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Female remating propensity contingent on sexual cannibalism in sagebrush crickets, *Cyphoderris strepitans:* a mechanism of cryptic female choice

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Male sagebrush crickets (*Cyphoderris strepitans*) permit females to engage in an unusual form of sexual cannibalism during copulation: females feed on males' fleshy hind wings and ingest hemolymph oozing from the wounds they inflict. These wounds are not fatal, and normally only a portion of the hind wings are eaten at any one mating, so that mated males are not precluded from mating again. As a result, nonvirgin males have fewer material resources to offer females than do virgin males, such that females should be selected to preferentially mate with high-investment virgin males. We tested the hypothesis that female mating preferences favor males capable of supplying females with the highest material investment. Our results indicate that both female diet and opportunities for sexual cannibalism influence female mating behavior. Females maintained on a low-nutrient diet mounted males significantly sooner than females maintained on a high-nutrient diet, indicating that a female's overall nutrient intake may determine her propensity to mate. In addition, females were significantly more reluctant to mount and mate with males whose hind wings had been surgically removed and thus were incapable of providing females with a wing meal. Finally, females initially mated to dewinged males remated with winged males significantly sooner than females allowed to feed freely during their initial mating, resulting in cryptic female choice of investing males. *Key words:* courtship feeding, cryptic female choice, *Cyphoderris strepitans,* sagebrush crickets, sexual cannibalism, sexual selection. *[Behav Ecol 10:227–233 (1999)]*

Cryptic female choice refers to mechanisms of mate choice that operate after copulation has begun but before fertilization occurs (Eberhard, 1996; Thornhill, 1983). Female control over the reproductive process and the resultant potential for postcopulatory forms of female choice to affect sexual selection are currently receiving widespread attention (Eberhard, 1996, 1997; Eberhard and Cordero, 1995). Insect mating systems that involve male-donated courtship food gifts provide ideal systems for the study of cryptic female choice because they offer an obvious target for such preferences. In sagebrush crickets, *Cyphoderris strepitans,* males permit females to engage in an unusual form of sexual cannibalism during copulation: females feed on males' fleshy hind wings and ingest hemolymph oozing from the wounds they inflict (Dodson et al., 1983). These wounds are not fatal, and normally only a portion of the hind wings are eaten at any one mating, so that mated males are not precluded from mating again. However, nonvirgin males have fewer material resources to offer than virgin males, such that females should be selected to mate preferentially with virgin males (Dodson et al., 1983; Thornhill and Alcock, 1983).

Previous studies have shown that virgin males do secure significantly more matings than nonvirgin males, based on their relative abundance in the population (Morris et al., 1989; Snedden, 1996). Although this effect has been shown to be partly a result of the decreased calling activity of recently mated males (Sakaluk and Snedden, 1990; Sakaluk et al., 1987), the degree to which female choice contributes to this virgin-male mating advantage remains uncertain. Studies to date suggest that females do not differentiate among virgin and nonvirgin males based on qualitative differences in males' songs (Sakaluk and Ivy, unpublished data; Snedden and Greenfield, 1995), nor do they appear to discriminate in terms of their willingness to mount and complete copulations with nonvirgin males (Snedden and Sakaluk, 1992). However, Eggert and Sakaluk (1994) showed that virgin males whose hind wings had been surgically removed were less likely to complete matings than males with intact wings, even though males of both treatments did not differ in the time taken to elicit female mountings. They concluded that wing feeding keeps females preoccupied during the time needed by males to transfer the spermatophore. However, the degree to which this result can be extended to nonvirgin mating success in the field remains uncertain because typically nonvirgin males retain at least some wing material with which to provision other mates (Dodson et al., 1983; Eggert and Sakaluk, 1994; Morris et al., 1989).

The lack of evidence showing any discrimination against nonvirgins calls into question the prevalence and efficacy of precopulatory female choice in this mating system. Benefits of outright mate rejection would appear to be low given that the duration of mating is short relative to the time required by females to localize calling males (Snedden, 1995) and that females can usually derive a meal, albeit reduced, from most nonvirgin males. For these reasons, one might expect females to adopt a strategy of material-benefit polyandry (Thornhill and Alcock, 1983), accepting matings and wing-feeding without regard to a male's mating status. However, if the nutrition derived through courtship feeding is important to female reproduction, nonvirgin males could still be subject to cryptic mate choice exerted after copulation has occurred. Females may accept matings with nonvirgin males, but if the resources

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derived through wing feeding on these males are insufficient to satisfy females' nutritional requirements, they may remate sooner than they otherwise would after matings with virgin males. Such postcopulatory behavior, in conjunction with the last-male sperm precedence that is common in insect mating systems characterized by high male material investment (Gwynne, 1984), would result in higher reproductive success of those males offering the greatest nutritional rewards. Although a female's choice under these circumstances might best be viewed as an incidental consequence of adopting a strategy of exchanging matings for food, this does not preclude the possibility that females secure indirect genetic benefits as well, particularly if a male's investment at mating is an honest indicator of his viability (Thornhill and Alcock, 1983).

