

BENEFITS OF MULTIPLE MATES IN THE CRICKET *GRYLLUS BIMACULATUS*

TOM TREGENZA¹ AND NINA WEDELL²

¹Ecology and Evolution Group, Department of Biology, University of Leeds, Leeds LS2 9JT, United Kingdom
E-mail: gentbt@leeds.ac.uk

²Department of Zoology, University of Stockholm, S-106 91 Stockholm, Sweden
E-mail: nina.wedell@zoologi.su.se

Abstract.—Despite the importance of polyandry for sexual selection, the reasons why females frequently mate with several males remain poorly understood. A number of genetic benefits have been proposed, based on the idea that by taking multiple mates, females increase the likelihood that their offspring will be sired by genetically more compatible or superior males. If certain males have intrinsically “good genes,” any female mating with them will produce superior offspring. Alternatively, if some males have genetic elements that are incompatible with a particular female, then she may benefit from polyandry if the sperm of such males are less likely to fertilize her eggs. We examined these hypotheses in the field cricket *Gryllus bimaculatus* (Orthoptera: Gryllidae). By allocating females identical numbers of matings but different numbers of mates we investigated the influence of number of mates on female fecundity, and both short- and long-term offspring fitness. This revealed no effect of number of mates on number of eggs laid. However, hatching success of eggs increased with number of mates. This effect could not be attributed to nongenetic effects such as the possibility that polyandry reduces variance in the quantity or fertilizing ability of sperm females receive, because a control group receiving half the number of copulations showed no drop in hatching success. Offspring did not differ in survival, adult mass, size, or development time with treatment. When males were mated to several different females there were no repeatable differences between individual males in the hatching success of their mate’s eggs. This suggests that improved hatching success of polyandrous females is not due to certain males having genes that improve egg viability regardless of their mate. Instead, our results support the hypothesis that certain males are genetically more compatible with certain females, and that this drives polyandry through differential fertilization success of sperm from more compatible males.

Key words.—Female choice, genetic incompatibility, good genes, *Gryllus bimaculatus*, inbreeding, polyandry, sperm competition.

Received August 12, 1997. Accepted April 30, 1998.

Numerous animals have been shown to mate far more frequently than is necessary to ensure the production of zygotes. We expect this sort of behavior from males competing for fertilizations, but why females do this is more puzzling. Matings are frequently costly to females. Apart from taking time and energy, copulation may leave pairs vulnerable to predation, provide an opportunity for disease transmission, and in some cases have direct costs through pathological properties of seminal fluid (Chapman et al. 1995). In some species, these costs are offset by direct benefits through nutrient donations (Gwynne 1984) or the replenishment of sperm stores (Sakaluk and Cade 1980). Alternatively females may be coerced into matings (Thornhill 1980) or may be bet-hedging against infertile males (Walker 1980).

Although these nongenetic benefits provide an explanation for polyandry in some species, for many, they do not seem feasible; this has led to the proposal of various genetic benefits that females may gain for their offspring through multiple mating. Unlike nongenetic benefits, which may accrue from repeated copulations with the same male, all genetic explanations depend upon females mating with several different males (polyandry). In monogamous birds, extrapair copulation may benefit females if it allows them to mate with males of a higher genetic quality than their own partner (Kempnaers et al. 1992). For hymenopterans, evidence from comparative studies suggests that multiple mating may be advantageous because it increases sibling diversity (Ridley 1993; Keller and Reeve 1994; but see Boomsma and Ratnieks 1996). In addition to these explanations, a number of more generally applicable hypotheses have recently been put forward. It has been argued that females may mate with several

males to promote sperm competition. This may benefit females because their sons will inherit traits giving them an advantage in sperm competition (Keller and Reeve 1995). Alternatively, sperm competition will be beneficial if there are correlations between sperm and offspring quality (Madsen et al. 1992). Finally, genetic incompatibility between mates may be common and multiple mating may be a female adaptation to reducing its deleterious effects. Such incompatibility may result from inbreeding (Stockley et al. 1993; Olsson et al. 1996a) or as a result of the presence of selfish genetic elements (Zeh and Zeh 1997a,b).

