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FEMALE-FEMALE COMPETITION IN KATYDIDS: SEXUAL SELECTION FOR INCREASED SENSITIVITY TO A MALE SIGNAL?

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Abstract.—In contrast to studies of sex-specific weaponry and other sexually selected traits, there has been no examination of Darwin's (1871, p. 418) suggestion that elaborations or enlargements of "the organs of sense" function to enhance mating success. In certain katydids the size of thoracic spiracles, which are a main input into the hearing system, determines auditory sensitivity of females. Here we present evidence that sexual dimorphism in the spiracle size of a pollen katydid, *Kawanaphila nartee,* is a result of sexual selection on females competing to locate nuptial-gift giving males. In field experiments in which female *K. nartee* were attracted to a calling male, we show a pairing advantage to females with larger auditory spiracles. The spiracle-size advantage was not a correlated result of a larger body size or mass of winners. Finally, there was no spiracle-size advantage or body-mass advantage for mating females in a later stage of competition when experimental females struggled for access to a silent male. We suggest that research on the detection of displays has lagged behind work on the displays themselves; the focus has been on the species specificity of signal perception rather than on the fitness consequences of variation in the ability to detect cues from mates or predators.

Key words.—Auditory sensitivity, courtship role-reversal, mate-feeding, sexual selection, Tettigoniidae.

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Darwin's (1859, 1871) argument that sexual selection causes sexual dimorphism in mating displays and characters that function in sexual contests has been well supported in studies that relate variation in these reproductive traits to mating success (Clutton-Brock 1988; Andersson 1994). However, no study of mating success has tested Darwin's (1871, p. 418) hypothesis that "The sexes, also, often differ in their organs of sense . . . so that the males may quickly discover . . . the females" (see also Thornhill and Alcock 1983; Andersson and Iwasa 1996).

Darwin's and most of the subsequent observations of sexual selection and sexual dimorphism have dealt mainly with elaborated traits of males (Andersson 1994), but recent work with some species has revealed behavioral and other evidence of strong sexual selection on females (reviews in Gwynne 1991; Owens and Thompson 1994; Kvarnemo and Ahnesjö 1996). This research on female sexual selection has focussed on male mating preferences, with less attention being paid to characters important in direct "scrambles" and "contests" (Andersson and Iwasa 1996) between females for access to males (e.g., Hieber and Cohen 1983; Johnson and Hubbell 1984; Lawrence 1986; McLain and Boromisa 1987; Svensson and Petersson 1988; Wiernasz 1995). In this paper we examine competition between female katydids, *Kawanaphila nartee* (Orthoptera: Tettigoniidae) for access to singing males and show a mating advantage for females with larger spiracular ears, structures that are directly related to auditory sensitivity in females of another katydid (Bailey 1998).

In katydids such as *K. nartee* there is both choice of males by females and direct competition between females. This reversal in the typical mating roles occurs only in food-stressed populations because there are more sexually active females than males due to a relative scarcity of males able to produce a nuptial meal—the spermatophylax that envelops the spermatophore—and hungry females have an increased propensity to forage for these mating meals (Gwynne 1990, 1993; Gwynne and Simmons 1990; Simmons and Bailey 1990).

Sexual competition among female katydids begins with the race to locate a singing male, that is, one able to supply a spermatophylax meal (Gwynne 1981, 1984; Simmons and Bailey 1990). Traits that aid in swift detection or location of the caller, such as increased auditory sensitivity, should provide an advantage, particularly in populations of *K. nartee* showing role reversal. In these populations males reduce their continuous calling song to an occasional, brief "click" when the encounter rate with sexually responsive females is high (see Results). Some evidence that sexual selection may have operated on the auditory system of female *K. nartee* is a sexual dimorphism in the auditory system. Females have higher auditory sensitivity to calls than males because they possess large, open auditory spiracles on the thorax. In contrast, male thoracic spiracles are small, closed structures, which is typical of spiracles with a respiratory function. Moreover, males lack the horn-shaped tracheae associated with the spiracles in females (Bailey and Römer 1991). Enlarged tracheae in female *K. nartee,* and both sexes in certain other katydids, function in amplifying sound into the auditory system (Bailey 1990, 1993). Variation in the size of this important spiracular input into the ears explains almost half of the substantial variation in female sensitivity to the male call in another katydid, *Requena verticalis* (Bailey 1998).

