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Female Preference for Large Males in the Bushcricket *Requena* sp. 5 (Orthoptera: Tettigoniidae)

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Receptive females of the bushcricket Requena *sp. 5 (Orthoptera: Tettigoniidae) are attracted to male calls. In this experiment we investigate whether females discriminate between males on the basis of their calls. When virgin females were presented with two males of different size, they preferred the larger male. Larger males produce calls with a lower carrier frequency compared to smaller males, suggesting that females may use male carrier frequency as a predictor of male size. Furthermore, larger males produce heavier spermatophores. This suggests that females may prefer to mate with larger males to receive large nuptial gifts.*

KEY WORDS: female choice; spermatophores; acoustics; Tettigoniidae; body size; nuptial gift.

INTRODUCTION

Females may benefit in several ways by discriminating between potential mates. These benefits can either be indirect and related to "good genes," whereby females choose their mates on the basis of traits that may indicate heritable variation in viability (e.g., Watt *et al.*, 1986), or production of "sexy sons" (Fisher, 1930). Alternatively, females can gain direct benefits from males in the form of material goods or resources (e.g., Gwynne, 1982). It is therefore important to females, if males differ in quality, to find a "suitable" partner, and equally important for males to convey information regarding their quality to females in order to be chosen. In acoustic insects where receptive females are

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attracted by male calls, it is conceivable that females can use information conveyed in the song to make an assessment of the quality of different males (Crankshaw, 1979; Gwynne, 1982; Hedrick, 1986; Latimer and Schatral, 1986; Simmons, 1988a). In general, selection will favor signals that reveal reliable information about male quality and a preference for these traits in females (Zahavi, 1977; Grafen, 1990; Iwasa *et al.*, 1991).

During mating male bushcrickets (Orthoptera: Tettigoniidae) provide the female with a nuptial gift that she feeds on during insemination. In two bushcricket species it has been demonstrated that males provide nutrients in the spermatophore to the female that are used in egg production, thereby increasing the reproductive output of females (Gwynne, 1984; Bowen *et al.*, 1984; Simmons, 1990; Simmons and Gwynne, 1993). Positive correlations between male body size and spermatophore size have been documented for several bushcricket species (e.g., Gwynne, 1982; Gwynne *et al.*, 1984; Gwynne and Bailey, 1988; Wedell and Arak, 1989; Wedell, 1993). Hence, female bushcrickets may benefit by preferentially mating with larger males if larger males produce bigger spermatophores.

In many insect species larger males achieve a higher mating success than smaller individuals (e.g., see Borgia, 1980; Sigurjónsdóttir and Parker, 1981; Partridge *et al.*, 1987; Gwynne and Bailey, 1988; Simmons, 1988b; Gilburn *et al.*, 1992; Souroukis and Cade, 1993). However, the degree to which this skewedness is due to male–male competition and/or female choice is generally not clear. In crickets and bushcrickets it has been shown that larger males produce louder calls (Bailey and Thiele, 1983; Forrest, 1983; Bailey, 1985; Latimer and Sippel, 1987) or calls with a lower carrier frequency (Latimer, 1981; Latimer and Schatral, 1986; Latimer and Sippel, 1987). In several species of orthopterans it has been shown that females prefer the song of larger males (Morris *et al.*, 1978; Gwynne, 1982; Simmons, 1986; Latimer and Sippel, 1987; Bailey and Yeoh, 1989).

In this study we investigate whether females of an undescribed bushcricket species of the genus *Requena* discriminate between different males and whether males convey reliable cues that can provide information regarding male quality to females. Since females of the congeneric *R. verticalis* use nutrients transferred in the spermatophore to increase their reproductive output (Gwynne, 1984; Gwynne *et al.*, 1984), it is conceivable that females of the species in this study may benefit by mating with larger males if larger males provide them with bigger spermatophores containing more nutrients.

MATERIALS AND METHODS

The Animal. The bushcricket *Requena* sp. 5 is an undescribed listroscelidine bushcricket occuring in coastal and tableland areas in eastern Australia. Animals were collected from the New South Wales coast about 100 km south

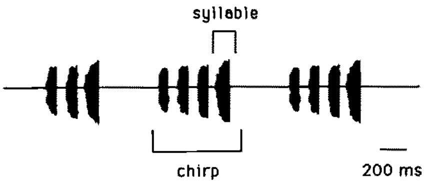

Fig. 1. A schematic oscillogram of a *Requena* sp. 5 call at 24°C. The call consists of several chirps containing three or four syllables.

of Sydney. Voucher specimens are deposited in the Australian National Insect Collection. Population densities can be as high as 5 singing males/m^3 in *Lomandra* bushes (N.W., personal observation), suggesting that females have ample opportunities to assess males.