The objective of this study was to test the hypothesis that postcopulatory female mating preferences favor males capable of supplying females with the highest material investment. Specifically, we predicted that females paired with dewinged males, and thus experimentally prevented from wing feeding during their initial matings, would remate sooner than females allowed to feed freely in their initial mating. In addition, we predicted that if nutrient intake influences female mating decisions, then females maintained on a low-nutrient diet should have a higher propensity to mate than females maintained on a high-nutrient diet.

METHODS

Overview and natural history

C. strepitans is one of only five extant species belonging to an obscure orthopteran family, the Haglidae, and occurs exclusively in mountainous areas of the western United States, where it is often found in high-altitude sagebrush meadows (Morris and Gwynne, 1978). Adults become sexually active in late spring, shortly after the snow melts, and remain active for the next 4–6 weeks. The acoustic signals produced by males function to attract females (Snedden and Irazuzta, 1994) and are the principal means of pair formation (Sakaluk et al., 1995b; Snedden and Sakaluk, 1992). Copulation is initiated when a receptive female climbs onto the dorsum of a male, immediately after which the female chews on the male's fleshy hind wings that the male exposes by raising his forewings. Successful mating requires the transfer of a spermatophore, the bulk of which remains outside the female's body after mating. Females may prevent mating by dismounting the male before spermatophore transfer has occurred, but they are hindered from doing so by the gin trap, an abdominal clasping device used by the male (Sakaluk et al., 1995a). Completed matings, however, are terminated by the male, who pulls away from the female as soon as spermatophore transfer has been accomplished (Dodson et al., 1983). Approximately 3 h after mating, on average, females begin feeding on the spermatophore, which they eventually consume (Sakaluk and Snedden, unpublished data).

Study site and collection procedures

The study was conducted at the University of Wyoming-National Park Service Research Center, the site of previous studies (Eggert and Sakaluk, 1994; Sakaluk et al., 1995b; Snedden and Sakaluk, 1992). Male and female crickets were collected early in the breeding season (May–June) from several populations within Grand Teton National Park and transported to the field station. All males used in the study were virgins, as evidenced by the presence of intact hind wings; females were of unknown mating status. Crickets were maintained according to standard procedures (Eggert and Sakaluk, 1994; Snedden and Sakaluk, 1992).

Matings were staged in specially constructed, Plexiglas viewing chambers divided into two equal compartments (10×6.8×4.4 cm). Each compartment was equipped with a small stick placed diagonally across the chamber to provide males with a calling perch. Experimental pairs were established early in the evening when the crickets become sexually active, and their mating behavior was directly observed over the next 8 h under red light. Throughout the observations we used a 5-min sampling protocol to determine the number of 5-min intervals in which a male called. No food or water was provided during mating trials. Upon completion of the experiment, crickets were returned to the population from which they were collected. Two different experiments were conducted over consecutive field seasons.

1996: diet and female mating behavior

The objective of this experiment was to examine the effect of dietary regime and wing feeding on female mating and remating propensity. We established two dietary regimes, one in which females were maintained solely on lettuce (low-nutrient diet), and another in which females were maintained on apple and bee pollen supplied ad libitum (high-nutrient diet). Feeding regimens were initiated the morning after females were collected. Females were held on their respective dietary regimes for a minimum of 48 h before being used in a mating trial and thereafter until they completed the study. Females from each of the dietary regimes were first paired either with virgin males whose hind wings had been left intact or with virgin males whose hind wings had been surgically removed, thereby precluding wing feeding. The hind wings of dewinged males were removed 24 h before the beginning of mating trials to permit their full recovery from the procedure (see Eggert and Sakaluk, 1994; Sakaluk et al., 1995a,b).

Females were randomly assigned to one of four experimental treatments for their initial matings (sample sizes in parentheses): (1) females held on the low-nutrient diet and paired with a winged, virgin male ($n = 12$); (2) females held on the high-nutrient diet and paired with a winged, virgin male ($n = 14$); (3) females held on the low-nutrient diet and paired with a dewinged, virgin male ($n = 11$); (4) females held on the high-nutrient diet and paired with a dewinged, virgin male ($n = 6$). We recorded the time at which females first mounted males and the time at which spermatophore transfer (i.e., mating) occurred relative to the beginning of the trial. Females that did not mate within the 8-h observation period were paired with a different male the next night and each subsequent night until mating occurred; in calculating the time to mating, we included only those hours during which females were paired with males. Whenever a female mated, another replicate within the treatment was established; this resulted in unequal sample sizes across treatments, but there was no significant difference in the date on which pairs across treatments were established ($\chi^2 = 3.78$, $p = .28$), thereby ameliorating any seasonal effects should such exist.

