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Courtship feeding in decorated crickets: is the spermatophylax a sham?

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Abstract. The spermatophore transferred by a male decorated cricket, *Gryllodes sigillatus*, at mating includes a large gelatinous spermatophylax, devoid of sperm, which the female removes and feeds on after copulation. Previous studies have shown that consumption of the spermatophylax keeps the female preoccupied while sperm from the remaining portion of the spermatophore is expelled into her reproductive tract; hence, the spermatophylax functions to ensure complete sperm transfer. To determine whether consumption of the spermatophylax also provides significant nutritional benefits to females and whether such benefits are contingent on food availability, female *G. sigillatus* were allowed to consume zero, one, or three spermatophylaxes per day and were either deprived of food, fed 30% of ad libitum food demands, or allowed unrestricted access to food (Purina® cricket chow). The number of spermatophylaxes consumed by females had no significant effect on the mass of eggs or number of nymphs produced, and there was no significant interaction between the number of spermatophylaxes consumed and food availability. Although there may be other benefits to its consumption, the present study suggests that as a food 'gift', the spermatophylax is a sham.

In various insect species, males provide females with a courtship food gift at the time of mating (Thornhill 1976; Zeh & Smith 1985; Quinn & Sakaluk 1986). In the ensiferan Orthoptera, such gifts often take the form of a spermatophylax, a large gelatinous mass forming part of the spermatophore and consumed by the female after copulation. The spermatophylax normally surrounds a smaller, sperm-containing ampulla, and in most species this bipartite spermatophore remains attached outside the female's body after mating. The female begins feeding on the spermatophylax shortly after copulation, and invariably removes and eats the sperm ampulla upon completion of the spermatophylax (Alexander & Otte 1967). Although it is generally held that the spermatophylax originated as a device to ensure complete sperm transfer, the consumption of which preoccupies the female during the evacuation of sperm from the ampulla (Sakaluk 1984, 1985; Wedell & Arak 1989; Wedell 1993a), studies of spermatophylax-bearing ensiferans have revealed a basic dichotomy: in some species, the spermatophylax is barely sufficient in size to ensure maximum insemination (Sakaluk 1984; Wedell & Arak 1989; Wedell 1993a), whereas in others, it is much larger than necessary to achieve complete sperm transfer (Gwynne et al. 1984; Gwynne 1986).

Studies of those katydid species whose spermatophylaxes are of an excessive mass have revealed that consumption of the spermatophylax yields significant fitness benefits to females and/or their offspring (but see Reinhold & Heller 1993). Gwynne (1984, 1988a) reported a positive correlation between the number of spermatophylaxes a female consumed and the number and weight of eggs produced in *Requena verticalis* (Orthoptera: Tettigoniidae). Similarly, Simmons (1990) showed that spermatophylax consumption increases egg number and mass in a zaprochiline katydid, *Kawanaphila nartee*, and more recently demonstrated that male energy investment in eggs equals that of females under certain circumstances (Simmons 1992). These observations have led some authors to suggest that the function of the spermatophylax has been elaborated beyond an ejaculate-protection role to one in which the spermatophylax constitutes a form of pre-zygotic male parental investment (Gwynne 1984, 1986, 1988b; Gwynne & Simmons 1990).

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The decorated cricket, *Gryllodes sigillatus* (Orthoptera: Gryllidae), and the wartbiter bushcricket, *Decticus verrucivorus* (Orthoptera: Tettigoniidae), are species in which the male's spermatophylax is of barely sufficient mass to ensure maximum insemination (Sakaluk 1984; Wedell & Arak 1989; Wedell 1993b). In contrast to the studies of Gwynne (1984, 1988a) and Simmons (1990), nutritional benefits that females derive through consumption of the spermatophylax remain unclear in such species. Wedell & Arak (1989) found no effect of spermatophylax consumption on the longevity, fecundity, or egg weight of female *D. verrucivorus*. Spermatophore size was, however, positively correlated with the duration of ampulla attachment, ultimately leading to increased oviposition rates. Burpee & Sakaluk (1993a) found that female *G. sigillatus* given unlimited mating opportunities lived longer and produced more offspring than females with limited mating opportunities. However, similar benefits of repeated mating were found in a non-spermatophylax bearing species, *Gryllus veletis* (Burpee & Sakaluk 1993a), suggesting that benefits of repeated mating accrue as much from the receipt of additional sperm and/or oviposition stimulants, as they do from spermatophore consumption.

