

# Male Aggregation Pheromones Inhibit Ideal Free Habitat Selection in Red Flour Beetles (*Tribolium castaneum*)

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**Abstract** The ideal free distribution (IFD) predicts that individuals should be distributed between habitats in proportion to habitat suitability such that mean fitness is equal in each habitat. The IFD is useful in studies examining habitat selection, yet its key assumptions are often violated and the expected IFDs are not consistently detected. While the use of aggregation pheromones by insects is expected to evolve in systems that experience positive density dependence (Allee effect), through a series of experiments we test the hypothesis that aggregation pheromones may limit the ability of individuals to achieve an IFD. Using red flour beetles (*Tribolium castaneum*), we specifically test the prediction that beetles in groups with an equal sex ratio or in the presence of an artificial aggregation pheromone will deviate from an IFD, whereas female-only groups will achieve an IFD. We also test the hypothesis that aggregation pheromones evolved to promote Allee effects by testing the prediction that beetle fitness will show positive density dependence at low densities. Consistent with our first hypothesis, female groups achieved an IFD, while mixed sex groups and females in the presence of an aggregation pheromone in the low food habitat under-matched the IFD. We found no evidence of Allee effects at low density, but we did find evidence of strong negative density dependence. We demonstrate that the use of aggregation pheromones may negatively impact a population's ability to achieve an IFD and cast doubt on the hypothesis that male aggregation pheromones evolve to promote Allee effects.

**Keywords** Allee effect · fitness · habitat matching · ideal free distribution · oviposition · patch selection

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## Introduction

The ideal free distribution (IFD; Fretwell and Lucas 1969) is the predominant theoretical framework underlying habitat selection models (e.g., Rosenzweig 1981; Rosenzweig and Abramsky 1986; Houston and McNamara 1988; Morris 1988, 2003, 2011; Tregenza 1995). The IFD predicts that organisms will distribute themselves between habitats in proportion to the suitability of each habitat (Fretwell and Lucas 1969), where habitat suitability is based on the relationship between fitness and density in a habitat. Individuals are thus predicted to distribute themselves between habitats such that every individual obtains the same amount of resources, and thereby has the same fitness. The IFD is considered an evolutionarily stable strategy (Maynard Smith 1976; Milinski 1979; Cantrell et al. 2011) because at equilibrium the IFD is the best strategy for optimizing fitness by all individuals. Since the IFD was proposed, the validity of its assumptions has repeatedly been questioned (see Kennedy and Gray 1993; but see also Åström 1994 and Milinski 1994). Yet, there is abundant empirical support for organisms distributing themselves between habitats in proportion to depletable resources (e.g., Fretwell 1969; Fretwell and Calver 1969; Milinski 1979; Godin and Keenleyside 1984; Grand 1997; Steward and Komers 2012; Moritz et al. 2015) and the IFD remains a key concept in ecology.

The assumptions of the IFD include ideal knowledge (the ability of individuals to know the distribution of habitats, of resources, and of competitors), freedom of movement (the ability of individuals to move between habitats), and that all competitors are equal. All of these assumptions can be considered unrealistic and in most studies at least one of the three is not met (Milinski 1988). For example, the assumption of ideal knowledge is often unmet because resources change through time, as does the distribution of competitors. Less than ideal knowledge typically leads to undermatching of the IFD (Abrahams 1986), where individuals use low quality habitats more than expected. The assumption of equality of competitors is often unmet because larger and more experienced individuals have an advantage, or because a dominance hierarchy exists. Differences in competitive abilities do not necessarily cause a departure from the IFD (Milinski 1984), but they can cause undermatching (Houston and McNamara 1988). Dominant individuals can also interfere with the choice of subordinates, which would also cause undermatching of the IFD (Sutherland 1983). The latter case is referred to as the ideal despotic distribution (Fretwell and Lucas 1969) and methods have been developed to tease apart ideal free and ideal despotic distributions without monitoring interference (Morris 1988, 1994). Finally, the freedom of movement assumption is often unmet because of significant travel costs or barriers between habitats, which should lead to overmatching (more individuals than expected in high quality habitats) when travel costs are high and to undermatching when it is difficult for organisms to discriminate between habitats (Kennedy and Gray 1993). High travel costs may also lead to undermatching (Korona 1990).

Male aggregation pheromones are known to influence the distribution of individuals within a population (Wertheim et al. 2005) and have yet rarely been considered as a potentially important factor that limits a population's ability to match an expected IFD. While aggregation pheromones could have evolved for multiple reasons, including increasing the efficiency of resource use, finding mates, protection from natural enemies, and protection from environmental conditions (Wertheim et al. 2005), their

effects on the distribution of individuals may run counter to those expected when only considering the distribution of resources themselves. For instance, if the species experiences positive density dependence at low population density (Allee effects; Allee et al. 1949), then perhaps the benefits of finding mates through the emission of aggregation pheromones at low density outweigh the costs of departing from the IFD and having reduced access to resources. Can aggregation pheromones cause a departure from an IFD and, if so, are there benefits to departing from it?