After females of the four different treatments had completed their initial matings, they were given an opportunity to remate with an unmanipulated (winged) virgin male on each subsequent night until remating occurred or the season ended. Rematings were staged under identical conditions as the initial matings (see above). Thus, the intervals between initial spermatophore transfer and time to mounting and time to mating with the replacement male were used as measures of each female's propensity to remate.

1997: wing feeding and postcopulatory female choice

Results from 1996 allowed us to assess the influence of diet on female mating propensity, but a paucity of initial matings

Table 1

Mating propensity of females held under different dietary regimes and paired initially with males of differing wing status, 1996

	Time to event (h)			
	Initial mating		Remating	
Treatment	Mounting[a]	Mating[b]	Remounting[a]	Remating[b]
Wing+, diet−	2.92 ± 1.42 (12)	11.20 (11)	3.60 ± 1.61 (11)	22.00 (7)
Wing+, diet+	5.95 ± 1.38 (14)	30.80 (13)	5.36 ± 1.53 (13)	39.6 (8)
Wing−, diet−	5.11 ± 1.44 (11)	71.50 (5)	12.02 ± 2.03 (5)	25.0 (5)
Wing−, diet+	12.97 ± 1.63 (6)	55.30 (3)	8.02 ± 2.50 (3)	73.7, 100.6, 136.8[c] (3)

Diet−, lettuce; diet+, bee pollen and apple; wing+, paired initially with a male with intact hind wings; wing−, paired initially with a male whose hind wings had been experimentally removed.

[a] Mounting data are reported as back-transformed least-square means ± SE (*n*).

[b] Mating data are reported as medians (*n*) (censorship of failure-time data precluded the calculation of interquartile ranges).

[c] Raw data for the three males in this treatment are shown; values were censored, precluding calculation of the median.

of females paired with dewinged males (see below) precluded any assessment of postcopulatory mating preferences. Accordingly, our focus in 1997 was on sexual cannibalism and its influence on female remating behavior, with all females maintained on the same diet of natural vegetation (fresh sagebrush clippings). Upon their capture, females were assigned to either of two experimental treatments: (1) females allowed to wing feed on their initial mate ($n = 13$) or (2) females prevented from wing feeding on their initial mate ($n = 15$). Males paired with females of treatment 2 had their hind wings surgically removed 24 h before the mating trial. Mating trials were staged as in the previous field season. As before, we used the time from trial initiation to mounting and mating as measures of female willingness to mate.

One hour after initial copulations had been completed, mated males were replaced with unmanipulated virgin males, and females of both treatments were given the opportunity to remate with a winged male. The intercopulatory interval was used to assess female remating propensity across treatments.

Statistical analyses

We conducted analyses using procedures of SAS for personal computers (SAS Institute, 1988). Student's *t* tests were used to evaluate any potential effect of wing removal on male calling ability. All of our measures of the latency to mount and mate were non-normally distributed. Therefore, comparisons between treatments of the time to mounting and time to remounting were made on log-transformed data using log-transformed ANOVA and *t* tests.

In contrast to data on female mounting latency, comparisons of time to mating and remating were performed using the nonparametric testing procedures of failure-time analysis (Fox, 1993b; Kalbfleisch and Prentice, 1980). Failure-time analysis accommodates censored data, observations in which an event such as mating may not have occurred by the end of the study, as was the case here. Omission of such data, as is frequently done in behavioral studies, may lead to a serious bias in comparisons across treatments (Fox, 1993b). For the 1996 two-way design, we performed four planned contrasts across treatments within (1) dietary regime and (2) wing treatment when the initial analysis indicated significant differences existed across groups; in these comparisons, the appropriate Bonferroni-adjusted significance level was employed.

In principle, we also could have employed failure-time analysis in the analysis of mounting data, but we did not do so because all females in both years mounted males at least once, even if all of them did not successfully complete a mating. When there are two main effects, as in the case of the 1996 experiment, a two-way ANOVA is preferable because, unlike failure-time analysis, it allows the interaction between the two main effects to be assessed.

RESULTS

1996: diet and female mating behavior

We compared the calling activity of winged and dewinged males, restricting our analysis to each male's first mating trial to ensure statistical independence of observations. Dewinged males ($n = 27$) called on average in 62% of the 5-min sampling intervals monitored over the 8-h observation period, whereas winged males ($n = 84$) called in 63% of the intervals; this difference is not statistically significant ($t = 0.24$, $p = .81$). For males successful at mating, there were no differences in the time spent calling by winged males ($n = 40$, 57% of intervals) and de-winged males ($n = 8$, 50% of intervals; $t = 0.65$, $p = .52$).

Table 1 summarizes female mounting, mating, remounting, and remating data across diet regimes and wing treatments for the 1996 experiment. For initial pairings, a log-transformed, two-way ANOVA [reported as back-transformed least square means (hours) ± SE] revealed that diet had a significant influence on a female's latency to mount, with low-diet females mounting males sooner than high-diet females (3.80 ± 1.29 and 8.70 ± 1.35 h, respectively; $F = 4.51$, $p = .04$). The effect of wing condition on latency to mounting was not statistically significant ($F = 3.00$, $p = .09$). There was no interaction between diet and wing condition on the latency to mounting ($F = 0.08$, $p = .77$).

