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Cryptic female choice predicated on wing dimorphism in decorated crickets

Scott K. Sakaluk
Ecology Group, Department of Biological Sciences, Illinois State University, Normal, IL 61790-4120, USA

Male decorated crickets, *Gryllodes sigillatus*, normally lack hind wings and are incapable of flight (short-winged males), but occasionally exhibit fully developed hind wings that make rudimentary flight possible (long-winged males). Long-winged males bear a cost of flight in the form of decreased insemination success, which arises as a consequence of two interrelated factors: (1) long-winged males exhibit a lower reproductive investment relative to short-winged males, as measured by the mass of a male's spermatophore and reproductive organs and (2) the postcopulatory behavior of females favors males that maximize their reproductive investment. Of particular importance to male mating success is the spermatophylax, a large gelatinous mass forming part of the spermatophore and consumed by the female after mating. Consumption of the spermatophylax keeps the female preoccupied while sperm are discharged from the remaining portion of the spermatophore (sperm ampulla) into her reproductive tract. The spermatophylax of long-winged males is significantly smaller than that of short-winged males and consequently requires less time to consume. As a result, the sperm ampulla of long-winged males is frequently removed before its complete evacuation and significantly sooner than that of short-winged males. Because the spermatophore-removal behavior of females mediates the relative insemination success of short-winged and long-winged males, it can be considered a form of cryptic female choice. *Key words:* crickets, *Gryllodes sigillatus*, mate choice, nuptial food gift, sexual selection, spermatophore, wing dimorphism. *[Behav Ecol 8:326–331 (1997)]*

In many insect species, females retain control of sperm transfer and usage and can thereby influence the paternity of their offspring (e.g., Sakaluk, 1984; Thornhill, 1976; Ward, 1993). The intrinsically greater female control of the reproductive process means that females are capable of exerting mating preferences even after copulation has occurred (review in Eberhard, 1996). Crickets offer an ideal model with which to identify male traits that are subject to female postcopulatory preferences: the ejaculate of a male typically remains outside the female's genital opening after mating in the form of an externally attached spermatophore (Alexander and Otte, 1967), and females are thus well positioned to determine the fate of their mates' gametes through the judicious removal of spermatophores (Sakaluk, 1984; Simmons, 1986).

In decorated crickets, *Gryllodes sigillatus*, the spermatophore includes a large gelatinous mass, the spermatophylax, which the female detaches and feeds on after mating (Sakaluk, 1984, 1987). While the female consumes this nuptial food gift, sperm are evacuated from the remaining portion of the spermatophore (sperm ampulla) into her reproductive tract. Smaller spermatophylaxes require less time to consume, and males providing small gifts are penalized in the form of premature ampulla removal and reduced sperm transfer (Sakaluk, 1984, 1985, 1987). Females can greatly influence the paternity of their offspring through their ampulla-removal behavior (Sakaluk, 1986; Sakaluk and Eggert, 1996), and hence this behavior constitutes a powerful mechanism of postcopulatory female choice.

Gryllodes sigillatus is a wing-dimorphic species dominated by the common short-winged form (Ghouri and McFarlane, 1958; Toms, 1993). Males normally lack hind wings and are incapable of flight (short-winged form), but occasionally exhibit fully developed hind wings (long-winged form) that make rudimentary flight possible (Sakaluk SK, personal observation); long-winged *G. sigillatus* occur both in nature and in laboratory colonies (Toms, 1993; Sakaluk, personal observation). Wing polymorphisms are common in insects and appear to reflect a fundamental trade-off between energy devoted to dispersal and energy devoted to reproduction (Dingle, 1985; Harrison, 1980). Numerous studies of wing-polymorphic species have shown that long-winged, flighted females typically have a lower fecundity and reproduce at a significantly later age than short-winged, flightless females (review in Roff and Fairbairn, 1991). Comparisons of different wing morphs with respect to reproductive parameters have rarely involved males, however, perhaps because males typically have a reduced gametic investment relative to females and are thus less likely to reveal costs of flight through a reduction in reproductive output. In support of this proposition, Roff and Fairbairn (1993) found no difference in the mass of testes of short-winged and long-winged male sand crickets, *Gryllus firmus*, nor were there any differences between males of the two morphs in their ability to sire offspring when pairs of males were permanently confined with single females. Similarly, Holtmeier and Zera (1993) found no difference in the ability of short-winged and long-winged male *Gryllus rubens* to sire offspring when males of the two morphs were paired in similar competitive interactions.