A later stage of competition between female *K. nartee* occurs when a female locates a rival who has mounted a male. In subsequent struggles on top of the male (Fig. 1) calling is rare. During the approximately 30 min mounting phase of mating, that is, before the spermatophore is transferred (Gwynne and Bailey 1988), the mounted female uses the base of her ovipositor to grasp the male in a "genital hold" but can still be unseated in subsequent interactions with rivals (Fig. 1) (Simmons and Bailey 1990; Gwynne et al. 1998). Size should be important in female interactions at any stage

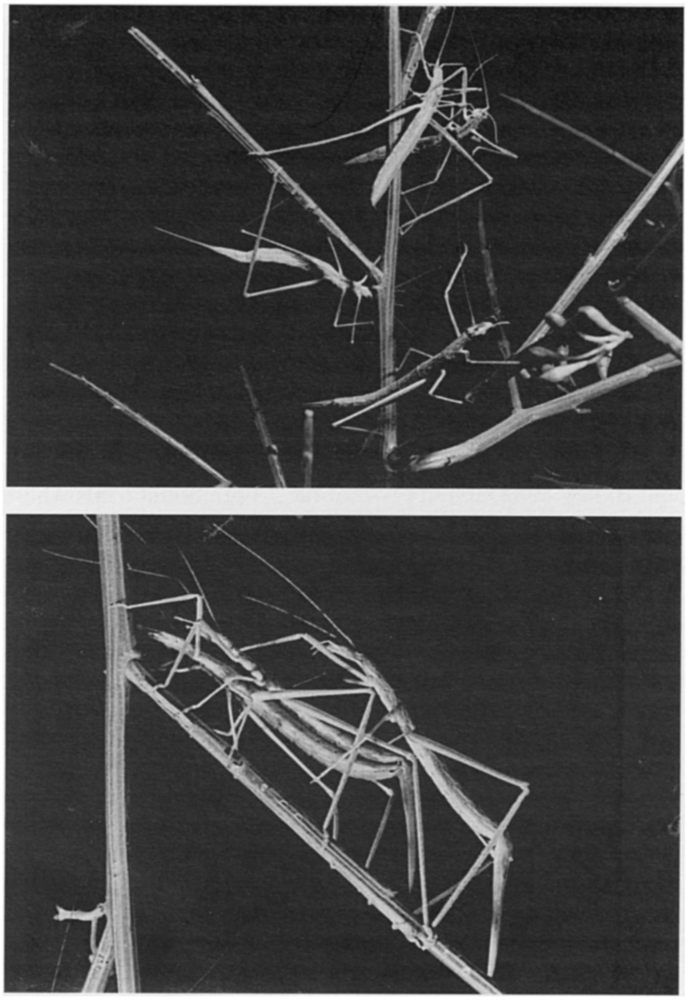

FIG. 1. Top: Three female *Kawanaphila nartee* approach a male (top) who has just stopped calling. Note the slightly arched abdominal tips of the responsive females. Bottom: A female mounts a mated pair. The mating female has grasped the male in a genital hold.

of competition because large mass is an advantage in struggles between female *K. nartee* over food (i.e., pollen; Simmons and Bailey 1990) and, in another katydid, larger females tend to win fights for calling males (Gwynne 1984).

Our present study uses experimental males to elicit sexual competition between females in nature and tests the hypotheses: (1) that female *K. nartee* with larger auditory spiracles have a mating advantage because they can more swiftly locate the caller; and (2) that larger females should win in struggles for access to sexually responsive males.

