Sexual Difference Theory: Mormon Crickets Show Role Reversal in Mate Choice

Abstract. *Male Mormon crickets produce a large spermatophore that the female eats. Spermatophore proteins are important to female reproduction, and females compete for access to singing males. Males reject most receptive females as mates, and those accepted are more fecund than rejected individuals. This role reversal in courtship is in contrast to the behavior of the sexes in katydid species in which the males produce small spermatophores.*

Modern evolutionary theory predicts that the differences between the sexes in mating behavior should be strongly influenced by the relative parental investment of the sexes in offspring (*1, 2*). In most species females take more risk and use more energy than males to enhance offspring survivorship and are usually the more choosy sex. Males usually compete for and court females. In a few species, males provide most of the parental care, and information, on some of these species, including insects (*3*), fish (*4*), anurans (*5*), and birds (*6*), reveals that at least a partial reversal in roles or the differences between the sexes occurs; females often are the competitive sex, and both sexes participate in courtship.

Insects rarely show paternal care (*7*), but males in several groups do provide prezygotic nourishment to the female at mating (*8, 9*). Male katydids (Orthoptera: Tettigoniidae) produce a large proteinaceous mass attached to a sperm-containing area that provides nourishment for the female (*10*). The female eats this spermatophore after mating (Fig. 1C) and uses the nutrients, in part, for reproduction (*11*). Mormon cricket (*Anabrus simplex* Haldeman) males have a very large spermatophore and lose up to 27 percent of their body weight as a result of spermatophore production. If female reproduction is limited by the availability of this nutrient, a reversal in the behavior of the sexes during mating would be expected. Results of a field study show that among Mormon crickets (i) females compete for access to singing males and (ii) males discriminate among females, preferring larger individuals that are likely to be more fecund. These findings demonstrate a sex role reversal in mate choice and mate competition for an insect species.

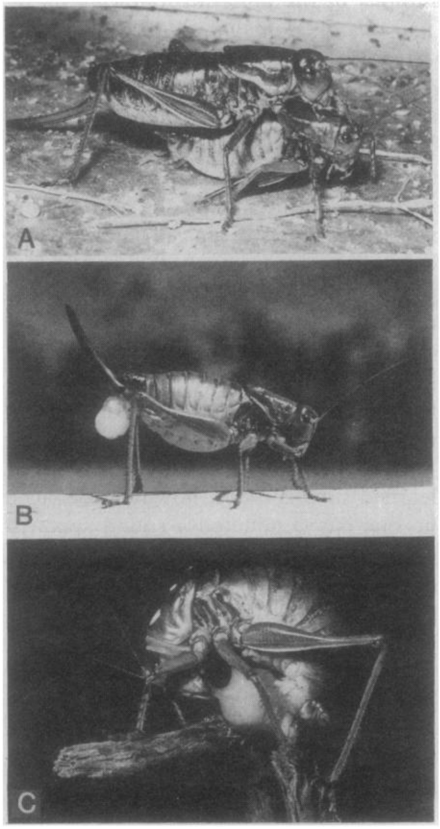

Fig. 1. A female Mormon cricket is shown (A) mounting a male, (B) with attached spermatophore, and (C) consuming the spermatophore.

The density of Mormon crickets at the study site (*12*) was very high, and, during the cooler daylight hours, most insects moved in a band that was approximately 500 m wide and contained up to 12 adults per square meter (*13*). Males that were ready to mate called from shrubs a short distance away (~ 5 to 20 m) from the band. Very few males called at one time, but overall 110 singing males were observed. (Mating was not observed in the band.)

One to three females responded quickly [1.95 ± 0.58 minutes (mean and 95 percent confidence interval), $N = 59$] to the singing male by moving rapidly over the ground and into the shrub from which the male called. If no female reached the male in a certain interval (4.32 ± 1.24 minutes, $N = 51$), the male left the perch and moved to another. In 11 of the 59 instances of female response, more than one female approached the male. In eight of these instances, the females interacted: in three cases, females pushed past one another, and in five cases, at least two females interacted aggressively by grappling.

In 45 of 52 male-female interactions observed, the female moved behind the male and mounted him and the pair coupled (Fig. 1A). In 29 of these 45 interactions, the male pulled away from the female after 1 to 2 minutes without transferring the spermatophore, and in 16 cases the female pulled away from the male as soon as the spermatophore was transferred (Fig. 1B).