Despite the importance of multiple mating for sexual selection, there remains a dearth of experimental tests of the hypotheses to explain it. Female adders with higher mating frequency have been found to produce fewer stillborn young (Madsen et al. 1992) and sand lizards mating to several males had young that were fitter in a number of respects (Olsson et al. 1994). However, these field studies cannot exclude the likelihood that better females attract more mates or that better habitats lead to contact with more males (Parker 1992). Additionally, these studies confound number of mates and number of matings, making it impossible to ascribe benefits to polyandry as opposed to simply mating several times. Zeh’s (1997) laboratory study of pseudoscorpions addresses this issue by showing that repeated matings with the same male do not increase offspring fitness, whereas females mated to several males had fewer brood failures and increased embryo survival.

In this study, we examine the benefits of multiple mating in the field cricket *Gryllus bimaculatus* (Orthoptera: Gryllidae). By allocating females the same number of matings but

different numbers of mates, we explicitly control for possible benefits of multiple copulations (such as avoiding sperm depletion) independent of benefits of polyandry. Genetic benefits can be divided into short- and long-term effects on offspring fitness. Hatching success is considered to be a short-term effect, whereas long-term effects may be detected in posthatching life history.

MATERIALS AND METHODS

The field cricket *Gryllus bimaculatus* is widely distributed in southern Europe, where it frequently occurs in high-density populations. Females in the laboratory have been shown to mate repeatedly, and males are capable of mating at least 40 times in three days (Simmons 1986). The lack of a female postmating refractory period combined with the likelihood of frequent encounters with males in the field makes it unlikely that polyandry is a laboratory artifact. Furthermore, gryllids in general are noted for repeated matings by females (Alexander and Otte 1967) and field studies of its closest relative, *Gryllus campestris* (Rost and Honegger 1987), indicate that *G. bimaculatus* is unlikely to be an exception. Females mating several times are able to maintain hatching success over a longer period than single- or double-mated females (Simmons 1988a). This provides a possible explanation for polyandry, although one might expect females to cease mating once they had acquired enough sperm. More importantly, there is no reason to expect that polyandry will have a single evolutionary explanation within or between species.

In our population, females unmated for an hour invariably mated with any courting male. Males will not initiate matings until they have produced a new spermatophore, a process that takes approximately an hour. The amount of sperm in subsequent spermatophores produced by a single male does not decline over at least the first five matings (Simmons 1986, 1987a) and there is no evidence that it declines thereafter. Spermatophore size is unrelated to male size (Simmons 1988b). Because the spermatophore is produced in advance of encountering the female, males do not have the option of manipulating their ejaculate in response to individual mates. This eliminates the possibility that males might transfer less sperm to females with whom they had mated in the past or in response to other cues such as female size, relatedness, or risk of sperm competition.

We isolated late-instar nymphs from a large laboratory stock in separate 9-cm diameter pots at 29°C and 18:6 hr light:dark and checked them daily to ascertain date of final molt to adulthood. On her 10th adult day, we placed each female into a 30 x 30 cm enclosure and allowed her to mate four times, at hourly intervals. Males used were all 10 days old and had mated once previously. We allowed males to remain with the female for an hour postmating, thus preventing the female from removing the spermatophore until sperm transfer had taken place by his guarding her and physically intervening if she attempted to remove the spermatophore. Females were allocated either the same male four times, two different males twice each, or four different males. Each male was used once in all three treatments, so he was the sole partner of one female as well as mating with one

female in each of the other treatment groups. Hence each male mated a total of eight times: an initial mating to a female not used in the study so that all males were nonvirgins and subsequently (each mating in random order) four times to one female, twice to another, and once to a third. To increase the sample size of the four-mates treatment, four males which were randomly chosen from among the already used males, were used twice as the mate of a female mating to four different males, so that these males mated nine times. Hence we produced three treatment groups of females, all mating four times: 48 females mated to one male, 24 females mated to two males, and 16 females mated to four males. We scheduled matings at random such that there was no bias in the mating history of males with regard to treatment group. Using the same males in different treatment groups is pseudoreplicative, but is preferable to using different males because it controls for variation between treatments resulting from differences between males. Females were not reused because it is the differences between females under different mating regimes that is the subject of this study.