In most cricket species, the male's spermatophore does not include a spermatophylax, but consists solely of a small sperm ampulla (Alexander and Otte, 1967). When the ampulla is augmented with a spermatophylax, as is the case in *G. sigillatus*, a sixfold increase in the total mass of the spermatophore accrues (Sakaluk and Smith, 1988). As a consequence of their investment in a food gift (spermatophylax), minimum refractory periods of male *G. sigillatus* are about an order of magnitude longer than those of non–gift-giving cricket species (Sakaluk, 1985). Given that the synthesis of food gifts is costly, costs of flight are more likely to be manifest in reduced reproductive performance of long-winged male *G. sigillatus* than has proved to be the case for long-winged males of other cricket species (e.g., Holtmeier and Zera, 1993; Roff and Fairbairn, 1993). Specifically, we might expect long-winged male

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Table 1
Mass (mg) of the spermatophore and reproductive organs of short-winged and long-winged male decorated crickets

	Short-winged			Long-winged				
	n	Mean	SE	*n*	Mean	SE	*t*	*p*
Body mass (wet)	34	266.8	7.3	34	248.0	6.4	1.94	.057
Wet measurements								
Spermatophore	34	7.08	0.40	34	5.40	0.39	3.00	.004
Spermatophylax	34	5.96	0.37	34	4.32	0.35	3.21	.002
Ampulla	34	1.11	0.05	34	1.08	0.06	0.47	.638
Accessory glands	32	25.97	1.37	31	20.29	1.15	3.17	.002
Testes	32	29.84	1.06	31	22.16	1.18	4.83	<.001
Dry measurements								
Spermatophore	34	1.56	0.08	34	1.21	0.07	3.24	.002
Spermatophylax	34	1.04	0.06	34	0.74	0.06	3.61	<.001
Ampulla	34	0.52	0.02	34	0.48	0.02	1.46	.150
Accessory glands	32	3.13	0.21	31	2.29	0.12	3.47	.001
Testes	32	3.46	0.14	31	2.71	0.11	4.17	<.001

Probabilities based on two-tailed *t* tests.

G. sigillatus to be compromised in their ability to synthesize food gifts and hence to be at a disadvantage with respect to the postcopulatory preferences of females. I tested this prediction by comparing the mass of reproductive organs of short-winged and long-winged male *G. sigillatus*, the mass of their ejaculates, the size of their food gifts, and their insemination success in mating trials with virgin females.

METHODS

Reproductive investment

Male *G. sigillatus* were obtained from a stock colony that was initiated from approximately 60 adults collected at Tucson, Arizona, USA, in May 1987 and maintained according to standard procedures (see Sakaluk, 1991). Measurements and observations on short-winged and long-winged individuals extended over 2.5 years and several generations (F_5–F_{13}) because long-winged individuals appeared in lab colonies only intermittently, and it was not always possible to measure long-winged males each time they became available. Whenever a long-winged male was removed for observation and measurement, a short-winged male was randomly selected from the same rearing cage to control for any effects of local rearing environment and to ensure that equal numbers of long-winged and short-winged males were measured each generation. Because breeding cages were stocked with nymphs of the same cohort, short-winged and long-winged males taken from the same colony were of similar, albeit unknown, age.

I obtained a spermatophore from each experimental male by manually removing it from the male's spermatophoric pouch (Sakaluk and Smith, 1988); the two components of the spermatophore were easily separated and weighed to the nearest 0.01 mg using a Fisher XA analytical balance. I weighed males after their spermatophores were removed. One day after these initial measurements, experimental males were used in mating trials (see below). After mating trials, males were killed and their reproductive organs were dissected. For each male, I determined the mass of the testes and that of the accessory glands, a collection of tubules that secrete the materials used in spermatophore synthesis (Leopold, 1976). The accessory glands were removed in a single mass, although they actually consist of various clusters of tubules (Nandchahal, 1972; Narula, 1969). Spermatophore components and reproductive organs were dried to constant weight at 60°C in a drying oven for 24 h before being reweighed.