Acoustics. Males produce a call by tegminal/tegminal stridulation. The call consist of several chirps, each containing three or four syllables (Fig. 1). Stridulation occurs during both the day and the night. However, the peak of activity in the laboratory, measured as the number of males singing at any one time, was greatest between 0900 and 1500 h. Therefore all experiments were carried out between these times. Each male was recorded at least once using a D-960 Ultrasound detector on time expansion mode at 24°C, connected to a Sony TC-D5M cassette recorder. The time-expanded signals (frequency-reduced 10 times) were analyzed on a Uniscan 4500 sonograph to determine frequency characteristics of songs. Temporal properties (i.e., chirp length) of the calls were measured directly from the screen (see Fig. 1). The spectral width of the syllables was measured at 50 kHz. For each male only three syllables were included in the statistical analyses since not all males produced chirps with four syllables (see Results).

Choice Experiments. Male size was established by measuring the length of the hind femur with a pair of digital calipers to the nearest 0.01 mm. All males were weighed (±0.1 mg) prior to the start of the choice experiments. All males and females were previously unmated. Virgin females were presented either with two males the same approximate size (weight difference less than 5 mg; $N = 11$) or with two males differing in size (weight difference between 50 and 110 mg; $N = 19$). The two males were placed individually in 9.5 × 4.5 × 3.5-cm black net cages placed 80 cm apart. After a 10-min habituation period a virgin female was introduced between the two males. This time was long enough to make sure that both males were stridulating. Females were allowed to make a choice during a 20-min period. A female was considered to have made a choice if she approached one of the stridulating males and moved on to the top of his net cage. A total of 30 trials with 17 females and 19 males was performed. None of the females were used more than twice; and none of the males were used more than three times. The room temperature was 24 + 1.0°C throughout the experiments. Results are given as means ± SE.

Spermatophore Size. After the choice experiments males were mated to virgin females. During mating, males transfer a spermatophore to the female.

The spermatophore consists of a sperm-containing ampulla attached to the female's genital opening and a sperm-free spermatophylax which the female feeds on following copulation, during which time insemination occurs. Spermatophore size was determined by weighing males and females to the nearest 0.1 mg on a precision balance (Sartorius 1602 MP) before and immediately following spermatophore transfer.

RESULTS

Body weight varied between 270 and 400 mg ($N = 19$) for males and 250 and 460 mg ($N = 22$) for females. Male femur length ranged between 11.7 and 13.7 mm. Not surprisingly, males with larger femur dimensions weighed more ($y = 37.8x - 137.5$; $r^2 = 0.4$, $N = 19$, $P = 0.0024$; Fig. 2). Males produce calls containing three or four syllables per chirp (Fig. 1). The first syllable in a chirp was between 70 and 170 ms long; the second, 70 and 195 ms long; and the third, 100 and 230 ms long. The first syllable was significantly shorter in duration compared to the second and third [repeated-measure ANOVA $F(2,38) = 16.4$, $N = 57$, $P = 0.0001$], but there was no difference in syllable length for all three syllables among the 19 males [$F(2,38) = 1.20$, $P = 0.3058$]. This suggests that syllable lengths may be a species-specific characteristic of the song. The mean peak carrier frequency was 22 kHz but varied between 17 and 30 kHz between males. There was a significant difference in the carrier frequency between males (repeated-measure ANOVA $F = 12.33$, $P = 0.0001$, $N = 19$), but not between the three syllables in a chirp of each of the 19 males ($F = 0.12$, $P = 0.883$). Furthermore, there was a significant negative relationship

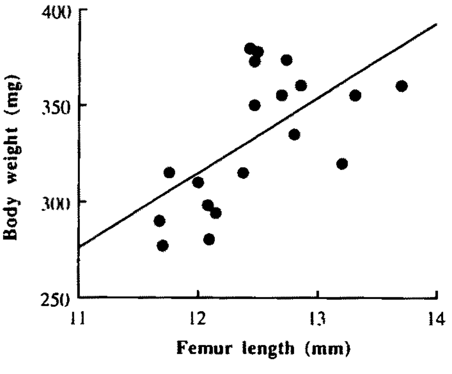

Fig. 2. Larger males weighed more. There was a positive relationship between male size and body weight: $r^2 = 0.4$, $N = 19$, $P = 0.0024$ ($y = 37.8x - 137.5$).

