

# Precopulatory choice for cues of material benefits in tree crickets

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The relative importance of direct and indirect benefits models of mate choice is a central question in sexual selection, but separating the two models is very difficult because high quality males often provide both better direct benefits and better genes. In tree crickets, *Oecanthus nigricornis*, females have the opportunity to gain both directly and indirectly from mate choice. Female tree crickets exercise premating choice for large males, but the model underlying this choice is unknown. In this study we examine the proximate cues used by female tree crickets to reject males, and show that the ability of males to provide food is a central cue. In contrast, we find no evidence that the relative size of mates is important in mate rejection. The fact that the major phenotypic cues of male quality are related to food provisioning suggests that the role of genetic benefits in shaping female preferences is limited by the extent to which food provisioning signals genetic quality. *Key words*: courtship feeding, direct benefits, good genes, Gryllidae, mate choice, nuptial gifts. [*Behav Ecol*]

Female animals are expected to exercise choice whenever that choice produces a net gain in fitness. This net gain can arise as a result of direct benefits, for example, because the chosen mate possesses a high-quality territory or provides better parental care or better food to the female herself. The fitness benefit can also arise through indirect benefits if a female's offspring inherit superior genes from the chosen sire. These genetic benefits are said to be indirect because selection acts via the covariance between the female preference and the male good genes rather than directly on the female preference genes themselves (Kokko et al., 2003).

The importance of direct versus indirect benefits in driving the evolution of female choice and male characters is at the heart of some recent debate in evolutionary theory (Houle and Kondrashov, 2002; Kirkpatrick, 1996; Kirkpatrick and Barton, 1997; Møller and Jennions, 2001). As a result, there has been concerted interest among behavioral ecologists to empirically classify specific examples of female preferences as resulting from either direct or indirect benefits. However, discerning between the two models of preference is very difficult when both occur in the same model organism. Direct benefits are almost always accompanied by an indirect component, because any genes that improve a male's ability to provide direct benefits will quickly associate with female preference genes in linkage disequilibrium (Kokko et al., 2003). As a result, whenever any aspect of the provision of goods and services by males is heritable, female choice for direct benefits will confer indirect benefits as well. For example, if the ability to provide direct benefits depends on heritable variation in condition (Rowe and Houle, 1996), choice for direct benefits will favor males of high genetic quality (Iyengar and Eisner, 1999b; Johnson et al., 1999).

Female tree crickets have the potential to gain both direct and indirect benefits from their mating decisions. In this article we study the proximate cues used by female tree

crickets in distinguishing between potential mates. Although these cues cannot conclusively support one model of mate choice or the other, they may at least suggest whether it is the material benefits themselves rather than other aspects of phenotype that are the primary target of choice.

## Biology of black-horned tree crickets

Female black-horned tree crickets, *Oecanthus nigricornis* (Walker), mount males and feed from secretions of a specialized gland on the male's thorax before and after copulation. Unlike many courtship-feeding insects (see Vahed, 1998), in this system the gift is secreted gradually, as the female consumes it. This food gift is valuable to females because it extends their lifespan (Brown, 1997a), and costly to males because repeated mating appears to reduce the ability of males to feed subsequent mates (Brown and Kuns, 2000). Indeed, a single mating is sufficient to cause significant depletion in male courtship-feeding glands, and at high mating rates the ability to provide food gifts limits male access to females (Bussière et al., 2005).

Females tree crickets mate very frequently in nature (on average, once per day, Bussière LF, Basit, and Gwynne, in preparation), and hungry females mate more often than do controls (Brown, 1997b), consistent with the established nutritional benefits of mating (Brown, 1997a). Females also preferentially orient to the calling songs of larger males (Brown et al., 1996), who provide higher-quality food gifts (Bussière LF, Basit, and Gwynne, in preparation) although not larger quantities of food (Brown, 1994; Bussière et al., 2005).