Male mating success

I conducted mating trials in which experimental males were paired individually with virgin female *G. sigillatus*. Matings were staged in plastic shoe boxes (16.5 × 30.5 × 8.5 cm) during the dark portion of a 12:12 h light–dark cycle, a period during which decorated crickets are reproductively most active (Burpee and Sakaluk, 1993). Observations were made under red light, and no food or water was provided during trials. For each mating, I determined the time taken by the female to fully consume the spermatophylax (duration of courtship feeding) and the time after mating at which the female removed and consumed the sperm ampulla. Occasionally (n = 9), females consumed only a portion of the spermatophylax and subsequently discarded the uneaten portion; data from such trials were excluded from further analysis, and the male was paired with a different female the next day.

I determined mating success on the basis of the duration of ampulla attachment, as it is directly related to the number of sperm transferred (Sakaluk, 1984) and, ultimately, male fitness (Sakaluk, 1986; Sakaluk and Eggert, 1996). Data were analyzed using SAS for personal computers (SAS Institute, 1988). Preliminary analyses revealed no systematic change in the mass of any reproductive character over successive generations; hence, in comparisons between wing morphs, data were pooled across generations.

RESULTS

Reproductive investment

Univariate comparisons of reproductive investment by long-winged and short-winged males are shown in Table 1. The accessory glands and testes of short-winged males were of significantly higher mass than those of long-winged males. The spermatophores of short-winged males were also significantly larger than those of long-winged males, but this difference was due entirely to the spermatophylax portion of the spermatophore; spermatophylaxes of short-winged males were significantly larger than those of long-winged males, but there was no difference in ampulla mass between the two groups.

Pearson correlations between male body mass and the mass of spermatophore components and reproductive organs are shown in Table 2; correlational patterns were similar across wet and dry measurements, so for convenience, only correlations for wet measurements are given. Correlational patterns

Table 2
Pearson correlations between body mass and mass of spermatophore components and reproductive organs (mg; wet measurements only) of male decorated crickets

	Spermatophylax	Ampulla	Accessory glands	Testes
Short-winged				
Body mass	0.37*	0.11	0.24	0.12
Spermatophylax		0.67***	0.12	0.34
Ampulla			0.23	−0.03
Accessory glands				0.02
Long-winged				
Body mass	0.42*	0.43*	0.55**	0.40*
Spermatophylax		0.56***	0.17	0.11
Ampulla			0.18	−0.03
Accessory glands				0.32

* $p < .05$; ** $p < .01$; *** $p < .001$.

were similar across the two wing morphs. Correlations between male body mass and mass of spermatophore components and reproductive organs were all positive, but not all of them were significant. In both wing morphs, spermatophylax mass was highly correlated with ampulla mass. The mass of the testes and the mass of the accessory glands were not correlated for either wing morph. Masses of reproductive organs also were not correlated with masses of spermatophore components.

I examined variation in the mass of reproductive organs and spermatophore components using principal components analysis, a multivariate technique in which a series of independent variables (principal components) is derived from the original measurements. The advantage of this kind of analysis is that it reduces the number of original variables to a smaller set of components that are uncorrelated, and hence it measures different dimensions of the data set (Manly, 1986). The first principal component emerging from an analysis of all wet and dry measurements (excluding male body mass) accounted for 56% of the total variance in the data set and had weak to moderate positive loadings on all of the original variables (Table 3). Essentially, the first principal component (PC1) appears to measure a male's overall reproductive investment. PC1 score was positively correlated with male body mass in both short-winged ($r = .40$, $p = .024$) and long-winged males ($r = .74$, $p < .001$). Hence, I used an ANCOVA to compare PC1 scores of short-winged and long-winged males, with male body mass entered as the covariate. The least-squares mean PC1 score (± SE) of short-winged males (0.62 ± 0.33) was significantly higher than that of long-winged males (−0.64 ± 0.34, $p = .012$), suggesting that short-winged males make a greater reproductive investment than do long-winged males, even after accounting for variation due to body mass.