For initial pairings, failure-time analysis revealed significant differences across treatments in the time taken by females to mate (Figure 1; $\chi^2 = 10.26$, $p = .02$). There was no significant effect of diet on the time to first mating ($p > .05$). The wing condition of males had a significant effect on the time at which females first mated, with females paired with dewinged males taking much longer to mate than those paired with winged males. However, this difference was significant only for

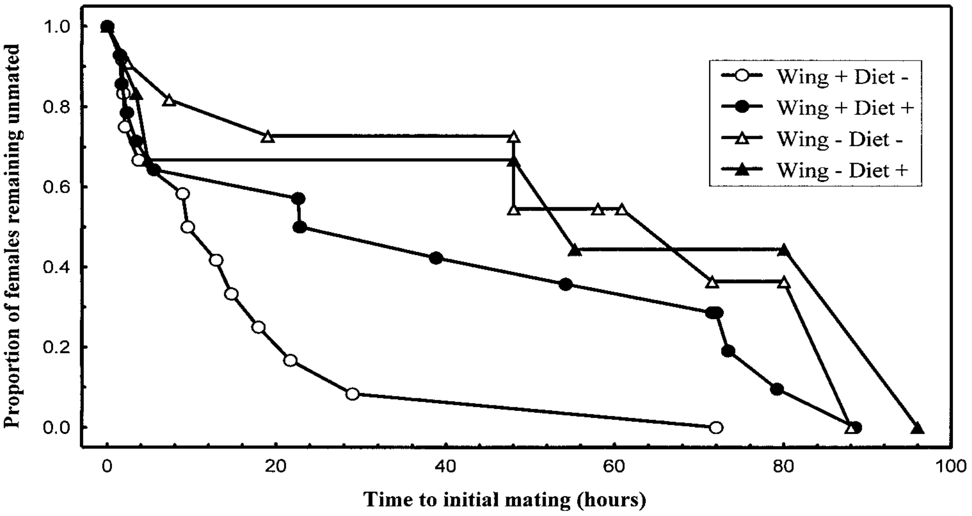

Figure 1
Survival distribution function of time to initial mating for the 1996 experiment. The proportion of females remaining unmated is compared across treatments as a decreasing function of time.

low-diet females (χ^2 = 6.98, p = .01; high-diet females: χ^2 = 2.00, p = .16).

Too few of the females paired with dewinged males completed their initial matings, precluding any assessment of the effect of wing condition on a female's propensity to remate (see instead results for 1997). There were, however, a sufficient number of initial matings by females paired with winged males to assess the effect of diet on remounting and remating propensity. In pairwise comparisons of females allowed to wing feed on their initial mate, there was no effect of diet regime on the time taken by females to mount the replacement male (t = 0.58, p = .56) or the time taken by females to remate (χ^2 = 0.004, p = .95).

1997: wing feeding and postcopulatory female choice

There was no difference in the proportion of time spent calling across wing treatments (winged males: n = 29, 60% of intervals; dewinged males: n = 33, 59% of intervals; t = 0.06, p = .95). Among males successful at acquiring matings, calling proportions were also similar across wing treatments (winged males: n = 9, 64% of intervals; dewinged males: n = 12, 68% of intervals; t = 0.27, p = .79).

Table 2 summarizes female mounting, mating, remounting, and remating data for the 1997 experiment. Female latency to mount (log-transformed) was significantly greater for females paired with dewinged males than for those paired with winged males (t = 2.09, p = .05). In addition, failure-time analysis showed that females took significantly longer to mate with dewinged males than they did with winged males (Figure 2; χ^2 = 15.83, p = .0001). Females initially mated to a dewinged male remounted replacement males significantly sooner than females allowed to feed on their initial mate (t = 2.81, p = .01). Failure-time analysis showed an equally strong effect of wing feeding on the latency to remating. Females prevented from wing feeding on their initial mate took one-third of the time to remate compared to females who were allowed to feed on their initial mate (Figure 3; χ^2 = 13.00, p = .0003).

DISCUSSION

Our results suggest that opportunities for sexual cannibalism, as well as female nutrient load, influence precopulatory mechanisms of mate choice through both female mounting and mating propensity. In addition, our results provide evidence of cryptic mate choice employed after mating, manifest in a female remating propensity that is contingent on a male's ability to provide wing material. Differential male mating success across treatments cannot be attributed to a lowered calling ability resulting from the surgical removal of a male's hind wings because in both years of the study dewinged males called at rates equivalent to winged males (see also Eggert and Sakaluk, 1994). Given that stridulation is perhaps the most energy-consuming activity in which a male can engage (Ho-

Table 2
Mating propensity of females provisioned with natural foliage (moistened sagebrush clippings) and paired initially with males of differing wing status, 1997

	Time to event (h)			
	Initial mating		Remating	
Treatment	Mounting[a]	Mating[b]	Remounting[a]	Remating[b]
Wing+	2.33 ± 1.44 (13)	16.90 (13)	4.68 ± 1.61 (13)	16.90 (13)
Wing−	8.53 ± 1.44 (15)	74.40 (12)	1.14 ± 1.41 (12)	6.00 (12)

Wing+, paired initially with a male with intact hind wings; wing−, paired initially with a male whose hind wings had been experimentally removed.