In this study, we use red flour beetles (*Tribolium castaneum* Herbst 1797), an organism known to secrete male aggregation pheromones (Suzuki 1980), to examine two hypotheses. First, we test the hypothesis that male aggregation pheromones limit the ability of flour beetles to achieve an IFD. Specifically, we test the prediction that beetles in groups with a 1:1 sex ratio or females in the presence of aggregation pheromones will deviate from an IFD, whereas female-only groups will achieve an IFD. Second, we test the hypothesis that aggregation pheromones evolved in response to Allee effects to increase fitness at low density. Specifically, we test the prediction that beetle fitness will show positive density dependence at low density, but negative density dependence at high density.

## Methods

### Study Species

We conducted all experiments with a colony of red flour beetles (*Tribolium castaneum*) originally obtained from Carolina Biological Supply Company (Burlington, North Carolina, USA). We started with 200 individuals and let the colony grow to approximately 5000 individuals. We maintained all cultures in 95 % wheat flour and 5 % brewer's yeast (henceforth referred to as flour). We housed beetles in an environmental chamber set at 25 °C and 70 % relative humidity. We sexed beetles at the pupa stage (Good 1936), and separated pupa into male and female containers with ad libitum flour for single-sex experiments.

### Experiment 1: Effect of Male Presence on Aggregation

We first quantified aggregations in groups with 1:1 sex ratios (mixed groups) and in groups of females only, with each treatment replicated ten times. We placed 30 beetles in small plastic containers ( $1 \times w \times h = 31 \times 17 \times 10$  cm) with 2 mm of sand substrate. Each container had a food patch (2.5 ml of flour on a glass slide; mass =  $1.36 \pm 0.01$  g) in the center. After 24 h, we took pictures of the distribution of the beetles and measured the number of aggregations, the number of individuals per aggregation, the density of aggregations (beetles/cm<sup>2</sup>), and the distance of each aggregation to the food patch and to the closest neighbouring aggregation. Based on preliminary observations, we defined an aggregation as three or more beetles within an area < 1.5 cm in diameter.

We compared the number of aggregations between treatments using a *t* test in R (package: stats; function: t.test; R Core Team 2012; version 2.15.2). We then compared the number of individuals per aggregation, density of aggregations, and the distance of aggregations from the food patch and nearest aggregation between treatments using a

MANOVA in R (package: stats; function: manova). All means are presented with their standard errors. For all analyses, we tested the appropriate statistical assumptions (i.e. normality, homoscedasticity, etc.) and found they were always met.

### Experiment 2: Effect of Male Presence on Habitat Selection

We quantified the effect of male presence on the distribution of beetles among food patches. We placed two food patches on opposite sides of the same containers used previously. Food patches were 20 cm apart to avoid high travel costs associated with habitat selection (Korona 1990). We created four food treatments with different proportions of flour in each patch: 1:1, 1:2, 1:4, and 1:8. One food patch contained 0.625 ml of flour while the second food patch contained 0.625 ml (1:1 treatment), 1.25 ml (1:2 treatment), 2.5 ml (1:4 treatment), or 5.0 ml (1:8 treatment) of flour. We used two sex-ratio treatments (1:1 and all females) and three density treatments (10, 30, and 50 beetles) for each food treatment in a fully factorial design with ten replicates of each treatment combination. Females in the female-only treatment were virgins, whereas those in the 1:1 treatment were not virgins. At the start of each experiment, we placed the beetles in the center of the container approximately equidistant from each food patch. After 24 h, we counted the number of beetles in each food patch and the number of beetles not in a food patch.

We first analysed the data using isodars (Morris 1988) because isodars are a powerful tool for quantifying density-dependent habitat selection in two habitats (e.g., Morris 1988; Ovadia and Abramsky 1995; Rodríguez 1995; Halliday and Blouin-Demers 2014). We used geometric mean regression in R (package: lmodel2; function: lmodel2; Legendre 2014) to build isodars for each sex ratio treatment in each food treatment, with the number of individuals in the high food patch as  $y$  and the number of individuals in the low food patch as  $x$ . We compared isodars using the confidence intervals around the intercept and slope of each isodar, as well as by comparing  $R^2$  and  $p$ -values. Isodars with an intercept significantly different from zero demonstrate habitat preference at low density, and isodars with a slope different from one demonstrate a change in habitat preference with density (Morris 1988). We followed our isodar analysis with a multiple linear regression (package: stats; function: lm) that examined the proportion of individuals in the low food patch (number of individuals in the low food patch divided by total number of individuals in both food patches). We used the proportion of food in the low food patch (amount of food in the low food patch divided by total amount of food in both patches), the sex ratio, density, and all interactions as independent variables. We compared models using Akaike's information criterion (AIC; package: stats; function: AIC), and selected the best model as the model with the lowest AIC. If models were within 2 AIC units (Bozdogan 1987), we considered them competing and used model averaging (Burnham and Anderson 2002).