The second (PC2) and third (PC3) principal components accounted for an additional 17% and 14% of the variation in the data set, respectively; collectively, the first three components explained about 86% of the variation. PC2 had strong positive loadings on wet and dry testes mass, whereas the third principal component had strong positive loadings on wet and dry accessory gland mass. There was no significant correlation between PC2 and PC3 scores and male body mass for either wing morph. PC2 scores of short-winged males (0.54 ± 0.19) were significantly higher than those of long-winged males (−0.55 ± 1.26, $t = 3.68$, $p < .001$); however, there was no significant difference between the wing morphs with respect to PC3 scores ($t = 1.61$, $p = .11$).

Table 3
Principal components (PC) analysis of wet (W) and dry (D) weights of spermatophore components and reproductive organs of male decorated crickets

	Eigenvalues of correlation matrix		
Component	Eigenvalue	Proportion of variation explained	Cumulative
PC1	5.584	0.558	0.558
PC2	1.664	0.166	0.725
PC3	1.363	0.136	0.861
PC4	0.541	0.054	0.915

	Eigenvectors		
	PC1	PC2	PC3
Spermatophore (W)	0.400	−0.047	−0.186
Spermatophylax (W)	0.393	−0.002	−0.198
Ampulla (W)	0.300	−0.368	−0.026
Spermatophore (D)	0.411	−0.070	−0.106
Spermatophylax (D)	0.401	−0.013	−0.145
Ampulla (D)	0.339	−0.207	0.026
Accessory glands (W)	0.192	0.180	0.674
Testes (W)	0.171	0.642	−0.093
Accessory glands (D)	0.220	−0.108	0.654
Testes (D)	0.190	0.598	−0.023

Male mating success

Females that were mated to long-winged males took significantly less time to consume the spermatophylax (28.9 ± 2.6 min) than did females mated to short-winged males [39.1 ± 3.9 min; t test (approximated for unequal variances), $t = 2.13$, df = 43.2, $p = .038$]. Females that were mated to long-winged males removed the sperm ampulla significantly sooner after copulation (38.2 ± 2.8 min) than did females mated to short-winged males [51.0 ± 4.4 min; t test (approximated for unequal variances), $t = 2.42$, df = 42.5, $p = .020$].

The time taken by the female to consume the spermatophylax was regressed against the mass of the spermatophylax that had been removed from her mate the previous day (the mass of a male's spermatophylax remains relatively constant across successive matings; see Sakaluk and Smith, 1988). The analysis revealed that as the size of the food gifts provided by males increases, so does the duration of courtship feeding (Figure 1A, $b = 4.08$, $r^2 = 0.21$, df = 48, $p < .001$). The time after mating at which the female removed and consumed the sperm ampulla also increased significantly with the mass of her mate's previous spermatophylax (Figure 1B, $b = 3.68$, $r^2 = 0.14$, df = 48, $p = .007$). An increase in male reproductive investment, as measured by PC1 score, also resulted in longer durations of courtship feeding (Figure 2A, $b = 3.67$, $r^2 = 0.21$, df = 48, $p < .001$) and extended retention of sperm ampullae (Figure 2B, $b = 3.45$, $r^2 = 0.16$, df = 48, $p = .005$).

DISCUSSION

Long-winged male *G. sigillatus* bear a cost of flight in the form of decreased mating success, which arises as a consequence of two interrelated factors: long-winged males exhibit a lower reproductive investment relative to short-winged males, and the postcopulatory behavior of females favors sperm transfer by males who maximize their reproductive investment. Of particular importance to male insemination success is the spermatophylax, the large gelatinous mass forming part of the spermatophore and consumed by the female after

