Does habitat quality affect density-dependent habitat selection by *Tribolium castaneum*?

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II. ABSTRACT

Density-dependent habitat selection inherently relies on the relationship between population density and fitness in different habitats. Habitats differing in quality, such as different food sources or habitat structure can have very different density-dependent relationships, which can then affect patterns of density dependence in habitat selection. I tested the hypothesis that patterns in fitness dictate the patterns in density-dependent habitat selection and tested the prediction that individuals will prefer the higher quality habitat over the lower quality habitat because it offers the best fitness, as demonstrated by fitness patterns. I tested this hypothesis using controlled experiments with red flour beetles (*Tribolium castaneum*), and examined density-dependent habitat selection by beetles in wheat, corn, and soy flour habitats, and compared these results to the fitness achieved in each of those habitats. Despite large differences in fitness, where fitness was highest in wheat flour, lower in corn flour, and nill in soy flour, beetles showed weak preference for wheat over corn flour and corn over soy flour, but strong preference for wheat over soy flour. These preferences were strongest at low density, but less obvious at higher densities. Beetles did not consistently match fitness predictions as they may use the lower quality habitat such as corn and soy as a structure for cover or because of space availability, and not directly as a food source. This study gives insight into the relationship between habitat quality and density-dependent habitat selection. It also suggests that other factors other than food sources determine habitat quality.

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VII. INTRODUCTION

Resources vary spatially and temporally across landscapes, and the distribution of organisms across landscapes will depend on the quality (or suitability) of those resources. Habitat selection and habitat preference are determined by an individual's fitness in different habitats, which can be based on the availability of shelters, the quantity and quality of food, or access to mates (Cody, 1985); individuals should prefer and select habitats that offer the greatest fitness rewards (Fretwell and Lucas, 1969). In habitat selection, fitness decreases as population density increases, which might cause different habitat selection patterns at different densities (Morris, 1988; Rosenzweig, 1981). Different forms of density-dependent habitat selection occur, such as ideal free distributions, where individuals are distributed proportionally between habitats depending on the amount of resources available in each habitat so that each individual obtains the same fitness, and ideal despotic distributions, where dominant individuals have higher fitness and are in higher quality habitats than subordinate individuals (Fretwell and Lucas, 1969).

In this study, I examine density-dependent habitat selection by red flour beetles *(Tribolium castaneum*) in habitats of different quality, where habitat quality is defined by the quality of the food sources (wheat, corn, and soy flour). Red flour beetles are stored grain pests that eat grain and oilseed (Good, 1936). Red flour beetles also use their food source as a habitat, where all of their life stages occur within that food source. This makes them a good model organism for testing habitat selection theory because it is easy to manipulate habitat quality by varying the food source. I hypothesize that patterns in fitness dictate the patterns in density-dependent habitat selection. Wheat flour is considered the optimal food source for flour beetles (Kheradpir, 2014) and previous studies have demonstrated that flour beetles have higher fitness in wheat than in corn flour, and also show a preference for living in wheat over corn flour (King and Dawson 1973). This is likely due to the differences in nutrient content, where corn has higher fat and fiber content, while wheat has higher protein content. Both wheat and corn are high in carbohydrate content. Meanwhile, soy flour is low in carbohydrates, but has higher protein, fat, and fiber than both wheat and corn flour, making it too harsh for the beetles (Mickel, 1947).

Fitness experiments with red flour beetles (Halliday, unpublished data) demonstrate that egg production is highest in wheat flour, lower in corn flour, and the lowest in soy flour, and that the number of eggs produced decreases with density in wheat and corn flour, but not in soy flour (Figure 1A). Another experiment examining population growth rate over six weeks in each flour type at three starting densities (Halliday, unpublished data) demonstrated that flour beetles in wheat had an increase in the total number of adults at the lowest starting density, and maintained population size at the higher starting densities, while beetles in corn had a slight decrease in the number of adults at all densities, and beetles in soy all died in six weeks (Figure 1B). Meanwhile, when population size was measured as the number of individuals in all life stages, total population size was higher for beetles in wheat than corn at low starting densities, equal at medium starting densities, and higher in corn than wheat at high starting densities; there were no living individuals in soy flour at any life stage (Figure 1C). These fitness results drive my prediction that beetles should always prefer living in the higher quality habitat over the lower one, meaning the beetles will prefer wheat over corn and soy, and corn over soy, regardless of the population density. Although fecundity and development time is higher in wheat than corn, total population size is higher in wheat at low starting densities, and higher in corn at higher starting densities. These fitness results might lead to conflicting habitat preference between wheat and corn as density changes, with beetles preferring wheat at low densities and corn at higher densities, even though corn is a lower quality habitat.

