Spermatophore size and its role in the reproductive behaviour of the cricket, *Gryllodes supplicans* (Orthoptera: Gryllidae)

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The spermatophore that a male cricket of *Gryllodes supplicans* transfers to the female during mating, includes a large gelatinous portion (spermatophylax) that is removed and consumed by the female after mating. In other North American cricket species, the spermatophore consists solely of a small sperm-containing ampulla. In this study, the role of spermatophore size in the reproductive behaviour of *G. supplicans* was examined, along with the costs associated with the provision of a more complex spermatophore. The mean intercopulatory interval of male *G. supplicans* that were allowed constant access to receptive females was 3.25 h; this period is long relative to those of other crickets. The estimated weight of spermatophores produced by males did not differ significantly from that of spermatophores produced by these same males 24 h later; males apparently hold constant their investment in subsequent copulations. The time taken by females to consume the spermatophylax fully increased linearly with the weight of the spermatophore. Females remove the sperm ampulla soon after consuming the spermatophylax and thus penalize males that provide smaller "nuptial meals." Larger males produce heavier spermatophores; thus, small males often may be at a selective disadvantage. These results, when examined in the light of the ampulla-removal behaviour of females, suggests that females are capable of adaptive mate choice.

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Le spermatophore que transmet le mâle de *Gryllodes supplicans* à la femelle au cours de la copulation comporte une portion gélatineuse de grande taille (spermatophylax) que détache et mange la femelle après l'accouplement. Chez les autres espèces nord-américaines de grillons, le spermatophore ne comporte qu'une petite ampoule remplie du sperme. Au cours de cette étude, le rôle de la grande taille du spermatophore dans le comportement reproducteur de *G. supplicans*, de même que les coûts associés à la possession d'un spermatophore plus complexe ont été examinés. L'intervalle moyen entre les copulations chez des mâles de *G. supplicans* laissés en présence de femelles réceptives était de 3,25 h; cette période est longue comparativement à celle qui prévaut chez d'autres espèces. La masse estimée des spermatophores produits par les mâles ne diffère pas significativement de celle des spermatophores produits par les mêmes mâles 24 h plus tard; les mâles semblent donc maintenir constante leur contribution au cours des copulations subséquentes. La durée de la consommation complète du spermatophylax par la femelle augmente linéairement en fonction de la masse du spermatophore. Les femelles retirent l'ampoule séminale peu de temps après avoir consommé le spermatophylax et pénalisent ainsi les mâles qui donnent de plus petits "repas nuptiaux". Les mâles les plus gros produisent les spermatophores les plus gros; la sélection désavantage donc souvent les mâles les plus petits. Ces résultats, examinés à la lumière du comportement par lequel la femelle retire l'ampoule séminale, indiquent que les femelles exercent de fait une sélection des mâles.

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Introduction

Males invest little energy in their gametes relative to that of females (Bateman 1948; Trivers 1972), although the costs that males incur in the production and packaging of ejaculates are not always trivial (Dewsbury 1982). Such costs may be manifest in a variety of ways: (*i*) longer intercopulatory intervals, (*ii*) increased copulation times, and (*iii*) decreased ejaculate volumes accompanying subsequent matings. In insects, these higher investment effects have been documented best in the Lepidoptera. In this group, a decrease in the size of spermatophores with additional matings has been demonstrated in those cases where the male was presented with a female immediately after or within 24 h of a previous mating (George and Howard 1968; Outram 1971; Rutowski 1979; Sims 1979); in one study (Sims 1979), this decrease in spermatophore size was accompanied by extended copulation durations. Correspondingly, there may also be a decrease in the quantity of sperm contained within subsequent spermatophores (Sims 1979), resulting in a substantial drop in fertility of females mated with nonvirgin males (George and Howard 1968; Outram 1971; Sims 1979).

Alternatively, males may hold constant their investment in successive copulations, but this may increase the time required to replenish spent ejaculates. Few data addressing this hypothesis are available, but the lengthy refractory periods exhibited by some male katydids (Orthoptera: Tettigoniidae) have been attributed to increased investment in their spermatophores (Busnel *et al.* 1956; Feaver 1977). In the acalypterate flies, *Anastrepha suspensa* (Diptera: Tephritidae) and *Drosophila melanogaster* (Diptera: Drosophilidae), recently mated males had a much lower mating success than virgin males when placed together with virgin females (Markow *et al.* 1978; Sivinski 1984). This disadvantage was abolished when mated males were allowed time to recover. The reduced mating success of freshly mated males was not due to a reduction in courtship activity. Females apparently rejected these males, thereby avoiding infertile matings. Thus, female choice also may act to increase intercopulatory intervals of recently mated males.