[a] Mounting data are reported as back-transformed least-square means ± SE (n).

[b] Mating data are reported as medians (n) (censorship of failure-time data precluded the calculation of interquartile ranges).

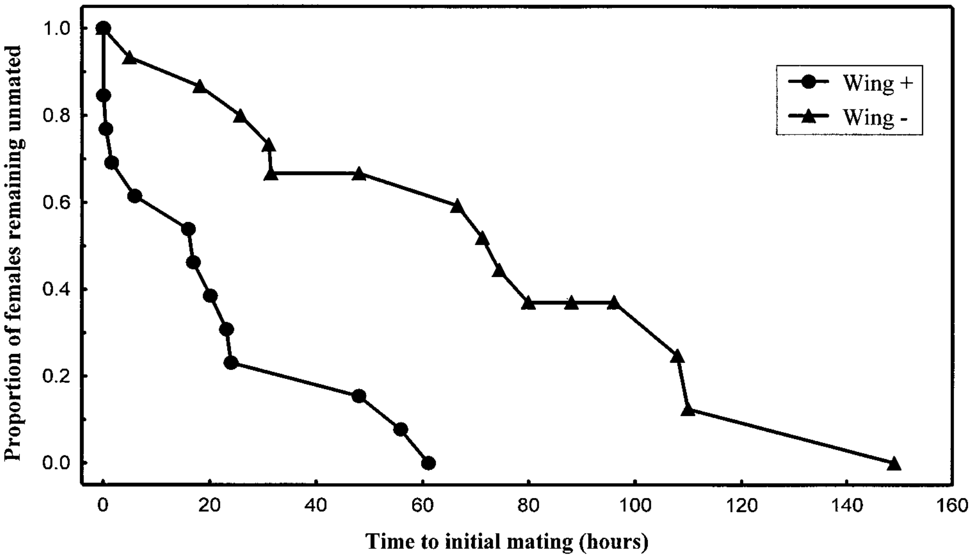

Figure 2
Survival distribution function of time to initial mating for the 1997 experiment. The proportion of females remaining unmated is compared across treatments as a decreasing function of time.

back and Wagner, 1997; Lee and Loher, 1993; Prestwich and Walker, 1981), this observation suggests that dewinged males were not appreciably weakened by their operations.

Precopulatory mate choice

Our manipulation of female diet in 1996 revealed that low-diet females mount their mates more readily than high-diet females. Similarly, when paired with a winged male, low-diet females took only about one-third as long to mate, on average, as did high-diet females. A similar effect of heightened female mating propensity under conditions of food stress has been documented in a variety of gift-giving insects (Brown, 1997; Fox, 1993a; Gwynne, 1990; Markow and Ankney, 1984; Simmons and Gwynne, 1991; Steele, 1986). These findings are consistent with the hypothesis that polyandry in gift-giving species functions, at least in part, in the acquisition of material benefits from males (Thornhill and Alcock, 1983).

In the 1997 experiment, females mounted winged males significantly sooner than they mounted males whose hind wings had been removed. This result is in direct contrast to a previous study showing no difference in the time at which winged and dewinged males were first mounted (Eggert and Sakaluk, 1994). The only obvious difference in the two studies is in the diet on which experimental females were maintained; in the 1997 experiment, all females were maintained on a natural diet of moistened sagebrush clippings, whereas in Eggert and Sakaluk's (1994) study, females were fed on pieces of apple and carrot. Any mounting preference for winged males would require a discriminatory mechanism that operates prior to mounting and before the onset of female wing feeding. Perhaps the most efficient mechanism for discrimination at this level would be acoustic differentiation of certain aspects of males' calls. Morris et al. (1989) suggested that the loss of hind-wing material lying beneath the sound-producing tegmina might alter male calling parameters. The ability to acoustically discriminate between virgin males and non-virgins at long distances would carry obvious selective advantages for females by eliminating situations in which females expend energy locating a male incapable of providing a large wing meal