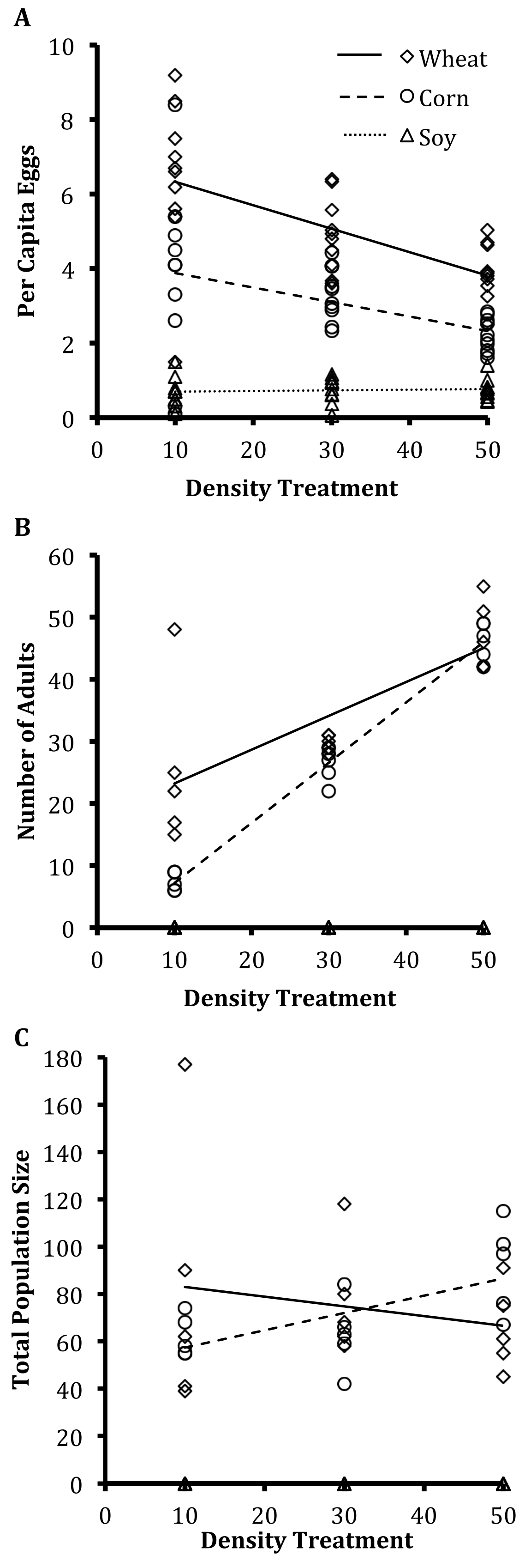

Figure 1. Fitness of red flour beetles (*Tribolium castaneum*) in wheat, corn, and soy flour, as measured by their per capita egg output (A), the number of adults in a population after six weeks (B), and the total population size (adults, larva, and pupa) after six weeks (C) at three starting density treatments.

VIII. METHODS

I conducted my experiment using females from a colony of red flour beetles (*Tribolium castaneum*) originally obtained from Carolina Biological Supply Company (Burlington, NC). The original colony consisted of 200 mixed individuals and the colony was grown to approximately contain 5000 individuals. The beetles were kept in large cultures containing 95% all-purpose wheat flour and 5% brewer's yeast. The cultures were maintained at 30°C and 70% humidity, with a 12 h light and 12 h dark photoperiod. Only female red flour beetles were used because males produce an aggregation pheromone (Suzuki, 1980), which has the potential to obscure habitat selection patterns (Halliday and Blouin-Demers, 2014). As a result, I had to first sex *Tribolium castaneum* pupae from the mixed colonies and establish an all-female colony from which I used the individuals in my experiments. Sexing was done during the pupae stage, as female ovipositors are only clearly discernable during this stage (Park, 1934).

I introduced three densities (10, 30, and 50 beetles) of female red flour beetles to the middle of a clear plastic container (31 × 17 × 10 cm) with sand as a substrate. Each container had two habitats, consisting of 2.5 ml of flour placed on glass slides at opposite ends of the container. I used three food sources (wheat, corn, and soy flour) to create three types of habitats, and compared the preference for each of these habitats using binary comparisons for a total of three treatment combinations at each density with 10 replicates of each treatment by density combination. After 24 hours, I counted the number of beetles in each half of the container. I maintained ambient temperature at 30°C because it is the preferred temperature of red flour beetles (Halliday and Blouin-Demers, 2014), and is also the optimal temperature for fitness, as measured by the number of eggs laid (Halliday et al. 2015).