In species where male investment in ejaculates is high, significant variation among males, with respect to the size of ejaculates, also may exist. Male body size is one important source of such variation. In katydids (Gwynne 1982; Gwynne *et al.* 1984) and moths (Greenfield 1982), an increase in the weight of spermatophores with increased male body weight has been reported.

In the decorated cricket, *Gryllodes supplicans* (Orthoptera: Gryllidae: Gryllinae), a male transfers a spermatophore consisting of a small sperm-containing ampulla and a larger

gelatinous spermatophylax devoid of sperm. As in other gryllines, the spermatophore remains outside the female's body afer mating, but the provision of a spermatophylax is unusual, at least for the North American species (Alexander and Otte 1967). A female *G. supplicans* detaches the spermatophylax from the sperm ampulla with her mouthparts within seconds of dismounting the male (Alexander and Otte 1967; Sakaluk 1984). An average period of 40 min is required for the female to consume fully the spermatophylax; several minutes later she removes and eats the sperm ampulla (Sakaluk 1984).

Previously I demonstrated that the spermatophylax functions to deter the female from removing the sperm ampulla before the ampulla is emptied of sperm (Sakaluk 1984). Here I examine experimentally the role of spermatophore size in the reproductive behaviour of males and females and attempt to define some of the costs associated with the provision of a more complex spermatophore. Specifically I examine (*i*) intercopulatory intervals of males provided with continuous access to sexually receptive females, (*ii*) the relationship between a male's body size and the weight of the spermatophore he produces, (*iii*) the weight of spermatophores produced in successive matings, and (*iv*) the relationship between a female's nuptial feeding behaviour and the weight of the spermatophore with which she is provided.

Methods of study

Crickets used in the present experiments were from two groups: (*i*) descendants of crickets originally collected at Gainesville, FL, in July 1981 and (*ii*) late-instar nymphs and adults collected at Tucson, AZ, in April 1984. For each experiment, the origin of crickets is shown in parentheses.

Crickets were provided with water contained in test tubes plugged with cotton wicks and ample food (Purina® cat chow). The surface areas of terraria were increased by the addition of egg cartons. Moistened vermiculite in a petri dish served as an oviposition substrate. Crickets were kept at 28 ± 2°C and 30% relative humidity on a 12 h light : 12 h dark photoperiod.

Data were analysed with a Hewlett–Packard statistical analysis package. All values are means ± SE.

Male intercopulatory interval (Florida)

Males were isolated from females 4–5 days prior to the start of the experiment, whereas females were kept separate for at least 24 h. All males were of unknown age; females were less than 3 weeks beyond the imaginal molt.

Matings were observed on 3 separate days. Observations began at about the midpoint of the dark portion of the photoperiod and continued for 6 h. In total, 27 males were tested. A male and two females were placed into each mating container, a 2-L plastic margarine tub. After the first mating, the mated female was removed and replaced with a new female. Following this first mating, females were checked for the presence of a new spermatophore at 30-min intervals for the next 2 h. Previous observations showed that males never mated twice within 2 h (S. K. Sakaluk, unpublished). Subsequently, the crickets were monitored continuously until the end of the 6-h observation period. The times at which first and second matings occurred were recorded for each male.

Male size and weight of spermatophore (Florida)

Males and females were isolated for at least 24 h before mating. Males were weighed before and after mating with a Roller-Smith precision balance accurate to 0.2 mg. Crickets were weighed in a small plastic bag suspended with a paper clip. The bag and clip were reweighed before weighing each cricket to eliminate the effects of fingerprints and cricket feces.

The experiment was conducted over 5 consecutive days requiring 5 h each day. No food or water was provided to males during 5-h experimental periods. Males were weighed prior to mating over the first 2 h, placed with one or two females for the next hour, and then reweighed over the final 2 h. The order in which crickets were weighed was the same both before and after mating, so that the intervening period was approximately the same for all males. Males placed in containers with no females and males confined with females but that did not mate served as a control for weight loss as a result of metabolic activity.

Thirty-one experimental males and 18 control males were tested. Premating and postmating weights were recorded for each individual.

