Journal of Insect Behavior (© 2007)
DOI: 10.1007/s10905-007-9076-1

Sex Differences in "Time Out" from Reproductive Activity and Sexual Selection in Male Bushcrickets (Orthoptera: Zaprochilinae: *Kawanaphila mirla*)

Gerlind U. C. Lehmann[1,2] and Arne W. Lehmann[1]

Animals of many species prefer some partners over others. Discriminating among potential mates causes strong sexual selection that shapes characters and behaviors. In bushcrickets the sexes shows different latencies to remate due to differences in investment in production of the nuptial gift by males and the induced refractory period in females. We conducted experiments with the Australian bushcricket Kawanaphila mirla *to test the variation in male mating success by female choice.*

Male remating intervals under unlimited access to food and mates were around two days, whereas most females did not remate within 12 days. Males had therefore a much shorter "time-out" from mating than females. The adult sex ratio from field samples was near to 1:1. Consequently, the OSR was male-biased with more males than females ready to mate. This male-biased OSR led to mating competition in males and choosiness in females. In a field enclosure with unlimited supply of receptive females the number of matings varied widely between males, with twenty percent of males neglected by the females. The number of matings within this enclosure was neither related to male size nor to song characters, recorded previously in the lab. However, the number of matings by individual males was positively correlated to the size of their spermatophore producing accessory gland. Females appear to prefer males with a large nutritive donation, thereby receiving a direct fitness benefit.

---

[1] School of Animal Biology, University of Western Australia, Perth, Western Australia; e-mail: arne.w.lehmann@t-online.de.

[2] To whom correspondence should be addressed at Institut für Zoologie, Freie Universität Berlin, Abteilung Evolutionsbiologie, Königin-Luise-Straße 1-3, 14195 Berlin, Germany; e-mail: gerlind.lehmann@t-online.de.

KEY WORDS: female choice; male-male-competition; mating success; calling; spermatophore; nuptial gifts.

INTRODUCTION

Animals of most species do not mate indiscriminately but prefer some partners over others (Andersson, 1994). Several benefits may be gained by discriminating among potential mates, especially when they provide direct benefits (Johnstone, 1995; Møller and Jennions, 2001; Kokko *et al.*, 2003). Mate choice is an important evolutionary process that imposes sexual selection on the opposite sex. The resulting sexual selection can be a strong force in shaping characters and behaviors (Andersson, 1994; Andersson and Iwasa, 1996; Andersson and Simmons, 2006). In most cases, sexual selection is stronger in males than in females, with males having more conspicuous sex traits, whereas females exerts some choice. A main determinant of the opportunity for sexual selection is the *operational sex ratio*: the ratio of fertilizable females to sexually active males at any given time and place (Emlen and Oring, 1977). Two components influencing the OSR are the sex ratio and the *potential reproductive rate*. It is widely argued, that a more accessible empirical approach is to measure the sexual difference in the PRR of a population and then to estimate the OSR (Clutton-Brock and Vincent, 1991; Clutton-Brock and Parker, 1992; Parker and Simmons, 1996; Ahnesjö *et al.*, 2001), instead of interfering the OSR directly. The PRR corresponds inversely to the *time-out*, the state when individuals have mated and recovering before being ready to mate again (Clutton-Brock and Parker, 1992; Parker and Simmons, 1996; Ahnesjö *et al.*, 2001). If one sex remates quicker than the other one, such a sexual difference may influence the direction of sexual selection. However, without further study of mating behavior, one can not take sex differences in potential reproductive rates as evidence for sexual selection (Andersson, 1994). It is necessary to show, that a biased OSR imposes variance in mating numbers and is correlated to phenotypic (male) traits.

The reproductive behavior of bushcrickets show a diversity of ways in which individuals compete for and select mates. In the majority of bushcricket species, males transfer a nuptial gift during mating (Gwynne, 1995). This spermatophore works as sperm protection device and at least sometimes also as parental investment (Wedell, 1994; reviews in Gwynne, 1997; Vahed, 1998). The mass of the spermatophore can be as much as 40 percent of the male body-mass (Wedell, 1993; Vahed and Gilbert, 1996), with the males unable to remate for a couple of days after spermatophore transfer at mating (Gwynne, 1997). Ingredients in the spermatophore are incorporated into the somatic tissue by females (Voigt *et al.*, 2006) also induce a refractory period in females, during which they are reluctant to remate (review in Gwynne, 1997; see also Lehmann and Lehmann, 2000b). Under high-quality and abundant food, male bushcrickets usually remate quicker than their females (Gwynne, 1990; Simmons and Gwynne, 1991; Simmons, 1995a). We assume therefore, that the OSR is likely to be male-biased in most bushcrickets, and that females exhibit choice on male characters.

