

# A model of the interaction between 'good genes' and direct benefits in courtship-feeding animals: when do males of high genetic quality invest less?

Luc F. Bussière

*Biology Group, The University of Toronto at Mississauga, Mississauga, Ontario, Canada L5L 1C6  
(lbussier@credit.erin.utoronto.ca)*

Conflict between mates over the amount of parental investment by each partner is probably the rule except in rare cases of genetic monogamy. In systems with parental care, males may frequently benefit by providing smaller investments than are optimal for individual female partners. Females are therefore expected to choose males that will provide the largest amounts of parental investment. In some species, however, the preferred males provide less care than their rivals. Focusing on species in which males invest by feeding their mates, I use a simple model to demonstrate the conditions under which males preferred by females may have optimal donations that are smaller than those of less-preferred rivals. Pre-mating female choice may sufficiently bias the perception of mate availability of preferred males relative to their rivals such that preferred males gain by conserving resources for future matings. Similarly, 'cryptic' biases in favour of high-quality ejaculates by females can compensate for smaller than average donations received from preferred males. However, post-fertilization cryptic choice should not change the optimal donations of preferred males relative to their rivals. I discuss the implications of this work for understanding sexual selection in courtship-feeding animals, and the relevance of these systems to understanding patterns of investment for animals in general.

**Keywords:** courtship feeding; cryptic choice; differential allocation; direct benefits; good genes; parental investment

## 1. INTRODUCTION

Sexual conflict over levels of parental care is probably ubiquitous in species that are not genetically monogamous. In these species, the optimal levels of investment for one member of a mating pair will probably differ from the levels of the other. This conflict reaches an extreme level in some systems in which a male's reproductive effort is almost entirely devoted to the acquisition of mates, such that his own offspring gain very little from this effort. In these systems, the male's optimal investment in offspring-directed benefits would be negligible provided it secured him fertilizations, while the female would benefit from securing as large a male investment as possible (Trivers 1972).

Females are expected to choose in order to obtain mates that will provide large investments. But this choice may conflict with female choice for indirect (good genes) benefits: in many species, the preferred males provide fewer direct benefits than their rivals, while in other species there is no conflict between choice for direct and indirect benefits, because the preferred males provide the largest investments (Møller & Thornhill 1998). This variation between species may be due in part to variation in the relative importance of genetic benefits (Møller & Thornhill 1998), or in the nature of returns on expenditure to sexual advertisement by males (Kokko 1998). In this paper I describe

an additional factor that may determine whether preferred males invest more or less than their rivals: the stage of the mating sequence at which female choice is exerted. I outline a model that focuses on systems that feature a form of male investment that is perhaps taxonomically more widespread than postnatal parental care: the transfer of food from males to females during mating (e.g. Royama 1966; Vahed 1998).

Courtship-feeding arthropods are ideal systems for studying the relationship between direct (material) and indirect (genetic) benefits to female choice. Unlike other systems for which there is growing evidence that chemicals in the ejaculate may be harmful to females (Fowler & Partridge 1989; Chapman *et al.* 1995; Civetta & Clark 2000), female courtship-feeding arthropods benefit from the nutritious secretions or gifts of prey that may accompany sperm transfer (Gwynne 1984; Brown 1997a). While I cannot rule out the possibility that courtship-food gifts can include toxic components, it seems unlikely that gifts that evolved because of their attractive properties to females would have adopted components that females should avoid. In any case, the subject of toxic ejaculates is beyond the scope of this paper. Due to the fact that male investment in courtship-feeding systems is typically limited to prey or an edible glandular secretion transferred during courtship, it is readily quantifiable, e.g. by measuring weight loss during mating (Brown & Kuns 2000) or by measuring the dimensions (Thornhill 1976) or mass (Simmons & Kvamemo 1997) of the gift itself. Further-

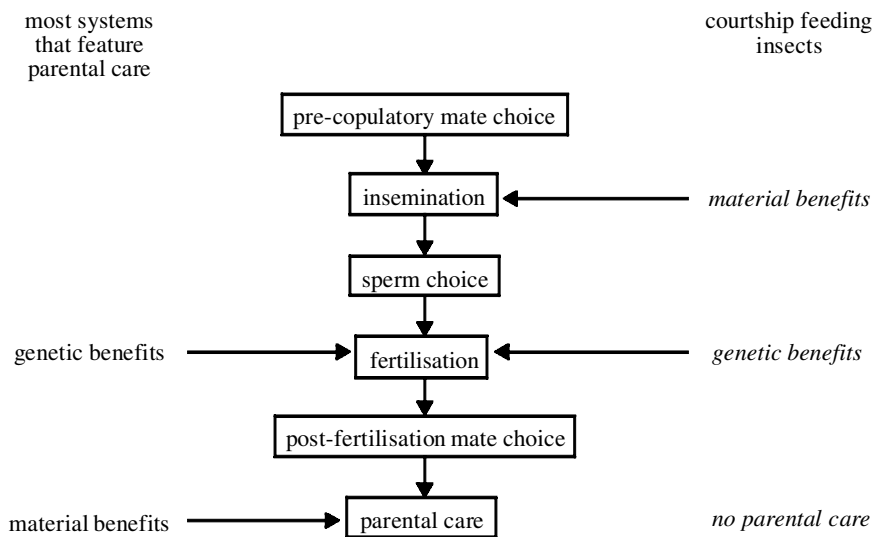


Figure 1. A diagrammatic representation of the generalized sequence of behaviours and female-choice opportunities in a mating episode. The events flow in sequence from the top of the figure to the bottom. In most systems featuring parental care, the all-important material benefits are accrued after fertilization. In courtship-feeding arthropods, however, the early acquisition of the food gift allows females to separate pre-copulatory choice for material benefits from cryptic choice for genetic benefits.

more, since many female insects store sperm from more than one male, there is the potential for females to separate choice for material benefits associated with mating from 'cryptic' (or post-copulatory) choice for genetic benefits by favouring certain sperm over others (L. Rowe, personal communication). This is because, unlike most systems featuring parental care, the male investment in courtship-feeding systems occurs early in the mating sequence, long before fertilization takes place (figure 1).