The reduced mass of the spermatophylax of *G. sigillatus*, relative to such species as *R. verticalis* and *K. nartee*, suggests that selection may have favoured males that minimize the costs, and hence the nutritional value, of their spermatophores. Here we test two competing, though non-mutually exclusive hypotheses concerning the functional significance of courtship feeding in *G. sigillatus*: (1) the spermatophylax is nutritionally beneficial to females and functions to enhance female reproductive success and (2) the spermatophylax functions primarily to protect the male's ejaculate. It has been suggested that spermatophylax consumption may be of nutritional value to females only when females are under food stress (Wedell & Arak 1989). Although previous investigations have been conducted using either well-fed or food-deprived females (Wedell & Arak 1989; Simmons 1990), these studies have not attempted to establish the predicted interaction effect between food availability and spermatophylax consumption within a single experiment. Here we employ a two-factor design, simultaneously varying both food availability and spermatophylax consumption to identify any such interaction.

METHODS

Experimental *G. sigillatus* were descendants of approximately 60 adults collected in Tucson, Arizona, in 1987. Crickets were housed in 75·7-litre terraria, provisioned with Purina® cricket chow and water in culture flasks plugged with cotton wicks. Egg cartons were placed in the terraria to provide shelter and increase surface area. Adult females were allowed to oviposit in plastic weigh boats filled with an equal mixture of sand and vermiculite, and moistened daily. Nymphs were reared in plastic shoe boxes (16·5 × 30·5 × 8·5 cm) provisioned with ample food, water, and sections of egg carton for shelter.

We placed newly emerged adult females (day 1 virgins) individually in 1-litre plastic containers after weighing them to the nearest 0·01 mg. Each female was provided with an oviposition dish and a piece of egg carton for shelter. Water was provided in test-tubes plugged with cotton wicks. Newly emerged males were held together in a 75·7-litre terrarium along with water, food and shelter. All crickets were maintained on a 12:12 h light:dark cycle at 30°C.

We permitted each female to mate twice, once on each of 2 consecutive days, starting on day 3. To ensure complete sperm transfer and equivalent insemination across treatments, we prevented females from removing the ampulla for 50 min, which corresponds to the time it takes the ampulla to empty of sperm (Sakaluk 1984). This was accomplished by placing the female in a small test-tube that restricted movement, thus preventing the female from bending around to remove the ampulla.

We randomly assigned experimental females to one of three treatments in which females were fed zero, one, or three spermatophylaxes per day and held under one of three nutritional regimes: (1) females provided with no food, (2) females provided with 30% of ad libitum food demands and (3) females provided with food ad libitum. We obtained spermatophylaxes by removing them from the spermatophoric pouches of males (Sakaluk & Smith 1988) and placed them on the bottoms of the cages of experimental females. Preliminary observations showed that females

readily found and consumed spermatophylaxes provided in this manner. We subsequently placed males with non-experimental females to stimulate subsequent spermatophore production. We determined the daily food demand of females by establishing seven groups of five newly emerged females, confining each group in a plastic shoe box with a known mass of Purina® cricket chow. After 4–6 days, depending on the group, we removed the food, cleaned it of faeces, and weighed it. We calculated the average daily food demand of females in each group as the total mass of food consumed divided by the number of days over which consumption occurred, divided by the number of females in the group. Across groups, the mean ($\pm$ SE) mass of food consumed/female/day was $14{\cdot}49 \pm 1{\cdot}29$ mg ($N=7$, range=10·19–19·34 mg).