To examine the effects of number of matings as opposed to number of mates, we conducted an additional experiment in identical fashion, using individuals from the same generation: 38 females were mated to the same male twice and thus provided a contrast to those females mated to a single male four times. Males used in this experiment had previously mated three times, so their final mating was their fifth, whereas in the main experiment the final mating of a male mating four times to the same female is on average its sixth, a difference that the work cited above (Simmons 1986, 1987a) indicates is unlikely to be significant.

Due to sperm mixing, the order of mating does not affect paternity in *G. bimaculatus* (Simmons 1987a), provided that all matings occur before egg laying begins (as in our experiments). Females were never observed to remove or consume the spermatophore after mating. After four matings, we placed females in separate containers provided with wet sand for oviposition. The eggs produced by each female in the three days after she began laying were counted, transferred to a petri dish containing damp cotton, and maintained under the same conditions as the adults. After laying, females were killed by freezing, dissected, and a count was made of the number of mature eggs remaining in her ovaries. This allowed us to examine whether the proportions of available eggs females chose to lay were affected by the number of mates. We checked eggs daily for hatching until seven days after the last emergence.

We transferred the first 40 nymphs from each female to an aerated 5-liter plastic container, provided them with water and paper towels for cover, and fed them rat pellets ad libitum. After rearing, we removed newly eclosed adults daily and recorded their mass, pronotum width (across the widest point), and hind femur length.

Data and regression residuals did not deviate from normal and there were equal variances between ANOVA groups. All tests are two tailed.

RESULTS

There were no significant differences between treatments in number of eggs laid (ANOVA $F_{2,85} = 1.0$, $P = 0.37$) or

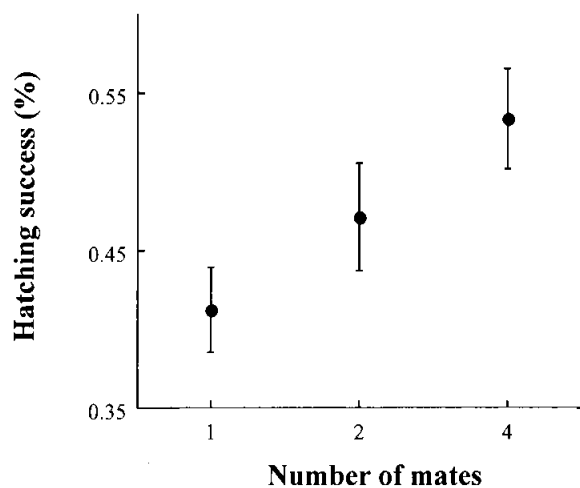


FIG. 1. Egg viability increases with number of mates: proportion of eggs hatching from females mated to one male four times, two males twice, or four males once (means \pm standard errors).

in the proportion of available eggs laid by females (arcsine-transformed proportions $F_{2,85} = 0.43$, $P = 0.65$). However, we did find evidence for short-term benefits to offspring whose mother had an increase in the number of mates. There was a significant increase in the proportion of eggs hatching from females mated to more than one male (Fig. 1); one mate, mean = 0.41 ± 0.03 SE, $n = 48$; two mates, mean = 0.47 ± 0.03 SE, $n = 24$; four mates, mean = 0.53 ± 0.03 SE, $n = 16$; ANOVA on arcsine-transformed proportions $F_{2,85} = 3.47$, $P = 0.036$; regression on arcsine-transformed proportions $r^2 = 0.275$, $n = 88$, $P < 0.01$). Furthermore, variation in hatching success declined with number of mates (coefficient of variation [CV] adjusted for variation in sample size [Sokal and Rohlf 1995], one mate, CV = 0.449; two mates, CV = 0.356; four mates, CV = 0.244). Using Lewontin's variance ratio test on arcsine-transformed data (Lewontin 1966; Zar 1984), these differences in CV are significant for one mate versus four mates ($F_{47,15} = 4.60$, $P < 0.0001$) and for two mates versus four mates ($F_{23,15} = 2.18$, $P = 0.023$), but not for one mate versus two mates ($F_{47,23} = 2.11$, $P = 0.10$), although this may be explained by the smaller sample size of this comparison.