In systems featuring post-fertilization parental care, female choice for indirect benefits cannot easily be dissociated from choice for genetic benefits. This is because the crucial direct benefits are acquired after the genetic benefits are fixed at fertilization. If direct benefits are normally much more important to choosy females than indirect benefits, as recent theory has concluded (Kirkpatrick 1996; Kirkpatrick & Barton 1997; but see also Møller & Jennions 2001; Houle & Kondrashov 2002), it seems unlikely that females in systems with paternal care will allow preferred males to invest fewer resources in care because of the male's superior genetic quality. In courtship-feeding systems, however, the male investment precedes fertilization. Females may thus use pre-mating choice to secure mates providing direct benefits, and subsequently use cryptic mate choice to favour the paternity of males providing indirect benefits irrespective of the material donations of those males. In fact, if active female choice occurs after the transfer of direct benefits, it cannot be choice for those benefits since there is no direct selection on females for material benefits at this stage (Parker & Simmons 1989; Brown 1999).

At this point it is worth taking a moment to attend to terminology (Birkhead 2000; Eberhard 2000; Pitnick & Brown 2000). Eberhard (1996) defined cryptic choice as follows: any 'female controlled process or structure that selectively favours paternity by conspecific males with a particular trait over that of others that lack the trait when

the female has copulated with both types'. The definition I use in this paper differs slightly. First, I agree with Pitnick & Brown (2000) that the word 'control' is problematic, and so have not included that word in my definition. Second, I wish to include in my definition all processes following copulation by which females exert mate choice (including those that do not manipulate paternity *per se*). I therefore use the term 'cryptic choice' interchangeably with 'post-copulatory choice', but I do not wish to imply that any of the processes involved are actually 'cryptic' or concealed from the males under selection or the investigators. I use the terms pre-fertilization and post-fertilization to distinguish between cryptic choice exerted before and after fertilization. The importance of distinguishing between female-choice mechanisms exerted at different stages of the reproductive cycle was recently discussed by Cunningham & Birkhead (1998). Pre-fertilization cryptic choice includes mechanisms of choice that manipulate paternity *per se* (e.g. by using the sperm of certain males preferentially over that of others; Ward 1993, 2000). Pitnick & Brown (2000) suggest using the following definition for sperm choice, that corresponds well to my notion of pre-fertilization choice: 'nonrandom paternity biases resulting from female morphology, physiology, or behaviour that occur after coupling'. Since I wish to emphasize the importance of the timing of events relative to fertilization, I will use the term 'pre-fertilization choice' rather than 'sperm choice' in this paper. Post-fertilization choice involves mechanisms by which females adjust the fitness of certain mates without biasing paternity. A well-known example is when females favour high-quality males by preferentially allocating nutrients to the offspring of those males, or to clutches in which the favoured males have high paternity (Burley 1986). Note that although the fitness of a focal male may be altered by post-fertilization choice, his representation in the female's sperm stores is not.

Recently, Parker (1998) has suggested that male insects favoured by cryptic female choice should be able to invest less in ejaculates than their rivals and nonetheless achieve success in sperm competition. As the nuptial gifts in most courtship-feeding insects are thought to be maintained in the context of maximizing sperm transfer (Gwynne 1997; Vahed 1998), males favoured by female cryptic choice should be able to invest less in courtship gifts than their rivals and nonetheless achieve high fertilization success. These males should subsequently be able to reinvest the conserved resources into other mating opportunities.

An example will help illustrate how female choice can operate to favour both direct and indirect benefits in a courtship-feeding insect. Female black-horned tree crickets (*Oecanthus nigricornis*), mount the males and feed from a specialized gland on the thorax for a brief period prior to copulation and for an extended period following copulation. This glandular secretion is valuable to females because it extends their lifespan (Brown 1997a). The pre-copulatory feeding is likely to give a female valuable information about the quality or quantity of nutrients she is to receive from the male. Before the pair make contact, females receive a signal of body size through the male calling song, and will preferentially orient towards larger males (Brown *et al.* 1996). This preference does not appear to be for material benefits: although large males tend to have larger total gift reserves, the correlation between body size and gift size is weak (Brown 1994; L. F. Bussière, unpublished data), partly because gift-giving ability fluctuates temporally depending on the male's recent mating frequency (Brown & Kuns 2000). Alternatively, females may seek larger males not for direct benefits, but for genetic benefits. This idea is especially compelling because larger male tree crickets are more successful in competition for mates (Brown 1994) and female tree crickets appear to exhibit cryptic choice for large males by increasing their oviposition rate following a high-quality mating irrespective of the size of gift received (Brown 1997b). If this increase in oviposition is an adaptation for female choice, it cannot be choice for material benefits, since it occurs after all material benefits have been transferred (Brown 1999; Parker & Simmons 1989). Thus a female tree cricket may be able to use cryptic choice to favour fertilization by males of high genetic quality (large size) without impairing her ability to obtain additional glandular meals through multiple matings. Consequently, high-quality males may provide smaller courtship gifts than expected and nonetheless achieve optimal insemination.

In this paper, I model the influence of female choice at several stages of the mating sequence on male investment behaviour, to determine the conditions under which negative correlations between male genetic quality and investment are likely to occur in courtship-feeding systems. I will demonstrate that the stage at which choice occurs is crucial in defining the nature of selection and the resulting patterns of investment across genotypes. I will also generate testable qualitative predictions about how male investment should evolve in response to changes in several aspects of the mating biology of a species.