Australian bushcrickets of the genus *Kawanaphila* are unusual tiny (pronotum length <4 mm, male weight <60 mg), strictly nocturnal and feed exclusively on nectar and pollen (Rentz, 1993). To test the pattern of female choice and an expected variance in male mating success, we conducted experiments with *K. mirla*. We measured body dimensions, body weight and song parameters of males, characters likely to be shaped as response to female choice. Body dimensions are fixed at adult molt and therefore likely to reflect differences in genetics and/or life history (Gwynne, 2004). In contrast, body weight varies with food availability (Simmons and Bailey, 1990; Gwynne, 1993) and the time since last mating (Simmons, 1990, 1995b; Reinhold and von Helversen, 1997; Lehmann and Lehmann, 2000a).

Our study consist of two parts. In the first part, samples of both sexes were brought into the laboratory, fed ad libitum and provided with free access to mates to measure the time-out from mating and estimate the OSR. Secondly, in a field enclosure males competed and were chosen by females. If sexual selection is operating in *K. mirla*, female choice in this situation will impose variance in male mating numbers and correlate with male traits.

MATERIAL AND METHODS

K. mirla is a comparatively small *Kawanaphila* species (males: pronotum length <3.0 mm, hind femur <10 mm, weight <40 mg), and produces songs with a peak frequency around 70 kHz, which is comparatively high for bushcrickets. *K. mirla* is restricted to Western Australia, where it inhabits the costal heath region along the southern coast (Rentz, 1993). All individuals tested here were caught as subadult individuals at Two Peoples Bay near Albany in spring 1998, preferentially on white flowers at night. 135 males and 120 females were held for four weeks in the lab and fed with commercial pollen available from a health food store ad libitum until their final molt.

Adults were sampled ($n = 255$) at Two Peoples Bay over the course of five nights, one week after the first adult has been heard using an ultrasound detector, to determine the adult sex ratio.

Remating Interval

We measured the time from an initial mating until remating separately in males and females. Individuals of both sexes were kept individually in between mating trials in 200 mL containers in the lab. The jars contained a stick on which to rest and pollen ad libitum. Because acoustic rivalry between males is demonstrated in *K. mirla* (Mason and Bailey, 1998), males were held in a separate room away from the females. Containers with males were isolated from each other by 2 cm thick polystyrene walls to prevent acoustic interference. Males were tested for matings six days after their final molt. Eight males were mated with virgin, receptive females. After an observed mating, the female was removed and replaced with a new virgin female. Every night individual males were placed with a fresh virgin female for four hours or until mating took place. Females were processed in a similar way, but separately. Ten females were initially mated and were allowed to consume the spermatophore. Females were tested for sexual receptivity each night for 12 nights. Females were placed on sand to allow for oviposition between matings. We counted the days from the initial mating until remating, meaning that an individual mating at two consecutive days have a remating interval of one day.

When have mated and spend time recovering, they are said to be in a time-out state. The mean time-out from mating is then used to calculate the PRR, by 1/time-out$_{\text{females}}$/1/time-out$_{\text{males}}$. The PRR multiplied by the adult sex ratio found in the field can be used to estimate the OSR (Parker and Simmons, 1996).