Although large male size thus appears to be a cue of the quality (but not the quantity) of direct benefits, whether or not it signals male breeding value (i.e., genetic benefits) in tree crickets remains unknown. A preliminary analysis of broad-sense heritabilities indicates that larger males sire offspring with higher fitness even after the quantity of paternal investment is controlled (Bussière, 2003), but eliminating the potentially confounding effects of differential maternal allocation and the quality of paternal investment is difficult and the subject of ongoing study. Our purpose in the current work was not to test the association between large size and breeding value, but instead to determine whether the food gift itself or other aspects of male phenotype were more important cues for females making mating decisions. In the first experiment, we

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manipulated the ability of males to provide food while controlling other aspects of phenotype. In the second, we manipulated the relative body size of subsequent males while controlling the ability of males to provide food.

## METHODS

We housed the crickets in individual cylindrical containers (10-cm diameter  $\times$  10-cm height) covered by fiberglass mesh. All housing and experimental work took place in a controlled environmental chamber at 25°C with a 12-h light/12-h dark cycle. We fed all crickets a diet of peeled apple pieces, bee pollen, and commercial cricket chow ad libitum (Fluker's Cricket Farm). This diet was designed to approximate the high-quality diet provided by Brown (1997b), because it was in the high-quality diet treatment that Brown observed high rates of rejection by females. Female crickets also received small sections of raspberry cane (*Rubus* spp.) as oviposition substrate.

### Experiment 1: Do females reject males that are experimentally depleted of food gifts?

We collected adult *O. nigricornis* from an old field on campus at the University of Toronto at Mississauga, Ontario, Canada, from 18–23 September 1998 and 30 July–15 August 1999. For mating interactions, we used two housing chambers placed end to end and lined with fiberglass mesh for substrate. In each year, we randomly assigned cricket pairs to each of two treatments and conducted trials in the two treatments simultaneously. In the first treatment, postcopulatory feeding was interrupted either mechanically by using a blade of grass or by picking up the mating arena immediately after spermatophore transfer. Interrupting matings in this way did not appear to cause undue stress to the animals (we have observed wind-blown leaves and stems interrupting mating pairs in the field, and it is therefore reasonable to expect that natural matings are often interrupted). Furthermore, interrupted animals that were reunited or given a different mating partner readily accepted (if female) or courted (if male) the new partner almost immediately. Precopulatory feeding bouts in this treatment (i.e., total courtship-feeding time) varied in duration (mean  $\pm$  SE = 41.50  $\pm$  8.09 s), but never exceeded 3 min. In the second treatment, the courtship-feeding bouts were interrupted in the same manner, but much later after spermatophore transfer than in the first treatment (948.28  $\pm$  129.26 s). In this way, males in both treatments transferred a spermatophore to their first mate, but those in the second treatment transferred much more glandular food than did those in the first treatment (feeding duration strongly correlates with male weight loss during mating, Brown, 1997b; Brown and Kuns, 2000). In each year, six of the 24 initial pairings (three from each treatment) did not result in any mating and so were discarded from the analysis.

One hour after copulation, we paired males of both treatments with a second female and noted rejections by this second female. This interval between matings is realistic given the potentially high mating rates of tree crickets in nature (Bussière et al., 2005). For each male, we recorded the duration (in seconds) of courtship-feeding and the number of bouts of courtship song performed by the male in his interaction with the second female (courtship song is a lower-intensity version of calling song that is produced by male crickets in near proximity to females; Alexander, 1961). Because courtship song is only produced in the context of courtship, it was used as an index of male motivation to mate in the second interaction (song production is known to decrease after mating in some Orthoptera; Sakaluk et al., 1987).

### Experiment 2: Do females reject males that are relatively smaller than previous mates?

To assess the importance of alternative phenotypic cues of male quality in female premating choice, we examined the role of body size in mating rejections. Body size is known to be an important phenotypic cue for mate choice in other crickets (Simmons, 1986) and is correlated with female precopulatory choice (Brown et al., 1996) and the quality of male courtship gifts (Bussière et al., 2005) in tree crickets. For the present study, we used male crickets collected as larvae and reared to adulthood in isolation in the laboratory. Because these males were laboratory-reared, well-fed virgins, they were less likely to differ in their ability to provide a courtship meal than were field-collected males with unknown feeding and mating histories. Thus, we were able to manipulate a natural phenotypic cue of male quality while minimizing differences in material benefits between experimental males.

