal thermal quality treatment than in the unequal thermal quality treatment ( $t_{1,156} = 3.91$ ,  $P = 0.0001$ ) and the relationship



**Figure 2** The proportion of red flour beetles *Tribolium castaneum* using the low food habitat (Proportion occupying low food) as the amount of food in the high food habitat increased (Ratio of food abundance). Habitats either had equal thermal quality (30°C) or unequal thermal quality (20 and 30°C), and the low food habitat was always set at 30°C. Ratio of food abundance (x-axis) refers to how much more food the high food habitat had compared to the low food habitat. Linear regression best described the unequal thermal quality treatment (solid line) and the equal thermal quality treatment (dashed line). Each point represents the mean value for that treatment ( $n = 10$ ), and the error bars represent the standard error of the mean.

between the proportion of beetles in the low food habitat and the abundance of food in the high food habitat was different between thermal quality treatments (Food  $\times$  Treatment:  $t_{1,156} = 2.61$ ,  $P = 0.01$ ), where the slope was steeper for the



**Figure 3** Per capita fecundity of red flour beetles *Tribolium castaneum* in treatments set at 30°C with 0.625 mL of flour (a) and 2.5 mL of flour (b), and set at 20°C with 0.625 mL of flour (c) and 2.5 mL of flour (d) as density increases from 10 to 50 beetles. Density is the total number of individuals in a treatment, and per capita fecundity is the number of eggs laid over 4 days divided by the density of beetles in the treatment.  $n = 10$  replicates for each density treatment. Points are darker where they are overlapping. The lines in (a) and (b) represent the polynomial line of best fit, and the lines in (c) and (d) represent the linear line of best fit.

unequal thermal quality treatment than for the equal thermal quality treatment (Fig. 2). Two closely competing, but less parsimonious models (see Supporting Information Table S2) included the non-significant effect of food<sup>2</sup>, and were therefore not considered the best models.

### Fitness consequences of habitat selection

Per capita fecundity was higher at 30°C (high thermal quality) than at 20°C (low thermal quality; temperature:  $t_{1,193} = 23.60$ ,  $P < 0.0001$ ), and per capita fecundity decreased as food availability decreased (food:  $t_{1,193} = 9.84$ ,  $P < 0.0001$ ; full model:  $R^2 = 0.80$ ,  $P < 0.0001$ ; Fig. 3, see Supporting Information Table S3). Negative density dependence was strong and curvilinear in the 30°C treatments, but was linear and nearly absent in the 20°C treatment (Density  $\times$  Temperature:  $t_{1,193} = 4.99$ ,  $P < 0.0001$ ; Density<sup>2</sup>  $\times$  Temperature:  $t_{1,193} = 3.04$ ,  $P < 0.01$ ).

### Discussion

Theories of density-dependent habitat selection were originally adapted for endothermic animals and focus on the effect of the quantity of depletable resources, such as food, yet many ectothermic animals may be limited more by environmental

temperature than by food (e.g. Huey, 1991; Buckley *et al.*, 2012). Our habitat selection experiments with red flour beetles demonstrate that ectotherms do select habitats based upon conspecific density, but the effects of thermal quality and of food abundance on habitat selection interact. Beetles in the equal food and in the high food in warm habitat treatments both preferred the warm habitat across all densities, despite the differences in food between these treatments. The distribution of beetles in the high food in cool habitat treatment provided clear evidence of the interaction between thermal quality and food abundance in the habitat selection of ectotherms: beetles demonstrated a preference for the warm habitat at low density and an increasing preference for the cool habitat as density increased. This suggests that under low competition (low density), beetles select their preferred temperature rather than more food in the cool habitat; but as competition increases, individuals are forced to use temperatures outside their preferred range to obtain sufficient food. In this way, individuals are potentially maximizing fitness by trading off heat and food in their habitat preference. It also appears that beetles were competing for food through exploitative competition rather than through interference competition, as demonstrated by our linear (rather than curvilinear) isodars (Morris, 1988).

Our experiment, designed to assess the relative effects of food abundance and thermal quality on habitat selection, demonstrated that beetles in the equal thermal quality treatment followed the predictions of habitat matching, whereas beetles in the unequal thermal quality treatment followed a distribution that depended partly upon food, but was strongly modified by thermal quality. Beetles switched habitat preference for the cool habitat when the cool habitat had four times more food than the warm habitat, and beetles continued to show increased preference for the cool habitat as food increased in that habitat. These results are strong indications that habitat selection is based upon both food and thermal quality in red flour beetles.