I analyzed the data using isodar analysis (geometric mean regression) in R (package: lmodel2; function: lmodel2; Legendre 2014). I built an isodar for each habitat comparison, and compared the confidence interval around the intercept and slope to 0 and 1, respectively, which represent equal selection of both habitats (Morris, 1988).

According to the isodar theory of habitat selection (Morris, 1988), habitats differ in both quality and quantity. Quality refers to the basic suitability of a habitat, or the fitness that can be achieved in the absence of competition. Quantity refers to the overall amount of energy available in a habitat that can be split between individuals. According to isodar theory, habitats with different qualities will have an isodar intercept different than zero, and habitats with different quantities will have an isodar slope different than one. Habitats can differ in both quality and quantity, or only in one of these aspects.

IX. RESULTS

Red flour beetles preferred the high quality habitat over the low quality habitat in all comparisons (Figure 2, Table 1). Wheat was preferred over corn and soy, while corn was also preferred over soy.

The confidence intervals for the slopes in all comparisons overlapped with 1, which indicates that this preference for the higher quality habitat was not very strong (Table 1). The confidence intervals for the intercepts overlapped with zero for wheat vs. corn and for corn vs. soy, which indicates that the preference for the high quality habitat is not strong. The confidence intervals for wheat vs. soy did not include zero, which indicates that beetles do prefer living in wheat rather than soy.

Treatment	**Equation**	**Intercept C.I.**		**Slope C.I.**		**P-value**	**R^2**
Wheat vs. Corn	Wheat=0.09+1.20*Corn	-6.62	4.84	0.85	1.70	0.02	0.18
Wheat vs. Soy	Wheat=5.72+1.17*Soy	0.66	9.35	0.84	1.62	0.005	0.24
Corn vs. Soy	Corn=2.89+1.04*Soy	-2.43	6.72	0.75	1.44	0.003	0.27

Table I. Isodars for red flour beetles (*Tribolium castaneum*) in three treatments that contained two different habitats. Treatment = Wheat vs. Corn, Wheat vs. Soy and Corn vs. Soy. In the equation, Wheat refers to the number of beetles in the wheat habitat, Corn refers to the number of beetles in the corn habitat and Soy is the number of beetles in the soy habitat. Intercept C.I. is the 95% confidence interval for the intercept and Slope C.I. is the 95% confidence interval for the slope.