On day 14, we randomly removed five eggs from each oviposition dish. After the eggs had been held in a drying oven for 2 days at 65°C, we weighed them to the nearest 0·1 μg (dry weight) using a Cahn C-31 microbalance. We removed emerging nymphs with a mouth aspirator and counted them daily. We determined female longevity as the day of emergence to the day of death.

All analyses were performed using the Statistical Analysis System (SAS) for personal computers (SAS Institute 1988). Data were transformed where required to meet the assumptions of parametric statistical tests. For pair-wise comparisons within treatments ($k=3$), the sequential Bonferroni technique was employed to control for the increase in the type I error rate associated with multiple statistical tests (Rice 1989). For such comparisons, the initial table-wide α was set at 0·017 (α/k where $\alpha=0{\cdot}05$).

RESULTS

There was no significant difference in the mean body mass of females across treatments (two-way ANOVA, $F_{8,81}=1{\cdot}50$, $P>0{\cdot}05$). Female body mass also was not significantly correlated with female longevity, egg mass, or number of nymphs produced.

The least-squares mean of female longevity for each nutrition and spermatophylax regime is shown in Table I. A two-way ANOVA ($\log_{10}$ transformed) revealed a significant effect of food regime ($F=26{\cdot}44$, $P=0{\cdot}0001$) and number of spermatophylaxes consumed ($F=3{\cdot}35$, $P=0{\cdot}0401$) on female longevity; there was no food*spermatophylax interaction ($F=0{\cdot}32$, $P=0{\cdot}8620$). Pair-wise comparisons (least-square means) showed that females deprived of food had a reduced longevity relative to females in the low ($P=0{\cdot}0132$) and high ($P<0{\cdot}0001$) nutrition regimes, and that females in the low food regime had a reduced longevity compared with those in the high food regime ($P<0{\cdot}0001$). Least-square means also showed that the longevity of females given one spermatophylax per day was reduced compared with those given three spermatophylaxes per day ($P=0{\cdot}0124$), but was not significantly different from those given no spermatophylaxes ($P=0{\cdot}113$). There was no significant difference in the longevity of females given zero and three spermatophylaxes a day ($P=0{\cdot}3386$).

Table I. Least-squares mean longevities of female *G. sigillatus* held under different nutritional regimes and fed different numbers of spermatophylaxes (back transformed from means of log-transformed values)

	N	$\bar{X}$ (days)*	Lower limit†	Upper limit
Food level				
High	30	$23{\cdot}5^{a}$	21·9	25·3
Low	29	$14{\cdot}8^{b}$	13·8	15·9
None	30	$11{\cdot}4^{c}$	10·6	12·3
Number of spermatophylaxes				
0	30	$16{\cdot}2^{ab}$	15·1	17·4
1	30	$13{\cdot}8^{a}$	12·8	14·8
3	29	$17{\cdot}9^{b}$	16·6	19·2

*Means with different letters are significantly different at $P<0{\cdot}05$.

†Lower and upper limits represent 95% confidence intervals.

Mean offspring production for each treatment is shown in Table II. Although nutritional regime had a significant effect on offspring production (log transformed) ($F=46{\cdot}71$, $P<0{\cdot}0001$), there was no effect of the number of spermatophylaxes consumed ($F=2{\cdot}39$, $P=0{\cdot}0978$), nor was there any significant interaction effect ($F=1{\cdot}26$, $P=0{\cdot}2922$). Least-square means revealed that females deprived of food produced significantly fewer nymphs than females on a limited nutritional diet ($P=0{\cdot}0009$), which in turn produced significantly fewer nymphs than females fed ad libitum ($P<0{\cdot}0001$).