## 2. THE MODEL

The model detailed in this section is based on mating systems in which males transfer material benefits to females during mating. It makes the following assumptions: (i) all materials that a female will receive from a given male are transferred at the time of mating (in the form of a prey item or glandular secretion, for example); (ii) the larger the gift a male produces (or the longer he feeds his mate), the greater his representation in the female's sperm stores (Gwynne *et al.* 1984; Wedell & Arak 1989; Simmons 1995b); (iii) sperm compete in an ideal lottery (Parker 1970) for access to ova; (iv) the availability of the gift or the resources required to produce it can in some cases limit male reproduction (Gwynne 1985, 1993; L. F. Bussière, unpublished data); (v) males have the ability to assess either the availability of receptive females or their own genetic quality relative to other males in the same population (Shelly & Bailey 1992; Simmons 1995c; Simmons & Kvarnemo 1997); (vi) females may exert cryptic choice for indirect benefits (Brown 1999); and finally (vii) for simplicity, I do not allow males to adjust their investment throughout their mating life, but rather maintain a constant investment level for all matings. I will discuss the limitations imposed by the model's assumptions in § 4.

Male fitness ( $W$ ) is expressed as a function of the size of each nuptial gift offering ( $x$ ). Gift size determines fitness via three components (see figure 2).

- (i) The first component defines the number of gifts a male can produce,  $n(x)$ , and decreases with gift size,  $x$ , as follows:

$$n(x) \propto \frac{\rho}{x},$$

where  $\rho$  is a term describing food availability in the population, and therefore defines how many nuptial gifts can be produced. The curve is necessarily concave-up, because the larger each individual gift a male makes, the smaller the total number of gifts he can give.

- (ii) The second component of male fitness defines the probability that gifts will be transferred to receptive females,  $p(x)$ , and increases with gift size. This is because when males make a large number of very small gifts, females rather than gift nutrients will be a limiting resource; the greater the gift number,  $n(x)$ , the lesser the likelihood of transferring all gifts to receptive females.

$$p(x) \propto \frac{ox}{\rho},$$

where  $o$  is the ratio of sexually receptive females to males, i.e. the OSR of Emlen & Oring (1977). Food availability,  $\rho$ , appears in this function because it influences the quantity of gifts a male can potentially present to females, and thus the number of receptive females required to accept all of a male's gifts.

- (iii) The third component defines the reproductive returns per gift,  $i(x)$ , and increases with gift size as follows:

$$i(x) \propto xf$$

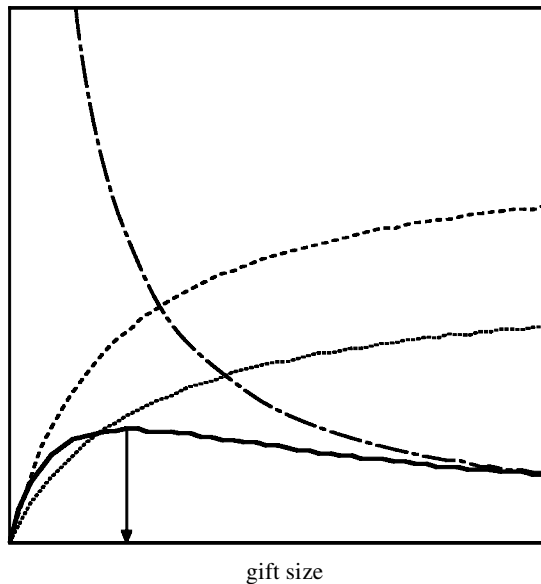


Figure 2. Male reproductive success,  $W(x)$ , modelled as a function of gift size (solid line). The three component factors of reproductive success are also illustrated, where  $n(x)$  represents the number of gifts a male can produce (dashed and dotted line),  $i(x)$  represents a male's reproductive returns per gift (dashed line) and  $p(x)$  illustrates the probability that a gift will be successfully transferred to a receptive female (dotted line). The arrow indicates the optimal gift size, i.e. the  $x$ -value corresponding to the maximum value of  $W(x)$ .

where  $f$  is a term describing female choice. This curve will assume a concave downward shape (as in Gwynne *et al.* 1984; Simmons 1986), according to the marginal value theorem (Charnov 1976). This is because increased expenditure on the ejaculate (the number of sperm transferred) yields increasing fitness benefits with diminishing returns. Additional sperm increase a male's representation in the female sperm store, but the gains per unit effort diminish as the male's representation approaches 100%.

Female choice ( $f$ ) can influence the curve describing fitness in several ways. I have distinguished between traditional pre-mating choice, pre-fertilization cryptic choice, and post-fertilization cryptic choice. Choice exerted before copulation influences male perceptions of their mating opportunities, such that the preferred males perceive females to be more abundant than do their rivals. Pre-mating choice is therefore modelled as a direct influence on the OSR of preferred males.

Cryptic pre-fertilization choice influences fertilization in the same way that the food gift itself does. Whereas the food gift passively modifies female behaviour (typically, the longer a female is preoccupied with feeding, the longer insemination proceeds; Vahed 1998), pre-fertilization choice actively influences the insemination success of a particular male.

Choice exerted after copulation influences neither the number of receptive females nor a male's insemination success, but a male's reproductive returns given these two previous factors. Thus a female may allocate more or fewer resources to a clutch sired by a preferred male, or even the size of the clutch itself,

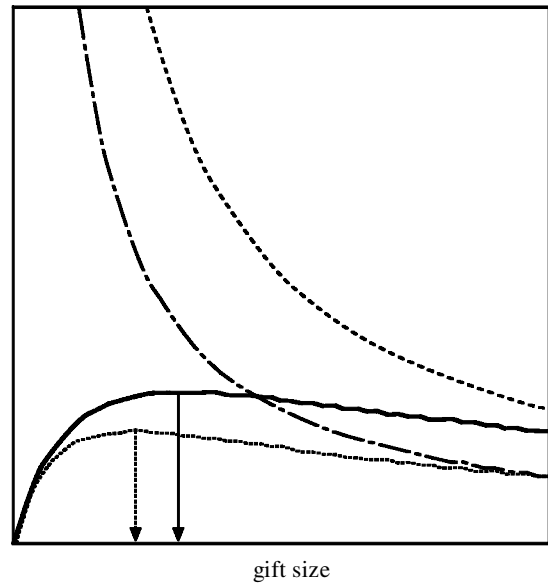


Figure 3. The influence of increased food availability on the optimal gift size of a male. As food availability in the environment increases, so does the optimal gift size of a male. The solid arrow represents the optimal gift size given more abundant food resources than in the environment indicated by the hatched arrow. Dashed and dotted line,  $n(x)$  lower food availability; dotted line,  $W(x)$  lower food availability; dashed line,  $n(x)$  higher food availability; solid line,  $W(x)$  higher food availability.

but the fraction of the clutch that he has sired will be unaffected by this kind of female preference.