Because the same males were used in the single-mate treatment and in the multiple mate treatments, we can directly compare observed hatching success of females mated to multiple males with expected values derived from the hatching success of females mated to single males. For instance, for a female mated to two males, A and B, her expected hatching success is (proportion of eggs hatching from female mated solely to male A + proportion of eggs hatching from the female mated solely to male B)/2. For females mated to four males, we used the mean hatching success of the four females for whom each male was their sole mate. Because we are interested in differences between males, not between treatments, the 24 females mated twice can be pooled with the 16 females mated four times, thus giving 40 observed and expected values. There is no evidence of a correlation between observed and expected values ($r = 0.17$, $n = 40$, $P = 0.29$). This could be because there is differential fertilization

TABLE 1. Posthatching summary data. Groups of 40 first-instar nymphs were reared to adulthood from females mated four times to either one, two, or four mates. Two broods were lost due to an accident. Sex ratio, arcsine-transformed sex ratio of nymphs surviving to adulthood; survival, arcsine-transformed proportion of nymphs surviving to adulthood; development time, mean time (d) for nymphs to reach adulthood; mass, mean adult mass (g); femur, mean adult femur length (mm); pronotum, mean adult pronotum width (mm).

	One mate, $n = 47$		Two mates, $n = 23$		Four mates, $n = 16$	
	Mean	SD	Mean	SD	Mean	SD
Sex ratio	0.76	0.13	0.76	0.12	0.80	0.11
Survival	0.65	0.12	0.69	0.16	0.60	0.23
Development time	39.4	3.94	39.0	3.43	40.4	4.22
Mass	6.71	0.53	6.78	0.55	6.81	0.57
Femur	11.1	0.30	11.0	0.31	11.1	0.28
Pronotum	6.83	0.20	6.80	0.20	6.82	0.20

success between males, so that our expected values, which are based on equal fertilization success of males, are too low. However, if we calculate our expected values as the hatching success of the female with the highest hatching success of the single mated females, there is still no correlation ($r = 0.29$, $n = 40$, $P = 0.26$). Additionally, in another experiment (Wedell and Tregenza, unpublished manuscript) where males were mated to two different females, we found no correlation between hatching success of each male's two mates ($r = -0.24$, $n = 12$, $P = 0.44$).

Females in our additional group mated to a single male twice showed no difference in hatching success to those mated to the same male four times (two matings, $n = 38$, mean = 0.44 ± 0.03 SE; four matings, $n = 48$, mean = 0.41 ± 0.03 SE; comparison of arcsine-transformed proportions $t = 0.73$, $P = 0.47$).

With regard to the post hatching life histories of the offspring, there was an equal adult sex ratio (one sample t -test, $t = 0.83$, $df = 85$, $P = 0.41$). The sexes weighed the same (mean mass of both sexes = 0.673 ± 0.003 g), but differed in femur length (female = 11.16 ± 0.17 mm, male = 10.95 ± 0.20 mm; $t = 6.15$, $df = 2020$, $P < 0.001$), and pronotum width (female = 6.89 ± 0.11 mm, male = 6.75 ± 0.13 mm; $t = 8.58$, $df = 2134$, $P < 0.001$). Despite achieving the same mass, females reached adulthood quicker than males (females = 38.6 ± 0.15 days, males = 40.1 ± 0.15 days, $t = 6.90$, $df = 2144$, $P < 0.001$).

There were no detectable differences between treatments (see Table 1) The mean mass, pronotum width, and femur length of offspring from different females did not vary significantly between treatments (ANOVA, mass: $F_{2,85} = 0.296$, $P = 0.74$; pronotum width: $F_{2,85} = 0.483$, $P = 0.62$; femur length: $F_{2,85} = 0.668$, $P = 0.52$). Additionally, there was no difference in mean time to adulthood (ANOVA $F_{2,85} = 0.662$, $P = 0.52$); sex ratio (ANOVA $F_{2,85} = 1.13$, $P = 0.33$); or proportion of nymphs surviving to adulthood (ANOVA $F_{2,85} = 1.53$, $P = 0.22$). There were no differences between treatments in the level of variation between broods. Using Lewontin's log variance ratio test, for all comparisons between treatments $P \geq 0.4$.