### Experiment 3: Aggregation Pheromone Experiment

To test if the patterns of habitat selection documented in the previous experiment were actually caused by aggregation pheromones, we conducted another set of habitat selection experiments using Bullet Lure *Tribolium* aggregation pheromones (Insects Limited,

Westfield, Indiana, USA). We set up four treatments, each with 0.625 ml of flour in one habitat (low food) and 2.5 ml of flour in the other habitat (high food) and: 1) only females with no aggregation pheromones; 2) only females with aggregation pheromone suspended above the high food patch; 3) only females with aggregation pheromones suspended above the low food patch; and 4) a mixed group without any pheromone. In the two treatments with aggregation pheromones, we attached the lure to a piece of pipe cleaner, which was then attached to the lid of the container. The lure was suspended approximately 1 cm above the food patch. We used five densities of beetles (10, 20, 30, 40, 50 beetles) and replicated the 20 treatment combinations 10 times. We counted the number of beetles in each food patch after 24 h. We built isodars for each treatment as above.

#### **Experiment 4: Fitness Effects of Habitat Selection**

We quantified the fitness effects of habitat selection by measuring the number of eggs laid over 4 days by different densities of beetles in different quantities of flour. Although egg laying rate is not an ultimate measure of fitness (Campbell and Runnion 2003; Halliday and Blouin-Demers 2015), it is strongly correlated with ultimate measures of fitness such as the number of adult descendants (Halliday et al. 2015). We sifted the flour through a 250  $\mu\text{m}$  sieve before using it in this experiment so that we could differentiate eggs from flour particles after the experiment. We used nine density treatments (2, 4, 6, 8, 10, 20, 30, 40, and 50 beetles) and four food treatments (0.625, 1.25, 2.5, and 5.0 ml). For density treatments of 2 to 8 individuals, we added an equal number of previously sexed (sexed as pupa) males and females; all individuals had been adults for at least 2 weeks. For treatments with densities from 10 to 50, we used individuals randomly selected from our main culture, where the sex ratio was 1:1 (Halliday and Blouin-Demers *unpublished data*); all individuals had been adults for less than 2 months. The 36 treatment combinations were each replicated ten times. We placed the beetles in petri dishes ( $d = 10$  cm,  $h = 1.5$  cm) with the flour in an incubator set at 25 °C. After 4 days, we removed the beetles and sifted the flour through a 250  $\mu\text{m}$  sieve to collect and count all the eggs that were laid. We allowed beetles to lay eggs for 4 days because egg-laying rate stays constant for at least the first 4 days in a food patch (Halliday and Blouin-Demers *unpublished data*). We calculated mean per capita fitness as the number of eggs in a dish divided by the number of individuals in that dish.

We analysed variation in mean per capita fitness as a function of density in two ways. First, we tested for Allee effects (Allee et al. 1949) by using only the data with densities from two to eight individuals. Second, we tested for negative density dependence by analysing the data with densities from ten to 50 individuals. We used multiple linear regression for both analyses, with food, density, and their interaction as independent variables. We again used AIC for model selection.

## **Results**

### **Experiment 1: Effect of Male Presence on Aggregation**

The presence of males increased the number and size of aggregations, which suggests that males are releasing aggregation pheromones. Mixed groups had 3 times more

aggregations than female-only groups ( $t_{17.7} = 4.97$ ,  $p = 0.0001$ ). On average, mixed groups also had 0.6 more individuals per aggregation ( $F_{1,40} = 4.88$ ,  $p = 0.03$ ), had aggregations located 12.7 cm closer to the nearest aggregation ( $F_{1,37} = 34.11$ ,  $p < 0.0001$ ), and had aggregations located 4.5 cm closer to the food patch ( $F_{1,40} = 15.8$ ,  $p < 0.001$ ) than female-only groups. There was no difference in the density of aggregations between mixed and female-only groups ( $F_{1,40} = 2.30$ ,  $p = 0.14$ ).