Total male fitness ( $W$ ), is the product of the number of successful copulations,  $n(x) \times p(x)$ , and the reproductive returns per copulation,  $i(x)$ , as follows:

$$W(x) = n(x) \times p(x) \times i(x).$$

Figure 2 illustrates male fitness as a function of gift size. The peak in fitness represents the optimal gift size. By modelling changes in the component functions of male fitness, I will show how these changes influence the value of this optimal donation (shifting the peak gift size to the right or left).

### 3. RESULTS

Changes in food availability,  $\rho$ , influence the extent to which nuptial gifts limit male success in two ways. If one holds the number of receptive females constant, simply increasing the condition of a male leads to a larger optimal gift size, as illustrated in figure 3. This is because with increasing environmental resources, gift reserves become less limiting (i.e. there is less incentive to conserve gift reserves for future matings). Males then gain in fitness by producing a larger number of larger gifts. Food availability may also influence sexual receptivity (and thus the OSR), since hungry females are more likely to mate in order to obtain the food gifts associated with mating, whereas hungry males have a decreased capacity to provide such food gifts (as in Gwynne 1993; Gwynne & Simmons 1990). This also results in a shift in optimal gift size: the more female biased the sex ratio, the smaller the optimal

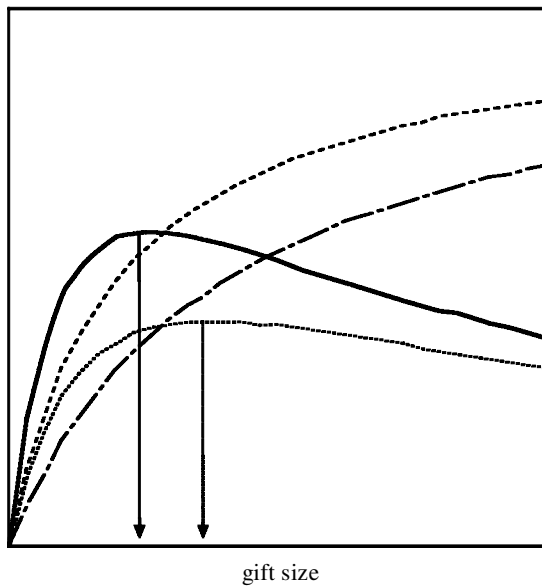


Figure 4. As the sex ratio becomes more female biased, the optimal gift size decreases. The solid arrow represents the optimal gift size given a relatively more female-biased OSR than that indicated by the hatched arrow. Pre-mating female choice may increase the encounter rates of preferred males with receptive females such that they perceive a more female-biased sex ratio than rivals. Dashed and dotted line,  $p(x)$  female-biased sex ratio; dotted line,  $W(x)$  male-biased sex ratio; dashed line,  $p(x)$  female-biased sex ratio; solid line,  $W(x)$  female-biased sex ratio.

donation strategy (figure 4). This supports the intuition that males should conserve gift resources for subsequent matings when the probability of future matings is high.

The sex ratio may also shift independently of environmental food availability and cause a shift in optimal gift sizes (figure 4). The greater the relative abundance of receptive females, the smaller the optimal food gift.

The influence of female choice on optimal gift size is more complex. Pre-copulatory female choice for high-quality males results in a skew in mating opportunities across male phenotypes, such that the preferred males encounter more receptive females. In this case, preferred males should decrease gift size to take advantage of the greater returns per unit effort of smaller gifts (figure 4). In nature, this should be distinguished from decreases in gift size that result from depletion of resources as a result of multiple mating (but which would also produce a negative correlation between male quality and material donations). In the model, gift size in subsequent mating events remains constant.

Due to the fact that both the food gift and pre-fertilization cryptic choice act to influence the representation of a male's sperm in the female's storage organ, a decrease in the size of the food gift can be compensated by pre-fertilization cryptic choice, and vice versa. This kind of female preference therefore allows the preferred males to donate smaller gifts and nonetheless achieve optimal insemination rates (figure 5a).

In contrast, post-fertilization female choice has no influence on the optimal gift size. Males favoured by post-fertilization choice have higher fitness levels at all gift sizes (see figure 5b), but the optimal gift size is identical to that