STUDY SITE AND METHODS

Kawanaphila nartee is a common nocturnal insect in Kings Park (Gwynne et al. 1988; Rentz 1993), 400 ha of natural bushland in the center of Perth, Western Australia (Main and Serventy 1957) and the site of all previous studies of this species of pollen-eating katydid (subfamily Zaprochilinae). We conducted three experiments in October and November 1993 in the "few-flowers" site, where little pollen was available and sexually responsive females greatly outnumbered responsive males (Gwynne et al. 1998). In all experiments, trials began by attracting females to a calling male caged in a 5-liter plastic jar with panels of fiberglass screen (which allowed the call to radiate freely from the cage). No male was used in more than one trial. There were many responsive females present at the site; males that called continuously attracted from one to 14 (median = 2) females in the first two minutes of calling (n = 22 males). In our first two experiments we allowed females to interact, timed the period during which these interactions occurred, and recorded whether the male produced continuous or click calls. The ultrasonic call was detected using an a QMC Mini Bat Detector set to the call's main frequency of 50 kHz (Gwynne and Bailey 1988).

Our first experiment examined spiracle size and other differences of winners and losers during competition for a calling male, that is, before he was mounted by a female. In this premount experiment the speed of the female response to the caller was expected to be important both during initial pair formation and especially later, after the females had made contact and the male reduced his signal to the occasional "click" when separated from the grappling females. In each of the 22 trials we waited until at least two females were attracted to the calling cage, then removed the top of the cage to allow the calling male to interact with two females while crawling along a grass stem into the natural vegetation above the cage. We ended each trial after one female—denoted the winner—had mounted the male and grasped him in a genital hold. In 20 of the 22 trials we monitored behavior and determined whether males called after they contacted the female. In this premount experiment we predicted both a large ear and a body-size advantage for the winning female.

The second experiment examined differences between winners and losers in a late stage of mating, when males usually do not sing; and therefore a spiracle-size advantage was not expected. We released a responsive female near a mounted pair. For each of the 25 trials in this postmount experiment, we waited until at least two females were attracted to the caged caller, then released the male and allowed just one haphazardly selected (i.e., statistical random selection methods were not used) female to mount the silent male and genitally hold him. At this point, one of the other responsive females was selected haphazardly and allowed to crawl onto a grass stem that was placed next to the mounted pair. Responsive females were recognized by their ovipositor being slightly depressed in apparent preparation for the genital hold (Fig. 1). The two females were allowed to struggle over the male and to interact. We recorded whether the initial pair broke up and we continued the trial until one of the females (the winner) had mounted the male and received a spermatophore from him. We monitored female behavior in 15 of the 25 postmount trials and whether males called in these trials. In this postmount experiment we predicted a body-size advantage, but no advantage for females with large auditory spiracles because the male was almost always silent.

Our third experiment was a control that determined whether the breakup of the mounted pair in the postmount experiment can occur in the absence of a rival female, for example, through rejection by the male (Gwynne and Simmons 1990;

Simmons and Bailey 1990). Ten females were attracted to callers and allowed to interact with them in the absence of competition from other females.

Winning and losing females in pre- and postmount experiments were captured and weighed alive to the nearest 0.1 mg and then frozen for later measurements in the laboratory. Female body mass did not include spermatophore mass. Our measure of the open auditory spiracle in females was the diameter of the circular opening. We also measured pronotum length, a reliable measure of body size in this species (Simmons and Bailey 1990). Spiracles were first measured using an ocular micrometer in a stereoscope. Because the spiracle is such a small structure, its diameter was measured a second time (both people being unaware of the winner or loser status of the specimens) from a video image digitized into a computer using NIH Image 1.60 (a program developed at the U.S. National Institutes of Health and available on the Internet at http:\\rsb.info.nih.gov\nih-image\). The correlation between the two estimates of mean spiracle diameter (Pearson's *r)* was 0.75 ($P < 0.001$, $n = 90$). Finally, we compared the condition of winning and losing females by comparing the residuals from the regression of female body mass on pronotum length ($F = 13.9$, $P < 0.001$, $n = 94$).