While the spatial distribution of animals is the focus of work on habitat selection, variation in population growth across habitats is an important mechanism driving variation in density. Our oviposition results demonstrate a clear fitness difference between warm and cool habitats. In warm habitats, negative density dependence was strong and a decrease in food abundance caused a sharp decrease in oviposition (although not exactly in proportion to food abundance). In cool habitats, however, negative density dependence was weak, and the effect of food abundance on oviposition was also weak. This suggests that when thermal quality is low, the ability to process resources, not the ability to acquire resources, is the rate-limiting factor for fitness in ectotherms. Transposed to our habitat selection experiments, these results indicate that beetles selecting the cool habitat would only have achieved equal fitness to beetles selecting the warm habitat when food was low in the warm habitat and when beetles were at the highest density. This raises a very interesting question: why did beetles select the cool habitat at all when it would have yielded lower fitness? One possible explanation is that beetles moved to the cool habitat to forage, but then moved back to the warm habitat to process their food. As our habitats were relatively close together, this behavioural response was possible. Future studies could test this hypothesis by marking the beetles and monitoring their movements to determine if beetles move between habitats more often when habitats differ in thermal quality than when thermal quality is equal. Alternatively, oviposition rates may not be an ultimate measure of fitness and a better measure of fitness, such as the number of descendants reaching reproductive age, may have indicated perfect habitat matching. Future work should examine the ultimate fitness consequences of habitat selection in flour beetles. Finally, another alternative hypothesis to explain this surprising pattern of beetle distribution is that beetles are also selecting habitat based upon the size of the habitat, and not just on food abundance. Flour is the food source for flour beetles, but it is also the substrate in which they conduct many of their activities. While our fitness experiment related oviposition rates to the availability of heat and food, it was not designed to assess the effect of habitat size because beetles were forced to live within one habitat in a finite space. Our habitat selection experiment, on the other hand, allowed individuals to select between habitats that differed in the amount of food, but also in the size of the food patch because food abundance and patch size are confounded in our design.

Although the habitats were the same size (one half of the container), the food patches within the habitats differed in volume. It is thus possible that space was limiting in the low food patch. Beetles could therefore be distributing themselves based upon the number of individuals that can fit in the food patch rather than based upon the amount of food in that habitat. Future work could assess this hypothesis by mixing wheat flour with a lower quality food, such as corn flour, and allowing beetles to select between patches of equal size, but with different food quality (King & Dawson, 1973).

Thermal quality is clearly an important aspect of habitat selection by ectotherms, and theories of habitat selection should reflect this importance. In fact, under some circumstances, thermal quality is the rate-limiting factor for fitness of ectotherms. All ectotherms require food, but they also all require a high thermal quality habitat to process food. While we expect thermal quality to be most important in predicting habitat selection patterns in ectotherms given their reliance on environmental temperature to regulate their body temperature, thermal quality actually also influences habitat selection by endotherms. Indeed, some large mammalian herbivores must select habitats to avoid heat stress (Schwab & Pitt, 1991), whereas some small hibernating mammals must select hibernacula that are not too cold (Humphries *et al.*, 2002). Therefore, including thermal quality as a factor that modifies habitat suitability would allow for a more accurate prediction of the distribution of animals between habitats.

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## Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Figure S1.** The temperatures selected by red flour beetles (*Tribolium castaneum*) in a thermal gradient ranging from 25 to 40°C. The box represents the interquartile range, the line within the box represents the median value, and the whiskers represent the maximum and minimum values.

**Table S1.** Isodars for red flour beetles (*Tribolium castaneum*) in three treatments that varied the quantity of food in habitats when habitats differed in thermal quality. Treatment = Equal (equal food between habitats), High (4 times more food in warm than in cool habitat), and Low (4 times more food in cool than in warm habitat). In the equation, Warm refers to the abundance of beetles in the warm habitat, and Cool is the number of beetles in the cool habitat. C.I. (Int) is the 95% confidence interval for the intercept and C.I. (Sl) is the 95% confidence interval for the slope.

**Table S2.** Model selection (top section) and parameters of the final model (bottom section) describing habitat selection of red flour beetles (*Tribolium castaneum*) in habitats differing in thermal quality and food as food increases in one habitat. Proportion = # beetles in low food habitat/total # of beetles; Treatment = equal thermal quality and unequal thermal quality (intercept in bottom panel); Food = multiples of food in the high food habitat; Food<sup>2</sup> = square of Food;  $k$  = number

of parameters in a model; AICc = bias-corrected Akaike's information criteria value;  $\Delta$ AICc = difference between AICc of the best model (bolded) and each other model. \*represents a competing, but less parsimonious model.

**Table S3.** Model selection (top section) and parameters of the final model (bottom section) describing per capita fitness (square root-transformed) of red flour beetles (*Tribolium castaneum*) as temperature, food abundance, and population

density are varied. Fitness = per capita # of eggs laid over four days; Temperature = temperature treatment (20 or 30°C); Food = food treatment (0.625 or 2.5 mL of flour); Density = number of beetles in a treatment; Density<sup>2</sup> = square of Density;  $k$  = number of parameters in a model; AICc = bias-corrected Akaike's information criteria value;  $\Delta$ AICc = difference between AICc of the best model (bolded) and each other model. \*represents a competing, but less parsimonious model.