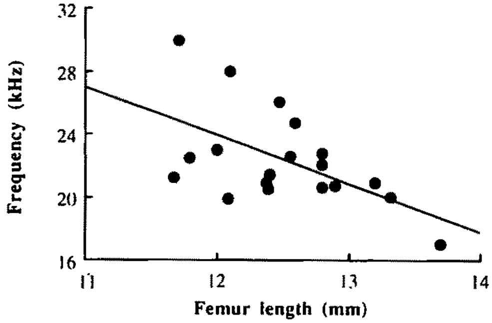

Fig. 3. Larger males produce calls with a lower carrier frequency: $r^2 = 0.3$, $N = 19$, $P = 0.0141$ ($y = 3.2x + 61.8$).

between a male's size and his carrier frequency, with larger males having calls with a lower carrier frequency ($y = -3.2 + 61.8$; $r^2 = 0.3$, $P = 0.0141$, $N = 18$; Fig. 3).

Of the 30 trials performed in this study, females were allowed to choose between different-sized males in 19 of these trials. In 16 of those females made a choice and in 14 of these 16 cases the female preferred the larger male (χ^2 $P = 0.0221$). Females made a choice in 7 of 11 trials in which there was no significant weight difference between the males. In three of these seven choices the females moved toward the slightly larger male (χ^2 $P = 0.7887$). Preferred males in trials where males were of different sizes had significantly lower carrier frequencies than rejected males (paired t test $t = 2.20$, $P = 0.0416$, df $= 14$; Fig. 4).

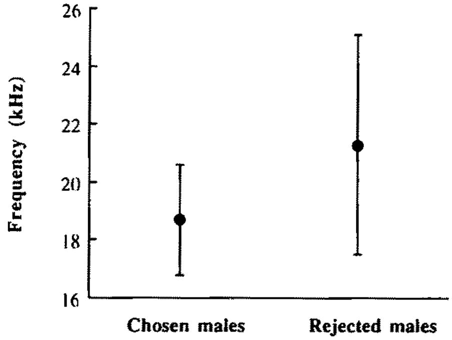

Fig. 4. Females prefer to mate with males with a lower carrier frequency. Chosen males had a significantly lower carrier frequency than rejected males (paired t test $t = 2.20$, df $= 14$, $P = 0.0416$).

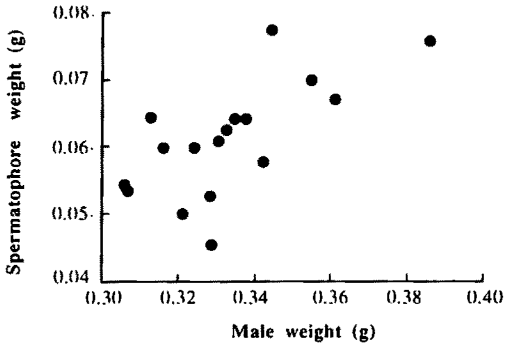

Fig. 5. Heavier males produce bigger spermatophores. There was a positive correlation between male body weight and spermatophore weight: $r = 0.67$, $N = 17$, $P = 0.0032$.

At their first mating, males produced spermatophores representing on average 18 ± 0.6% of their body weight (range, 12.7 to 22.5%; $N = 17$). There was a positive correlation between spermatophore weight and male weight before mating ($r = 0.67$, $P = 0.0032$, $N = 17$; Fig. 5), with larger males producing heavier spermatophores.