We collected larval tree crickets in early August of 1998 and 1999, from the same site as experiment 1. In each year we assigned experimental males to females in a nonrandom fashion in order to ensure that each focal female would encounter males of substantially different size (as approximated by mass). This was done by weighing all males on eclosion to adulthood, and systematically assigning a pair of males with posteclosion masses differing by  $>0.02$  g to each female. Males were then reweighed before mating trials, and those premating masses are those reported below and used in all analyses featuring male mass. Males ranged in premating mass from 0.040–0.086 g (mean  $\pm$  SE = 0.062  $\pm$  0.004), and the difference in premating mass between two males presented to the same female ranged from 0.007–0.025 g (mean  $\pm$  SE = 0.015  $\pm$  0.004). Although mass is an imperfect index of body size, it is correlated with other indices of body size such as pronotum length and femur lengths (Brown, 1997a), and it was the most convenient index to use on live animals. To verify the accuracy of our size estimates (based on mass), after the experiment we took five morphological measures (mean hind femur length, mean forewing length, mean hindwing length, pronotum length, and head width) of the 44 males paired with females that mated at least once. We then conducted a principal components analysis (PCA) on these five measures to extract a single variable reflecting body size. This index of size was then used along with male mass in analyses of the influence of size on female mate rejection.

For mating interactions, we used two housing chambers placed end to end and lined with fiberglass mesh for substrate, as in experiment 1, above. In each year, half of the females ( $N = 14$  females in 1998 and 18 females in 1999) were randomly assigned to one of two treatments. In the first treatment, females first encountered the larger of the two males assigned to her, whereas in the second treatment females encountered the smaller of two potential mates first. Those females that successfully mated ( $N = 10$  females in 1998 and 12 females in 1999) were allowed to complete postcopulatory courtship without interruption. Once the female and her first mate had separated for at least 10 min after the last bout of postcopulatory feeding, the first mate was replaced with the second suitor. We recorded the number of rejections of the second suitor by these females, as well as the premating masses of both males and the duration of courtship-feeding (where applicable) in both mating events.

### Mate rejection

We reasoned that mate rejection was a more complete index of premating choice than was phonotaxis because it allowed females to incorporate multiple aspects of male phenotype in

**Table 1**  
The influence of the amount of previous courtship-feeding on the likelihood of a male mating with a second female

Treatment	Rejected	Mated	Total
Courtship-feeding interrupted	9	9	18
Courtship-feeding uninterrupted (depleted)	15	3	18
Total	24	12	36

their mating decisions. For both experiments, female mate rejection was defined as the failure of a female to respond to male courtship behavior by mounting and accepting a spermatophore within the first hour after the initial antennal contact between the two individuals. Although we cannot with certainty exclude a role for males in this assessment (i.e., male mate rejection), in all but three of the 58 trials in which mate rejection was observed, males produced bouts of courtship song indicating their willingness to mate. Moreover, in all trials (including those in which males produced no courtship song) males engaged in other courting activities, including raising the wings when near the female, attempting to back under the female, and following the female as she walked within the courtship arena.

### Statistical analyses

We first compared the data collected from 1998 and 1999 in order to determine whether there was a difference in effects produced between years. Because the year of study had no effect either independently or when crossed with treatment in ANOVA (effect of treatment and year on likelihood of mating in the second trial;  $F_{\text{ratio}_{\text{year}}(1,32)} = 0.232$ ,  $p = .633$ ,  $F_{\text{ratio}_{\text{year} \times \text{treatment}}(1,32)} = 0.232$ ,  $p = .633$ ), for all remaining analyses we pooled the data from different years. We used one-way Fisher's Exact tests to determine the effect of treatment on mate rejection for both experiments, because the marginal totals for each of the treatments was fixed (category 2 contingency table, Zar, 1999). We used  $t$  tests and logistic regression analyses to determine the influence of variables potentially confounded with treatment (such as the number of song bouts and the duration of courtship-feeding in previous matings) on mate rejection. All statistics were computed by using Systat software (Wilkinson, 1999), except one-way Fisher's Exact tests, which were calculated by hand according to the method of Zar (1999).