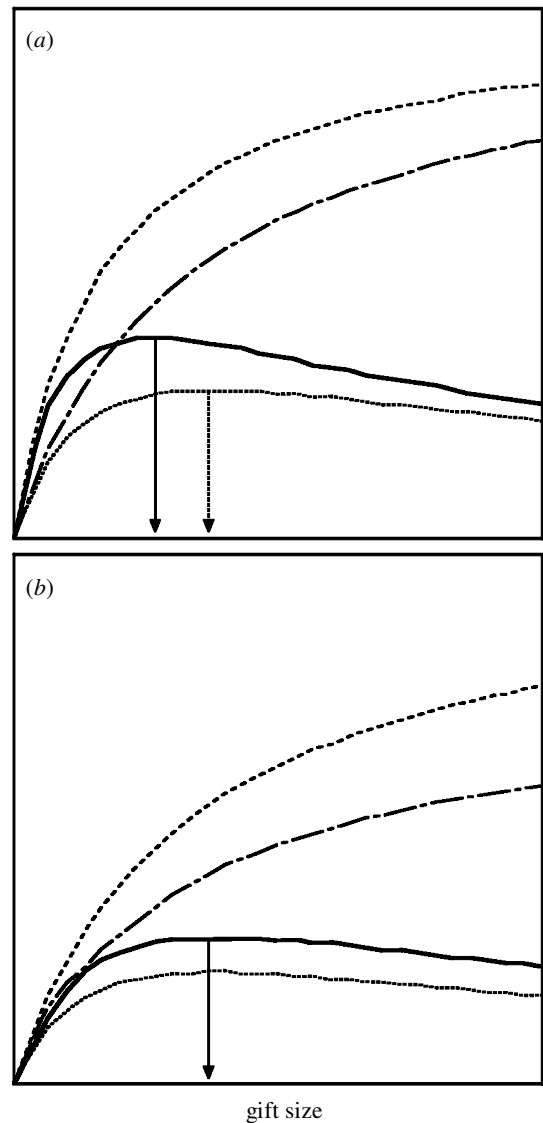


Figure 5. The influence of cryptic female choice on the optimal male donation size. (a) Pre-fertilization mechanisms allow preferred males (solid arrow) to invest less than their rivals (hatched arrow). (b) In contrast, post-fertilization mechanisms of female choice do not influence the optima of preferred males relative to the optima of less preferred males (both optima indicated by the solid arrow). (a) Dashed and dotted line,  $i(x)$  without pre-fertilization preference; dotted line,  $W(x)$  without pre-fertilization preference; dashed line,  $i(x)$  with pre-fertilization preference; solid line,  $W(x)$  with pre-fertilization preference. (b) Dashed and dotted line,  $i(x)$  without post-fertilization preference; dotted line,  $W(x)$  without post-fertilization preference; dashed line,  $i(x)$  with post-fertilization preference; solid line,  $W(x)$  with post-fertilization preference.

of less-preferred rivals. This is because post-fertilization female choice has no influence on insemination, and the preferred males thus have to ensure optimal insemination by feeding the females as much as their less-preferred rivals. For example, if a female increased her oviposition rate after mating with a preferred male (or decreased the number of eggs laid following mating with a lower-quality male), she would increase the number of eggs produced in the period immediately following mating with the pre-

ferred male, but the fraction of those eggs that were actually sired by the preferred mate would still depend on the size of his nuptial gift.

#### 4. EFFECTS OF VIOLATING THE ASSUMPTIONS

In constructing this model, many assumptions were inevitable. The assumptions detailed in § 2 produced the simplest and most easily interpreted results; however, the broad qualitative results usually remained even when assumptions were violated. I now describe in detail the consequences of violating each of the assumptions as follows.

- (i) The basic model assumes that all materials received from a given male are transferred at the time of mating. This simplifies the benefits to mate choice from the female perspective because, provided there are no direct benefits after mating, cryptic choice following mating is likely to be directed towards genetic benefits. If this assumption is violated (e.g. if there is some level of paternal care), a negative correlation between male genetic quality and nuptial gift investment is less likely because females cannot as easily dissociate choice for direct benefits from choice for genetic benefits. As a consequence, cryptic choice is less likely to reflect only genetic benefits, and high-quality males will have to provide more direct benefits to benefit from any cryptic choice.
- (ii) The model also assumes that the larger the gift a male produces (or the longer he feeds his mate), the greater his representation in the female's sperm stores. This is a reasonable assumption because courtship food gifts are generally thought to be adaptively maintained in the context of maximizing sperm transfer (Vahed 1998). However, if females use pre-fertilization cryptic choice to favour certain males irrespective of their donations, the correlation between gift size and insemination success is diminished. In theory, individual mating investment should correlate with confidence in paternity (Gwynne 1984; but see also Simmons & Siva-Jothy 1998), and so one could argue that selection should promote a decrease in gift size across all male phenotypes. However, low-quality males have only one option to increase sperm transfer success to its optimal level, and that is to increase gift size. In a sense, low-quality males are making the 'best of a bad job' by providing larger gifts, and consequently I expect no uniform decrease in gift sizes as a result of female cryptic choice.
- (iii) Sperm compete in an ideal lottery for access to ova. This is perhaps the most questionable assumption of my model, especially because insects are well known for their varied patterns of sperm competition, both within and among species (Danielsson 1998; Simmons & Siva-Jothy 1998). In my model, I made the assumption of an ideal lottery because it imposed sharply diminishing returns on ejaculate expenditure. Alternative models of sperm competition (e.g. sperm flushing or partial sperm displacement) will also probably confer diminishing returns, but the function describing those returns

would be more complex. For example, if some degree of sperm displacement occurred, the returns on gift expenditure would diminish more gradually. Perfect sperm displacement is unlikely in nature, but so is the ideal lottery I initially assumed. Thus, in reality, the effect of pre-fertilization choice on optimal donation size is likely to be weaker than in my model as a result of some sperm displacement, but nevertheless present.

- (iv) The model assumes that the availability of the gift or the resources required to produce it can in some cases limit male reproduction. If this is not the case, then males should simply provide the largest possible gifts for each mating event.
- (v) The model assumes that males have the ability to assess either the availability of receptive females or their own genetic quality relative to other males in the same population. This is crucial, because if males cannot predict the likelihood of future mating encounters, they cannot optimize their donations based on future opportunities for reproduction. The literature on courtship-feeding insects suggests that males may alter their sexual behaviour according to their perceptions of the availability of mates (Kvarnemo & Simmons 1998; Shelly & Bailey 1992; Simmons 1995c). Males may also use any signal that functions in male-female communication to discern relative quality. The acoustic signals of Orthoptera (well known to indicate male quality in several species (Simmons 1995a; Simmons & Ritchie 1996; Brown *et al.* 1996; De Luca & Morris 1998)) could easily function in this context because males can eavesdrop on the calls of rivals.
- (vi) Females may exert cryptic choice for indirect benefits. This assumption is required only for the sections dealing with cryptic choice. Obviously, if females of a given species do not exert choice after mating, that component of the model does not apply.
- (vii) Male gift sizes are fixed for each of their copulations. Although this assumption is unrealistic for natural systems (where males are likely to experience temporal changes in resource availability and copulation frequency), it simplifies the model greatly, and its violation does not change any of the qualitative predictions of the model. This is because the decision rules regulating the trade-off between current and future reproduction will apply regardless of the current value of immediate versus future reproduction.