Table II. Mean offspring production of female *G. sigillatus* held under different nutritional regimes and fed different numbers of spermatophylaxes (back transformed from means of log-transformed values)

	N	$\bar{X}$*	Lower limit†	Upper limit
Food level				
High	30	320·2[a]	246·4	416·1
Low	29	33·3[b]	25·6	43·3
None	30	9·3[c]	7·2	12·1
Number of spermatophylaxes				
0	30	35·6[a]	27·4	46·3
1	30	37·7[a]	29·0	49·0
3	29	73·9[a]	56·9	96·0

*Means with different letters are significantly different at $P<0·05$.

†Lower and upper limits represent 95% confidence intervals.

Table III. Least-squares mean mass of eggs produced by female *G. sigillatus* held under different nutritional regimes and fed different numbers of spermatophylaxes

	N	$\bar{X}$ (mg)*	Lower limit†	Upper limit
Food level				
High	28	0·1879	0·1859	0·1898
Low	27	0·1811	0·1790	0·1831
None	22	0·1880	0·1857	0·1903
Number of spermatophylaxes				
0	24	0·1820	0·1798	0·1842
1	26	0·1861	0·1840	0·1881
3	27	0·1889	0·1868	0·1909

*Only food level had a significant effect on mean egg mass, but pair-wise comparisons could not reveal the source of the effect.

†Lower and upper limits represent 95% confidence intervals.

Least-squares mean egg mass for each food and spermatophore treatment is shown in Table III. A two-way ANOVA revealed a significant effect of nutritional regime ($F=3·72$, $P=0·0291$), but there was no effect of the number of spermatophylaxes consumed ($F=2·62$, $P=0·0803$), nor was there a significant interaction ($F=1·18$, $P=0·3264$). Pair-wise comparisons did not reveal where differences in egg mass between nutritional treatments occurred.

DISCUSSION

The number of spermatophylaxes consumed by female *G. sigillatus* had no significant effect on either the number of nymphs or mass of eggs they produced. These results suggest that with respect to its nutritional value, the spermatophylax is a sham gift; its primary function is keeping the female preoccupied while sperm are discharged from the ampulla into the female's reproductive tract (Sakaluk 1984, 1985). Further support for the sham-gift hypothesis is provided by the lack of an interaction between food availability and spermatophylax consumption; consumption of the spermatophylax had no effect on female reproduction even when females were deprived of food. Indeed, the only factor that had a significant effect on female reproductive output was the nutritional regime under which females were held; as food availability was increased, the mass of eggs and number of nymphs produced also increased. Similar results have been reported for a katydid, *D. verrucivorus*, with general dietary protein intake having the predominant effect on female fitness and spermatophylax consumption having little impact (Wedell & Arak 1989). More recently, Reinhold & Heller (1993) found no significant effect of spermatophylax consumption on the number of eggs laid, weight of eggs, and mass of larvae in the katydid, *Poecilimon veluchianus*. Although the spermatophylax constitutes approximately one-quarter the mass of a male in *P. veluchianus*, its size appears to be adjusted in accordance with the length of time females must be kept preoccupied for complete ampulla evacuation to be achieved (Reinhold & Heller 1993), as is also the case in decorated crickets (Sakaluk 1984). Assuming spermatophylax production has a cost, it would be disadvantageous for males to produce an oversized spermatophylax because the energy and time invested in additional material might ultimately reduce male mating opportunities (Sakaluk 1985; Burpee & Sakaluk 1993b).

With one exception (Wedell & Arak 1989), the effect of spermatophylax consumption on the fitness of nutritionally stressed females has been examined only for females deprived of adequate nutrition during the adult stage (e.g. Gwynne 1984; Gwynne et al. 1984; present study). Under natural circumstances, however, earlier nymphal stages might also be subject

periodically to food deprivation, leading to even greater nutritional differences between individuals than those established in the present study. It is unclear, however, whether a more prolonged period of food limitation would have led to more pronounced fitness effects of spermatophylax consumption than those reported here or in previous studies.