Male size, weight of spermatophore, and duration of nuptial feeding (Arizona)

Males and females were isolated 24 h before mating. Males were weighed before and after mating with a Mettler PC 440 electronic balance accurate to 1 mg. This balance required less time for weighing crickets than the Roller-Smith model, so that control weight losses could be minimized. Males each were weighed in a 150-mL plastic cup.

The experiment was conducted over 8 days with 20 different males; many males were used more than once, both as controls and experimentals. Additionally, some of the males ($N = 9$) were not used until the 5th day of the study, because initially they were not sexually mature. The interval between weighings was exactly 2 h for each cricket. No food or water was provided during this period. Experimental males each were confined with one or two females; controls were established as described previously.

All premating and postmating weights were recorded. Additionally, the time taken by the female to consume fully the spermatophylax, or the time subsequent to spermatophylax removal, at which she dropped it, was noted for each mating.

Results

Male intercopulatory interval (Florida)

All 27 males mated and 24 of the 27 remated within the 6-h observation period. All males, with one exception, mated within the first 11 min of the start of observations. The single exception first mated after 283 min; this male was one of the three that did not remate. The mean intercopulatory interval for the 24 males that remated was 196.0 ± 8.8 min (range, 136–322 min).

Male size and weight of spermatophore (Florida)

The mean weight of experimental males was 281 ± 6.3 mg before mating (range, 226.6–371.0 mg) and 269.4 ± 6.2 mg after mating, representing an average loss in weight of 11.8 ± 0.8 mg. The corresponding mean weights of control males before and after confinement were 291.5 ± 9.1 mg (range, 223.8–367.8 mg) and 288.3 ± 9.3 mg, respectively, representing an average reduction in weight of 3.2 ± 0.5 mg.

The weight of the spermatophore produced by an experimental male was estimated as the weight lost in mating less the mean control weight loss. Thus, the mean estimated weight of the spermatophore was 8.6 ± 0.8 mg (range, 0.2–18.6 mg), representing, on average 3.1 ± 0.3% of the male's initial body weight (range, 0.07–5.94%). There was no significant correlation between a male's initial body weight and the estimated size of the spermatophore he produced (Fig. 1*a*; $r = 0.23$, $t = 1.30$, $p > 0.05$).

Male size, weight of spermatophore, and duration of nuptial feeding (Arizona)

The mean initial weight of males was 206.8 ± 7.3 mg ($N = 20$; range, 167–295 mg), significantly less than that of males reared from crickets collected in Florida ($F = 69.9$, $p < 0.001$).

Seventeen males accounted for 59 matings, an average mating frequency of 3.5 ± 0.6 (range, 1–8). The mean weight

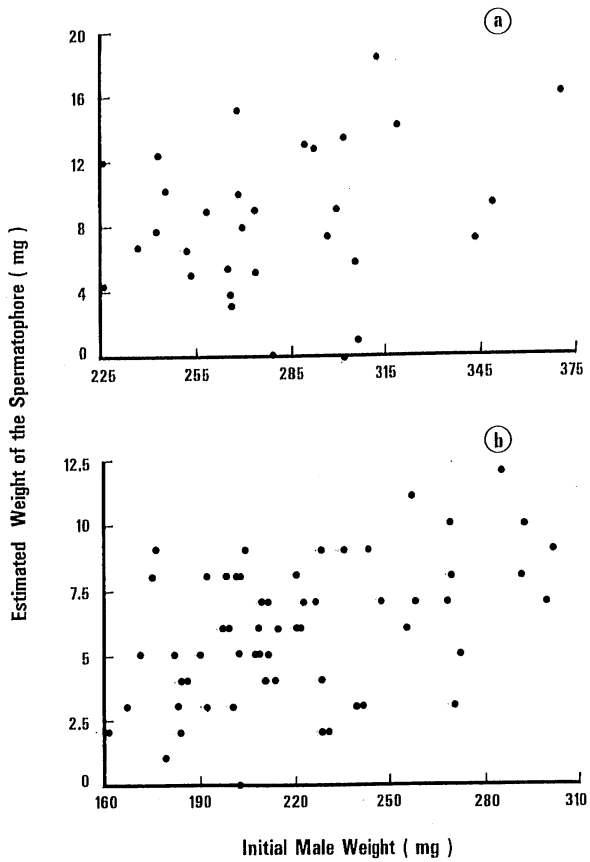

FIG. 1. The relationship between the weight of a male *G. supplicans* before mating and the estimated weight of the spermatophore transferred to the female during mating (weight loss during mating minus control weight loss). (*a*) Florida cricket group ($r = 0.23$, $t = 1.30$, $p > 0.05$). (*b*) Arizona cricket group ($r = 0.45$, $t = 3.81$, $p < 0.001$).