## RESULTS

### Experiment 1: Do females reject males that are experimentally depleted of food gifts?

Females were more likely to reject males experimentally depleted of courtship gift than males from the treatment in which courtship-feeding was interrupted soon after copulation (Pearson's  $\chi^2 = 4.50$ ,  $df = 1$ , Fisher's Exact test one-way  $p = .032$ ) (Table 1). Because we were interested in female choice, we wanted to ensure that this effect was not owing to a decreased motivation on the part of depleted males. First we tested whether our treatments differed in motivation. Given the cost of trilling song in crickets (Prestwich and Walker, 1981), we reasoned that if depleted males were less motivated to mate, they should produce fewer bouts of courtship song, and that the number of bouts should correlate negatively with the duration of courtship-feeding in the first mating. We found no relationship between treatment and the number of courtship song bouts performed by the male in his second

**Table 2**  
Component loadings for five separate body size indices on the first principal component (PC1) extracted from an unrotated principal component's analysis on the correlation matrix of these indices

Body size index	PC1 loadings
Mean hind femur length	0.910
Mean forewing length	0.906
Mean hindwing length	0.845
Pronotum length	0.870
Head width	0.803

Overall, PC1 explained 75.3% of the variance in the body size indices.

courtship ( $t = 0.748$ ,  $n = 36$ ,  $p = .46$ ), nor between the duration of courtship-feeding in the first mating interaction and the number of courtship song bouts in the second courtship ( $r = -.20$ ,  $n = 36$ ,  $p = .24$ ). However these analyses had limited power for detecting a weak effect of treatment on male calling. Therefore, we tested whether the observed male calling behavior could have influenced female receptivity. We found no such relationship: the number of courtship song bouts in the second mating interaction did not influence the likelihood of mating (log-likelihood  $\chi^2 = 0.567$ ,  $df = 1$ ,  $p = .73$ ). Therefore we are confident that even if there was a weak effect of treatment on male motivation, it could not account for the effect of treatment on female choice that we observed.

### Experiment 2: Do females reject males that are relatively smaller than previous mates?

First we determined whether our estimates of body size based on male mass reflected body size as represented by the length of several body structures. We combined the five morphometric measures using an unrotated PCA on the correlation matrix of the five body measures. The PCA extracted a single significant principal component (PC1) that accounted for 75.3% of the variance in the matrix, and loaded positively with each of the individual measures of body size (Table 2). Body size PC1 was significantly correlated with male mass ( $r = .721$ ,  $n = 44$ ,  $p < .001$ ), and using PC1 rather than male mass did not change the treatment designation (i.e., whether the second male was larger or smaller than the first) for any of the females.

The size of a female's first mate did not influence the likelihood of accepting her first suitor as a mate (log-likelihood  $\chi^2 = 0.099$ ,  $df = 1$ ,  $p = .753$ ). This is not surprising because females were virgins and may have been predisposed to accept any mate because they required sperm. We expected discrimination based on body size only after this initial mating. However, the size of a second male suitor relative to a female's first mate did not influence her likelihood of accepting the second mate (Pearson's  $\chi^2 = 0.21$ ,  $df = 1$ , one-way Fisher's Exact test  $p = 1.0$ ; see Table 3). Note that this  $p$  value is one because the difference between treatments is opposite to that which we predicted (females rejected larger males in one more instance than smaller males). This result did not change when we treated the difference in male sizes as a continuous variable rather than a categorical one (using differences in male mass: log-likelihood  $\chi^2 = 0.017$ ,  $df = 1$ ,  $p = .897$ ; using differences in male PC1: log-likelihood  $\chi^2 = 0.044$ ,  $df = 1$ ,  $p = .835$ ). Furthermore, although the power of this test was not high, there was no trend in the data that suggested expanding the sample would reveal a significant result (females mated smaller second males in one more instance than larger second males).

