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# Paternity of offspring in multiply-mated female crickets: the effect of nuptial food gifts and the advantage of mating first

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The spermatophore transferred by male decorated crickets (*Gryllobates sigillatus*) includes a large gelatinous mass, the spermatophylax, that is consumed by the female after mating. This nuptial gift preoccupies the female while sperm are discharged from the remaining portion of the spermatophore, the sperm ampulla, into her reproductive tract. There is considerable variation in the mass of the spermatophylax, and about half of all males produce spermatophylaxes that are too small to ensure complete sperm transfer. We tested two hypotheses concerning the maintenance of this variation: (i) males trade-off investment in spermatophylaxes against copulation frequency; and (ii) males synthesize the largest spermatophylaxes of which they are physiologically capable. Males synthesizing large and small food gifts were permitted multiple mating opportunities with the same females, and allozyme markers were used to establish the paternity of offspring. There was a significant advantage to those males that mated first irrespective of gift size. This advantage probably arose, in part, because the sperm of first males would have had exclusive access to females' eggs during the first 24 hours of oviposition, and underscores the benefits of matings with virgin females. The paternity of 'small-gift' males increased with gift mass, but there was no such increase in 'large-gift' males. This difference probably stems from the relationship between gift mass and sperm transfer: most of the gifts of the large-gift males would have been above the threshold needed to achieve complete inseminations, whereas those of small-gift males would have been below the threshold. Within mating-order positions, there was no significant difference in the paternity of large-gift and small-gift males, a result seemingly consistent with the 'trade-off' hypothesis. However, there was no correlation between spermatophylax mass and male mating frequency, so that the mechanism by which small-gift males offset their fertilization disadvantage remains unknown.

**Keywords:** crickets; nuptial food gifts; sperm competition; sexual selection; *Gryllobates sigillatus*

## 1. INTRODUCTION

Males of various insect species provide nuptial food gifts to females at mating that come in a variety of forms including prey items captured by the male, glandular secretions, regurgitated crop contents, and even parts of the male's body (Thornhill 1976; Zeh & Smith 1985; Quinn & Sakaluk 1986; Vahed 1998). In crickets and katydids, nuptial food gifts often take the form of a spermatophylax, a gelatinous adjunct to the male's spermatophore that is consumed by the female after mating (Sakaluk 1986a; Brown & Gwynne 1997). In decorated crickets (*Gryllobates sigillatus*), the spermatophylax envelops a small, sperm-containing ampulla, whose contents are emptied through a narrow spermatophore tube threaded into the female's genital chamber; the bulk of the spermatophore remains attached outside the female's body after mating. Almost immediately after the spermatophore has been transferred, the female detaches the spermatophylax from the ampulla with her mandibles

and begins to consume it. Spermatophylax feeding lasts anywhere from 5 min to 2 h, and typically within a few minutes of the complete consumption of the spermatophylax, the female removes and eats the sperm ampulla (Sakaluk 1984, 1985, 1987).

In both crickets and katydids, the time required for the complete consumption of the spermatophylax is determined primarily by its mass, which in turn influences the number of sperm that a male transfers. Smaller spermatophylaxes require less time to consume, and males providing such gifts are penalized in the form of premature ampulla removal and reduced sperm transfer (Sakaluk 1984, 1985; Wedell & Arak 1989; Reinhold & Heller 1993). The amount of sperm transferred can influence a male's reproductive success, particularly when his sperm must compete with another male's sperm for the fertilization of a female's eggs (Sakaluk 1986b; Simmons 1987; Wedell 1991; Sakaluk & Eggert 1996).

Notwithstanding the importance of gift size to male fertilization success, roughly half of all male *Gryllobates sigillatus* synthesize spermatophylaxes that are too small to ensure complete sperm transfer (Sakaluk 1984, 1985, 1987). There are at least two hypotheses that could

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account for this variation. One possibility is that males who supply females with small food gifts, trade-off investment in spermatophores against copulation frequency ('trade-off' hypothesis). Males that synthesize small spermatophylaxes may be able to mate more frequently than those that invest in larger ones, thereby offsetting the fertilization disadvantage that they accrue owing to reduced sperm transfer. This hypothesis predicts that over the long term, the reproductive success of 'large-gift' and 'small-gift' males should be about the same. Alternatively, males may synthesize the largest spermatophylaxes of which they are physiologically capable, so that small-gift males may be unable to offset the cost of reduced sperm transfer with increased copulation frequency ('honest-male' hypothesis). This hypothesis predicts that large-gift males should exhibit greater reproductive success than small-gift males.