In two instances, a pair made contact, but the female did not mount the male, and in four cases, the pair was hidden in vegetation before male rejection. In only one interaction did a female clearly abandon a male by leaving before mounting. A sample of rejected and mated females was collected (*14*). The mean weight of mated females (3.766 ± 0.275 g, $N = 22$, spermatophore removed) was significantly greater than that of rejected females (3.198 ± 0.304 g, $N = 17$) (Mann-Whitney U test, $P < .01$). These data suggest that males may assess the weight of females during mounting.

Males accrue advantages in mating with heavier females since these females are more fecund. In the sample of mated and rejected females there was a statistically significant positive correlation between female weight and both ovary weight and the number of mature eggs (*15*) (Fig. 2). The latter may be especially

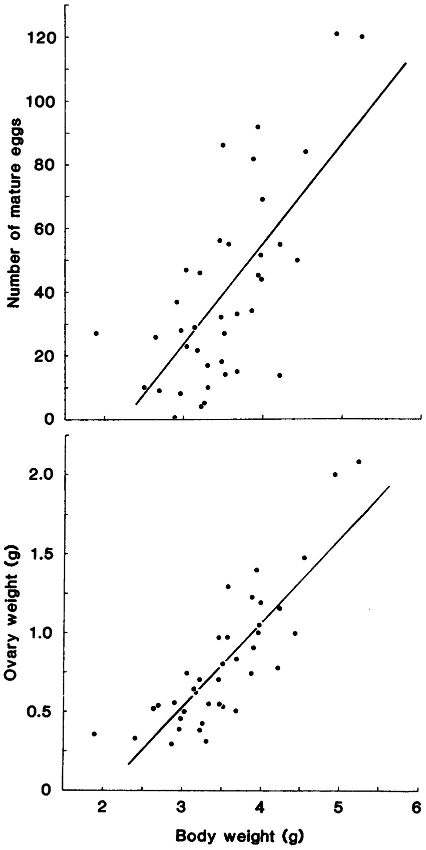

Fig. 2. Female weight plotted as a function of ovary weight ($r = .84$, $P < .01$; linear regression equation: $y = 0.54x - 1.09$) and the number of mature eggs ($r = .69$, $P < .01$; linear regression equation: $y = 31.8x - 72.1$).

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important since the male's sperm is very likely to fertilize almost all of the mature eggs that the female lays after mating (*16*). Among the variables that contribute to the variation in female weight, an important one is the large amount of fat noted in the abdomens of heavy females. A female with large fat reserves would be a good mate choice since she has demonstrated abilities to store resources in a situation where there is intense competition for food (*17*).

The tettigoniids are an ideal group in which to examine differences in sex roles within a discrete taxon. Neither sex of any species is known to exhibit care of offspring. Interspecific variation in female egg investment does not appear to vary as much as male contribution to spermatophores. Male weight loss per spermatophore ranges from 2 to 3 percent in some species (*18*) to 30 percent in others (*19*). There should, therefore, be differences in the behavior of the sexes of species with low male investment and those with high male investment. Studies of the reproductive behavior of katydids indicate that males of many species vigorously compete. Males of the genus *Orchelimum* space themselves acoustically and often fight for the best singing perches, that is, perches likely to have females nearby (*20, 21*). Females in the field often take several hours to select a mate (*21*). Male *Orchelimum* invest about 10 percent of body weight (*21*). *Copiphora rhinoceros*, a neotropical species, has a very large spermatophore; males of this species prolong courtship by repeatedly withdrawing from the female (*22*). Mormon crickets lose an average of 20 percent of their body weight. In this species, spermatophores are likely to be a limiting resource for female reproduction. Since food, especially protein sources, is vigorously contested by both sexes in the band (*17*), spermatophore nutrients may be very important to female reproduction. A behavioral sex role reversal with female competition and male mate discrimination results.