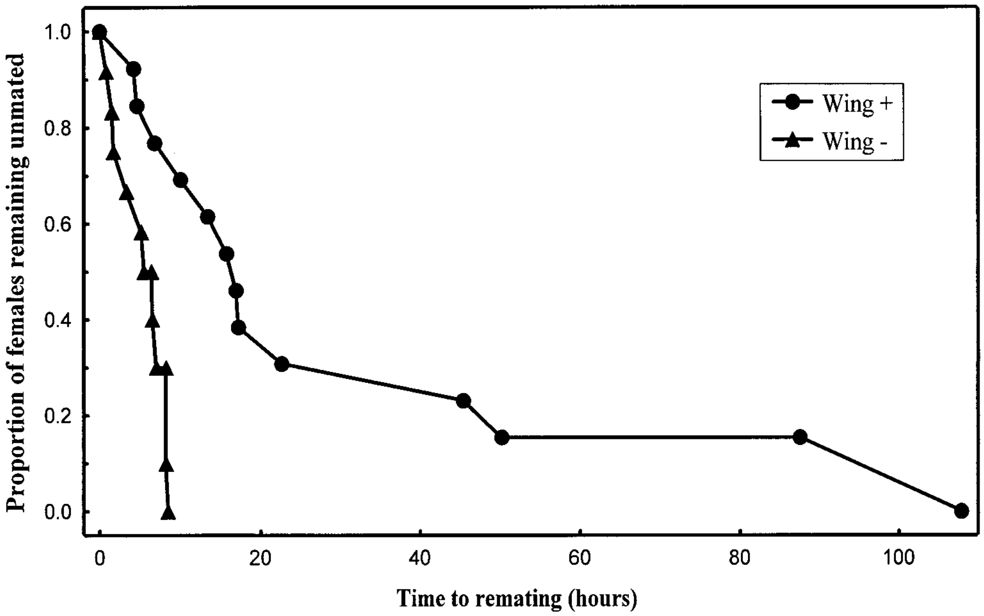

Figure 3
Survival distribution function of time to remating for the 1997 experiment. The proportion of females failing to remate with a replacement male (virgin with intact hind wings) is compared across treatments as a decreasing function of time.

(Boggs, 1990) and/or by minimizing predation risks associated with phonotaxis (Sakaluk, 1990; Sakaluk and Belwood, 1984). Indeed, acoustic analyses of digitized calls of virgin, non-virgin, and experimentally de-winged males indicate possible differences in the amplitude, and perhaps, spectral components of the signals (Snedden and Greenfield, 1995; Ritchie MG, personal communication). A more recent study has shown, however, that the asymmetrical removal of one hind wing does not influence female willingness to mount males in the laboratory or reduce male mating success in the field (Sakaluk and Ivy, unpublished data), results that are inconsistent with an acoustically mediated mounting preference.

Other proximate mechanisms that potentially could mediate female mounting preferences include visual and/or tactile detection of the presence/absence of wing material before mounting. One possibility is that the creamy white color of the hind wings against a dark background could serve as a close-range visual cue alerting females to wing-feeding opportunities. Alternatively, there may be occasions in which the females do not mount the male, but get sufficiently close to palpate the dorsum of the male with their mouthparts. In support of this possibility, females occasionally were observed hanging upside down from the calling perch above a calling male in an apparent attempt to wing feed without mounting the male.

In the 1997 experiment, and within the low-diet treatments in the 1996 experiment, we found a statistically significant female mating preference for winged males. In both cases females were markedly more reluctant to complete matings with dewinged males, waiting on average 50 h longer to mate than females allowed to wing feed. These findings support previous studies showing that wing-feeding females are much more likely to allow spermatophore transfer than females prevented from wing feeding (Eggert and Sakaluk, 1994; Sakaluk et al., 1995b).

Postcopulatory mate choice

Due to small sample sizes in 1996, we were able to compare the effect of diet regime on female remating propensity only for females initially mated to males with intact hind wings. Following such matings in which wing feeding was permitted, low-diet females did not remount or remate significantly sooner than their high-diet counterparts. Thus, while female mating propensity appears to be accelerated by a lack of adequate nutrition, the refractory period following an initial mating involving wing feeding is not affected by diet regime. This raises the possibility that consumption of the food gift in the initial mating may weaken the effect of previous food stress, rendering females from both diet regimes equally ready to remate. Similarly, Simmons and Gwynne (1991) showed that nutrient stress in a zaprochiline katydid shortens female refractory periods only when females are restricted from feeding on their initial male's food gift, a gelatinous spermatophylax.

Previous studies of *C. strepitans* have focussed on factors that favor male success in obtaining matings. Unique to the present study is the finding that female refractory periods vary as a function of the ability of the initial male to provide wing material. Our data indicate that 9 of 12 females restricted from wing feeding on their initial mate remated within the same night, with the remaining 3 females remating within the first hour of the following night's mating trial. In contrast, only 3 of 13 wing-fed females remated within the same night, and the remaining 10 females typically waited 3 nights before remating. While little is known of female oviposition patterns in this species, this differential in remating propensity should almost certainly influence male fertilization success given any degree of last-male sperm precedence.