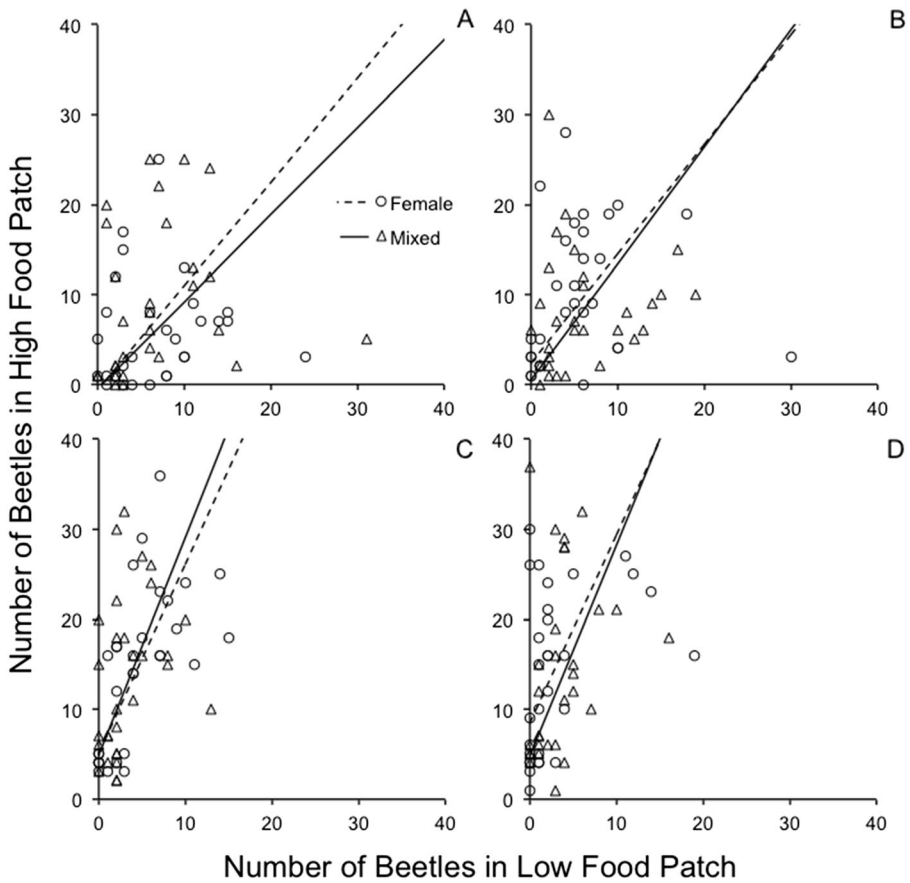
## Experiment 2: Effect of Male Presence on Habitat Selection

Our isodar analysis indicated density-dependent habitat selection, as predicted by the IFD, and the slopes and intercepts tended to increase as food increased in the high food patch (Fig. 1, Table A1). Female group isodars were not significantly different from mixed group isodars according to their slopes and intercepts (Fig. 1, Appendix Table A1); however, female group isodars had higher  $R^2$  than mixed group isodars (Appendix Table A1), which suggests that the presence of males weakens the isodar, but does not change its slope or its intercept.

The presence of males caused a departure from the IFD. The proportion of individuals in the low food patch in female-only groups was significantly different from that of mixed groups ( $t_{1,237} = 2.77$ ,  $p < 0.01$ ). In both sex ratio treatments, the proportion of individuals in a patch increased with the proportion of food in that patch ( $t_{1,237} = 9.84$ ,  $p < 0.0001$ ; Appendix Table A2). Mixed groups under-matched the IFD (intercept =  $0.08 \pm 0.03$ ; slope =  $0.97 \pm 0.10$ ; Fig. 2A), whereas female-only groups conformed to the IFD (intercept =  $0.006 \pm 0.03$ ; slope =  $0.97 \pm 0.10$ ; Fig. 2B). Both sex ratio treatments fit the expected slope of the IFD, but the intercept for mixed groups was higher than expected.

## Experiment 3: Aggregation Pheromone Experiment

Isodars are interpreted by comparing the intercept to zero and the slope to one, the null model for isodars, which represents a situation where individuals do not differentiate between habitats (Morris 1988). The intercepts and slopes for all four isodars overlapped which demonstrates that these isodars are not significantly different from one another. However, the isodar for the female-only treatment without pheromones and the isodar for the treatment with pheromones in the high food patch had intercepts significantly greater than zero, whereas the other two isodars had intercepts that overlapped with zero (Table 1). Despite the lack of statistical difference between the four isodars, the biological interpretation of each isodar based on comparison to the null model is important. In the absence of aggregation pheromones, females had a significant preference for the high food patch at low density (intercept  $> 0$ ), and this preference strengthened as density increased (slope  $> 1$ ). When pheromones were in the high food patch, females similarly had a preference for the high food patch at low density (intercept  $> 0$ ), and this preference strengthened as density increased (slope  $> 1$ ). When pheromones were in the low food patch, females showed equal preference for both patches at low density (intercept  $\neq 0$ ), but had an increasing preference for the high food patch as density increased (slope  $> 1$ ); however, this isodar was not statistically significant ( $p = 0.05$ ). The mixed group of beetles had equal preference for both patches at low density (intercept  $\neq 0$ ), and had an increasing preference for the high food patch