DISCUSSION

There are two classes of hypotheses that might explain the observed increase in hatching success with degree of polyandry. These are variation in ejaculate characteristics other than their genotype (e.g., volume, sperm number, nutrients, hormones, etc.), or a genetic correlation between male fertilization success and genetic traits influencing offspring viability.

Because females in all treatments received the same total number of matings from males mating the same number of times, the first hypothesis (nongenetic) could explain our results only if females benefit from reduced variance in ejaculate properties. Variation between males in the quantity, viability, or nutrient content of inseminations will mean that polyandrous females tend to receive a total ejaculate quantity and (nongenetic) quality closer to the mean than those mated to a single male. This reduction in variance might be advantageous if there are diminishing improvements in hatching success with increased ejaculate quantities and qualities. For instance, if females are sperm limited, receiving more than a certain amount of sperm might not bring any additional benefits; females simply need to ensure that they receive enough to fertilize all their eggs. In this case, reduced variance may be advantageous even if the mean quantity of ejaculate received does not improve. The same argument could apply to other ejaculate characteristics, for instance females may need a threshold amount of some hormone (such as prostaglandin) contained in male inseminations (Leopold 1976).

We can test this hypothesis because it predicts a difference in proportional hatching success between females mated twice and four times to the same male. Unless there are extreme differences between individual males in their capacity to fertilize the female's eggs, any advantages of reduced variance will be minor compared to receiving half the mean ejaculate quantity (two vs. four matings). No such difference was found in our population: offspring of females mated twice to the same male had greater hatching success (although there was no significant difference) as those mated to the same male four times. Because we cannot detect a difference between two matings and four matings, it is unlikely that the differences we see between females mated to single males as opposed to those mated to multiple males with equal numbers of matings can be explained by the sperm-limitation or other nongenetic hypotheses. Because all males were the sole mate of one female, we know that although the decrease in variance of hatching success with number of mates indicates that males vary in traits affecting offspring viability, all the males were at least partially fertile. Microscopic examination of 100 eggs that failed to hatch showed well developed embryos in 33 eggs. This represents a conservative minimum because embryos dying early in their development could not be detected. With such a large proportion of fertilized eggs failing to develop, there is clearly the potential for the differences between mating treatments to be due to differences in offspring viability rather than paternal fertility.

The genetic variability hypothesis depends on males conferring higher viability also being more likely to fertilize eggs, because otherwise we would expect lower variance in

offspring viability of multiply mated females (as is seen) but no difference in mean viability. There are two possible processes that could create this scenario. Males may vary genetically, such that some individuals confer higher viability on their offspring regardless of their mate, with the sperm of these males more likely to fertilize the female's eggs (Madsen et al. 1992). Alternatively, there may be genetic incompatibility between certain pairs of mates, with females able to preferentially use the sperm of compatible males (Olsson et al. 1996a; Zeh 1997). We can attempt to distinguish between these hypotheses because only the intrinsic-male-quality hypothesis predicts that certain males should increase the hatching success of offspring regardless of the female to which they are mated. Our results suggest that this is not the case.

If certain males were intrinsically better fathers, we would expect a correlation between the hatching success of females mated to several males and expected values derived from females mated solely to each of the males. A male conferring high hatching success on a female when he was her sole mate would be expected to improve the hatching success of a female for whom he was one of several mates. This effect will be somewhat obscured by differential fertilization success of males conferring higher viability. However, the lack of a correlation between observed and expected values when assuming either equal fertilization success of all males or that only the male conferring highest hatching success fertilizes all the female's eggs suggests that certain males are not intrinsically superior. Rather, this result is consistent with the hypothesis that certain males are more compatible with certain females. This is supported by the lack of correlation between the hatching success of 12 pairs of females mated to the same male. Although this sample is too small to draw firm conclusions, the fact that the correlation is negative indicates that male influence on hatching success is unlikely to be repeatable across females.