of these males was 221.9 ± 4.6 mg before mating (range, 162–302 mg) and 214.0 ± 4.5 mg after mating, representing an average loss in weight of 7.9 ± 0.3 mg. Control weights ($N = 43$) were 212.3 ± 5.5 mg before mating (range, 161–295 mg) and 210.5 ± 5.5 after mating, representing an average weight loss of 1.8 ± 0.4 mg.

The mean estimated weight of the spermatophore produced by experimental males was 6.1 ± 0.3 mg (range, 0.2–12.2 mg), representing, on average, 2.7 ± 0.1% of the male's initial body weight (range, 0.1–5.2%). Here also there was a positive correlation between a male's initial body weight and the weight of the spermatophore he produced (Fig. 1*b*), except that in this case, the relationship was significant ($r = 0.45$, $t = 3.81$, $p < 0.001$).

Females fully consumed the spermatophylax in 32 of 59 matings (54.2%) and partially ate the spermatophylax before dropping the remaining portion in 18 matings (30.5%). The fate of the spermatophylax was unknown in the remaining nine cases. The mean time females spent fully consuming the spermatophylax was 36.7 ± 3.5 min (range, 11–89 min). The relationship between the estimated weight of the spermatophore produced by the male and the time taken by the female to consume fully the spermatophylax is shown in Fig. 2. The duration of spermatophylax consumption increased linearly with respect to spermatophore size and this relationship was significant ($r^2 = 0.49$, $F = 29.0$, $p < 0.001$). For females that only partially ate the spermatophylax, the mean time after mating at which the uneaten portion was dropped was 16.2 ±

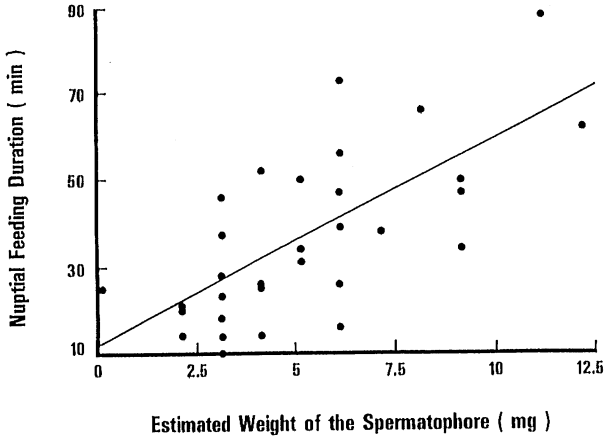

FIG. 2. Estimated weight of the spermatophore and the time taken by a female *G. supplicans* to fully consume the spermatophylax. Fitted regression: $y = 4.81x + 11.54$ ($r^2 = 0.49$, $F = 29.0$, $p < 0.001$).

2.8 min (range, 3–39 min). The mean estimated weight of dropped spermatophores (7.1 ± 0.6 mg) was significantly greater than that of spermatophores that were fully consumed (5.2 ± 0.5 mg; $F = 6.02$, $p < 0.025$).

In 21 instances, males were remated 24 h after a previous mating. There was no significant difference in the estimated weight of spermatophores produced by these males initially and that of spermatophores produced by these same males 24 h later (paired t-test: $t = 1.74$, $p > 0.05$).

Discussion

Male *G. supplicans* remated, on average, 3.25 h after a previous mating. Insofar as males were provided with optimal mating conditions, this observed intercopulatory interval likely corresponds to the physiological limits of spermatophore production. Specifically, males were isolated several days prior to the experiment and, therefore, should have had fully charged accessory glands. They were permitted continuous access to sexually receptive females during the experimental period and provided with ample food and water. Spermatophore replacement times for other male gryllines, whose spermatophores do not include a spermatophylax, usually are less than 1 h (Khalifa 1950; Alexander and Otte 1967; Loher and Rence 1978) and as little as 17 min (Khalifa 1950). Fewer data are available on intervals between matings for these males. According to Alexander (1961), matings by male *Gryllus pennsylvanicus* occur at intervals of 1 hour or less. Male *Gryllus integer* (under taxonomic revision; W. H. Cade, personal communication) exhibited an average mating rate of 0.85 matings/h when confined with females over 2 consecutive nights (Sakaluk and Cade 1980); this is a conservative estimate relative to that for *G. supplicans* in that mated *G. integer* females were not replaced with different individuals. In a study of *Anurogryllus arboreus*, Walker (1983) observed two males that mated twice over intervals of 4 and 14 min, respectively. *Teleogryllus commodus* males are able to replace spent spermatophores within 30 min, but courtship activity is not renewed for 2–2.5 h subsequent to a previous mating. In this species, a period of mate guarding by the male follows a copulation and this must occur before a male will initiate additional courtships (Loher and Rence 1978).