To ensure that we had properly controlled for nuptial gift-giving abilities in the experimental males, we tested the influence of the first mate's nuptial gift size and the absolute

**Table 3**  
**The influence of the relative size of a female's first suitor on the second suitor's likelihood of mating**

Treatment	Rejected	Mated	Total
Second male smaller than first	3	8	11
Second male larger than first	4	7	11
Total	7	15	22

size of the second mate on mate rejection. The size of a female's first meal (as measured by the duration of courtship-feeding in the first mating) did not influence her likelihood of remating (log-likelihood  $\chi^2 = 0.567$ ,  $df = 1$ ,  $p = .451$ ) nor did the absolute size of her second mate (using male mass: log-likelihood  $\chi^2 = 0.208$ ,  $df = 1$ ,  $p = .649$ ; using male PC1: log-likelihood  $\chi^2 = 0.904$ ,  $df = 1$ ,  $p = .342$ ). Moreover, because the size of courtship meals in the two consecutive encounters were not negatively correlated ( $r = -.052$ ,  $n = 15$ ,  $p = .855$ ), it is unlikely that females who mated twice were merely attempting to compensate for small gifts in the first mating.

## DISCUSSION

Our results show that the ability to provide food during courtship is a central cue to choosy females. However, we failed to provide any evidence that the relative size of successive males influences mate rejection. Although the power of this second test was low, the variation in mate rejection behavior explained by male body size (approximated by McFadden's Rho squared in the logistic regression, Tabachnick and Fidell, 2001) is 0.002, which suggests that even if the power of our test were expanded, male size difference has a small capacity for explaining mate rejection relative to courtship-feeding ability. The influence of genetic benefits on premating preferences may therefore be constrained by the extent to which food provisioning predicts male genetic quality. The relationship between food provisioning and male breeding value will therefore help to clarify the relative importance of direct and indirect benefits in shaping female preferences in tree crickets.

We did not specifically study the mechanisms by which females assess male gift-giving ability. In three trials, females engaged in brief precopulatory feeding bouts before rejecting the male. These bouts may allow females to "taste-test" male donations before committing to copulation. In the other trials, mate rejection occurred in the absence of precopulatory feeding, and so other mechanisms for assessing male gift-giving potential must exist. The mechanisms by which females discriminate between males merit further study.

Brown (1997b) examined the potential role of premating female choice in driving remating behavior in *O. nigricornis*. He used a statistical approach to dissect factors affecting variation in female remating behavior, and tested whether variation in female remating rates could be explained by three alternative hypotheses: (1) nutritional benefits, such that hungrier females remate more quickly; (2) postcopulatory choice, where females remate quickly when their previous mate is of low quality (providing either poor material or genetic benefits); and (3) precopulatory mate choice, where females remate quickly when the current mate is high-quality, regardless of the quality of previous mates. Brown's (1997b) study showed that female remating rates increased in nutrient-deprived females, supporting the hypothesis that material benefits were implicated in female precopulatory choice. In contrast, his results provide less support for the hypothesis that female remating was

influenced by genetic benefits. Specifically, although Brown (1997b) showed that females maintained on high quality diets had longer refractory periods when their initial mate was large as opposed to when he was smaller (supporting the notion that females remate to improve the genetic quality of their sperm), he also found that females whose first mate was in relatively high condition had shorter refractory periods than females mated to lower-condition males. One possibility is that the effect of male size on female refraction was a direct result of the higher-quality courtship gifts provided by large males (Bussière et al., 2005), rather than representing choice for indirect benefits.