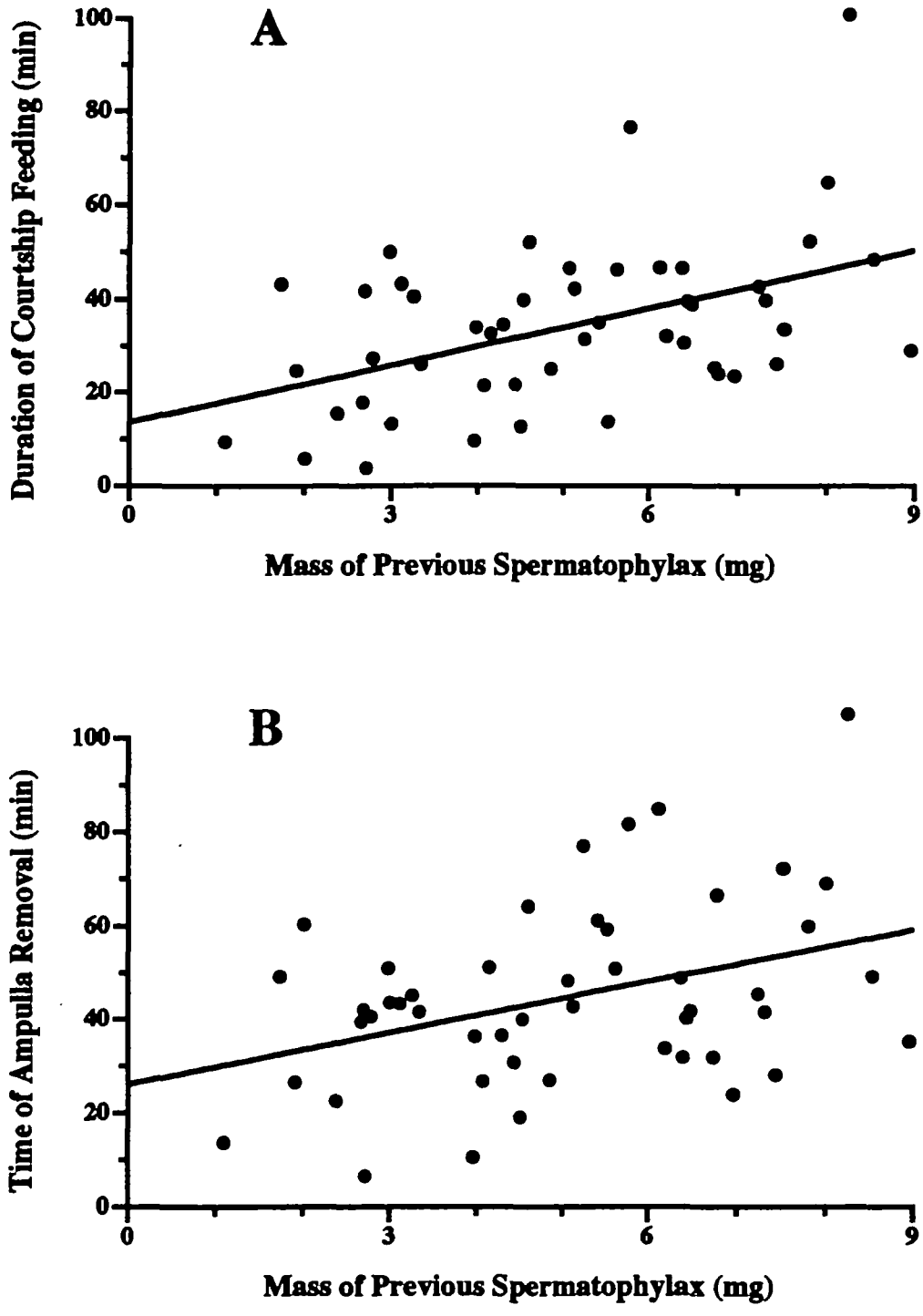

Figure 1
(A) The time required for the complete consumption of the spermatophylax and (B) the time after mating at which the sperm ampulla was removed by the female after copulation plotted as a function of the mass of the previous spermatophylax produced by a male. Data pooled for short-winged and long-winged males. Both regressions are statistically significant ($p < .001$ and $p = .007$, respectively).

mating. Spermatophylax feeding lasts anywhere from 5 min to 2 h, and typically within a few minutes of the complete consumption of the spermatophylax, the female removes and eats the sperm ampulla. The smaller spermatophylaxes of long-winged males require less time to consume, and males providing such gifts are penalized in the form of premature ampulla removal and reduced sperm transfer (Sakaluk, 1984, 1985, 1987). The amount of sperm transferred is vital to male fitness because it is the principal determinant of a male's fertilization success, particularly when his ejaculate must compete with those of other mating partners of the female (Sakaluk, 1986; Sakaluk and Eggert, 1996).