We found no evidence for posthatching life-history differences between treatments (Table 1). There were also no differences in heterogeneity of broods between treatments. Sex ratio was unaffected by treatment, suggesting that if genetic incompatibility is the cause of lower hatching success in females mated to fewer males, it is not due to sex-linked segregation distorters (Lyttle 1991).

There are a number of possible reasons for genetic incompatibility between pairs in our population. Our laboratory population is likely to be subject to inbreeding; the population has been established for around 30 years, so it is possible that inbreeding avoidance mechanisms could have evolved in the laboratory. Additionally, the demography of natural populations may be such that inbreeding threatens offspring fitness in the wild. Alternatively, there may be other sources of genetic incompatibility such as cytoplasmic endosymbionts or transposable elements (Zeh and Zeh 1997a). We can only speculate on the mechanisms by which females mated to several males fertilize a greater proportion of their eggs with sperm from more compatible males. Females may be able to manipulate sperm utilization using information gained during mating. There are large differences between the sexes in cuticular pheromones (Tregenza and Wedell 1997), and it has been shown that females are capable of discriminating

between related and unrelated males (Simmons 1990). Therefore, it is possible that females make use of differences between males in their cuticular composition for mate assessment. Additionally, chemical properties of male ejaculates may be detected by females or simply cause reactions within them such that ejaculates conferring higher offspring viability are more likely to be used in fertilizing eggs. Regardless of the mechanism involved, it is clear that mating with several different males provides females with the opportunity to choose sperm from the most suitable of a number of potential fathers (Eberhard 1996). Precopulatory mate choice is known to occur in this species (Simmons 1987b). Any postcopulatory system will provide a further opportunity for females to maximize offspring fitness. Whether we are observing the benefits of active sperm selection by females or a passive process remains to be investigated.

ACKNOWLEDGMENTS

We thank R. Butlin, L. Keller, J. Mallet, J. Schneider, L. Simmons, and an anonymous referee for discussion and comments on the manuscript. NW was supported by grants from the Swedish Natural Science Research Council.