Competition over Females for Males in a Field Enclosure

We measured the number of matings for males who had unlimited availability to virgin females. Nine individually marked males were released in an outdoor enclosure [dimensions: 1.60 × 0.80 × 1.00 m]. This outdoor enclosure was placed at Two Peoples Bay, including the natural mixture of bushes found within the habitat of *K. mirla*. The density can be calculated to 7 males per m^2, which falls into the observed range of this species. Males were evenly distributed within the enclosure and relocated every night to a random chosen place in the cage. We placed a large number of cotton buds soaked and covered with commercial pollen in the enclosure, which exceeded the daily dietary needs (two to six mg pollen per day and male; Simmons, 1995a). Every night a new randomly chosen subset of nine virgin females were released into the cage, in total 72 virgin females. All animals were observed under red light for potential matings. Using virgin females every day meant that males were not limited by mating partners. Main mating-activity in the closely related species *K. nartee* is between 18:30 h and 21:30 h (Simmons and Bailey, 1990). Therefore, females were released at 18:00 h and recaptured from the enclosure at 22:00 h. We also measured the time of pairs from first physical contact until transfer of the spermatophore as precopula plus copula time. We used the mean if multiple data from one male exist to avoid non-independence. This experiment was conducted for eight nights.

Body Dimensions

To identify possible parameters used by females to choose a male we measured body dimensions and song parameters. Five days after the end of the experiments we determined the wet mass of the males and then killed them, measured body dimensions and dissected and weighed the wet weight of the accessory glands. Feeding for five additional days was used to compensate for different mating history during the course of the experiment. For measurements of the body size we used the length of the pronotum and the length of the right hind femur. Measurements were obtained with a Mitutoyo caliper rule (accuracy 0.01 mm). The spermatophylax producing accessory glands were weighed fresh immediately after death to avoid weight losses due to desiccation. Measurements of mass were made to the nearest 0.01 mg on a Mettler Toledo AG 245 scale. The eight males used in the lab to test for the remating interval were similar in size to the nine males used in the enclosure experiment (pronotum length, hind femur length and wet glandular mass in percent of body wet mass: *t* test for homogen variances, *NS*).

Temporal Patterns of Calling Songs

Before we started the experiments, the temporal structure of the songs (Gerhardt and Huber, 2002) of the nine males used in the field enclosure experiment were recorded from acoustical isolated males at 25°C in the lab. Songs were recorded with a Sennheiser microphone ME66 and stored on a Sony Cassette recorder. This devices sample frequencies up to 20 kHz, which is fare less than the peak frequency at 70 kHz. However *K. mirla* produces songs with broadband frequencies (Mason and Bailey, 1998), so sampling had reduced the intensity but did not alter the temporal structure of songs. Analog recorded songs were A/D converted to a PC with a sampling rate of 1 kHz. Temporal patterns of songs were analyzed using the program Signal® (Noldus/Technical Engineering). The acoustic elements were classified according to Gerhardt and Huber (2002). *Pulses* are defined as the sound unit made during one movement of the stridulatory structures. The *number of pulses* produced during one closing movement of the wings, are grouped into a *verse*. After a variable time the next verse follows, so *verse duration* and *pause duration* sum up to the *verse period*.

RESULTS

The eight males fed ad libitum in the lab remated within three nights after their initial mating (Fig. 1). The time-out due to the remating interval was 2.38 ± 0.74 (mean ± SD) days (normal distributed: $\chi^2 = 0.16$, $P = 0.92$). In contrast, nine out of 10 females showed no remating within 12 days, with one exceptional female remating after 3 days. Female time-out from mating is therefore at least 12 days. Males remate much quicker than females under maximal food conditions (t test, $t_{\text{adjusted for heterogen variances}} = 9.31$, $df = 10.50$, $P < 0.001$). As the PRR is inversely correlated to the time-out from mating, the PRR is at least five times higher in males than in females. The adult sex ratio from the field sample was near equal with a quotient of 1.125:1 males to females ($n = 255$). The operational sex ratio (OSR) is largely male-biased, with a 5.7 times larger number of males than females ready to mate. Thus males are predicted to be the main competitors and females exhibiting intense choice on male traits.