Here we test the 'trade-off' and 'honest-male' hypotheses by comparing the reproductive success and copulation frequency of males synthesizing large and small gifts, and competing directly for fertilizations of the same females' eggs. An important element of our experimental design is that males were afforded the opportunity to engage in multiple matings with females, thereby allowing any trade-off in gift investment and copulation frequency to be made manifest. Previous investigations of the influence of nuptial-gift investment on male paternity have involved doubly-mated females mated once to each of two males (Sakaluk 1986*b*; Wedell 1991; Gwynne & Snedden 1995; Sakaluk & Eggert 1996). Although these studies have demonstrated that an increase in the size of the nuptial gift enhances male paternity in the context of single matings by male competitors, they do not address the possibility of reproductive trade-offs in males. Moreover, recent work has shown that the pattern of sperm precedence revealed by doubly-mated females may not hold for females mating more than twice (Zeh & Zeh 1994; Radwan 1997; but, see Eady & Tubman 1996). This result is particularly relevant to gryllid mating systems, where females typically engage in multiple matings (Alexander & Otte 1967; Sakaluk & Cade 1980, 1983; Burpee & Sakaluk 1993*a,b*), and often mate repeatedly with the same male (Loher & Rence 1978; Rost & Honegger 1987; Zuk 1987; Hissmann 1990).

## 2. METHODS

### (a) *General methods*

Experimental *Gryllobates sigillatus* were obtained from a stock colony initiated with approximately 200 crickets collected in Tucson, AZ, USA, in October 1995 and maintained according to standard procedures (Sakaluk 1991; Burpee & Sakaluk 1993*a*). Male and female crickets were held separately after they eclosed to ensure their virginity.

We determined the mass of the first spermatophylax produced by each of 74 males to assess the variation in gift size present in the study population. Spermatophylax mass ranged from 2.8 mg to 8.13 mg (mean mass ( $\pm$ s.e.) =  $5.49 \pm 0.13$  mg), and the distribution of spermatophylax masses did not deviate significantly from normality (Lilliefors maximum difference = 0.059,  $p = 0.72$ ). We selected as experimental individuals 54 new males falling in the upper and lower ends of the distribution, and designated them 'large-gift' and 'small-gift' males, respectively.

We determined the combined mass of the first two consecutive spermatophylaxes produced by each male to the nearest 0.01 mg. This was taken as a measure of the level of a male's investment in nuptial feeding, as previous studies have shown that the mass of the spermatophylax remains relatively constant over successive matings and even longer intervals (Sakaluk & Smith 1988; Sakaluk 1997). The mean combined spermatophylax mass of large-gift males was  $14.42 \pm 0.29$  mg ( $\pm$ s.e.) ( $n = 27$ , range = 11.95–18.23 mg), and that of small-gift males was  $10.47 \pm 0.25$  mg ( $n = 27$ , range = 8.74–13.84 mg); the slight overlap in distributions occurred because some males were assigned to mating trials (see below) before all males were measured.

### (b) *Paternity study*

Experimental triads consisting of one virgin female, one small-gift virgin male and one large-gift virgin male were established. Males in each triad differed in their average spermatophylax mass by a mean of  $1.97 \pm 13$  mg (range = 0.8–3.4 mg); this difference represents *ca.* two standard deviations. One male was initially confined with the female in a plastic container (10.5 cm  $\times$  10.5 cm  $\times$  9.5 cm) for 24 h, after which he was replaced with the other male for a subsequent 24-h period. Daily alternation of males continued until each male had spent a total of five days with the female. Because males were prevented from competing directly for females, offspring paternity was not confounded by intrasexual competition. In half of the triads, the large-gift male was introduced first and vice versa for the remaining triads. The potentially confounding effect of male body mass on reproductive success was controlled by establishing similar numbers of two types of triads, those in which the small-gift male was the heavier of the two males and those in which the large-gift male was the heavier. In addition, males used in triads were of similar age (small-gift males, mean age =  $15.2 \pm 1.4$  d post-eclosion, range = 4–27 d; large-gift males, mean age =  $15.2 \pm 1.0$  d post-eclosion, range = 4–26 d); experimental females were  $16.9 \pm 1.5$  d old when first mated (range = 2–32 d). A portion of egg carton was added to each mating chamber to provide shelter for experimental individuals, and oviposition substrate, food and water were provided *ad libitum* throughout the experiment.