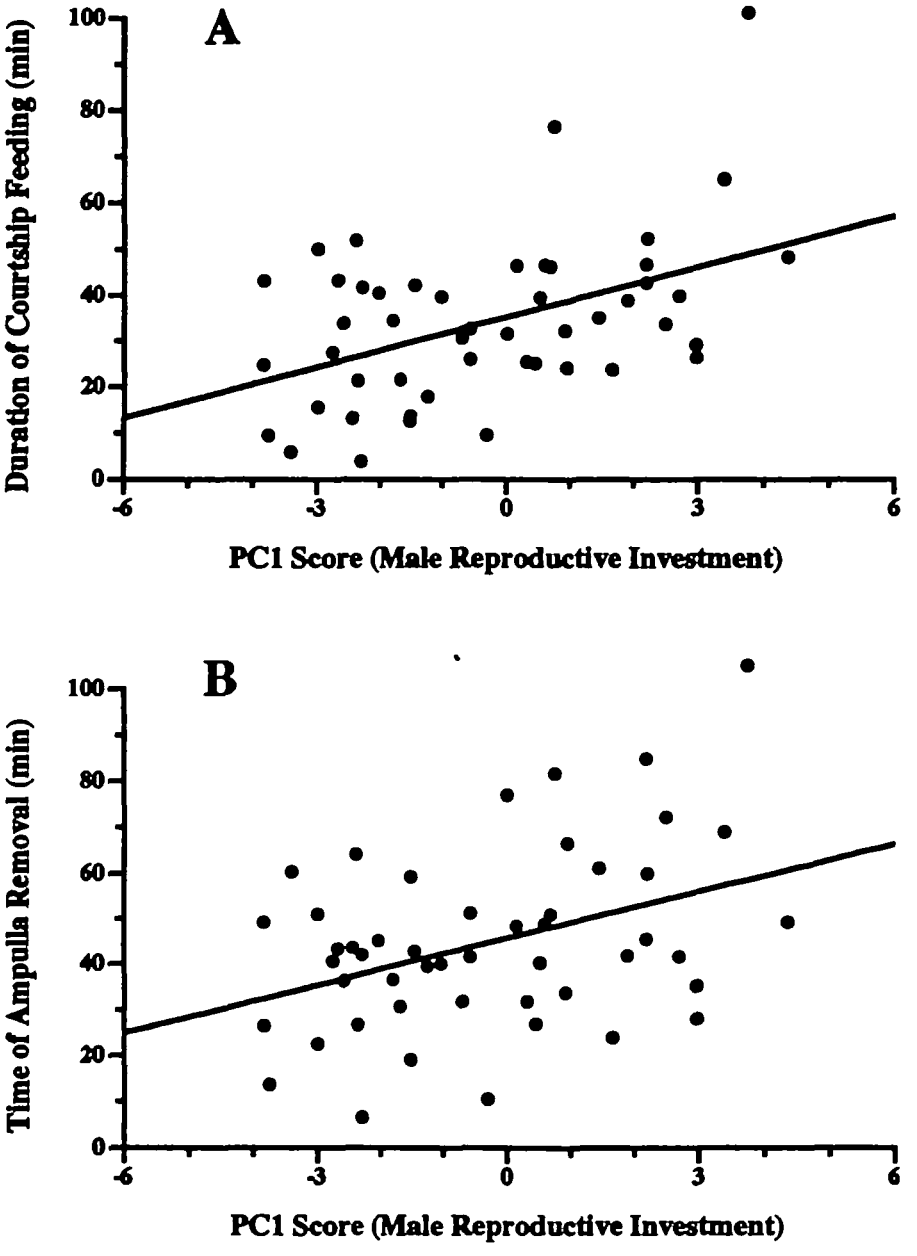

Figure 2
(A) The time required for the complete consumption of the spermatophylax and (B) the time after mating at which the sperm ampulla was removed by the female after copulation plotted as a function of the first principal component of a multivariate analysis of male spermatophore components and reproductive organs. Data pooled for short-winged and long-winged males. Both regressions are statistically significant ($p < .001$ and $p = .005$, respectively).