Most dependent variables were found to be normally distributed (Lillifor's tests, $P > 0.05$). We analyzed winner-loser differences in body measurements for the pre- and postmount experiments using paired tests (*t*-tests and Wilcoxon). The power of these tests was determined using the method of Zar (1996). Mean ± SE are used to describe normally distributed variables and medians ± ranges for nonnormal data. Because we had a second measure of both auditory spiracles, we analysed the mean size of the two spiracles using repeated-measures analysis of variance with two trial factors: the two estimates of mean spiracle size and the two females in each trial, winner and loser. This analysis also controlled for the effects of body size on ear size by including the covariate, difference in pronotum length (winner minus loser) (our statistical analyses used SYSTAT; Wilkinson 1990). Because winners and losers were compared with respect to four size variables in each experiment (ear size, pronotum length, body mass, and condition), we applied sequential Bonferroni corrections to alpha levels in the four tests within the pre- and postmount experiments.

RESULTS

Male Calling in Pre- and Postmount Experiments

Our study compared the initial female-female competition, which occurred when males called, to a later stage of mating when calling was not expected. Observations of mating confirmed this difference in male behavior. Males called in each of the 20 premount trials in which we continuously monitored the behavior of males, but only once in the 15 observed postmount trials. In all 22 premount trials males called not only before females were attracted, but also after attraction in 14 of the 20 trials in which male behavior was continuously observed. Singing after mate attraction in premount trials occurred when the male withdrew or was otherwise separated from a potential partner due to aggressive interactions in which females pushed against each other (in 11 of the 20 trials), or flailed at each other with legs (in five of the 20 trials). These physical interactions between females in trials in which the male stridulated after female attraction resulted in a median time of 6.5 min (range: 2–42 min, $n = 14$) before one of the females finally mounted and genitally held the male. In the six trials where males did not stridulate after female attraction the time until mounting was significantly shorter (median = 2 min, range 0.5–2.0 min: Mann-Whitney $U = 1.5$, $P = 0.002$). Stridulation after mate attraction in the premount trials and the single postmount trial usually sounded to our ears (via the bat detector) like a single, brief click. This appears to be a song with less risk of predator-attraction (see Burk 1982), that is produced by a male after detecting the presence of responsive females. After mate attraction, clicks changed to the continuous calling song (a rapid series of double clicks) typical of lone *K. nartee* males (Gwynne and Bailey 1988) in only two of the 14 premount trials where calling occurred after pairing. In response to male stridulation (both types), all females observed in the vicinity of the male immediately oriented to and moved toward him.

Premount Experiment

As predicted, in the premount experiment the mean diameter of the auditory spiracles of the winner (the first female to genitally hold the male) was significantly larger than that of the loser (within-trial difference between winner and loser: $F_{1,20} = 11.56$, $P = 0.003$, using a corrected $\alpha = 0.013$). For the first measure, winners had a spiracle diameter of 0.243 ± 0.005 mm ($\bar{x} \pm$ SE) and losers of 0.220 ± 0.007 mm; for the second measure, winners had a spiracle diamter of 0.238 ± 0.005 mm and losers of 0.215 ± 0.007 mm. There was no significant difference between these two estimates of mean spiracle size for each female ($F_{1,20} = 2.94$, $P = 0.10$), and none of the two- and three-way interactions between factors and the covariate were significant (for all, $P > 0.3$). The difference in spiracle size between winners and losers was not a result of a correlation with a larger body size of winners: there was no significant effect of the covariate, pronotum length, on spiracle size ($F_{1,20} = 0.35$, $P = 0.56$), and a separate paired test showed no significant difference between the pronotum length of winners (median length = 2.30 mm) and losers (median length = 2.25 mm) ($n = 22$, Wilcoxon signed-ranks test = 5.0, $P = 0.86$, $\alpha = 0.016$). Also, for the population of females sampled in both pre- and postmount experiments, there was no significant correlation between mean spiracle diameter and either body mass ($r = 0.08$, $P = 1.0$) or pronotum length ($r = 0.14$, $P = 0.56$; $n = 87$).

Finally, in this premount experiment there was no significant body-mass advantage or any difference in the condition of winners and losers (residuals from body mass x pronotum length regression, see Methods): the body mass of winners was 63.61 ± 1.52 mg and of losers was 62.12 ± 1.66 mg ($t_{21} = 0.69$, $P = 0.5$) and the condition of winners was 0.42 ± 1.55 and of losers was −1.19 ± 1.44 ($t_{21} = 0.85$, $P = 0.4$, corrected $\alpha = 0.016$). Although not significant, the winning females showed a trend to have greater values in each case (mass, size, and condition). However, the tests of these hypotheses were not strong because the statistical power was low ($P \ll 0.50$ for each).