The existence of cryptic female choice via remating propensity in sagebrush crickets adds to a growing number of studies that implicate sexual conflict over female remating intervals as a potential source of sexual selection. When food gifts are given at mating, females often remate more quickly following matings with low-investment males (Boggs, 1981; Kosal and Niedzlek-Feaver, 1997; Oberhauser, 1992; Savalli and Fox, 1998; Simmons and Gwynne, 1991; Thornhill, 1976, 1983). The results of our study closely parallel those of Thornhill's (1983) pioneering work on cryptic female choice in gift-giving scorpionflies, *Harpobittacus nigriceps*. In the mating systems of both species, female postcopulatory mating preferences impose strong selection on males to maximize their nutritional contributions. Additionally, females of both species exhibit precopulatory mating biases against low-investment males, suggesting that female choice may routinely be a complex of discrimination at multiple levels.

Much of what has been interpreted as cryptic female choice could alternatively be viewed as a form of male manipulation. For example, if chemical substances contained in male hemolymph function to diminish female sexual receptivity, then the inability of dewinged males to transfer such substances might explain the heightened mating propensity of females mated to these males. However, even if it could be shown that substances contained in the male's hemolymph induce a refractory period in females, their existence per se would not be sufficient evidence of male manipulation because "manipulation" implies that females are forced to behave in a way that is contrary to their own reproductive interests. Although males clearly benefit from a reduction in the sexual receptivity of their mates, females might also benefit from the refractory period that follows copulations with males offering substantial food rewards. Having met their immediate nutritional needs and secured sufficient sperm to fertilize their eggs, females' interests might best be served by focussing their efforts on oviposition and foregoing the attendant risks of seeking out additional mates (Csada and Neudorf, 1995; Hedrick and Dill, 1993; Sakaluk and Belwood, 1984). Hence, it might be advantageous for females to respond to any hormonal cues present in male hemolymph, in which case these substances might more properly be regarded as chemical signals rather than as a form of male manipulation.

Future studies should focus on assessing the degree to which female mating biases serve female interests and the degree to which these biases are the product of male manipulation. A complete understanding of mating system dynamics requires that they be viewed as the net result of an ongoing sexual arms race (Parker, 1979; Alexander et al., 1997). Just as male–male competition occurs at multiple levels before and after mating, precopulatory and postcopulatory mechanisms of female choice offer females an array of potential counter-adaptations to maintain control over the reproductive process.

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REFERENCES

Alexander RD, Marshall DC, Cooley JR, 1997. Evolutionary perspectives on insect mating. In: The evolution of mating systems in insects and arachnids (Choe JC, Crespi BJ, eds). Cambridge: Cambridge University Press; 4–31.

Boggs CL, 1981. Selection pressures affecting male nutrient investment at mating in heliconiine butterflies. Evolution 35:931–940.

Boggs CL, 1990. A general model of the role of male-donated nutrients in female insects' reproduction. Am Nat 136:598–617.

Brown WD, 1997. Female remating and the intensity of female choice in black-horned tree crickets, *Oecanthus nigricornis*. Behav Ecol 8: 66–74.

Csada RD, Neudorf DL, 1995. Effects of predation risk on mate choice in female *Acheta domesticus* crickets. Ecol Entomol 20:393–395.

Dodson G, Morris GK, Gwynne DT, 1983. Mating behavior in the primitive orthopteran genus *Cyphoderris* (Haglidae). In: Orthopteran mating systems: sexual competition in a diverse group of insects (Gwynne DT, Morris GK, eds). Boulder, Colorado: Westview Press; 305–318.

Eberhard WG, 1996. Female control: sexual selection by cryptic female choice. Princeton, New Jersey: Princeton University Press.

Eberhard WG, 1997. Sexual selection by cryptic female choice in insects and arachnids. In: The evolution of mating systems in insects and arachnids (Choe JC, Crespi BJ, eds). Cambridge: Cambridge University Press; 32–57.

Eberhard WG, Cordero C, 1995. Sexual selection by cryptic female choice on male seminal products—a new bridge between sexual selection and reproductive physiology. Trends Ecol Evol 10:493–496.

Eggert A-K, Sakaluk SK, 1994. Sexual cannibalism and its relation to male mating success in sagebrush crickets, *Cyphoderris strepitans* (Haglidae: Orthoptera). Anim Behav 47:1171–1177.

Fox CW, 1993a. Multiple mating, lifetime fecundity and female mortality of the bruchid beetle, *Callosobruchus maculatus* (Coleoptera: Bruchidae). Funct Ecol 7:203–208.

Fox GA, 1993b. Failure-time analysis: emergence, flowering, survivorship and other waiting times. In: Design and analysis of ecological experiments (Scheiner SM, Gurevitch J, eds). New York: Chapman and Hall; 253–289.

Gwynne DT, 1984. Male mating effort, confidence of paternity, and insect sperm competition. In: Sperm competition and the evolution of animal mating systems (Smith RL, ed). Orlando, Florida: Academic Press; 117–149.

Gwynne DT, 1990. Operational sex ratios and the control of sexual selection: a test with katydids (Orthoptera: Tettigoniidae). Am Nat 136:474–484.

