Behavioral Ecology Vol. 12 No. 6: 740–745

Ejaculate expenditures of male crickets in response to varying risk and intensity of sperm competition: not all species play games

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Costs incurred in the manufacture of ejaculates may constrain the number of sperm that males can produce, so males should show some economy in their allocation of sperm across multiple matings. In species in which females mate with multiple males and are capable of storing sperm for extended periods, sperm allocation of males should be tailored to the risk of sperm competition. Recent game theory predicts that males should transfer the least sperm when there are no other rivals, and the most sperm when only one other rival is likely to inseminate the female. However, as the numbers of competitors increases beyond two, the models predict a corresponding decrease in ejaculate expenditure. We tested these predictions in three cricket species, *Gryllodes sigillatus, Gryllus veletis,* and *Gryllus texensis,* assessing the sperm allocation of males held under three levels of apparent interrival competition: no rivals, one rival and six rivals. Sperm allocation of *G. veletis* varied according to theory: males increased their sperm allocation with an increased risk of sperm competition (no rivals vs. one), but decreased their allocation with an increased intensity of sperm competition (one rival vs. six). Sperm allocation of male *G. texensis* showed no significant response to the density of rivals, and sperm allocation in *G. sigillatus* was influenced by an unexpected interaction between treatment density and the order in which males experienced the three treatments. The observed interspecific variation in facultative sperm allocation may be due to interspecific differences in population density, rearing environment, or female mating behavior. *Key words:* crickets, *Gryllodes,* nuptial food gifts, sexual selection, spermatophore, sperm competition. *[Behav Ecol 12:740–745 (2001)]*

The conventional view of animal mating systems has been that sperm are cheap to produce, leaving males free to devote the majority of their reproductive investment to acquiring matings (Trivers, 1972). A growing body evidence suggests, however, that costs incurred in the manufacture of ejaculates limits the number of sperm that males can produce and predicts that males should show some economy in their allocation of ejaculates across multiple matings (Dewsbury, 1982; MacDiarmid and Butler, 1999; Marconato and Shapiro, 1996; Nakatsuru and Kramer, 1982). Nowhere should plasticity of male gametic investment be more evident than in the context of sperm competition (Parker, 1970, 1984). Many insect species are predisposed to high levels of sperm competition because females often mate with many different males and are capable of storing sperm of multiple mates over long periods of time (Parker, 1970). In such species, the number of sperm with which a male inseminates a given female will necessarily be a trade-off between two opposing selection pressures: the risk of sperm competition typically will favor an increase in the number of sperm transferred, but the increased gametic investment will come at the expense of the ability of males to invest in future matings or somatic maintenance.

Parker et al. (1996) recently derived a series of evolutionarily stable strategy models to determine optimal sperm expenditures under varying conditions of sperm competition. Their models distinguish between sperm competition risk, the probability that a male's ejaculate will compete with that of at least one other male, and sperm competition intensity, the number of competing ejaculates with which a male's ejaculate must contend given a high risk of sperm competition. Both within and across species, the models predict an increase in ejaculate expenditure with increased sperm competition risk. An increase in sperm competition intensity similarly predicts an increase in ejaculate expenditure across species, but within-species predictions differ. Here, the models predict that males should transfer the least sperm when there are no other competitors and the most sperm when only one other male is likely to inseminate the female. However, as the numbers of competitors increase beyond two, the models predict a corresponding decrease in ejaculate expenditure. This apparently counterintuitive result emerges because, as the number of competitors increases, the benefits derived from any additional expenditure on sperm increase at a diminishing rate.

Interspecific comparisons across a wide range of taxa have broadly supported the prediction that ejaculate expenditure should increase with an increase in the risk of sperm competition (Harcourt et al., 1981; Møller, 1991; Stockley et al., 1997; Svärd and Wiklund, 1989). A number of empirical studies have also demonstrated that males within species exhibit considerable plasticity in ejaculate expenditure in response to varying sperm competition risk (e.g., Gage, 1991, 1998; Gage and Baker, 1991; Baker and Bellis, 1993). Few studies, however, have assessed plasticity in ejaculate expenditure in response to varying sperm competition intensity (Gage and Barnard, 1996; Simmons and Kvarnemo, 1997; Wedell and Cook, 1999).