In the nemobine cricket, *Nemobius sylvestris*, a male transfers two spermatophores to the female during the course of a mating (Mays 1971; Campan and Demai 1983). The first

spermatophore contains no sperm and is removed by the female shortly after dismounting the male. The second spermatophore, which is about twice as large as the first, contains sperm and is retained by the female for a longer period. Both spermatophores, on average, are transferred to the female within 55 min (Campan and Demai 1983). Male *Hygronemobius alleni* (Nemobiinae) transfer as many as three spermatophores to the same female in little more than 1.5 h (Mays 1971).

Intercopulatory intervals for male *G. supplicans*, therefore, are long relative to those for other crickets; this undoubtedly is related to the size and complexity of the spermatophore produced by the male. In this study, the spermatophore assumed up to as much as 6% of a male's body weight and, although corresponding data are unavailable for other species, the spermatophore produced by a male *G. supplicans* is about 3–5 times larger in volume than those produced by *A. domesticus* and *Gryllus* males (S. K. Sakaluk, personal observation).

A single observation conflicts with this hypothesis. Alexander and Otte (1967) observed a spermatophylax-producing male *Teleogryllus africanus* (South African species) mate twice with the same female in about 15 min. However, the interval between matings for males should be affected by their investment in future spermatophores; a male that reduces his investment in a subsequent spermatophore may similarly reduce the time required for its production. In this study, the weight of spermatophores produced by male *G. supplicans* did not differ significantly from that of spermatophores produced by these same males 24 h later. Apparently, male *G. supplicans* hold constant their investment in subsequent copulations. In the case of *T. africanus*, it may be that spermatophore size decreases with additional matings, so that males can remate sooner than if ejaculate size was held constant. Clearly, further study is required on the plasticity in the size of spermatophores produced by males of different cricket species; differences in spermatophore size may be an important source of interspecific variation in mating behaviour (Gwynne 1983; Rutowski *et al.* 1983).

The time taken by female *G. supplicans* to consume fully the spermatophylax increased linearly with the estimated weight of the spermatophore. In a previous study, females usually removed the sperm-containing ampulla within several minutes of eating the spermatophylax, regardless of the feeding-phase duration (Sakaluk 1984). The ampulla must be attached for roughly 55 min before it is completely emptied of sperm. However, females often finish eating their "nuptial meal" long before this critical time and consequently remove the ampulla before complete sperm transfer has occurred. The results here demonstrate that it is the amount of feeding material provided to the female that determines how long it takes her to consume it fully. Males providing inadequately sized nuptial meals may therefore be penalized in two ways: (*i*) premature removal of the ampulla may result in the transfer of an insufficient number of sperm to fertilize all of a female's eggs (Sakaluk 1984) and (*ii*) the overall competiveness of a male's ejaculate in fertilizing eggs may be reduced, relative to that of other males (S. K. Sakaluk, in preparation).

The ampulla-removing behaviour of female *G. supplicans* can be construed as adaptive female choice only if the preference for males that provide larger spermatophores results in increased female reproductive success (Maynard Smith 1966). Discriminating females may experience enhanced fitnesses through the acquisition of material and (or) genetic benefits (see Thornhill and Alcock (1983) for a review of such benefits in insects; note also that the importance of female preference in obtaining "good genes" remains controversial; Bateson 1983). No data are available, as yet, on the effects of spermatophore consumption on reproduction in female *G. supplicans*. However, in *Acheta domesticus*, the consumption of the spermatophore by singly mated females did not result in increased offspring production over those females whose spermatophores had been removed with forceps (spermatophore attachment times were similar for both treatments; Sakaluk 1980). But in *A. domesticus*, the spermatophore does not include a spermatophylax. In the katydid, *Requena verticalis* (Orthoptera: Tettigoniidae), the male's spermatophore does includes a spermatophylax that the female consumes after mating (Gwynne *et al.* 1984); Gwynne (1984) demonstrated that the size and number of eggs produced by females increases when females are provided with additional spermatophylaxes. Additionally, proteins contained in the male's spermatophore are incorporated in the ovaries and eggs of the female shortly after mating (Bowen *et al.* 1984).