Matings in the field enclosure generally took place within one hour (at most two hours) after sunset. The time pairs spent in the precopula phase did not depend on the time of courtship initiation (Linear regression:

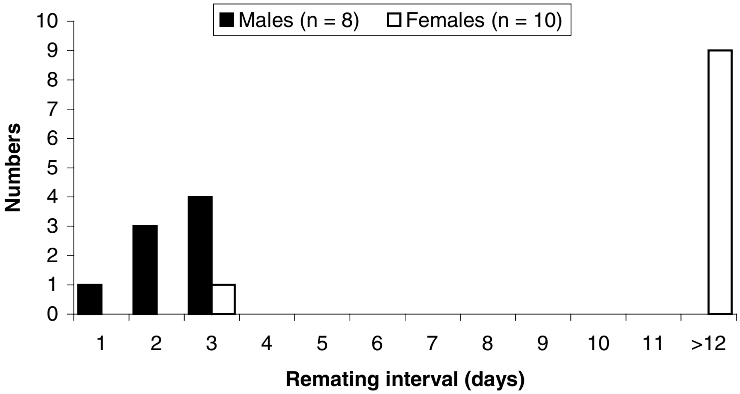

Fig. 1. Remating interval of males and females under laboratory conditions.

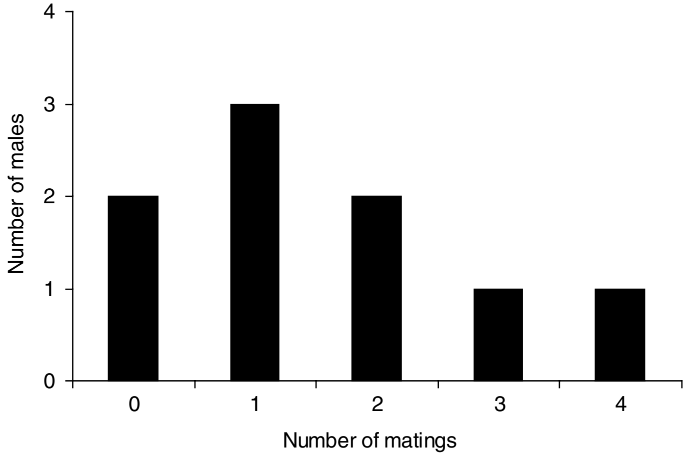

Fig. 2. Number of matings of males during eight nights in a field enclosure ($N = 9$).

$y = 58.30 + 4.29x$, $R^2 = 0.08$, $N = 14$). Mating number in the field was unequal between males and ranged from zero to four (Fig. 2), but the distribution of matings did not deviate from normal distribution ($\chi^2 = 0.20$, $df = 2$, $P = 0.91$). Two out of nine males (22%) did not mate at all. In contrast, only 19 of the 72 females (19.4%) placed into the field enclosure actually mated.

There was considerable variance in the mating number between males (1.77), larger than the mean mating number (1.56), revealing a potential for sexual selection acting on males ($s^2/\text{mean} = 1.14 > 1$).

To identify possible parameters used by females to choose a male we related body dimensions and song parameters to the observed mating number. The number of matings for males was related to body dimensions. In a multiple stepwise regression mating number was significantly related to the mass of the spermatophylax producing glands (expressed as percentage from live body weight; $N = 9$, R^2 adjusted for multiple regression $= 0.44$, $P = 0.03$), but not to pronotum or femur length (Fig. 3). Relative glandular mass is also negatively correlated to precopula plus copula duration ($y = 34.75 - 0.59x$, $R^2 = 0.17$, $N = 7$), meaning that males with a larger relative glandular mass spent less time in contact with their female.

The song of *K. mirla* males consists of discrete trains of pulses. Song parameters showed different levels of variation between males. Nearly equal and low levels of variation were found for the number of pulses within a verse, the pulse duration and as a consequence the verse duration. In

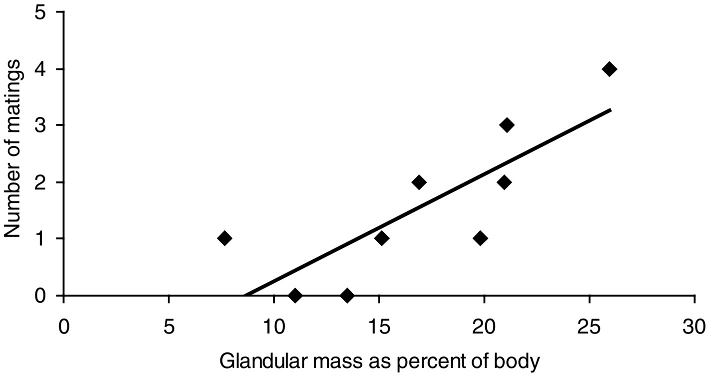

Fig. 3. Number of matings in the field enclosure in correlation to percentage glandular mass. Linear regression ($y = -11.78 + 2.93x$, $N = 9$, $R^2_{\text{adjusted for multiple regression}} = 0.44$, $P = 0.03$).

contrast, the pause duration between consecutive verses showed twice as much variation between males. Even with such variation, song characters were not related to the number of matings observed in the field enclosure (Table I).