Thornhill (1983) described as "cryptic" those forms of female choice that occur only after copulation has been initiated and that lead to certain males enjoying an advantage over others in achieving fertilizations (review in Eberhard, 1996; Eberhard and Cordero, 1995). For example, female scorpionflies (*Harpobittacus nigriceps*) that mate with males that provide them with inadequate nuptial prey are more likely to remate sooner and delay oviposition until after remating relative to females that receive larger prey items at mating; such behavior almost certainly reduces the fertilization success of those males offering meager food gifts (Thornhill, 1983). Similarly, in *G. sigillatus*, a male that provides a female with a small spermatophylax at mating is more apt to have his sperm ampulla removed prematurely and, as a result, transfer fewer sperm (Sakaluk, 1984, 1985). The behavioral rule of thumb that leads females to terminate sperm transfer after consumption of the nuptial food gift is perhaps one of the better understood mechanisms of cryptic female choice (Eberhard, 1996). In *G. sigillatus*, such choice likely imposes significant sexual selection on at least two phenotypic characteristics of males, body size and wing condition, as both of these traits influence the size of the spermatophylax that a male is able to synthesize; large males and those of the short-winged morph produce larger food gifts on average and are therefore at an advantage with respect to female postcopulatory preferences.

Roff and Fairbairn (1993) noted that the incidence of macroptery in males relative to females is generally much lower in Orthoptera than in other insect taxa. They proposed that the particular reliance of male orthopterans on costly long-range acoustic signals to attract females could exacerbate the costs of being winged for males of this group, a suggestion borne out by Crnokrak and Roff's (1995) study of differences in the calling behavior of the two wing morphs of male sand

crickets, *Gryllus firmus*. Given that the costs of flight are more readily apparent in male *G. sigillatus* relative to other cricket species, at least as manifest by morph-specific differences in reproductive investment (cf. Holtmeier and Zera, 1993; Roff and Fairbairn, 1993), we might expect a lower incidence of macroptery in males relative to females in keeping with the general orthopteran trend. In *G. sigillatus*, however, the incidence of macroptery is the same or only slightly higher in females (Mathad and McFarlane, 1968), suggesting that benefits to dispersal, where they exist, are similar across the sexes.

Although spermatophylaxes of short-winged male *G. sigillatus* were significantly larger than those of long-winged males, there was no difference in ampulla mass between the two groups. These results suggest that although males of the two morphs provide different-sized nuptial food gifts to females, they manufacture ejaculates of similar magnitude. Within both wing morphs, there was a significant positive correlation between the mass of the spermatophylax and the mass of the ampulla, a result which, superficially at least, appears to be inconsistent with the observed difference in spermatophylax mass and the absence of any such difference in ampulla mass between the two morphs. One possibility is that a biological difference in ampulla mass exists, but the statistical test lacked sufficient power to detect it. Even were this the case, however, it appears that any difference in ampulla mass between the two morphs is fairly trivial (mean difference in ampulla mass = 0.03 mg).

The correlation between spermatophylax mass and ampulla mass observed in *G. sigillatus*, has also been established for the spermatophores of numerous bushcricket species (Vahed and Gibert, 1996; Wedell, 1993). Such a correlation has been taken as evidence that males adjust the size of their food gifts in accordance with the size of their ejaculates; the rationale is that fewer sperm require less time to transfer, and hence a smaller food gift suffices to ensure the complete evacuation of a smaller ampulla. Whether the mass of the ampulla is related to the time required for its complete evacuation remains to be established for *G. sigillatus*, but recent work suggests that male crickets are capable of fine-grained adjustments in the number of sperm packaged in their ejaculates (Gage and Barnard, 1996). Notwithstanding this capability, long-winged male *G. sigillatus* do not appear to reduce the size of their ejaculates in a manner commensurate with the smaller food gifts they provide relative to short-winged males. It may be that any penalty for excessive sperm wastage is more than offset by the increased fertilization success that is realized when, as occasionally happens, a mated female fails to remove the sperm ampulla soon after consuming the spermatophylax (Sakaluk, 1984, 1987).

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REFERENCES

Alexander RD, Otte D, 1967. The evolution of genitalia and mating behavior in crickets (Gryllidae) and other Orthoptera. Misc Pub Mus Zool Univ Mich 133:1–62.