Postmount Experiment

In 23 of the 25 postmount trials the intruding female interacted with the mating pair by mounting the rival (mating) female at least once (Fig. 1). While mounted, the intruder typically moved her body up and down, side to side, or back and forth. Females also pushed against the mated pair. In 19 of the 25 trials the mated pair broke up in a median 6.0 min (range = 0.3–14.3) after introduction of the intruding female. Because there were no breakups of the 10 control trials (in which the male interacted with just one female), we conclude that it was the presence of the intruder that caused the pair to separate. In the 19 breakups in postmount trials, the intruder succeeded in mating with the male in 11 trials, whereas the "resident" female secured the male in eight. Thus, the resident female mated in 14 of 25 trials.

Our prediction about a body-mass advantage in postmount trials was not supported. There was no difference overall in body mass of winners (the female receiving a spermatophore) (61.60 ± 1.73 mg) and losers (61.90 ± 1.81 mg; paired $t_{24} = 1.33$, $P = 0.2$) or in condition of winners (0.66 ± 1.5) and losers (0.02 ± 1.75; paired $t_{24} = 0.3$, $P = 0.8$, corrected $\alpha = 0.013$). There was also no difference in the body mass of winners (61. 9 ± 3.0 mg) and losers (60.2 ± 2.7 mg) in the small sample of 11 trials where breakups occurred and the intruder won (paired $t_{10} = 0.47$, $P = 0.64$).

Male singing played virtually no role in the interactions in postmount experiments, and we found, as expected, no differences in the mean diameter of the auditory spiracles of winning and losing females (within-trial difference between winner and loser, $F_{1,21} = 2.42$, $P = 0.14$, $\alpha = 0.013$). For the first measure winners had a spiracle diameter of 0.224 ± 0.005 mm and losers of 0.232 ± 0.007 mm; for the second measure, winners had a spiracle diameter of 0.221 ± 0.004 mm and losers of 0.228 ± 0.005 mm. There was no significant difference between the two estimates of mean spiracle size ($F_{1,21} = 0.45$, $P = 0.51$) and none of the two- and three-way interactions between factors and the covariate were significant (for all, $P > 0.3$). Finally, there was no significant effect of the covariate, pronotum length, on spiracle size ($F_{1,21} = 3.01$, $P = 0.10$) and no difference between the pronotum lengths of the 25 winning and losing females (median of winner = 2.15 mm, loser = 2.12 mm, Wilcoxon = 37.5, $P = 0.17$, $\alpha = 0.013$).

As in the premount experiment, although the differences were not significant, the winning female tended to be larger and in better condition (in three of four comparisons). Again, however, the power of these tests was very low ($P \ll 0.50$).

DISCUSSION

Sexual dimorphism in the thoracic auditory system of the pollen katydid, *Kawanaphila nartee,* is unusual among singing insects (including other genera of pollen katydids: Bailey and Römer 1991; Rentz 1993) and reflects a history of different selection pressures on male and female ears. Our results suggest that the maintenance of a fully functional hearing system in female *K. nartee* is due to sexual selection acting on sensory structures in the way that Darwin (1871, p. 418) first suggested, to "quickly discover" the signaling sex. In the *K. nartee* population that we studied, females with large auditory spiracles gained a pairing advantage during the early stages of sexual competition for the fecundity-enhancing nuptial meals (Simmons 1990) available from singing males. Given the greater sensitivity of large auditory spiracles (in *Requena verticalis*; Bailey 1998), it seems likely that this pairing advantage was due not only to rapid responses during the initial female race to the continuous call, but also in further sorting among female phenotypes when relocating the male after losing contact with him, that is, during the average 6.5 min before copulation when interacting rival females reoriented several times to the greatly reduced "click" song of the reclusive male.