Two fairly obvious relationships where the coupling of the number of pulses with verse duration ($R^2 = 0.74$) and pause duration explains nearly all variance in verse period ($R^2 = 0.96$).

Pronotum length and femur length were correlated ($R^2 = 0.46$, $P < 0.05$ for the combined data set of males used in the lab and in the enclosure experiment, $N = 17$), however glandular mass showed no significant correlation with femur or pronotum length. Whilst the number of matings in the field enclosure was related to body dimensions, especially glandular mass (see multiple regression above, Fig. 3), the remating interval of males in the lab was independent of body-measurements (body weight, glandular

Table I. Multiple Regression of Temporal Patterns of Calling Songs -Recorded Previously in the Lab- with the Number of Matings Obtained by These Males Later in the Field Enclosure During Eight Nights

Song parameter	β	95%	SD	T	P	Mean	±SD	CV (%)
Verse duration (ms)	0.09	0.33	0.10	0.91	0.43	825.5	25.0	3
Pause duration (ms)	0.06	0.24	0.08	0.84	0.46	6088.1	417.6	7
Verse period (ms)	−0.06	0.24	0.08	−0.85	0.46	6912.6	416.6	6
Pulse duration (ms)	−0.69	3.96	1.24	−0.56	0.62	33.4	1.0	3
Pulse number/verse	−1.06	6.71	2.11	−0.50	0.65	25.0	0.7	3
(const.)	31.50							

weight, femur length, pronotum length) as revealed by multiple regression ($N = 8$, adjusted $R^2 = 0.16$, *NS*).

DISCUSSION

The concept of the OSR is a central tool to predict the opportunity for sexual selection. Furthermore, the OSR is a good predictor of contest competition for mates and to some extent mate choice (Kvarnemo and Ahnesjö, 1996). Especially when one sex has a considerable longer period of time-out from reproduction, this will in turn impose competition between the sex in access (Parker and Simmons, 1996). Under laboratory conditions with maximum food, males remated at least five times faster than females in *K. mirla*. Thus the PRR of males was larger than that of females. The adult sex ratio in turn was near unity, so that we calculated the OSR to be male-biased. Similar results were found in the congeneric *Kawanaphila nartee*, where well fed males remate in median within two days, whereas females remate within 20 days (Simmons and Gwynne, 1991). Such a strongly male-biased OSR exists in *K. nartee* under good food conditions in the laboratory (Gwynne and Simmons, 1990; Parker and Simmons, 1996) and is also a realistic situation found in nature when food is abundant (Simmons and Bailey, 1990; Gwynne *et al.*, 1998). An adequate pollen availability can occur in *K. mirla* habitats: we found many suitable flowering plants at the collecting site at Two Peoples Bay. In general, the OSR is predominantly male-biased in animals (Andersson, 1994). Contrary to our design with food in excess, the OSR becomes female biased in *K. nartee* under food shortage (Gwynne and Simmons, 1990; Simmons and Bailey, 1990; Simmons, 1992, 1995a). This difference in the OSR can occur over small spatial scale depending on pollen sources (Gwynne *et al.*, 1998) and reversing the sex roles with serious female-female competition (Simmons and Bailey, 1990; Gwynne and Bailey, 1999).

Based on the theoretical considerations, a male-biased OSR as in our study should lead to variance in male mating success under competition. We found a variance in male mating success in a way predicted by sexual selection theory, with the variance in mating numbers greater than the mean (Andersson, 1994). Two out of nine males loosed out completely, by getting no females at all. This is astonishing, as verbal descriptions and explicit models on mate searching and mate preferences predict that female choice is less strong if females are virgin (review in Reid and Stamps, 1997), like in our enclosure experiment.