DISCUSSION

In the present study we investigate whether females discriminate between males. When males differ in size, females seem to assess male size and moved toward the larger individuals. Several studies have shown that females of acoustic species prefer to mate with larger males [e.g, frogs (Ryan, 1985; Robertson, 1986) and insects (Morris *et al.*, 1978; Gwynne, 1982; Simmons, 1986; Latimer and Sippel, 1987; Bailey and Yeoh, 1989)]. It has also been demonstrated that females tend to choose the most active signalers (Arak, 1983; Arak *et al.*, 1990; Greenfield and Roizen, 1993) or the first male encountered (Arak, 1988; Arak *et al.*, 1990). Moreover, singing activity and male body size have been found to be positively correlated in several species (Simmons, 1988a; Arak *et al.*, 1990; Sakaluk and Snedden, 1990). In the present study, both males in the mate choice experiments stridulated throughout the trials, thereby minimizing the possibility that singing activity in itself may have influenced the choice made by females.

By approaching males singing with what females may perceive as the loudest call, which often is the nearest male, females will minimize the distance they are required to move. This process, termed "passive attraction" by Parker

(1982, 1983), is sufficient to explain why females would "prefer" certain males without assuming any other relationship between the characteristics of a male's calls and possible indirect or direct benefits to females. The population densities of *Requena* sp. 5 is high in the field, with up to 3–5 males/m^3. However, it is not known if females approach the closest male in the field, possibly to minimize their search costs (Searcy and Anderson, 1986), and discriminate between males only when they are calling from an equal distance. Since the amplitude of the calls (SPL) was not measured, this study cannot distinguish active female choice (i.e., choice on the basis of carrier frequency) from passive attraction to the loudest calling male in this species. It has also been shown that the amplitude of the song is positively correlated with male body size in several species (Bailey and Thiele, 1983; Latimer and Schatral, 1986). Thus, on average females may "choose" the largest male by moving toward males producing calls with the highest perceived amplitude.

Females discriminate between males on the basis of their size, and moved toward larger males that had a lower carrier frequency. Carrier frequency has been shown to be a reliable indicator of male size in other bushcricket species (Bailey, 1985; Latimer, 1981; Latimer and Schatral, 1986; Latimer and Sippel, 1987). Rejected males had a significantly higher carrier frequency than preferred males, indicating further that females may use carrier frequency when assessing males. In a congeneric species, *R. verticalis*, it was found that paired males in the field had a significantly lower carrier frequency compared to unpaired males, which were also significantly smaller, indicating that larger males may have a mating advantage in the field (Schatral, 1990). However, it is not clear whether the higher mating success of larger males in this species is the result of female choice or male–male competition. In a phonotaxis experiment females failed to show any preference for males with lower frequencies (Bailey and Yeoh, 1989), and in yet another study females approached the closest male, which were calling louder (Bailey *et al.*, 1990).

Heavier males produced larger spermatophores. Positive correlations between male body size and spermatophore size have been documented for several bushcricket species (e.g., Gwynne, 1982; Gwynne *et al.*, 1984; Gwynne and Bailey, 1988; Wedell and Arak, 1989; Wedell, 1993; but see Tuckerman *et al.*, 1993). Larger spermatophores may be beneficial to females in several ways. For example, in *R. verticalis* females use male-derived nutrients in subsequent egg production, and larger spermatophores increase a female's reproductive output (Gwynne, 1988). In *R. verticalis* spermatophore and male size are correlated (Gwynne *et al.*, 1984), and spermatophore consumption affects the fitness of the female's offspring by increasing their hatching success after winter diapause (Gwynne, 1988). Females may also benefit by mating with larger males if male body size is an indicator of high viability or survival. In *R. verticalis* Gwynne (1988) found that females mating with larger males that provided larger amounts of spermatophore material also tended to produce larger sons. This represent a fitness gain for the female, since large body size is correlated with reproductive success in this species.

Maynard Smith (1991) has argued that female choice is more likely to occur in situations when variation in the phenotype of males will have a direct benefit to female fecundity compared to indirect benefits related to possible future effects on the genotypes of the female's offspring. It is not known to what degree spermatophore consumption in *Requena* sp. 5 affects the reproductive success of females. The spermatophore represents on average about 18% of male body weight, which is very similar to that of *R. verticalis* [≈ 19% (Gwynne, 1986)]. Furthermore, the spermatophore of *Requena* sp. 5 has a high protein content, 20% wet weight (Wedell, 1994), compared to 13.5% for *R. verticalis* (Bowen *et al.*, 1984), suggesting that females may receive a fairly substantial amount of nutrients that may potentially affect their reproductive output. These findings indicate that the presence of female choice in this species may be the outcome of female preference for males providing large nuptial gifts, although additional work is needed to explore this possibility.

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