Larger male *G. supplicans* produced heavier spermatophores, although this relationship was statistically significant only for the Arizona crickets. This effect also has been demonstrated in other insects (Greenfield 1982; Gwynne 1982; Gwynne *et al.* 1984). Smaller male *G. supplicans* may therefore be at a selective disadvantage, because the smaller nuptial meals provided by these males often should result in the premature removal of their sperm ampullae. But this hypothesis is complicated by two additional observations. First, females do not always remove the sperm ampulla shortly after consuming the spermatophylax (Sakaluk 1984). This may represent an additional avenue of female choice, insofar as these females permit full insemination with no apparent regard to spermatophore size. Perhaps there are male traits other than the size of the nuptial meal by which females evaluate males. In crickets, such traits may include a male's dominance status (Crankshaw 1979), frequency of courtship stridulation (Burk 1983), and calling-song intensity (Forrest 1980, 1983). Second, the weight of spermatophores provided to females who subsequently dropped the spermatophylax was significantly greater than those provided to females who fully consumed the spermatophylax. The dropping of spermatophylaxes may represent a subtle form of female choice, related perhaps to the nutritional composition of the spermatophore (see Marshall 1982). Alternatively, females provided with the larger spermatophores may simply have become satiated before fully consuming the spermatophylax; no food or water was provided during 2-h experimental periods, but females had ready access to abundant food supplies at all other times. Regardless, the extended retention of the ampulla after consumption of the spermatophylax along with spermatophylax-dropping behaviour, represent plausible examples of "cryptic" female choice (Thornhill 1983) meriting further investigation.

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ALEXANDER, R. D. 1961. Aggressiveness, territoriality, and sexual behavior in field crickets (Orthoptera: Gryllidae). Behaviour, **17**: 130–223.

ALEXANDER, R. D., and D. OTTE. 1967. The evolution of genitalia and mating behavior in crickets (Gryllidae) and other Orthoptera. Misc. Publ. Mus. Zool. Univ. Mich. **133**: 1–62.

BATEMAN, A. J. 1948. Intra-sexual selection in *Drosophila*. Heredity, **2**: 349–368.

BATESON, P. (*Editor*). 1983. Mate choice. Cambridge University Press, Cambridge, England.

BOWEN, B. J., C. G. CODD, and D. T. GWYNNE. 1984. The katydid spermatophore (Orthoptera: Tettigoniidae): male nutritional investment and its fate in the mated female. Aust. J. Zool. **32**: 23–31.

BURK, T. 1983. Male aggression and female choice in a field cricket (*Teleogryllus oceanicus*): the importance of courtship song. *In* Orthopteran mating systems: sexual competition in a diverse group of insects. *Edited by* D. T. Gwynne and G. K. Morris. Westview Press, Boulder, CO. pp. 97–119.

BUSNEL, R.-G., B. DUMORTIER, and M.-C. BUSNEL. 1956. Recherches sur le comportement acoustique des éphippigères (Orthoptères, Tettigoniidae). Bull. Biol. Fr. Belg. **3**: 219–286.

CAMPAN, M., and F. DEMAI. 1983. Le comportement de *Nemobius sylvestris* (Orthoptera: Gryllidae). I. Répertoire comportemental du mâle et de la femelle. Biol. Behav. **3**: 185–204.

CRANKSHAW, O. S. 1979. Female choice in relation to calling and courtship songs in *Acheta domesticus*. Anim. Behav. **27**: 1274–1275.

DEWSBURY, D. A. 1982. Ejaculate cost and male choice. Am. Nat. **119**: 601–610.

FEAVER, M. 1977. Aspects of the behavioral ecology of three species of *Orchelimum* (Orthoptera: Tettigoniidae). Ph.D. thesis, University of Michigan, Ann Arbor, MI.

FORREST, T. G. 1980. Phonotaxis in mole crickets: its reproductive significance. Fla. Entomol. **63**: 45–53.