Offspring hatching from eggs collected over the lifetime of experimental females were reared and their paternity was established using cellulose-acetate protein electrophoresis. Offspring were screened at the phosphoglucosyltransferase (PGM) locus, which is diallelic in *G. sigillatus* (Sakaluk & Eggert 1996). In *G. sigillatus*, PGM is sex-linked and thus only the paternity of daughters can be resolved (Sakaluk & Eggert 1996). Offspring were reared to a stage at which they could easily be sexed and only female offspring were subjected to electrophoretic analysis. This protocol necessarily assumes that the pattern of sperm precedence revealed in female offspring is the same as that for male offspring. Experimental triads entailed females that were homozygous for either allele, and males that were hemizygous for alternate alleles. *G. sigillatus* adult phenotypes were determined by removing a single mesothoracic leg and homogenizing the femur in 15  $\mu$ l of Tris Glycine buffer (pH 8.5); the loss of a single leg did not hinder experimental crickets from mating. Allozymes were separated and stained using techniques adapted from Hebert & Beaton (1989).

### (c) *Video study*

To determine whether males trade-off investment in spermatophores against copulation frequency, the sexual activity of

Table 1. Mean paternity ( $\pm$ s.e.) of large-gift and small-gift males within mating-order positions

gift class	paternity							
	first male to mate				last male to mate			
	<i>n</i>	mean	s.e.	range	<i>n</i>	mean	s.e.	range
large-gift males	13	0.61	0.06	0.06–0.87	13	0.34	0.06	0.07–0.89
small-gift males	13	0.66	0.06	0.11–0.93	13	0.38	0.06	0.13–0.94

males of varying gift sizes was monitored using time-lapse video photography (see Burpee & Sakaluk 1993*a,b*). Crickets used in the video study were treated as in the paternity study. We monitored the mating activity of four pairs at a time over five consecutive days, the maximum number of pairs for which spermatophore transfer could be clearly resolved by the video camera (Burpee & Sakaluk 1993*a,b*). Each pair was placed in a clear Plexiglas cage (10 cm  $\times$  7.5 cm  $\times$  4 cm) and provisioned with food, water and moistened oviposition substrate *ad libitum*. The cages were arranged in a 2  $\times$  2 stack, and each five-day trial included a male from each quartile of the observed spermatophylax mass distribution. The position of males within the stacked cages was altered in each five-day trial with respect to the quartiles from which they had been drawn.

### 3. RESULTS

#### (a) Paternity study

Paternity analyses were based on the electrophoretic analysis of an average of  $138 \pm 9.8$  ( $\pm$ s.e.) female offspring reared per female ( $n=26$  sibships, range=40–230 offspring). One additional female produced too few female offspring ( $n=14$ ) to obtain reliable estimates of the proportion of offspring sired by each male, and proved to be an outlier in preliminary paternity analyses (studentized residual =  $-2.952$ ). This sibship was excluded from further analysis.

Mating order had a significant effect on male paternity irrespective of male gift size. When mated first to the female, large-gift males had a significantly higher paternity than when mated last (table 1; Student's *t*-test,  $t=3.52$ ,  $p<0.002$ ). The same was true of small-gift males ( $t=3.52$ ,  $p<0.002$ ). To examine the influence of gift size on male paternity, we used an ANCOVA in which the paternity of the large-gift (or small-gift) male was entered as the dependent variable, and the order in which the male was mated to the female (first or last) was entered as the categorical variable (table 2). The analysis included two covariates, the mass of the food gift of the large-gift male and the mass of the food gift of the small-gift male, measured as the combined mass of the first two spermatophylaxes produced by each male, respectively. An increase in the mass of the food gift of the small-gift male resulted in a decrease in the paternity of the large-gift male ( $p=0.016$ ), but the mass of the large-gift male's own food gift had no effect on his paternity. A parallel analysis using the small-gift male as the focal male necessarily yields the inverse result: the paternity of the small-gift male increased with the size of his own food gift, but the mass of the food gift of his large-gift rival had no significant influence. The effect of mating order on male