#### 5. DISCUSSION

I examined three variables in my investigation of male optimal donation strategies: (i) food resources available for gift production or transfer; (ii) the OSR; and (iii) female choice. Males should decrease allocation to individual gifts if total gift reserves are limiting; the more limiting the gift reserves, the smaller the optimal gift size. Optimal gift size should also decrease as the abundance of copulation opportunities increases. Finally, males preferred by pre-mating or pre-fertilization (but not post-fertilization) cryptic choice should donate smaller gifts than expected based on their condition.

These findings could help to explain a number of

empirical studies of courtship-feeding insects that demonstrate poor correlations between male quality and gift size or quality (e.g. Sakaluk 1985; Wiklund *et al.* 1993; Brown 1994; Cook & Wedell 1996; Calos & Sakaluk 1998). Notably, in an experiment using the katydid *Requena verticalis*, Simmons *et al.* (1999) show that asymmetrical (and thus probably low quality; Møller & Pomiankowski 1993) males provide food gifts containing more protein than symmetrical males. Simmons *et al.* (1999) concluded that males with high levels of asymmetry were anticipating lower mating rates and optimizing their investment accordingly. To my knowledge, this is the only published report of a significant negative correlation between male genetic quality and male gift quality.

My approach does not provide any quantitative predictions of the relative importance of the three variables I studied. Perhaps a more mathematically sophisticated approach than the one I adopted would generate such predictions. Nevertheless, the qualitative predictions of the model can be tested experimentally through careful manipulations of the availability of resources, the OSR, and the opportunity for female choice.

All of these variables should be considered concurrently to predict the correlation between male genetic quality and donation quality in any one system. If body size is a good index of male genetic quality (as it appears to be in tree crickets, for example, Brown (1997a, 1999)), then it is possible to speculate about how these three variables will interact. Larger males will usually have larger gift reserves than smaller males, and are thus less likely to be limited by gift reserves. This should promote a positive association between attractiveness and gift size. However, larger males may experience a higher female encounter rate because of their attractiveness, that should promote a decrease in gift size as expected opportunities for future copulations increase (see figure 4). These larger males may also adaptively decrease gift size because they are favoured by pre-fertilization cryptic female choice (see figure 5a).

In nature, one would rarely expect the correlation between genetic quality and material benefits to be strongly negative, because preferred genotypes are typically in better condition than their rivals, and can thus better afford to expend energy on mating. In fact, the optima for males of differing genotypes in some species may be beyond what any individual can actually produce, such that each male provides as large a gift as possible, and a resulting positive correlation between male quality and gift quality is observed despite the fact that the true optimum for preferred males may be smaller than it is for less-preferred males. Never the less, in other species cryptic female choice may decrease the strong relationship between genetic quality and gift size that would be expected in the absence of female choice, such that indices of genetic quality are relatively poorly correlated with material benefits (Brown 1994; L. F. Bussière, unpublished data; Simmons *et al.* 1999).

Interestingly, the conditions promoting weaker correlations between genetic quality and gift size are unlikely to occur in the laboratory, since most laboratory-reared insects receive food *ad libitum* and are isolated from females except during experimental manipulations, whereas in nature, matings may occur more frequently

and resources may be more limiting. Consistent with this intuition is the finding by Simmons *et al.* (1999) that positive correlations between measures of male quality and gift size were only detectable when there were long intervals between matings. The lack of reported negative male body size-gift size correlations in gift-giving insects may thus be partly attributable to the laboratory environment, and not reflect natural patterns of variation in material donations.

The fact that between-individual differences in the perception of mating opportunities can influence male donation strategies has important implications for our understanding of how parental investment and the OSR control sexual selection. Conventionally, discussions of factors controlling sexual selection have emphasized that relative parental investment by the sexes controls the OSR (Emlen & Oring 1977). It is clear that the OSR can also influence parental investment, and that it can influence different males within a single population quite differently. Preferred males may perceive a more female-biased OSR than rivals because they attract more receptive females, and adjust their behaviour accordingly. This notion has preliminary empirical support in tree crickets, where males appear to respond to increased female encounter rates by decreasing the size of their nuptial gifts (L. F. Bussière, unpublished data).

Testing the applicability of the model will involve careful assessment of natural mating conditions and a strong understanding of the mechanisms of mate choice (both before and after copulation). Although convincing evidence for both pre-fertilization and post-fertilization cryptic choice is elusive (Birkhead 1998, 2000; Eberhard 2000; Kempnaers *et al.* 2000; Pitnick & Brown 2000; Sheldon 2000), such evidence will be required to convincingly support the differential effect of pre-fertilization and post-fertilization mechanisms of cryptic choice suggested by this model. Cryptic choice has been well documented in several species of courtship-feeding insects, but to my knowledge all of the reported mechanisms of cryptic choice in these systems are either dependant on gift size (mediated by spermatophore consumption, and thus constitute cryptic choice for male quality only insofar as donation ability indicates male quality, for example, Sakaluk (1997)) or post-fertilization forms of cryptic choice (e.g. increased oviposition rate in tree crickets; Brown 1994, 1997b). To date there are no candidate systems featuring both courtship feeding and sperm choice in which the negative correlation between pre-fertilization cryptic choice and male investment could be tested.