Although spermatophylax consumption in *G. sigillatus* had no significant effect on female reproductive success, it had a statistically significant, although marginal effect ($P=0{\cdot}04$) on female longevity; females fed one spermatophylax per day had a shorter life span than females allotted zero or three spermatophylaxes per day. This result neither supports the sham-gift nor the paternal investment hypothesis, but instead suggests that when food-stressed females receive some nourishment, they alter the relative amounts of energy allocated to maintenance and reproduction. Alternatively, this result may in fact be an anomaly; in a pilot study involving the same number of females deprived of food, we found no significant effect of spermatophylax consumption on female longevity (unpublished data).

In a previous study, Burpee & Sakaluk (1993a) found that female *G. sigillatus* given unlimited mating opportunities lived longer and produced more offspring than females given only limited access to males. Although they suggested that this difference could be explained in part by differences in the number of spermatophylaxes consumed by females of the two treatments, the results of the present study suggest that this is unlikely to be the case. Instead, the increased fitness of females given unlimited mating opportunities may have occurred because these females received greater amounts of sperm or oviposition stimulants (Destephano & Brady 1977; Loher 1979; Murtaugh & Denlinger 1987), or because they were able to consume a greater number of sperm ampullae (including both those evacuated of sperm and those still retaining some ejaculate) over the course of their lifetimes (Sakaluk & Cade 1980, 1983; Simmons 1988). In the present experiment, both of these factors were controlled by holding constant the number of matings and the total duration of ampulla attachment.

The lack of a significant increase in offspring production, female longevity and egg mass with an increase in spermatophylax consumption suggests that females do not rely on the spermatophylax for any inherent nutritive value. If so, then what benefits do females derive through the complete consumption of the spermatophylax to offset any costs arising from the loss of space available in the digestive tract for high-quality food? Such costs may not be trivial; females consumed only about three times the weight of a spermatophylax in cricket chow per day. One possibility is that females treat the spermatophylax as they would any other secondary sexual character, assessing male quality on the basis of the size of the spermatophylax transferred by the male. If a male's ability to secure the resources necessary for producing a spermatophylax is related to his overall genetic quality, females may secure genetic benefits by penalizing males that transfer small spermatophylaxes. Indeed, the mass of the spermatophylax, as estimated by the weight loss of a male at mating, explains about half the variation in the duration of nuptial feeding (Sakaluk 1985). Size of the spermatophylax is not the only means by which females may assess males. The gummy consistency of the spermatophylax appears to render it inherently resistant to consumption; it may be that the 'gumminess' of the spermatophylax contributes to the remaining variation in the time required for its complete consumption. Hence, by removing the ampulla shortly after consuming the spermatophylax, females may select for increased mass and/or increased gumminess of the spermatophylax. This in turn may constrain males from evolving a spermatophylax that is entirely devoid of costs, and in this sense, the spermatophylax may represent an honest signal of a male's ability to secure resources (Kodric-Brown & Brown 1984). If the spermatophylax does indeed provide a reliable indicator of a male's prowess, then it should be considered a sham only from the narrow standpoint of its nutritive value. Otherwise, it may be more accurately described as a ritualized signal, functioning perhaps, in a manner analogous to the post-copulatory songs or tactile signals used by the males of other cricket species (reviewed by Loher & Dambach 1989; Sakaluk 1991).

In addition to the possibility that females rely on the spermatophylax as a means of assessing males, the spermatophylax may provide other benefits to females that would not have been detected within the context of the present experimental design. Approximately 82% of the wet

mass of the spermatophylax is water (S. K. Sakaluk, unpublished data), and it may be that under certain circumstances the spermatophylax serves as a valuable source of water to females, an idea first suggested by Reinhold & Heller (1993). *Gryllodes sigillatus* are extremely sensitive to desiccation and rarely live more than a day without access to water (personal observation). In the xeric environments in which the species is frequently found (e.g. southwestern U.S.A.), females may enhance their own survival by mating with males to secure the water contained in spermatophores. In the present experiment, females were provided with water ad libitum, such that any benefits brought about by the intake of additional water via spermatophylax consumption would have been obscured. That these or other benefits to spermatophylax consumption may exist is supported by the observation that individuals of both sexes steal the different components of the spermatophores from mated females and consume them (Sakaluk 1987).