We tested the hypothesis that sperm allocation in males is mediated both by the risk and intensity of sperm competition in three cricket species, *Gryllodes sigillatus, Gryllus veletis,* and *Gryllus texensis* (Orthoptera: Gryllidae: Gryllinae). Crickets represent ideal model systems with which to address these questions because multiple mating by females is widespread within the group (Zuk and Simmons, 1997), and females are

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Received 4 July 2000; revised 18 December 2000; accepted 6 March 2001.

capable of storing sperm from multiple mates for extended periods (Sakaluk, 1986), attributes conducive to a high degree of sperm competition (Parker, 1970). The success of a male in sperm competition depends, in part, on the number of sperm that he transfers to the female because the sperm of a female's various mating partners are recruited for fertilizations in direct proportion to their relative abundance in the female's spermatheca (Sakaluk, 1986; Sakaluk and Eggert, 1996; Simmons, 1987). Males transfer their sperm in the form of a spermatophore, a discrete vessel that remains attached outside the female's body after mating. The spermatophore is easily removed, simplifying the recovery and enumeration of sperm. Males typically manufacture their spermatophore well in advance of copulation and copulate only if a fully formed spermatophore is present in their spermatophoric pouch (Loher and Dambach, 1989). Hence, the number of sperm allocated to the spermatophore should reflect the number of competitors that a male encounters before locating a prospective mate.

METHODS

Experimental animals

Experimental crickets were obtained from stock colonies and maintained according to standard procedures (Burpee and Sakaluk, 1993; Sakaluk, 1991). *Gryllodes sigillatus* originated from approximately 200 subadult and adult crickets collected at Tucson, Arizona, USA, in October 1995. *Gryllus texensis* originated from crickets collected at Austin, Texas, USA, in summer 1995; in previous papers (e.g., Sakaluk, 2000; Sakaluk and Cade, 1980, 1983), this species has been incorrectly referred to as *G. integer* (see correction in Cade and Otte, 2000). *Gryllus veletis* were F_1 offspring of crickets collected locally. Late-instar nymphs were checked daily for adult eclosion, and adults were held individually to ensure their virginity. Experimental males, at least 4 days beyond the imaginal molt to ensure their sexual maturity, were weighed and marked with a spot of model paint on either the pronotum or hind femur to distinguish them from nonexperimental males.

Patterns of sperm allocation

Sperm allocation of experimental males was assessed under each of three levels of apparent inter-rival competition established before mating: (1) no rivals, (2) one rival, and (3) six rivals. This design simultaneously varies sperm competition risk (sperm allocation of males held with no rivals versus those held with one and six rivals, respectively) and sperm competition intensity (sperm allocation of males held with one rival versus those held with six rivals). The experiment was a repeated-measures design, with each experimental male experiencing each of the three treatment densities. Such a design controls for intermale variation in sperm production, and thereby affords greater statistical power in detecting differences between treatments. The order in which males experienced the three treatment densities was altered from one replicate to the next, and each of the six possible sequences (0–1–6, 0–6–1, 1–0–6, 1–6–0, 6–0–1, 6–1–0) was replicated four times, yielding a sample size of 24 males per species.

Each experimental male was mated once to a virgin female immediately before being assigned to their first treatment density, and the spermatophore was discarded. This ensured that the males were of the same mating status across all experimental treatments (i.e., nonvirgin) and that the number of sperm allocated to the spermatophore during the first prescribed treatment density reflected the number of competitors with which the male had been held. After this initial nonexperimental mating, each experimental male was housed in a 3.5-l plastic jar with the prescribed number of rivals for a period of 24 h. Cricket chow and water were provided ad libitum. After the 24-h period, the male was removed and placed in another jar with a virgin female of known mass and age and allowed to mate. If the pair failed to mate within 1 h, we reassigned the male to his current treatment density, and he was given an opportunity to mate with a different virgin female 24 h later. Upon mating, the spermatophore was immediately removed from the female with forceps, and the male was assigned to his next treatment density. We repeated this protocol until each male had experienced all three treatment densities.

In *G. veletis* and *G. texensis,* the spermatophore consists of a simple sperm-containing ampulla, whereas in *G. sigillatus,* the ampulla is accompanied by a gelatinous, non–sperm-containing mass, the spermatophylax, that functions to keeps the female preoccupied during the time it takes the ampulla to be emptied of sperm (Sakaluk, 1984, 1985). After matings in all three species, we immediately weighed the ampulla to the nearest microgram using a Cahn microbalance, except that in the case of *G. sigillatus,* this first necessitated the separation of the ampulla from the spermatophylax, after which we weighed the two components separately. The ampulla was subsequently placed in 4 ml of distilled water and cut into several pieces using microscissors, after which the mixture was forced repeatedly through a fine-gauge, 1-cc syringe until the ampulla had been sheared into smaller pieces. To prevent sperm agglutination, the solution was stirred vigorously for 1 min using a Fisher Vortex Genie 2. In the case of *G. sigillatus,* the solution was further diluted in half because of the higher density of sperm in this species. Five 10-μl samples were pipetted onto a uniquely labeled microscope slide equipped with a grid, which subsequently was set aside to dry. We determined the mean number of sperm per 10-μl sample at 100× magnification. Sperm counts were made blind to the experimental treatment from which the spermatophore had been drawn.