The model should apply whenever there is the opportunity for females to divorce choice for genetic benefits from choice for material benefits. I expect this to be reasonably common, especially in arthropods where material benefits are frequently transferred during courtship and where females can store sperm from more than one mate. I contend that a good understanding of the interaction between genetic (indirect) and material (direct) benefits might best be achieved in systems in which the choice for those benefits is disentangled, but the effects of such choice can nonetheless be measured in the common currency of offspring fitness. However, any investigation should take care to mimic natural mating conditions, since the strategies of preferred males are least

likely to diverge from those of poorer-quality rivals under some laboratory conditions.

The author thanks D. Gwynne, L. Rowe, W. Lasiuk and especially P. Lorch for many hours of discussion and advice. D. Gwynne, P. Lorch, C. Kelly, S. Balshine, B. Kempnaers, T. Szekely and two anonymous reviewers provided very helpful suggestions for improving the manuscript. This work was supported by a NSERC (Canada) research grant to D. T. Gwynne and a NSERC post-graduate scholarship to L.F.B.

## REFERENCES

- Birkhead, T. R. 1998 Cryptic female choice: criteria for establishing female sperm choice. *Evolution* **52**, 1212–1218.
- Birkhead, T. R. 2000 Defining and demonstrating postcopulatory female choice—again. *Evolution* **54**, 1057–1060.
- Brown, W. D. 1994 Mechanisms of female mate choice in the black-horned tree cricket, *Oecanthus nigricornis* (Orthoptera: Gryllidae: Oecanthinae). PhD thesis, Zoology Department, University of Toronto.
- Brown, W. D. 1997a Courtship feeding in tree crickets increases insemination and female reproductive life span. *Anim. Behav.* **54**, 1369–1382.
- Brown, W. D. 1997b Female remating and the intensity of female choice in black-horned tree crickets, *Oecanthus nigricornis*. *Behav. Ecol.* **8**, 66–74.
- Brown, W. D. 1999 Mate choice in tree crickets and their kin. *A. Rev. Entomol.* **44**, 371–396.
- Brown, W. D. & Kuns, M. M. 2000 Female choice and the consistency of courtship feeding in black-horned tree crickets *Oecanthus nigricornis* Walker (Orthoptera: Gryllidae: Oecanthinae). *Ethology* **106**, 543–557.
- Brown, W. D., Wiseman, J., Andrade, M. C. B., Mason, A. C. & Gwynne, D. T. 1996 Female choice for an indicator of male size in the song of the black-horned tree cricket (Orthoptera: Gryllidae: Oecanthinae). *Evolution* **50**, 2400–2411.
- Burley, N. 1986 Sexual selection for aesthetic traits in species with biparental care. *Am. Nat.* **127**, 415–445.
- Calos, J. B. & Sakaluk, S. K. 1998 Paternity of offspring in multiply mated female crickets: the effect of nuptial food gifts and the advantage of mating first. *Proc. R. Soc. Lond. B* **265**, 2191–2195. (DOI 10.1098/rspb.1998.0558.)
- Chapman, T., Liddle, L. F., Kalb, J. M., Wolfner, M. F. & Partridge, L. 1995 Cost of mating in *Drosophila melanogaster* females is mediated by male accessory gland products. *Nature* **373**, 241–244.
- Charnov, E. L. 1976 Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* **9**, 129–136.
- Civetta, A. & Clark, A. G. 2000 Correlated effects of sperm competition and postmating female mortality. *Proc. Natl Acad. Sci. USA* **97**, 13 162–13 165.
- Cook, P. A. & Wedell, N. 1996 Ejaculate dynamics in butterflies: a strategy for maximizing fertilization success. *Proc. R. Soc. Lond. B* **263**, 1047–1051.
- Cunningham, E. J. A. & Birkhead, T. R. 1998 Sex roles and sexual selection. *Anim. Behav.* **56**, 1311–1321.
- Danielsson, I. 1998 Mechanisms of sperm competition in insects. *A. Zool. Fenn.* **35**, 241–257.
- De Luca, P. A. & Morris, G. K. 1998 Courtship communication in meadow katydids: female preference for large male vibrations. *Behaviour* **135**, 777–794.
- Eberhard, W. G. 1996 *Female control: sexual selection by cryptic female choice*. Princeton University Press.
- Eberhard, W. G. 2000 Criteria for demonstrating postcopulatory female choice. *Evolution* **54**, 1047–1050.
- Emlen, S. T. & Oring, L. W. 1977 Ecology, sexual selection and the evolution of mating systems. *Science* **197**, 215–222.
- Fowler, K. & Partridge, L. 1989 A cost of mating in female fruit-flies. *Nature* **338**, 760–761.
- Gwynne, D. T. 1984 Courtship feeding increases female reproductive success in bushcrickets. *Nature* **307**, 361–363.
- Gwynne, D. T. 1985 Role-reversal in katydids: habitat influences reproductive behaviour (Orthoptera: Tettigoniidae: *Metaballus* sp.). *Behav. Ecol. Sociobiol.* **16**, 355–361.
- Gwynne, D. T. 1993 Food quality controls sexual selection in Mormon crickets by altering male mating investment. *Ecology* **74**, 1406–1413.
- Gwynne, D. T. 1997 The evolution of edible ‘sperm sacs’ and other forms of courtship feeding in crickets, katydids and their kin (Orthoptera: Ensifera). In *The evolution of mating systems in insects and arachnids* (ed. J. C. Choe & B. Crespi) pp. 110–129. Cambridge University Press.
- Gwynne, D. T. & Simmons, L. W. 1990 Experimental reversal of courtship roles in an insect. *Nature* **346**, 172–174.
- Gwynne, D. T., Bowen, B. J. & Codd, C. G. 1984 The function of the katydid spermatophore and its role in fecundity and insemination. *Aust. J. Zool.* **32**, 15–22.
- Houle, D. & Kondrashov, A. S. 2002 Coevolution of costly mate choice and condition-dependent display of good genes. *Proc. Natl Acad. Sci. USA* **269**, 97–104.
- Kempnaers, B., Foerster, K., Questiau, S., Robertson, B. C. & Vermeirssen, E. L. M. 2000 Distinguishing between female sperm choice versus male sperm competition: a comment on Birkhead. *Evolution* **54**, 1050–1052.
- Kirkpatrick, M. 1996 Good genes and direct selection in the evolution of mating preferences. *Evolution* **50**, 2125–2140.
- Kirkpatrick, M. & Barton, N. H. 1997 The strength of indirect selection on female mating preferences. *Proc. Natl Acad. Sci. USA* **94**, 1282–1286.
- Kokko, H. 1998 Should advertising parental care be honest? *Proc. R. Soc. Lond. B* **265**, 1871–1878 (DOI 10.1098/rspb.1998.0515.).
- Kvarnemo, C. & Simmons, L. W. 1998 Male potential reproductive rate influences mate choice in a bushcricket. *Anim. Behav.* **55**, 1499–1506.
- Møller, A. P. & Jennions, M. D. 2001 How important are direct fitness benefits of sexual selection? *Naturwissenschaften* **88**, 401–415.
- Møller, A. P. & Pomiankowski, A. 1993 Fluctuating asymmetry and sexual selection. *Genetica* **89**, 267–279.
- Møller, A. P. & Thornhill, R. 1998 Male parental care, differential parental investment by females and sexual selection. *Anim. Behav.* **55**, 1507–1515.
- Parker, G. A. 1970 Sperm competition and its evolutionary consequences in the insects. *Biol. Rev.* **45**, 525–567.
- Parker, G. A. 1998 Sperm competition and the evolution of ejaculates: towards a theory base. In *Sperm competition and sexual selection* (ed. T. R. Birkhead & A. P. Møller), pp. 1–54. San Diego, CA: Academic Press.
- Parker, G. A. & Simmons, L. W. 1989 Nuptial feeding in insects: theoretical models of male and female interests. *Ethology* **82**, 3–26.
- Pitnick, S. & Brown, W. D. 2000 Criteria for demonstrating female sperm choice. *Evolution* **54**, 1052–1056.
- Royama, T. 1966 A re-interpretation of courtship feeding. *Bird Study* **13**, 116–129.
- Sakaluk, S. K. 1985 Spermatophore size and its role in the reproductive behaviour of the cricket, *Gryllobates supplicans* (Orthoptera: Gryllidae). *Can. J. Zool.* **63**, 1652–1656.
- Sakaluk, S. K. 1997 Cryptic female choice predicated on wing dimorphism in decorated crickets. *Behav. Ecol.* **8**, 326–331.
- Sheldon, B. C. 2000 Differential allocation: tests, mechanisms and implications. *Trends Ecol. Evol.* **15**, 397–402.
- Shelly, T. E. & Bailey, W. J. 1992 Experimental manipulation of mate choice by male katydids: the effect of female encounter rate. *Behav. Ecol. Sociobiol.* **30**, 277–282.