In a comparative study of 28 species of tettigoniids across 19 genera, Wedell (1993c) found a positive correlation between the mass of the spermatophylax and ampulla mass, and no correlation between the mass of the spermatophylax and female fecundity. She concluded from this general pattern that the spermatophylax originated as an ejaculate-protection device rather than as a form of male parental investment, a conclusion supported by detailed experimental studies of two katydid species, *D. verrucivorus* (Wedell & Arak 1989; Wedell 1993a) and *P. veluchianus* (Reinhold & Heller 1993), and one cricket species, *G. sigillatus* (Sakaluk 1984, 1985, 1986, 1987; present study). In contrast to these results, strong positive effects of spermatophylax consumption on female fitness have been found in two other katydid species, *R. verticalis* (Gwynne 1984, 1988a) and *K. nartee* (Simmons 1990). Although the results of these studies appear to be diametrically opposed, Wedell (1993a) has recently identified a striking dichotomy in the protein content of katydid spermatophores, with most species producing protein-depauperate spermatophores and a few, presumably the ones effecting positive fitness benefits in females, producing protein-rich spermatophores. Future studies should focus on identifying the ecological and social factors that lead to the evolution of one spermatophore type over the other.

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REFERENCES

Alexander, R. D. & Otte, D. 1967. The evolution of genitalia and mating behavior in crickets (Gryllidae) and other Orthoptera. *Misc. Publs Mus. Zool. Univ. Mich.*, **133**, 1–62.

Burpee, D. M. & Sakaluk, S. K. 1993a. Repeated matings offset costs of reproduction in female crickets. *Evol. Ecol.*, **7**, 240–250.

Burpee, D. M. & Sakaluk, S. K. 1993b. The effect of pair formation on diel calling patterns in two cricket species, *Gryllus veletis* and *Gryllodes sigillatus* (Orthoptera: Gryllidae). *J. Insect Behav.*, **6**, 431–440.

Destephano, D. B. & Brady, U. E. 1977. Prostaglandin and prostaglandin synthetase in the cricket, *Acheta domesticus*. *J. Insect Physiol.*, **23**, 905–911.

Gwynne, D. T. 1984. Courtship feeding increases female reproductive success in bushcrickets. *Nature, Lond.*, **307**, 361–363.

Gwynne, D. T. 1986. Courtship feeding in katydids (Orthoptera: Tettigoniidae): investment in offspring or in obtaining fertilizations? *Am. Nat.*, **128**, 342–352.

Gwynne, D. T. 1988a. Courtship feeding and the fitness of female katydids (Orthoptera: Tettigoniidae). *Evolution*, **42**, 545–555.

Gwynne, D. T. 1988b. Courtship feeding in katydids benefits the mating male's offspring. *Behav. Ecol. Sociobiol.*, **23**, 373–377.

Gwynne, D. T., Bowen, B. J. & Codd, C. G. 1984. The function of the katydid spermatophore and its role in fecundity and insemination (Orthoptera: Tettigoniidae). *Austral. J. Zool.*, **32**, 15–22.

Gwynne, D. T. & Simmons, L. W. 1990. Experimental reversal of courtship roles in an insect. *Nature, Lond.*, **346**, 172–174.

Kodric-Brown, A. & Brown, J. H. 1984. Truth in advertising: the kinds of traits favored by sexual selection. *Am. Nat.*, **124**, 309–323.

Loher, W. 1979. The influence of prostaglandin E2 on oviposition in *Teleogryllus commodus*. *Entomologia exp. appl.*, **25**, 107–119.

Loher, W. & Dambach, M. 1989. Reproductive behavior. In: *Cricket Behavior and Neurobiology* (Ed. by F. Huber, T. E. Moore & W. Loher), pp. 43–82. Ithaca, New York: Cornell University Press.