Table 2. ANCOVA of the effect of mating order (first or last), mass of food gift of large-gift male (covariate), and mass of food gift of small-gift male (covariate), on the paternity of large-gift males

(Note that an analysis of the paternity of the small-gift male yields the identical ANCOVA table. SS, sum of squares; MS, mean squares.)

source of variation	SS	d.f.	MS	<i>F</i>	<i>p</i>
mating order	0.6027	1	0.6027	17.70	0.0004
small-gift mass	0.2320	1	0.2320	6.81	0.0160
large-gift mass	0.0801	1	0.0801	2.35	0.1392
error	0.7492	22	0.0340	—	—

Table 3. ANCOVA of the effect of the class of male (large-gift or small-gift male), mass of food gift of first male to mate (covariate), and mass of food gift of last male to mate (covariate), on the paternity of the first male

(Note that an analysis of the paternity of the last male yields the identical ANCOVA table. Abbreviations as in table 2.)

source of variation	SS	d.f.	MS	<i>F</i>	<i>p</i>
class of male	0.1898	1	0.1898	5.25	0.0318
mass of first male's gift	0.1026	1	0.1026	2.84	0.1062
mass of second male's gift	0.1771	1	0.1771	4.90	0.0375
error	0.7950	22	0.0361	—	—

paternity became even more apparent when adjusted for the effect of the covariates and, as in the previous analysis, showed a significant first-male mating-order advantage ( $p<0.001$ ).

There was no significant difference in the paternity of large-gift males and that of small-gift males within mating-order positions (table 1;  $t=0.53$ ,  $p=0.6$ ). To examine the influence of gift size on male paternity within mating-order positions, we used an ANCOVA in which the paternity of the first male (or last male) was entered as the dependent variable and the class of male (large-gift or small-gift) was entered as the categorical variable (table 3). The analysis included two covariates, the mass of the food gift of the first male to mate and the mass of the food gift of the last male to mate (table 2). The analysis revealed a significant effect of male class on paternity after adjusting for the effect of food gift-size

( $p=0.031$ ). Specifically, the adjusted least-squares mean paternity of small-gift males was significantly higher than that of large-gift males. This result indicates that for a given amount of food-gift material, small-gift males achieve a greater return on paternity than do large-gift males. The mass of the food gift of the first male to mate had no effect on the paternity of either the first or last male to mate ( $p=0.11$ ). In contrast, as the mass of the food gift of the last male to mate increased, his paternity increased while that of the first male to mate decreased ( $p=0.037$ ).

#### (b) Video study

Males mated, on average,  $12.03 \pm 0.59$  times over the course of the five-day observation period ( $n=30$ ). There were no significant correlation between a male's copulation frequency and the combined mass of his first two spermatophylaxes ( $n=30$ ,  $r=0.26$ ,  $p>0.05$ ), nor was male copulation frequency correlated with male body mass ( $n=30$ ,  $r=0.29$ ,  $p>0.05$ ) or female body mass ( $n=28$ ,  $r=0.28$ ,  $p>0.05$ ). There was a significant correlation between male body mass and combined spermatophylax mass ( $n=30$ ,  $r=0.55$ ,  $p=0.0015$ ).