An alternative hypothesis for the large-spiracle advantage in the premount experiment is that the larger spiracle size of winning females is correlated with a larger body size of winners. This alternative can be rejected because size was controlled in the analysis of spiracle size and we found no evidence of a competitive advantage for large body mass or size. The lack of a size or condition advantage in both pre- and postmount experiments was unexpected; we predicted such an advantage because heavier female *K. nartee* win in fights over pollen (Simmons and Bailey 1990). The body measure of the winner was (nonsignificantly) larger in six of seven comparisons in our experiments. Because the power of these tests was low, a larger sample size would be required to detect a possible real advantage.

Because our results are correlative, it remains possible that as-yet-unmeasured traits in females, such as their ability to detect male chemical cues, may explain the pairing advantage in reproductive competition. Such traits would have to be positively correlated with spiracle size, which seems unlikely.

The importance of sensitive ears to competing females in unmanipulated natural populations depends on a number of factors. First, because our measure of success in the premount experiment was a genital hold on the mounted male and many postmount experimental pairs were disrupted by the rival, the actual proportion of disrupted mountings in nature may affect the reproductive success of mounted females with sensitive hearing. The only field estimate of the potential for disruption of pairs in role-reversed populations of *K. nartee* is by Simmons and Bailey (1990), who reported multiple females attracted to callers in only 15% of observed cases of pair formation. Proportion of disruptions is expected to increase with higher population density (and density varies greatly; see Shelly and Bailey 1995).

Secondly, a high rejection rate by males during the mounting phase may reduce the mating success of the more sensitive females. Although over a third of mating females were rejected by males at this stage (in natural populations: Simmons and Bailey 1990), we did not observe rejection in our 10 single-female control matings, probably because these control males were well fed and isolated from females prior to the experiment. Males in pre- and postmount experiments experienced the same pre-trial conditions as control males. However, the subsequent high encounter rate with experimental females by pre- and postmount males appeared to cause some of these males to become more choosy (as has been demonstrated experimentally with this species; see Shelly and Bailey 1992). Male rejection of females was noted in three of these trials, and our premount males showed coyness after encountering more than one female by retreating from them and reducing postpairing stridulation to brief clicks.

A selective advantage may even accrue to males that favor females with large spiracles (perhaps by stopping calling when the first female arrives). If spiracle size has a heritable component, these males may gain by siring daughters with enhanced mate-locating abilities. Additionally, males may gain if daughters with large spiracles are genetically superior individuals that can overcome possible phenotypic costs of maintaining large open spiracles, for example, increased susceptibility to tracheal mites (Bailey and McCrae 1978) or water loss. The hypothesis that females with sensitive hearing gain a mating advantage assumes some cost to female *K. nartee* in maintaining constantly open auditory spiracles, a cost that prevents all females from achieving a maximum spiracular opening; all other spiracles (e.g., in the abdominal respiratory system) are almost fully occluded by valves, as are the auditory spiracles of conspecific males (Bailey and Römer 1991; Bailey and Simmons 1991).

Our conclusions about sexual selection on the sensory systems of female *K. nartee* can be generalized to other systems in which members of one sex compete when using long-distance signals in the race to locate the opposite sex. For example, sexual selection on males seeking out the calling signal of the female is thought to explain sexual dimorphism in antennal elaboration of certain insects (e.g., Thornhill and Alcock 1983); individual male mosquitoes and moths with more elaborate or larger antennae are expected to respond more quickly to, respectively, the sounds and calling pheromones of conspecific females. Furthermore, in taxa that parallel *K. nartee* in exhibiting a role-reversed mating system, there should be an advantage to competing females that are quick to perceive the sexual signals from males offering goods or services such as paternal care. Signals might include acoustic calls (e.g., midwife toads: Bush et al. 1996; Bush and Bell 1997) or visual displays (giant water bugs: Smith 1979).

In one important sense, research on perception of displays has lagged behind work on the displays themselves. In contrast to the study of the receptors, the focus of research on signal structure has changed from an interest in the species specificity to the emphasis of behavioral ecology—the importance of display variation (Zahavi 1979). A productive area for future research in sensory ecology will be the fitness consequences of variation in the abilities of animals to detect the signals of mates as well as predators.

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