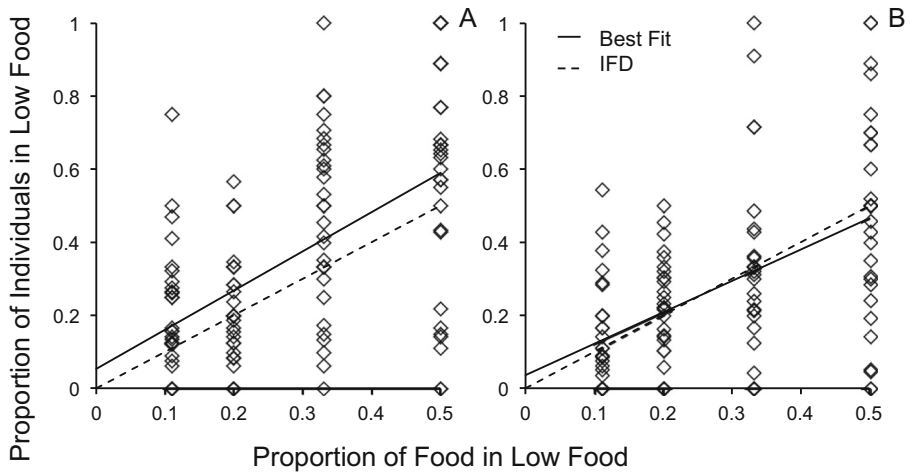


**Fig. 1** Isodars for mixed (solid line) and female-only groups (dashed line) of red flour beetles (*Tribolium castaneum*) when food was equal between patches (A), 2:1 in the high food patch (B), 4:1 in the high food patch (C), and 8:1 in the high food patch (D)

as density increased (slope > 1). Based on our comparisons of each isodar to the null model, aggregation pheromones in the low food patch weakened preference for the high food patch, and also weakened the strength of density-dependent habitat selection. Similarly, when males were present, the preference for the high food patch was weakened.

**Experiment 4: Fitness Effects of Habitat Selection**

We did not detect Allee effects at low density, but we did detect significant negative density dependence of fitness at high density. At low population densities, per capita fitness was unaffected by density ( $t_{1,148} = 0.04, p = 0.97$ ; Appendix Table A3), but per capita fitness increased as food increased (slope =  $0.13 \pm 0.04$ ;  $t_{1,149} = 3.62, p < 0.001$ ). At high population densities, there was strong negative density dependence of per capita fitness (slope =  $-0.02 \pm 0.001$ ;  $t_{1,188} = 12.97, p < 0.0001$ ; Appendix Table A3) and per capita fitness again increased as food increased (slope =  $0.67 \pm 0.06$ ;  $t_{1,188} = 11.02, p < 0.0001$ ).



**Fig. 2** Proportion of individuals using the low food patch in a habitat selection experiment with red flour beetles (*Tribolium castaneum*) where sex ratio was manipulated (1:1 sex ratio (A) or female-only (B)) and the proportion of food in the low food patch was manipulated. Food was in ratios of 1:1, 2:1, 4:1, or 8:1 between patches. The solid line represents the line of best fit and the dashed line represents the prediction from the ideal free distribution (IFD)

**Discussion**

Our experiments demonstrated that mixed groups of red flour beetles aggregated more than female-only groups. Additionally, we demonstrated that mixed groups under-matched the IFD whereas female-only groups achieved an IFD, and that female-only isodars explained more variance (higher  $R^2$ ) in the distribution of beetles than mixed group isodars. Finally, at low density, the presence of aggregation pheromones in low food patches led to no habitat preference, whereas the presence of aggregation pheromones in high food patches led to a preference for the high food habitat. Therefore, it appears that aggregation pheromones may cause deviations from the IFD.

The ability of animals to achieve an IFD depends in part on their ability to properly assess the suitability of available habitats (Fretwell and Lucas 1969). Aggregation pheromones are a cue that flour beetles react to in their habitat choice, but this cue does not necessarily match with habitat suitability. For example, if a male emits

**Table 1** Isodars for an experiment with red flour beetles (*Tribolium castaneum*) examining the effect and location of male aggregation pheromones on habitat selection, calculated using geometric mean regression. Female and Mixed are control treatments where no pheromones were added, whereas High had pheromones added to the high food patch, and Low had pheromones added to the low food patch. CI represents the 95 % confidence interval around the intercept and slope

Treatment	Intercept	Intercept CI	Slope	Slope CI	$R^2$	$p$
Female	5.49	0.19 to 9.52	2.20	1.67 to 2.89	0.09	0.03
Mixed	2.97	-2.36 to 7.11	2.20	1.71 to 2.83	0.23	< 0.01
High	5.37	0.94 to 8.86	2.00	1.58 to 2.54	0.31	< 0.01
Low	4.44	-0.59 to 8.25	1.64	1.25 to 2.16	0.08	0.05



pheromones in a low quality patch, then under-matching of the IFD would occur, whereas if a male emits pheromones in a high quality patch, then overmatching of the IFD would occur. Our experiment demonstrated undermatching of the IFD in the presence of males, suggesting that overall males may emit aggregation pheromones from low quality patches more than from high quality patches. As such, aggregation pheromones increase noise in habitat selection data, and make the relationship between habitat suitability and abundance weaker (lower  $R^2$ ). We indeed found that mixed treatments had weaker isodar relationships than treatments with females only. We do not suggest that aggregation pheromones are maladaptive, but rather that the IFD may not predict the optimal habitat selection strategy for non-social insects that secrete aggregation pheromones.