Murtaugh, M. P. & Denlinger, D. L. 1987. Regulation of long-term oviposition in the house cricket, *Acheta*

domesticus: roles of prostaglandin and factors associated with sperm. *Arch. Insect Biochem. Physiol.* **6,** 59–72.

Quinn, J. S. & Sakaluk, S. K. 1986. Prezygotic male reproductive effort *in insects*: why do males provide more than sperm? *Fla Entomol.*, **69,** 84–94.

Reinhold, K. & Heller, K.-G. 1993. The ultimate function of nuptial feeding in the bushcricket *Poecilimon veluchianus* (Orthoptera: Tettigoniidae: Phaneropterinae). *Behav. Ecol. Sociobiol.*, **32,** 55–60.

Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution*, **43,** 223–225.

Sakaluk, S. K. 1984. Male crickets feed females to ensure complete sperm transfer. *Science*, **223,** 609–610.

Sakaluk, S. K. 1985. Spermatophore size and its role in the reproductive behaviour of the cricket, *Gryllodes supplicans* (Orthoptera: Gryllidae). *Can. J. Zool.*, **63,** 1652–1656.

Sakaluk, S. K. 1986. Sperm competition and the evolution of nuptial feeding behavior in the cricket, *Gryllodes supplicans* (Walker). *Evolution*, **40,** 584–593.

Sakaluk, S. K. 1987. Reproductive behaviour of the decorated cricket, *Gryllodes supplicans* (Orthoptera: Gryllidae): calling schedules, spatial distribution, and mating. *Behaviour*, **100,** 202–225.

Sakaluk, S. K. 1991. Post-copulatory mate guarding in decorated crickets. *Anim. Behav.*, **41,** 207–216.

Sakaluk, S. K. & Cade, W. H. 1980. Female mating frequency and progeny production in singly and doubly mated house and field crickets. *Can. J. Zool.*, **58,** 404–411.

Sakaluk, S. K. & Cade, W. H. 1983. The adaptive significance of female multiple matings in house and field crickets. In: *Orthopteran Mating Systems: Sexual Competition in a Diverse Group of Insects* (Ed. by D. T. Gwynne & G. K. Morris), pp. 319–336. Boulder, Colorado: Westview Press.

Sakaluk, S. K. & Smith, R. L. 1988. Inheritance of male parental investment in an insect. *Am. Nat.*, **132,** 594–601.

SAS Institute. 1988. *SAS/STAT User's Guide*. Release 6.03 edn. Cary, North Carolina: SAS Institute.

Simmons, L. W. 1988. The contribution of multiple mating and spermatophore consumption to the lifetime reproductive success of female crickets (*Gryllus bimaculatus*). *Ecol. Entomol.*, **13,** 57–69.

Simmons, L. W. 1990. Nuptial feeding in tettigoniids: male costs and the rates of fecundity increase. *Behav. Ecol. Sociobiol.*, **27,** 43–47.

Simmons, L. W. 1992. Quantification of role reversal in relative parental investment in a bush cricket. *Nature, Lond.*, **358,** 61–63.

Thornhill, R. 1976. Sexual selection and paternal investment in insects. *Am. Nat.*, **110,** 153–163.

Wedell, N. 1993a. Evolution of nuptial gifts in bushcrickets. Ph.D. thesis, University of Stockholm, Stockholm, Sweden.

Wedell, N. 1993b. Mating effort or paternal investment? Incorporation rate and cost of male donations in the wartbiter. *Behav. Ecol. Sociobiol.*, **32,** 239–246.

Wedell, N. 1993c. Spermatophore size in bushcrickets: comparative evidence for nuptial gifts as a sperm protection device. *Evolution*, **47,** 1203–1212.

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.

Zeh, D. W. & Smith, R. L. 1985. Paternal investment by terrestrial arthropods. *Am. Zool.*, **25,** 785–805.