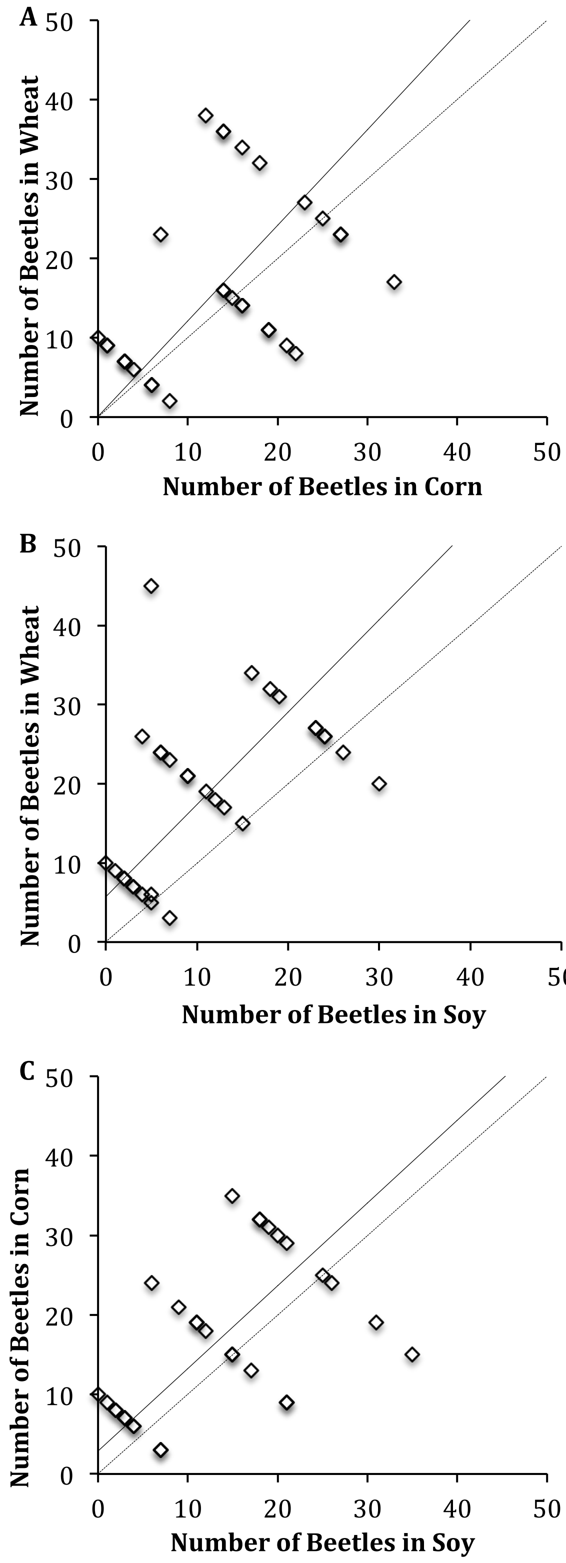

Figure 2. Isodars (calculated via geometric mean regression) for habitat selection by *Tribolium casteneum*. A) represents the isodar for habitat selection between wheat and corn, B) between wheat and soy and C) between corn and soy. Each diamond represents a single replicate indicating the number of beetles found in each habitat. Solid line indicates the habitat selection isodar and the dotted line represents the equality between habitats (a one for one selection between both habitats).

X. DISCUSSION

At lower densities, there was a larger proportion of beetles in the wheat habitat than in the corn habitat and therefore wheat was favoured, which reflects the results found in the fitness study (Halliday, unpublished data). However, at medium and higher densities, the proportion of beetles found in the wheat habitat decreased and the preference for wheat weakened with increasing density. The preference for wheat over corn at high densities contradicts the fitness pattern observed, where populations were higher in corn at high densities (Figure 1C). Although proven to provide optimal fitness, the wheat habitat was not significantly preferred over corn because the confidence interval for the slope overlapped with 1 and the confidence interval for the intercept overlapped with 0. The differing patterns depending on density observed in the fitness study were indeed reflected in the habitat comparisons, because although beetles did prefer the wheat habitat over the corn habitat, the ratios of beetles in each habitat did not remain constant with increasing density.

Tribolium castaneum displayed a significant preference for wheat over soy at all densities but especially at low and medium densities, where the ratio of beetles in wheat to beetles in soy was 8:2 at low density and 19:11 at medium density (Figure 2B). The patterns in habitat selection reflect the patterns in fitness in this comparison as beetles hardly chose soy, as they cannot subsist in a habitat of such low quality. The significant difference in habitat quality is represented by an intercept different than 0 (Figure 2B). A preference for corn over soy was observed, reinforcing the prediction that beetles will prefer higher quality habitat over the lower quality habitat. At lower densities, there was a stronger preference for corn over soy; however, this preference weakened with increasing density as the ratio of beetles between the habitats at lower density does not persist at higher densities and the proportion of beetles found in the higher quality habitat decreases. According to the fitness data, the soy habitat does not offer any fitness at all, as all the beetles die when left in soy. If patterns in fitness truly dictated patterns in density-dependent habitat selection, beetles should not have been found in the soy patch, as they cannot subsist in this harsh environment. The results in this habitat comparison indicate that there were other factors influencing habitat selection other than the fitness offered by the patch. Since the proportion of beetles found in corn decreases with density, there may be an inclination towards the availability for space as a factor in habitat selection.

A weaker preference for the higher quality habitat at higher densities was observed in all comparisons, as the proportion of beetles in the higher quality habitat decreased with increasing density. Thus habitat quality has a stronger effect on density-dependent habitat selection at lower densities, while other factors may influence habitat selection at higher densities as the higher quality patch fills up. *Tribolium castaneum* consistently disturbed the wheat flour patch, burrowing into the flour. This indicates a high preference for this habitat as it offers the highest fitness, where the beetles can efficiently extract nutrients. This was not the case for the corn and soy patches. *T. castaneum* very rarely disturbed the corn patch, reinforcing the fact that it is hard for them to exploit this habitat and this habitat is of lower fitness quality. Finally, red flour beetles never disturbed the soy flour patches. Beetles found in the lower quality habitat were mostly found wandering the perimeter of the container, most likely exploiting space rather than the food source as a result of the higher quality patch being filled up. Beetles will also select a habitat based on its available cover, provided by the patch (Romero et al., 2010). In the case of the beetles found in the corn patch, their habitat choice may have been influenced by the availability of cover that it offered and not by the actual food resource.

As this study demonstrates, quality of the food source is the deciding factor in habitat selection at low densities whereas other factors may have more of an influence in habitat preference at higher densities. Red flour beetles habitat selection patterns did not explicitly follow fitness patterns, implicating that factors other than habitat quality also modulate habitat selection. Also, density plays an important part in habitat selection, shifting the proportion of beetles found in one habitat over the other regardless of the habitat quality.

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