Male mating success was correlated to male traits, in accordance with sexual selection theory (Andersson, 1994). However, the length of the hind femur and the pronotum were not reliable cues for male mating success in our study. Another body dimension, the front-femur length in the congeneric species *K. nartee* seems to be less important to sexual competition, as there is no sex specific response to food stress in this character (Gwynne, 2004). Body dimensions are fixed at adult molt and therefore likely to reflect differences in genetics and/or life history.

In courtship-feeding systems, male investment precedes fertilization. Females may thus use pre-mating choice to secure mates providing direct benefits (Bussière, 2002). When males provide material (direct) benefits to their mates, females are expected to choose males providing large investments (Trivers, 1972). Despite basing their choice on static male body size, male mating success was strongly correlated to the dynamic criterion of the size of the accessory glands. We show that the ability of males to provide larger spermatophores is a central cue for female mate choice in the enclosure experiment. The glandular mass is known to be closely correlated to the transferred spermatophore size in other bushcricket species (Heller and Reinhold, 1994; Simmons, 1995b), making this measurement a direct indicator of a males investment capacity. The choice of larger males in several bushcricket species is also best seen as choosing males with a larger investment into the nuptial gift (Gwynne, 1982; Gwynne and Bailey, 1988; Lehmann and Lehmann, accepted).

Female choice on male songs is a common phenomenon in bushcrickets (reviews in Gwynne, 2001; Robinson and Hall, 2002; Gerhardt and Huber, 2002). As a basis for mate choice song variation is a prerequisite. As first found in treefrogs (Gerhardt, 1991) and later analyzed for a number of anuran and orthopteran species (Gerhardt and Huber, 2002), the level of variation between songs differ between the song properties. This conclusion is repeated in our study; as the pulse duration had a quite low level of variation. The same is true for the verse duration, which also corresponds with the short signal duration. This classifies both acoustic properties as static criteria, a result similar to other bushcricket species (Gerhardt and Huber, 2002). In contrast, the verse period had a much higher level of variation in *K. mirla*.

In our laboratory data we looked for a correlation between mating success and acoustic properties, but the tested regressions were not significant. However, we have not tested the performance of singing males in song contest, but rather the song characters in isolation. Given the strong acoustic male-male competition in *K. mirla*, a synchronization of songs might explain the results (Mason and Bailey, 1998). When one male ends up as the leader of a song contest between neighboring singing males this male will get the mating (Greenfield *et al.*, 1997). In a bushcricket, males that become leaders had a higher intrinsic chirp rate (Hartbauer *et al.*, 2005). Males reared on a low-nutrition diet where smaller but had similar chirp rates in comparison to males reared on a high-nutrition diet, indicating the independence of chirp rate from male condition (Hartbauer *et al.*, 2006). Whether the establishing of leadership is condition dependent needs further examination.

In our study we have found clear evidence for female mate choice in a way predicted by sexual selection hypothesis.

ACKNOWLEDGMENTS

This study would not have been possible without the help of Winston J. Bailey who invited us to the University of Western Australia, Zoology Department, and provided office and research space during our stay. Brenton Knott generously loaned us camping equipment for the field experiments. We thank Winston J. Bailey and Robert Hickson and three anonymous referees for comments on the manuscript. The research was funded by a postdoctoral grant from the DAAD to GL.

REFERENCES

Ahnesjö, I., Kvarnemo, C., and Merilaita, S. (2001). Using potential reproductive rates to predict mating competition among individuals qualified to mate. *Behav. Ecol.* **12:** 397–401.

Andersson, M. B. (1994). *Sexual Selection*, Princeton University Press, Princeton.

Andersson, M., and Iwasa, Y. (1996). Sexual selection. *Trends Ecol. Evol.* **11:** 53–58.

Andersson, M., and Simmons, L. W. (2006). Sexual selection and mate choice. *Trends Ecol. Evol.* **21:** 296–302.

Bussière, L. F. (2002). A model of the interaction between ‘good genes’ and direct benefits in courtship-feeding animals: When do males of high genetic quality invest less? *Phil. Trans. R. Soc. Lond. B* **357:** 309–317.

Clutton-Brock, T. H., and Parker, G. A. (1992). Potential reproductive rates and the operation of sexual selection. *Quart. Rev. Biol.* **67:** 437–456.