——— 1983. Calling songs and mate choice in mole crickets. *In* Orthopteran mating systems: sexual competition in a diverse group of insects. *Edited by* D. T. Gwynne and G. K. Morris. Westview Press, Boulder, CO. pp. 185–204.

GEORGE, J. A., and M. G. HOWARD. 1968. Insemination without spermatophores in the Oriental fruit moth, *Grapholitha molesta* (Lepidoptera: Tortricidae). Can. Entomol. **100**: 190–192.

GREENFIELD, M. D. 1982. The question of paternal investment in Lepidoptera: male-contributed proteins in *Plodia interpunctella*. Int. J. Invertebr. Reprod. **5**: 323–330.

GWYNNE, D. T. 1982. Mate selection by female katydids (Orthoptera: Tettigoniidae, *Conocephalus nigropleurum*). Anim. Behav. **30**: 734–738.

——— 1983. Male nutritional investment and the evolution of sexual differences in Tettigoniidae and other Orthoptera. *In* Orthopteran mating systems: sexual competition in a diverse group of insects. *Edited by* D. T. Gwynne and G. K. Morris. Westview Press, Boulder, CO. pp. 337–366.

——— 1984. Courtship feeding increases female reproductive success in bushcrickets. Nature (London), **307**: 361–363.

GWYNNE, D. T., B. J. BOWEN, and C. G. CODD. 1984. The function of the katydid spermatophore and its role in fecundity and insemination (Orthoptera: Tettigoniidae). Aust. J. Zool. **32**: 15–22.

KHALIFA, A. 1950. Sexual behaviour in *Gryllus domesticus* L. Behaviour, **2**: 264–274.

LOHER, W., and B. RENCE. 1978. The mating behavior of *Teleogryllus commodus* (Walker) and its central and peripheral control. Z. Tierpsychol. **46**: 225–259.

MARKOW, T. A., M. QUAID, and S. KERR. 1978. Male mating experience and competitive courtship success in *Drosophila melanogaster*. Nature (London), **276**: 821–822.

MARSHALL, L. D. 1982. Male nutrient investment in the Lepidoptera: what nutrients should males invest? Am. Nat. **120**: 27–35.

MAYNARD SMITH, J. 1966. The theory of evolution. Penguin Books Inc., Baltimore, MD.

MAYS, D. L. 1971. Mating behavior of nemobiine crickets—*Hygronemobius*, *Nemobius* and *Pteronemobius* (Orthoptera: Gryllidae). Fla. Entomol. **54**: 113–126.

OUTRAM, I. 1971. Aspects of mating in the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). Can. Entomol. **103**: 1121–1128.

RUTOWSKI, R. L. 1979. The butterfly as an honest salesman. Anim. Behav. **27**: 1269–1270.

RUTOWSKI, R. L., M. NEWTON, and J. SCHAEFER. 1983. Interspecific variation in the size of the nutrient investment made by male butterflies during copulation. Evolution (Lawrence, Kans.), **37**: 708–713.

SAKALUK, S. K. 1980. Sexual behaviour and factors affecting female reproduction in house and field crickets. M.Sc. thesis, Brock University, St. Catharines, Ont.

——— 1984. Male crickets feed females to ensure complete sperm transfer. Science (Washington, D.C. 1883–), **223**: 609–610.

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

SIMS, S. R. 1979. Aspects of mating frequency and reproductive maturity in *Papilio zelicaon*. Am. Midl. Nat. **102**: 36–50.

SIVINSKI, J. 1984. Effect of sexual experience on male mating success in a lek forming tephritid *Anastrepha suspensa* (Loew). Fla. Entomol. **67**: 126–130.

THORNHILL, R. 1983. Cryptic female choice and its implications in the scorpionfly *Harpobittacus nigriceps*. Am. Nat. **122**: 765–788.

THORNHILL, R., and J. ALCOCK. 1983. The evolution of insect mating systems. Harvard University Press, Cambridge, MA.

TRIVERS, R. L. 1972. Parental investment and sexual selection. *In* Sexual selection and the descent of man: 1871–1971. *Edited by* B. Campbell. Aldine–Atherton Inc., Chicago, IL. pp. 136–179.

WALKER, T. J. 1983. Mating modes and female choice in short-tailed crickets (*Anurogryllus arboreus*). *In* Orthopteran mating systems: sexual competition in a diverse group of insects. *Edited by* D. T. Gwynne and G. K. Morris. Westview Press, Boulder, CO. pp. 240–267.