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References and Notes

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9. Although male prezygotic nutrient investments have been described as parental effort (*8*), it has been argued that these investments are mating effort because they are used to acquire mates (*2*). They are, however, a kind of mating effort that benefits the female's reproduction and reduces the male's maximum number of fertilizations. As a result, they should influence the evolution of sexual differences in a way similar to true parental investment such as parental care [D. T. Gwynne, in *Sperm Competition and the Evolution of Animal Mating Systems*, R. L. Smith, Ed. (Academic Press, New York, in press)].
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11. Spermatophore proteins are known to be important to female reproduction. Labeled spermatophore proteins are incorporated into the ovaries of grasshoppers [T. Friedel and C. Gillott, *J. Insect Physiol.* **23**, 145 (1977)] and butterflies [C. L. Boggs and L. E. Gilbert, *Science* **206**, 83 (1979)]. Research with my co-workers has shown that labeled amino acids from katydid spermatophores are used in both eggs and somatic tissues. Spermatophore and glandular feeding by female tree crickets increases the number of eggs they lay [P. Bell, thesis, University of Toronto (1979)].
12. The study was conducted about 12 km southeast of Greystone, Colo., in a high plains sagebrush area during July 1980.
13. Mormon crickets commonly reach pest status in the western United States, where they move in large feeding bands [F. T. Cowan, *U.S. Dep. Agric. Tech. Bull. 161* (1929); C. Wakeland, *U.S. Dep. Agric. Tech. Bull. 1202* (1959)].
14. Several females that had fresh spermatophores but were not observed mating were included in the sample. All specimens were frozen and later weighed, measured, and dissected. Spermatophores were removed before weighing.
15. There were no statistically significant differences in the average sizes (head widths and pronotum lengths) of rejected and mated females. The average ovary weight and number of mature eggs of mated females were larger than those of rejected females. These differences were not significant, however, probably because sample sizes were not large enough (Mann-Whitney *U* tests). No observable differences in the ages of mated and rejected females were noted. Both groups were over 10- to-12-day-old adults as judged by the techniques described by A. C. Neville [*Oikos* **14**, 1 (1963)].
16. In *Anabrus*, oviposition follows a mating [N. Criddle, *Can. Entomol.* **58**, 261 (1926)]. G. A. Parker [*Biol. Rev. Cambridge Philos. Soc.* **45**, 525 (1970)] has reported that the last male to mate in most insects obtains a higher proportion of egg fertilizations. D. T. Gwynne (*9*) has shown that the sperm of the last male usually has precedence in groups where males invest nutrients, parental care, and so forth [see also R. L. Smith, *Science* **205**, 1029 (1979)].
17. Optimum food plants located by individuals are eaten very quickly. Both sexes aggressively interact over the bodies of dead conspecifics (*13*).
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23. I thank P. Bell, G. Dodson, L. George, H. Evans, R. Thornhill, and B. Woodward for their criticisms of the manuscript. Supported by NSF grant BNS–7912208.

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Sparrows Learn Adult Song and More from Memory

Abstract. *Male swamp sparrows reared in the laboratory and exposed to taped songs during infancy produce accurate imitations of the material following an 8-month interval with no rehearsal. When the first rehearsal occurs, at about 300 days of age, large numbers of syllables are perfected. They are developed through invention and improvisation as well as imitation. Most are discarded at the time of song crystallization. Hence, these songbirds learn more than they manifest in full adult song.*

Many and perhaps all songbirds acquire the normal song of their species through learning (*1*). Some songbirds retain an ability to develop new songs throughout life (*2*). Others lose this ability early, so that songs developed at sexual maturity remain virtually unchanged over subsequent breeding seasons. Sensitive periods for vocal learning are commonly found; laboratory-reared birds of several species learn from taped songs played to them in infancy more readily than later in life (*3*). In some this occurs even though full song does not commence until late adolescence or adulthood. Thus certain songbirds may be said to display a remarkable capacity to learn to sing from memory. There is an early perceptual phase of listening to others and learning from them and a later phase of sensorimotor development in which birds monitor their own voice in perfecting song production.

In the sensorimotor phase, song does not spring forth fully formed, but is prefaced by a period of subsong (*4*). In some species subsong begins in infancy, and can follow soon after the perceptual phase. Insofar as subsong might involve rehearsal of memorized song themes, it could be viewed as bridging the gap between the perceptual and sensorimotor phases, alleviating any undue burden on the bird's memory.

The question of early rehearsal of learned song is moot, however, because no one has conducted a sound spectrographic study of the early stages in the development of singing. We undertook such an investigation in the swamp sparrow, *Melospiza georgiana*.

Male swamp sparrows brought into the laboratory as nestlings learn readily from taped songs of their species when these are played from the third to the eighth week of life. Full song develops some 9 months later and often contains a certain proportion of "syllables" that match components on the training tapes (*5*). The diverse morphology of natural