Hedrick AV, Dill LM, 1993. Mate choice by female crickets is influenced by predation risk. Anim Behav 46:193–196.

Hoback WW, Wagner WE, 1997. The energetic cost of calling in the variable field cricket, *Gryllus lineaticeps*. Physiol Entomol 22:286–290.

Kalbfleisch JD, Prentice RL, 1980. The statistical analysis of failure time data. New York: Wiley.

Kosal EF, Niedzlek-Feaver M, 1997. Female preferences for large, heavy mates in *Schistocerca americana* (Orthoptera: Acrididae). J Insect Behav 10:711–725.

Lee H-J, Loher W, 1993. The mating strategy of the male short-tailed cricket *Anurogryllus muticus* de Geer. Ethology 95:327–344.

Markow TA, Ankney PF, 1984. Drosophila males contribute to oogenesis in a multiple mating species. Science 224:303–303.

Morris GK, Gwynne DT, 1978. Geographical distribution and biological observations of Cyphoderris (Orthoptera: Haglidae) with a description of a new species. Psyche 85:147–167.

Morris GK, Gwynne DT, Klimas DE, Sakaluk SK, 1989. Virgin male mating advantage in a primitive acoustic insect (Orthoptera: Haglidae). J Insect Behav 2:173–184.

Oberhauser KS, 1992. Rate of ejaculate breakdown and intermating intervals in monarch butterflies. Behav Ecol Sociobiol 25:237–246.

Parker GA, 1979. Sexual selection and sexual conflict. In: Sexual selection and reproductive competition in insects (Blum MS, Blum NA, eds). London: Academic Press; 123–166.

Prestwich KN, Walker TJ, 1981. Energetics of singing in crickets: effect of temperature in three trilling species (Orthoptera: Gryllidae). J Comp Physiol B 143:199–212.

Sakaluk SK, 1990. Sexual selection and predation: balancing reproductive and survival needs. In: Insect defenses (Evans DL, Schmidt JO, eds). Albany, New York: SUNY Press; 63–90.

Sakaluk SK, Bangert PJ, Eggert E-K, Gack C, Swanson LV, 1995a. The gin trap as a device facilitating coercive mating in sagebrush crickets. Proc R Soc Lond B 261:65–71.

Sakaluk SK, Belwood JJ, 1984. Gecko phonotaxis to cricket calling song: a case of satellite predation. Anim Behav 32:659–662.

Sakaluk SK, Morris GK, Snedden WA, 1987. Mating and its effect on acoustic signalling behaviour in a primitive orthopteran, *Cyphoderris strepitans* (Haglidae): the cost of feeding females. Behav Ecol Sociobiol 21:173–178.

Sakaluk SK, Snedden WA, 1990. Nightly calling durations of male sagebrush crickets, Cyphoderris strepitans: size, mating and seasonal effects. Oikos 57:153–160.

Sakaluk SK, Snedden WA, Jacobson KA, Eggert A-K, 1995b. Sexual competition in sagebrush crickets: must males hear calling rivals? Behav Ecol 6:250–257.

SAS Institute, 1988. SAS/STAT user's guide, release 6.03 ed. Cary, North Carolina: SAS Institute Inc.

Savalli UM, Fox CW, 1998. Sexual selection and the fitness consequences of male body size in the seed beetle Stator limbatus. Anim Behav 55:473–483.

Simmons LW, Gwynne DT, 1991. The refractory period of female katydids (Orthoptera: Tettigoniidae): sexual conflict over the remating interval? Behav Ecol 2:276–282.

Snedden WA, 1995. Correlates of male mating success and their implications for sexual selection in a primitive orthopteran insect (PhD dissertation). Toronto: University of Toronto.

Snedden WA, 1996. Lifetime mating success in male sagebrush crickets: sexual selection constrained by a virgin male mating advantage. Anim Behav 51:1119–1125.

Snedden WA, Greenfield MD, 1995. Virgins are louder: the effect of mating on acoustic signaling in sagebrush crickets. In: University of Wyoming-National Park Service Research Center, 19th annual report (Harlow HJ, Harlow M, eds). Moran, Wyoming: National Park Service Research Center; 78–83.

Snedden WA, Irazuzta S, 1994. Attraction of female sagebrush crickets to male song: the importance of field bioassays. J Insect Behav 7: 233–236.

Snedden WA, Sakaluk SK, 1992. Acoustical signalling and its relation to male mating success in sagebrush crickets. Anim Behav 44:633–639.

Steele RH, 1986. Courtship feeding in Drosophila subobscura: I. The nutritional significance of courtship feeding. Anim Behav 34:1087–1098.

Thornhill R, 1976. Sexual selection and paternal investment in insects. Am Nat 110:153–163.

Thornhill R, 1983. Cryptic female choice and its implications in the scorpionfly *Harpobittacus nigriceps*. Am Nat 122:765–788.

Thornhill R, Alcock J, 1983. The evolution of insect mating systems. Cambridge: Harvard University Press.