One potential issue with our experiment is that we were unable to differentiate males and females in the mixed treatments. Deviations from an IFD in mixed treatments could simply be due to different habitat selection behaviours by males (i.e. a consistent departure from an IFD) rather than due to males secreting pheromones. Our experiment with pheromone lures, however, demonstrated that habitat selection patterns for female groups when aggregation pheromones were in the low food patch mirrored habitat selection patterns for mixed groups of beetles. Conversely, treatments with females and no pheromones had similar patterns to treatments with pheromones in the high food patch. These results suggest that male beetles emitting pheromones in low food patches causes deviations from the IFD.

We did not detect Allee effects in flour beetles, but that does not mean Allee effects are not present at the very lowest densities. There will always be positive density dependence in sexual species as density changes from one individual to two individuals (assuming the two individuals are of opposite sex), therefore aggregation pheromones could have evolved to attract females to a single male. Perhaps food patches in the ancestral environment of flour beetles were scarce, therefore the aggregation pheromones could have evolved in response to having no potential mate at a new food patch. Aggregations caused by males in our experiment were centred on food patches, suggesting that males may only emit pheromones when they are at a food source. Obviously, a male able to attract a female to a new food patch will have higher fitness than a male unable to attract a female. Other males could also cue on these pheromones to help them locate new food patches, and potentially increase their own mating success. Alternatively, Allee effects may have been detected in fitness measures other than the number of eggs laid, such as number or quality of offspring. Despite the possibility that aggregation pheromones in red flour beetles may have evolved in response to Allee effects at very low density, evidence from other species suggests that not all aggregation behaviour evolved in response to Allee effects (Nufio and Papaj 2012). Allee effects occur because individuals in low density populations have a lower probability of finding mates. Because our experiments were conducted in constrained spaces, the probability of finding a mate was high. Future work could attempt to detect Allee effects in flour beetles in a more open system.

Aggregation pheromones are widespread in non-social insects (see Wertheim et al. 2005 for a review), but they likely evolved under different selection pressures in different species. For example, aggregation can increase environmental temperature for certain stored grain pests, thereby increasing fecundity (Howe 1962). Aggregations can also reduce predation risk through risk dilution or increased vigilance, as suggested

with gray pine aphids (*Schizolachnus pineti*; Kidd 1982). Boake (1986) suggested that female red flour beetles select higher quality males based on their aggregation pheromone. The adaptive value of aggregation pheromones, however, has been experimentally tested for very few species. Wertheim et al. (2005) proposed testable hypotheses for why aggregation pheromones persist in nature despite the obvious cost of negative density dependence, but further experiments are needed to determine whether these hypotheses are supported. Future experiments should investigate the relationship between food and the location of aggregations, which will allow us to understand better the adaptive value of aggregation pheromones, and allow us to determine whether they evolved in relation to feeding or in relation to mating opportunities at new or vacant food patches.

Our experiments on red flour beetles demonstrate that physiological mechanisms (i.e. secretion of pheromones) can inhibit the ability of organisms to achieve an IFD. Yet red flour beetles can clearly achieve an IFD in the absence of males and of aggregation pheromones, as shown by our female-only treatment and by experiments conducted by Korona (1990). These female-only experiments provide further support for the ability of the IFD to predict the distribution of organisms. Although it is often argued that the IFD is too simple (Kennedy and Gray 1993) and requires additional parameters, such as a limited ability to move or unequal competitors, the principle that organisms track depletable resources in the environment continues to provide surprising predictive power given its several unrealistic assumptions.

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## Appendix. Statistical Tables

**Table A1** Isodars for mixed versus female-only groups of red flour beetles (*Tribolium castaneum*) selecting between patches with different quantities of food, calculated using geometric mean regression. The ratios in the Treatment column represent the relative amount of food between the two patches. CI represents the 95 % confidence interval around the intercept and slope

Treatment	Intercept	Intercept CI	Slope	Slope CI	$R^2$	$p$
Mixed 1:1	-0.48	-2.63 to 1.18	0.97	0.75 to 1.25	0.006	0.56
Female 1:1	-0.66	-3.39 to 1.47	1.16	0.91 to 1.49	0.08	0.02
Mixed 2:1	0.44	-2.16 to 2.45	1.30	1.00 to 1.68	0.008	0.49
Female 2:1	2.38	0.00 to 4.22	1.22	0.95 to 1.58	0.02	0.32
Mixed 4:1	4.84	2.29 to 6.82	2.43	1.89 to 3.12	0.06	0.05
Female 4:1	5.10	2.84 to 6.94	2.11	1.72 to 2.59	0.39	< 0.0001
Mixed 8:1	4.81	2.29 to 6.78	2.35	1.84 to 3.00	0.11	< 0.01
Female 8:1	8.49	6.72 to 9.88	2.10	1.65 to 2.67	0.14	< 0.01