LITERATURE CITED

- ALEXANDER, R. D., AND D. OTTE. 1967. The evolution of genitalia and mating behaviour in crickets (Gryllidae) and other Orthoptera. *Misc. Publ. Mus. Zool. Univ. Mich.* 133:1-62.
- BOOMSMA, J. J., AND F. L. W. RATNIEKS. 1996. Paternity in eusocial Hymenoptera. *Philos. Trans. R. Soc. Lond. B.* 351:947-975.
- CHAPMAN, T., L. F. LIDDLE, J. M. KALB, M. F. WOLFNER, AND L. PARTRIDGE. 1995. Cost of mating in *Drosophila melanogaster* females is mediated by male accessory gland products. *Nature* 373:241-244.
- EBERHARD, W. G. 1996. *Female control: sexual selection by cryptic female choice*. Princeton Univ. Press, Princeton, NJ.
- GWYNNE, D. T. 1984. Courtship feeding increases female reproductive success in bushcrickets. *Nature* 307:361-363.
- KELLER, L., AND H. K. REEVE. 1994. Genetic variability, queen number and polyandry in social insects. *Evolution* 48:694-704.
- . 1995. Why do females mate with multiple males? The sexually selected sperm hypothesis. *Adv. Stud. Behav.* 24:291-315.
- KEMPENAERS, B., G. J. VERHEYEN, M. BAN DEN BROECK, T. BURKE, C. VAN BROEKHOVEN, AND A. A. DHONDT. 1992. Extra-pair paternity results from female preference for high-quality males in the blue tit. *Nature* 357:494-496.
- LEOPOLD, R. A. 1976. The role of male accessory glands in insect reproduction. *Annu. Rev. Entomol.* 21:199-221.
- LEWONTIN, R. C. 1966. On the measurement of relative variability. *Syst. Zool.* 15:141-142.
- LYTTLE, T. W. 1991. Segregation distorters. *Annu. Rev. Genet.* 25:511-557.
- MADSEN, T., R. SHINE, J. LOMAN, AND T. HÅKANSSON. 1992. Why do female adders copulate so frequently? *Nature* 355:440-441.
- OLSSON, M., T. MADSEN, R. SHINE, A. GULLBERG, AND H. TEGELSTRÖM. 1994. Rewards of promiscuity—reply. *Nature* 372:230.
- OLSSON, M., R. SHINE, T. MADSEN, A. GULLBERG, AND H. TEGELSTRÖM. 1996a. Sperm selection by females. *Nature* 383:585.
- OLSSON, M., A. GULLBERG, R. SHINE, T. MADSEN, AND H. TEGELSTRÖM. 1996b. Paternal genotype influences incubation period, offspring size and offspring shape in an oviparous reptile. *Evolution* 50:1328-1333.
- PARKER, G. A. 1992. Snakes and female sexuality. *Nature* 335:395-396.
- RIDLEY, M. 1993. Clutch size and mating frequency in parasitic Hymenoptera. *Am. Nat.* 142:893-910.
- ROST, R., AND H. W. HONEGGER. 1987. The timing of premating and mating behaviour in a field population of the cricket *Gryllus campestris* L. *Behav. Ecol. Sociobiol.* 21:279-289.
- SAKALUK, S. K., AND W. H. CADE. 1980. Female mating frequency and progeny production in singly and doubly mated house and field cricket. *Can. J. Zool.* 58:404-411.
- SIMMONS, L. W. 1986. Female choice in the field cricket, *Gryllus bimaculatus* (De Geer). *Anim. Behav.* 34:1463-1470.
- . 1987a. Sperm competition as a mechanism of female choice in the field cricket, *Gryllus bimaculatus* (De Geer). *Behav. Ecol. Sociobiol.* 21:197-202.
- . 1987b. Female choice contributes to offspring fitness in the field cricket, *Gryllus bimaculatus* (De Geer). *Behav. Ecol. Sociobiol.* 21:313-321.
- . 1988a. The contribution of male multiple mating and spermatophore consumption to the lifetime reproductive success of female field crickets (*Gryllus bimaculatus*). *Ecol. Entomol.* 21:313-321.
- . 1988b. Male size, mating potential and lifetime reproductive success in the field cricket (*Gryllus bimaculatus*) (De Geer). *Anim. Behav.* 36:372-379.
- . 1990. Pheromonal cues for the recognition of kin by female field crickets, *Gryllus bimaculatus*. *Anim. Behav.* 38:192-194.
- SOKAL, R. R., AND F. J. ROHLF. 1995. *Biometry*. Freeman, New York.
- STOCKELY, P., J. B. SEARLE, D. W. MACDONALD, AND C. S. JONES. 1993. Female multiple mating behaviour in the common shrew as a strategy to reduce inbreeding. *Proc. R. Soc. Lond. B Biol. Sci.* 254:173-179.
- THORNHILL, R. 1980. Rape in *Panorpa* scorpionflies and a general rape hypothesis. *Anim. Behav.* 28:52-59.
- TREGENZA, T., AND N. WEDELL. 1997. Definitive evidence for cuticular pheromones in a cricket. *Anim. Behav.* 54:979-984.
- WALKER, W. F. 1980. Sperm utilization strategies in non-social insects. *Am. Nat.* 115:780-799.
- ZAR, J. H. 1984. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, NJ.
- ZEH, J. A. 1997. Polyandry and enhanced reproductive success in the harlequin-beetle-riding pseudoscorpion. *Behav. Ecol. Sociobiol.* 40:111-118.
- ZEH, J. A., AND D. W. ZEH. 1997a. The evolution of polyandry. I. Intra-genomic conflict and genetic incompatibility. *Proc. R. Soc. Lond. B Biol. Sci.* 263:1711-1717.
- . 1997b. The evolution of polyandry. II. Post-copulatory defenses against genetic incompatibility. *Proc. R. Soc. Lond. B Biol. Sci.* 264:69-75.

Corresponding Editor: J. Mallet