Rather than using a statistical approach, we have adopted an experimental approach in attempting to manipulate the ability of males to provide food. This approach has advantages over a strictly correlational study in that the effect of experimental manipulation on differences between treatments can be inferred as causal. However, there are also limitations to our study relative to Brown's. For example, although size played no role in mate rejection in the initial mating, it is conceivable that because we discarded females who failed to mate in the first instance, our design may have unintentionally eliminated relatively coy females who were more likely to reject males based on their size relative to rivals. Brown (1997b) avoided this problem by retesting females that did not mate initially until they could be included in his experiment. In addition, our inability to detect an effect of size on mate choice could be because we did not control for condition. However, when we estimated condition in the same way that Brown did (as residuals of an exponential regression of body mass on male PC1, see Brown 1997b), whereas the regression was significantly positive (mass =  $\exp(-2.79 + 0.13 \times \text{MalePC1})$ ; mean corrected  $r^2 = .527$ ,  $n = 44$ ,  $p < .001$ ), there was no difference between large and small males in condition ( $t = 0.457$ ,  $n = 44$ ,  $p = .653$ ). It is therefore unlikely that condition itself obscured a strong effect of size on mate rejection in our study.

Our finding that female tree crickets reject males based on gift-giving ability adds to the literature supporting female choice for material benefits among insects (for review, see Vahed, 1998). Examples of taxa for which females use precopulatory choice to discriminate on the basis of material donations include courtship-feeding scorpionflies (see Bockwinkel and Sauer, 1994; Thornhill, 1980), and crickets and katydids (De Luca and Morris, 1998; Eggert and Sakaluk, 1994; Johnson et al., 1999). Other examples include premating (or preinsemination) discrimination of male ability to provide ejaculatory chemicals that females use to protect eggs in beetles (Eisner et al., 1996) and moths (Iyengar and Eisner, 1999a; Iyengar et al., 2002). In a similar experiment to our own, LaMunyon and Eisner (1994) showed that postcopulatory selection in an arctiid moth acts primarily on male courtship donations. They experimentally disassociated male size from spermatophore size and showed that males providing large donations sired more offspring irrespective of their body size.

There are far fewer documented examples of premating preferences based on phenotypic cues of quality that are unrelated to material benefits. One exception may be the spotted cucumber beetle (Coleoptera: Chrysomelidae), in which females selectively mate with males that court at a high rate (Tallamy et al., 2002). The rate of courtship indicates the genetic quality of sires (Tallamy et al., 2003), but does not appear to reflect the quantity of inseminated cucurbitacins (a substance that is translocated to eggs, endowing them with a chemical defense against predators, Tallamy et al., 2002). Other exceptions include systems in which the male investment has no nutritional benefit for females, and therefore may have evolved to indicate genetic quality, for example, some species of balloon flies (Diptera: Empididae) in which males provide nuptial gifts that are inedible (Sadowski et al., 1999). In still

other species, there is a demonstrable trade-off between male genetic quality and male investment, such that the highest quality males provide fewer material benefits than rivals (in some birds, Møller and Thornhill, 1998; and a katydid, Simmons et al., 1999). In these systems, any female preferences for males of high genetic quality over rival males providing more material benefits must be preferences for genetic benefits.

An alternative approach to studying choice for material and genetic benefits has been to experimentally manipulate access to the number of mating partners while controlling the number of matings. In two species of crickets, this kind of experiment has revealed genetic benefits to polyandry (Fedorka and Mousseau, 2002; Tregenza and Wedell, 1998). Moreover, in *Allonemobius socius*, a courtship-feeding cricket, the genetic benefits to polyandry appear to outweigh the material benefits conferred by nuptial feeding, suggesting that multiple mating is maintained via indirect selection (Fedorka and Mousseau, 2002). These results should be interpreted cautiously, however, because the comparison of the magnitudes of direct and indirect benefits in this experiment depends on the assumption that the regression between mate number and fitness gain is similar for both types of benefit. In fact, the genetic benefits of polyandry are likely to be maximized after a few matings, or at best suffer diminishing returns with additional mates, whereas the direct nutritional benefits in courtship feeding insects are likely to accrue in a more linear fashion. As a result, evaluating the relative importance of direct and indirect benefits will require better empirical estimates of total mating frequency and offspring performance using experiments that manipulate the quality of nutrients as well as the genetic diversity of mates available to females. Model systems such as the tree cricket, in which the ability of males to provide direct benefits can be manipulated experimentally, will be very useful in such studies.

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