Burpee DM, Sakaluk SK, 1993. The effect of pair formation on diel calling patterns in two cricket species, *Gryllus veletis* and *Gryllodes sigillatus* (Orthoptera: Gryllidae). J Insect Behav 6:431–440.

Crnokrak P, Roff DA, 1995. Fitness differences associated with calling behaviour in the two wing morphs of male sand crickets, *Gryllus firmus*. Anim Behav 50:1475–1481.

Dingle H, 1985. Migration. In: Comprehensive insect physiology, biochemistry and pharmacology (Kerkut GA, Gilbert LI, eds), vol. 9, Behaviour. Oxford: Pergamon Press; 375–415.

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

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.

Gage AR, Barnard CJ, 1996. Male crickets increase sperm number in relation to competition and female size. Behav Ecol Sociobiol 38: 349–353.

Ghouri ASK, McFarlane JE, 1958. Occurrence of a macropterous form of *Gryllodes sigillatus* (Walker) (Orthoptera: Gryllidae) in laboratory culture. Can J Zool 36:837–838.

Harrison RG, 1980. Dispersal polymorphisms in insects. Annu Rev Ecol Syst 11:95–118.

Holtmeier CL, Zera AJ, 1993. Differential mating success of male wing morphs of the cricket, *Gryllus rubens*. Am Midl Nat 129:223–233.

Leopold RA, 1976. The role of male accessory glands in insect reproduction. Annu Rev Entomol 21:199–221.

Manly BFJ, 1986. Multivariate statistical methods: a primer. London: Chapman and Hall.

Mathad SB, McFarlane JE, 1968. Two effects of photoperiod on wing development in *Gryllodes sigillatus* (Walk.). Can J Zool 46:57–60.

Nandchahal N, 1972. Reproductive organs of *Gryllodes sigillatus* (Walker) (Orthoptera: Gryllidae). J. Nat His 6:125–131.

Narula JS, 1969. The male genital system of the Indian house cricket *Gryllodes sigillatus* (Walker) (Gryllidae: Orthoptera). Bull Entomol 10:86–91.

Roff DA, Fairbairn DJ, 1991. Wing dimorphisms and the evolution of migratory polymorphisms among the Insecta. Am Zool 31:243–251.

Roff DA, Fairbairn DJ, 1993. The evolution of alternate morphologies: fitness and wing morphology in male sand crickets. Evolution 47: 1572–1584.

Sakaluk SK, 1984. Male crickets feed females to ensure complete sperm transfer. Science 223:609–610.

Sakaluk SK, 1985. Spermatophore size and its role in the reproductive behaviour of the cricket, *Gryllodes supplicans* (Orthoptera: Gryllidae). Can J Zool 63:1652–1656.

Sakaluk SK, 1986. Sperm competition and the evolution of nuptial feeding behavior in the cricket, *Gryllodes supplicans* (Walker). Evolution 40:584–593.

Sakaluk SK, 1987. Reproductive behaviour of the decorated cricket, *Gryllodes supplicans* (Orthoptera: Gryllidae): calling schedules, spatial distribution, and mating. Behaviour 100:202–225.

Sakaluk SK, 1991. Post-copulatory mate guarding in decorated crickets. Anim Behav 41:207–216.

Sakaluk SK, Eggert A-K, 1996. Female control of sperm transfer and intraspecific variation in sperm precedence: antecedents to the evolution of a courtship food gift. Evolution 50:694–703.

Sakaluk SK, Smith RL, 1988. Inheritance of male parental investment in an insect. Am Nat 132:594–601.

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

Simmons LW, 1986. Female choice in the field cricket *Gryllus bimaculatus* (De Geer). Anim Behav 34:1463–1470.

Thornhill R, 1976. Sexual selection and nuptial feeding behavior in *Bittacus apicalis* (Insecta: Mecoptera). Am Nat 110:529–548.

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

Toms RB, 1993. More winged females of the cricket *Gryllodes supplicans* (Walker). S Afr J Zool 28:122–124.

Vahed K, Gilbert FS, 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: 1257–1265.

Ward PI, 1993. Females influence sperm storage and use in the yellow dung fly *Scathophaga stercoraria* (L.). Behav Ecol Sociobiol 32:313–319.

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