**Table A2** Model selection (upper) and final model output (lower) for models examining habitat selection by red flour beetles (*Tribolium castaneum*) between low food and high food patches as sex ratio, density, and food changes. AIC is the Akaike’s information criterion value,  $\Delta$ AIC is the difference between a model and the model with the lowest AIC (bolded), and  $k$  is the number of parameters in the model. Competing models (\*) are within 2 AIC units of the best model. Final model output is based on model averaging of the competing models (\*) from model selection

Model	$k$	AIC	$\Delta$ AIC	
<b>Proportion = Food + Sex Ratio + Density + Food: Density</b>	<b>6</b>	<b>-34.01</b>	<b>0.00*</b>	
Proportion = Food + Sex Ratio	4	-33.83	0.18*	
Proportion = Food + Sex Ratio + Density + Food: Sex Ratio + Food: Density + Sex Ratio: Density	8	-32.67	1.34*	
Proportion = Food + Sex Ratio + Density	5	-31.84	2.17	
Proportion = Food + Sex Ratio + Density + Food: Sex Ratio + Food: Density + Sex Ratio: Density + Food: Sex Ratio: Density	9	-31.52	2.49	
Parameter	Estimate	S.E.	$t$	$p$
Intercept	0.02	0.06	2.42	0.02
Food	1.24	0.18	9.84	< 0.01
Sex Ratio (Mixed)	-0.08	0.05	2.71	< 0.01
Density	0.003	0.002	1.72	0.08
Food: Sex Ratio	-0.21	0.20	1.09	0.28
Food: Density	-0.01	0.006	2.03	0.04
Sex Ratio: Density	0.002	0.002	1.19	0.24

**Table A3** Model selection and final model output for models examining per capita fitness by red flour beetles (*Tribolium castaneum*) across food and density treatments when densities are low (upper) and densities are high (lower). AIC is the Akaike’s information criterion value,  $\Delta$ AIC is the difference between a model and the model with the lowest AIC (bolded), and  $k$  is the number of parameters in the model

Model	$k$	AIC	$\Delta$ AIC	
<b>Fitness = Food</b>	<b>3</b>	<b>367.10</b>	<b>0.00</b>	
Fitness = Food + Density	4	369.10	2.00	
Fitness = Food + Density + Food: Density	5	370.98	3.88	
Fitness = Density	3	379.58	12.48	
Parameter	Estimate	S.E.	$t$	$p$
Intercept	2.44	0.10	23.88	< 0.01
Food	0.13	0.04	3.58	< 0.01
Model	$k$	AIC	$\Delta$ AIC	
Fitness = Food + Density	4	87.04	0.00	
Fitness = Food + Density + Food: Density	5	89.04	2.00	
Fitness = Density	3	178.26	91.22	
Fitness = Food	3	205.10	118.06	
Parameter	Estimate	S.E.	$t$	$p$
Intercept	2.00	0.06	34.91	< 0.01
Food	0.68	0.06	10.81	< 0.01
Density	-0.02	0.001	12.73	< 0.01