#### 4. DISCUSSION

Within mating-order positions, there was no significant difference in the paternity of large-gift males and small-gift males. This result supports the 'trade-off' hypothesis for the maintenance of variation in the size of food gifts, but is inconsistent with the 'honest-male' hypothesis. However, the time-lapse video study revealed no significant correlation between the mass of the food gift and male mating frequency, a result that forestalls acceptance of the 'trade-off' hypothesis without some modification. The lack of a significant correlation cannot be attributed simply to low statistical power (power is 0.5 at moderate effect size ( $r=0.3$ ) with  $n=30$  and  $\alpha_1=0.05$  (Cohen 1988)), because the observed  $r$  of 0.26 is in the opposite direction of that predicted by the hypothesis. How small-gift males are able to offset their fertilization disadvantage over multiple matings remains unknown, but their ability to do so would account for the variation in gift size that persists in natural populations and the genetic variation that underlies investment in the spermatophylax (Sakaluk & Smith 1988). It may be that small-gift males are of greater genetic quality and hence able to 'cheat' on the size of their food gifts, perhaps because females selectively use their sperm (see Eberhard 1996); in some birds, for example, males that are preferred by females show lower offspring provisioning rates than unattractive males (Burley 1986; Møller 1994). Another possibility is that small-gift males emerge earlier than large-gift males and are hence more likely to accrue the advantages of first matings.

Although there was no difference in the paternity of small-gift and large-gift males, an ANCOVA suggests that for any given amount of food-gift material, small-gift males achieve a greater return on paternity than do large-gift males (table 3). This seemingly counter-intuitive result can best be explained on the basis of the trajectory of sperm transfer after mating. In gryllids, the number of sperm transferred increases with the duration of ampulla

attachment but at a diminishing rate, so that sperm transfer follows a curvilinear trajectory (Sakaluk 1984; Simmons 1986; Parker *et al.* 1990; Sakaluk & Eggert 1996). This means that the rate of sperm transfer early in the period of ampulla attachment is higher than it is later in the period of ampulla attachment. Because small-gift males normally have their ampullae removed sooner than large-gift males (i.e. earlier in the period of ampulla attachment), they achieve greater sperm transfer per unit mass of spermatophylax than do large gift males.

Within the framework of the multiple-mating design used in this study, there was a significant advantage to those males that mated first irrespective of gift size. One obvious explanation is that eggs laid by the female over the first 24 h could only have been fertilized by the first male, as there was no rival sperm with which to contend. The first male also would have shared in fertilizations even after the female had mated with the rival male because in gryllids, sperm are recruited for fertilizations in direct proportion to their relative abundance in the female's spermatheca (Sakaluk 1986b; Simmons 1987; Sakaluk & Eggert 1996). Moreover, the rate of egg laying in female crickets is at its maximum early in the adult life of the female and diminishes steadily thereafter (see Sakaluk & Cade 1983; Simmons 1988), so that the first male would have enjoyed a fertilization advantage at a time that the female was most productive.

To what extent can this first-male advantage be generalized to the natural situation? Female *G. sigillatus* that are confined continuously with males in the laboratory mate 2–2.5 times per 24-h period (Burpee & Sakaluk 1993a,b; present study), but field studies show that females in nature mate, on the average, less than once per night (S. K. Sakaluk, A.-K. Eggert and W. A. Snedden, unpublished data). This means that any male mating with a virgin female in nature would show the kind of advantage revealed in this study. This advantage, coupled with the pattern of egg-laying described above, would be expected to favour early male emergence or protandry, as has been documented in a gift-giving tettigoniid exhibiting similar reproductive characteristics (Wedell 1992). However, anecdotal observations made by one of us (S.K.S.), over many years of laboratory rearing of *G. sigillatus*, indicate that females typically emerge earlier than males in contradiction of the predicted pattern. Moreover, males must wait about a week after the imaginal moult before they are capable of transferring a spermatophore, whereas females will mate within as little of one day of the imaginal moult (Sakaluk 1987).

Despite the magnitude of the first-male advantage and the additional complexity engendered by multiple matings, there was still an discernible effect of gift size on the reproductive success of males. Specifically, there was an increase in the paternity of the small-gift male with gift mass, but no such increase was manifest in large-gift males. This difference is explicable when the relationship between nuptial gift mass and sperm transfer is taken into account. Many, if not all of the gifts of large-gift males would have been above the threshold size needed to achieve complete insemination, so that variation in gift mass in this group would be expected to have no discernible effect on paternity. In contrast, many, if not all of the gifts of small-gift males would have been below the

threshold, so that variation in the mass of these gifts would be expected to have some influence on the degree of insemination and hence, male paternity. Within mating-order positions, paternity increased with gift mass, but this relationship was statistically significant only for the last male to mate. It may be that the first-male advantage described above obscured any modest increment in paternity accruing to an increase in the mass of the food gift of the first male.

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