- Simmons, L. W. 1986 Female choice in the field cricket *Gryllus bimaculatus* (De Geer). *Anim. Behav.* **34**, 1463–1470.
- Simmons, L. W. 1995a Correlates of male quality in the field cricket, *Gryllus campestris* L.: age, size, and symmetry determine pairing success in-field populations. *Behav. Ecol.* **6**, 376–381.
- Simmons, L. W. 1995b Courtship feeding in katydids (Orthoptera: Tettigoniidae): investment in offspring and in obtaining fertilizations. *Am. Nat.* **146**, 307–315.
- Simmons, L. W. 1995c Male bushcrickets tailor their spermatophores in relation to their remating intervals. *Funct. Ecol.* **9**, 881–886.
- Simmons, L. W. & Kvarnemo, C. 1997 Ejaculate expenditure by male bushcrickets decreases with sperm competition intensity. *Proc. R. Soc. Lond. B* **264**, 1203–1208. (DOI 10.1098/rspb.1997.0166.)
- Simmons, L. W. & Ritchie, M. G. 1996 Symmetry in the songs of crickets. *Proc. R. Soc. Lond. B* **263**, 1305–1311.
- Simmons, L. W. & Siva-Jothy, M. T. 1998 Sperm competition in insects: mechanisms and the potential for selection. In *Sperm competition and sexual selection* (ed. T. R. Birkhead & A. P. Møller) pp. 341–434. San Diego, CA: Academic Press.
- Simmons, L. W., Beesley, L., Lindhjem, P., Newbound, D., Norris, J. & Wayne, A. 1999 Nuptial feeding by male bushcrickets: an indicator of male quality? *Behav. Ecol.* **10**, 263–269.
- Thornhill, R. 1976 Sexual selection and nuptial feeding behavior in *Bittacus apicalis* (Insecta: Mecoptera). *Am. Nat.* **110**, 529–548.
- Trivers, R. L. 1972 Parental investment and sexual selection. In *Sexual selection and the descent of man, 1871–1971* (ed. B. Campbell) pp. 136–179. Chicago, IL: Aldine Press.
- Vahed, K. 1998 The function of nuptial feeding in insects: a review of empirical studies. *Biol. Rev.* **73**, 43–78.
- Ward, P. I. 1993 Females influence sperm storage and use in the yellow dung fly *Scathophaga stercoraria* (L.). *Behav. Ecol. Sociobiol.* **32**, 313–320.
- Ward, P. I. 2000 Cryptic female choice in the yellow dung fly *Scathophaga stercoraria* (L.). *Evolution* **54**, 1680–1686.
- Wedell, N. & Arak, A. 1989 The wartbiter spermatophore and its effect on female reproductive output (Orthoptera: Tettigoniidae, *Decticus verrucivorus*). *Behav. Ecol. Sociobiol.* **24**, 117–125.
- Wiklund, C., Kaitala, A., Lindfors, V. & Abenius, J. 1993 Polyandry and its effect on female reproduction in the green-veined white butterfly (*Pieris napi* L.). *Behav. Ecol. Sociobiol.* **33**, 25–33.