## References

- Abrahams MV (1986) Patch choice under perceptual constraints: a cause for departures from an ideal free distribution. *Behav Ecol Sociobiol* 19:409–415
- Allee WC, Emerson AE, Park O, Schmidt KP (1949) Principles of animal ecology. WB Saunder, Philadelphia
- Åström M (1994) Travel cost and the ideal free distribution. *Oikos* 69:516–519
- Boake CRB (1986) A method for testing adaptive hypotheses of mate choice. *Am Nat* 127:654–666
- Bozdogan H (1987) Model selection and Akaike's information criterion (AIC): the general theory and its analytical extensions. *Psychometrika* 52:345–370
- Burnham KP, Anderson DR (2002) Model selection and Multimodel inference: a practical information-theoretic approach. Springer, Berlin
- Campbell JF, Rummion C (2003) Patch exploitation by female red flour beetles, *Tribolium Castaneum*. *J Insect Sci* 3:1–8
- Cantrell RS, Cosner C, Lou Y (2011) Evolutionary stability of idea free dispersal strategies in patchy environments. *J Math Biol* 65:943–965
- Fretwell SD (1969) On territorial behavior and other factors influencing habitat distribution in birds: III. Breeding success in a local population of field sparrows. *Acta Biotheor* 19:45–52
- Fretwell SD, Calver JS (1969) On territorial behavior and other factors influencing habitat distribution in birds: II. Sex ratio variation in the Dickcissel (*Spiza Americana* Gmel). *Acta Biotheor* 19:37–44
- Fretwell SD, Lucas HL (1969) On territorial behavior and other factors influencing habitat distribution in birds: I. Theoretical development. *Acta Biotheor* 19:16–36
- Godin J-GJ, Keenleyside MHA (1984) Foraging on patchily distributed prey by a cichlid fish (Teleostei, Cichlidae): a test of the ideal free distribution theory. *Anim Behav* 32:120–131
- Good NE (1936) The flour beetles of the genus *Tribolium*. USDA Tech Bull 498:47–58
- Grand TC (1997) Foraging site selection by juvenile coho salmon: ideal free distribution of unequal competitors. *Anim Behav* 53:185–196
- Halliday WD, Blouin-Demers G (2014) Red flour beetles balance thermoregulation and food acquisition via density-dependent habitat selection. *J Zool* 294:198–205
- Halliday WD, Blouin-Demers G (2015) A stringent test of the thermal coadaptation hypothesis in flour beetles. *J Therm Biol* 52:108–116
- Halliday WD, Thomas AS, Blouin-Demers G (2015) High temperature intensifies negative density dependence of fitness in red flour beetles. *Ecol Evol* 5:1061–1067
- Houston AI, McNamara JM (1988) The ideal free distribution when competitive abilities differ: an approach based on statistical mechanisms. *Anim Behav* 36:166–174
- Howe RW (1962) A study of the heating of stored grain caused by insects. *Ann App Biol* 50:137–158
- Kennedy M, Gray RD (1993) Can ecological theory predict the distribution of foraging animals? A critical analysis of experiments on the ideal free distribution. *Oikos* 68:158–166
- Kidd NAC (1982) Predator avoidance as a result of aggregation in the grey pine aphid, *Schizolachnus pineti*. *J Anim Ecol* 51:397–412
- Korona R (1990) Travel costs and the ideal free distribution of ovipositing female flour beetles, *Tribolium confusum*. *Anim Behav* 40:186–187
- Maynard Smith J (1976) Evolution and the theory of games. *Am Sci* 64:41–45
- Milinski M (1994) Ideal free theory predicts more than only input matching – a critique of Kennedy and Gray's review. *Oikos* 71:163–166
- Milinski M (1979) Evolutionarily stable feeding strategy in sticklebacks. *Z Tierpsychol* 51:36–40
- Milinski M (1984) Competitive resource sharing: an experimental test of a learning rule for ESSs. *Anim Behav* 32:233–242
- Milinski M (1988) Games fish play: making decisions as a social forager. *Trends Ecol Evol* 3:325–330
- Moritz M, Hamilton IM, Yoak AJ, Scholte P, Cronley J, Maddock P, Pi H (2015) Simple movement rules result in ideal free distribution of mobile pastoralists. *Ecol Model* 305:54–63
- Morris DW (1988) Habitat-dependent population regulation and community structure. *Evol Ecol* 2:253–269
- Morris DW (1994) Habitat matching: alternatives and implications to populations and communities. *Evol Ecol* 8:387–406
- Morris DW (2003) Toward an ecological synthesis: a case for habitat selection. *Oecologia* 136:1–13
- Morris DW (2011) Adaptation, habitat selection, and the eco-evolutionary process. *P Roy Soc Lond B Bio* 278:2401–2411
- Nufio CR, Papaj DR (2012) Aggregative behavior is not explained by an Allee effect in the walnut infesting fly, *Rhagoletis juglandis*. *J Insect Behav* 25:166–182

- Ovadia O, Abramsky Z (1995) Density-dependent habitat selection: evaluation of the isodar method. *Oikos* 73:86–94
- R Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>
- Rodríguez MA (1995) Habitat-specific estimates of competition in stream salmonids: a field test of the isodar model of habitat selection. *Evol Ecol* 9:169–184
- Rosenzweig ML (1981) A theory of habitat selection. *Ecology* 81:327–335
- Rosenzweig ML, Abramsky Z (1986) Centrifugal community organization. *Oikos* 46:339–348
- Steward A, Komers PE (2012) Testing the ideal free distribution hypothesis: moose response to changes in habitat amount. *Int Scholarly Res Net Ecol* 2012:945209. doi:[10.5402/2012/945209](https://doi.org/10.5402/2012/945209)
- Sutherland WJ (1983) Aggregation and the ‘ideal free’ distribution. *J Anim Ecol* 52:821–828
- Suzuki T (1980) 4,8-dimethyldecanal – the aggregation pheromone of the flour beetles, *Tribolium-castaneum* and *Tribolium-confusum* (Coleoptera, Tenebrionidae). *Agr Biol Chem* 44:2519–2520
- Tregenza T (1995) Building on the ideal free distribution. *Adv Ecol Res* 26:253–307
- Wertheim B, van Baalen E-JA, Dicke M, Vet LEM (2005) Pheromone-mediated aggregation in nonsocial arthropods: an evolutionary ecological perspective. *Annu Rev Entomol* 50:321–346