Clutton-Brock, T. H., and Vincent, A. C. J. (1991). Sexual selection and the potential reproductive rates of males and females. *Nature* **351:** 58–60.

Emlen, S. T., and Oring, L. W. (1977). Ecology, sexual selection and the evolution of mating systems. *Science* **197:** 215–223.

Gerhardt, H. C. (1991). Female mate choice in treefrogs: Static and dynamic acoustic criteria. *Anim. Behav.* **42:** 615–635.

Gerhardt, H. C., and Huber, F. (2002). *Acoustic Communication in Insects and Anurans—Common Problems and Diverse Solutions*, The University of Chicago Press, Chicago.

Greenfield, M. D., Tourtellot, M. K., and Snedden, W. A. (1997). Precedence effects and the evolution of chorusing. *Proc. R. Soc. Lond. B* **264:** 1355–1361.

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

Gwynne, D. T. (1990). Testing parental investment and the control of sexual selection in katydids: The operational sex ratio. *Am. Nat.* **136:** 474–484.

Gwynne, D. T. (1993). Food quality controls sexual selection in mormon crickets by altering male mating investment. *Ecology* **74:** 1406–1413.

Gwynne, D. T. (1995). Phylogeny of the Ensifera (Orthoptera): A hypothesis supporting multiple origins of acoustical signalling, complex spermatophores and maternal care in crickets, katydids, and weta. *J. Orth. Res.* **4:** 203–218.

Gwynne, D. T. (1997). The evolution of edible 'sperm sacs' and other forms of courtship feeding in crickets, katydids and their kin (Orthoptera: Ensifera). In Choe, J. C., and Crespi, B. J. (eds.), *The Evolution of Mating Systems in Insects and Arachnids*, Cambridge University Press, Cambridge, pp. 110–129.

Gwynne, D. T. (2001). *Katydids and Bush-Crickets: Reproductive Behavior and the Evolution of the Tettigoniidae*, Cornell University Press, Ithaka.

Gwynne, D. T. (2004). Sexual differences in response to larval food stress in two nuptial feeding orthopterans—implications for sexual selection. *Oikos* **105:** 619–625.

Gwynne, D. T., and Bailey, W. J. (1988). Mating system, mate choice and ultrasonic calling in a zaprochiline katydid (Orthoptera: Tettigoniidae). *Behaviour* **105:** 202–223.

Gwynne, D. T., and Bailey, W. J. (1999). Female-female competition in katydids: Sexual selection for increased sensitivity to a male signal? *Evolution* **53:** 546–551.

Gwynne, D. T., and Simmons, L. W. (1990). Experimental reversal of courtship roles in an insect. *Nature* **346:** 172–174.

Gwynne, D. T., Bailey, W. T., and Annels, A. (1998). The sex in short supply for matings varies over small spatial scales in a katydid (*Kawanaphila nartee*, Orthopetra: Tettigoniidae). *Behav. Ecol. Sociobiol.* **42:** 157–162.

Hartbauer, M., Kratzer, S., Steiner, K., and Römer, H. (2005). Mechanisms for synchrony and alternation in song interactions of the bushcricket *Mecopoda elongate* (Tettigoniidae: Orthoptera). *J. Comp. Physiol. A* **191:** 175–188.

Hartbauer, M., Kratzer, S., and Römer, H. (2006). Chirp rate is independent of male condition in a synchronising bushcricket. *J. Ins. Physiol.* **52:** 221–230.

Heller, K.-G., and Reinhold, K. (1994). Mating effort function of the spermatophore in the bushcricket *Poecilimon veluchianus* (Orthoptera, Phaneropteridae): Support from a comparison of the mating behaviour of two subspecies. *Biol. J Linn. Soc.* **53:** 153–163.

Johnstone, R. A. (1995). Sexual selection, honest advertisement and the handicap principle: Reviewing the evidence. *Biol. Rev.* **70:** 1–65.

Kokko, H., Brooks, R., Jennions, M. D., and Morley, J. (2003). The evolution of mate choice and mating biases. *Proc. R. Soc. Lond. B* **270:** 653–664.

Kvarnemo, C., and Ahnesjö, I. (1996). The dynamics of operational sex ratios and competition for mates. *Trends Ecol. Evol.* **11:** 404–408.

Lehmann, G. U. C., and Lehmann, A. W. (2000a). Spermatophore characteristics in bushcrickets vary with parasitism and remating interval. *Behav. Ecol. Sociobiol.* **47:** 393–399.

Lehmann, G. U. C., and Lehmann, A. W. (2000b). Female bushcrickets mated with parasitized males show rapid remating and reduced fecundity (Orthoptera: Phaneropteridae: *Poecilimon mariannae*). *Naturwissenschaften* **87:** 404–407.

Lehmann, G. U. C., and Lehmann, A. W. (accepted). Bushcrickets song is essential for female mate choice of heavier males, who provide larger direct (material) benefits. *Behav. Ecol. Sociobiol.*

Mason, A. C., and Bailey, W. J. (1998). Ultrasound hearing and male-male communication in Australian katydids (Tettigoniidae: Zaprochilinae) with sexually dimorphic ears. *Phys. Entomol.* **23:** 139–149.

Møller, A. P., and Jennions, M. D. (2001). How important are direct fitness benefits of sexual selection? *Naturwissenschaften* **88:** 401–415.

Parker, G. A., and Simmons, L. W. (1996). Parental investment and the control of sexual selection: Predicting the direction of sexual competition. *Proc. R. Soc. Lond. B* **263:** 315–321.

Reid, M. L., and Stamps, J. A. (1997). Female mate choice tactics in a resource-based mating system: Field tests of alternative models. *Am. Nat.* **150:** 98–121.

Reinhold, K., and von Helversen, D. (1997). Sperm number, spermatophore weight and remating in the bushcricket *Poecilimon veluchianus*. *Ethology* **103:** 12–18.

Rentz, D. C. F. (1993). *A monograph of the Tettigoniidae of Australia. Vol. 2, The Phasmodinae, Zaprochilinae and Austrosaginae*, CSIRO Australia, Victoria.

Robinson, D. J., and Hall, M. J. (2002). Sound signaling in Orthoptera. *Adv. Insect Physiol.* **29:** 151–278.

Simmons, L. W. (1990). Nuptial feeding in tettigoniids: Male costs and the rates of fecundity increase. *Behav. Ecol. Sociobiol.* **27:** 43–47.

Simmons, L. W. (1992). Quantification of role reversal in relative parental investment in a bush cricket. *Nature* **358:** 61–63.

Simmons, L. W. (1995a). Relative parental expenditure, potential reproductive rates, and the control of sexual selection in katydids. *Am. Nat.* **145:** 797–808.

Simmons, L. W. (1995b). Male bushcrickets tailor spermatophores in relation to their remating intervals. *Funct. Ecol.* **9:** 881–886.

Simmons, L. W., and Bailey, W. J. (1990). Resource influenced sex roles of zaprochiline tettigoniids (Orthoptera: Tettigoniidae). *Evolution* **44:** 1853–1868.

Simmons, L. W., and Gwynne, D. T. (1991). The refractory period of female katydids (Orthoptera: Tettigoniidae): Sexual conflict over the remating interval? *Behav. Ecol.* **2:** 276–282.

Trivers, R. L. (1972). Parental investment and sexual selection. In Campbell, B. (ed.), *Sexual Selection and the Descent of Man, 1871–1971*, Heinemann, London, pp. 136–179.

Vahed, K. (1998). The function of nuptial feeding in insects: Review of empirical-studies. *Biol. Rev.* **73:** 43–78.

Vahed, K., and Gilbert, F. S. (1996). Differences across taxa in nuptial gift size correlate with differences in sperm number and ejaculate volume in bushcrickets (Orthoptera: Tettigoniidae). *Proc. R. Soc. Lond. B* **263:** 1255–1263.

Voigt, C. C., Lehmann, G. U. C., Michener, R. H., and Joachimski, M. M. (2006). Nuptial feeding is reflected in tissue nitrogen isotope ratios of female katydids. *Funct. Ecol.* **20:** 656–661.

Wedell, N. (1993). Spermatophore size in bushcrickets: Comparative evidence for nuptial gifts as a sperm protection device. *Evolution* **47:** 1203–1212.

Wedell, N. (1994). Dual function of the bushcricket spermatophore. *Proc. R. Soc. Lond. B* **258:** 181–185.