To assess the pattern of sperm allocation for each species, we used a repeated-measures MANOVA in which the numbers of sperm allocated to ampullae at each of the three treatment densities were entered as the response variables, the experimental treatment (density of competitors) was entered as the within-subjects factor (henceforth, ''treatment''), and the order in which males experienced the three treatment densities was entered as the between-subjects factor (henceforth, ''order''). Profile analysis was used to addresses hypotheses concerning parallelism of profiles (a test for an order × treatment interaction), flatness of profiles (a test of the effect of treatment on sperm numbers) and levels of profiles (a test of the effect of order on sperm numbers). Individual contrasts were analyzed using the Profile and Contrast transformations included in the SAS GLM procedure (SAS Institute, 1988). A repeated-measures MANOVA is preferable to a univariate repeated-measures ANOVA because it avoids the assumptions of circularity and sphericity inherent to the latter (von Ende, 1993), and it is the recommended course of action when $N - M > k + 9$, where N = the number of subjects, M = the number of between-subject groups, and k = the number of variables (Maxwell and Delaney, 1990). This criterion was easily met for each of the species examined in the present study ($24 - 6 > 3 + 9$).

RESULTS

The mean, standard deviation, and range of male body mass, spermatophore mass, and sperm number are shown in Table 1.

There was a significant effect of treatment on the number

Table 1
Male body mass, spermatophore mass, and sperm number in 3 cricket species

	n	Mean	SD	Range
Gryllus veletis				
Body mass (mg)	24	450	109	271–640
Ampulla mass (mg)	67	0.77	0.16	0.47–1.27
No. sperm (per 10-μl sample)	72	158	107	4–460
Gryllus texensis				
Body mass (mg)	24	589	131	370–834
Ampulla mass (mg)	68	0.85	0.14	0.57–1.13
No. sperm (per 10-μl sample)	72	121	74	3–350
Gryllodes sigillatus				
Body mass (mg)	24	283	55	200–397
Spermatophylax mass (mg)	61	5.46	1.09	1.78–7.84
Ampulla mass (mg)	68	1.18	0.25	0.72–1.96
No. sperm (per 10-μl sample)[a]	72	159	65	50–390

[a] Samples were drawn from a solution that was twice as dilute as those prepared for the other two species, so that these values should be multiplied by a factor of two for direct comparisons between species.

of sperm allocated by male *Gryllus veletis* ($p = .0079$; Table 2). There was no effect of order on sperm allocation ($F_{5, 18} = 0.6$, $p = .70$), nor was there a significant order × treatment interaction ($p = .52$). Males, when held with one rival, allocated significantly more sperm to their ampullae than when held with no rivals ($F = 8.90$, $p = .008$) or when held with six rivals ($F = 9.79$, $p = .0058$). There was no difference in sperm allocation when males were held with no rivals versus when they were held with six rivals ($F = 0.00$, $p = .95$; Figure 1).

There was no effect of either treatment ($p = .39$; Table 2) or order ($F_{5, 18} = 1.56$, $p = .22$) on sperm allocation in male *Gryllus texensis,* nor was there a significant order × treatment interaction ($p = .72$; Table 2).

There was a significant order × treatment interaction on sperm allocation in *Gryllodes sigillatus* ($p = .0234$), obviating separate tests of the main effects. The interaction appeared to stem from sperm allocation of males when held with no rivals. Males appeared to allocate more sperm when they experienced this treatment first than when they experienced this treatment in the second or third position in the order. In contrast, sperm allocation of males held with one or six rivals appeared to be relatively unaffected by the order in which they experienced these treatments.

Table 2
Repeated-measures MANOVA of sperm allocation in male crickets subject to varying densities of male competitors

			df		
	Wilks' λ	*F*	Num.	Den.	*p*
Gryllus veletis					
Treatment	0.5657	6.52	2	17	.0079
Treatment × order	0.6155	0.93	10	34	.5155
Gryllus texensis					
Treatment	0.8948	1.00	2	17	.3886
Treatment × order	0.6892	0.70	10	34	.7215
Gryllodes sigillatus					
Treatment	0.9100	0.84	2	17	.4488
Treatment × order	0.3339	2.48	10	34	.0234

In the analysis, the density of competitors is the within-subjects factors (designated treatment), and the order in which males experienced the three treatment densities is the between-subjects factor (designated order).

Pearson product-moment correlations between male body mass, ampulla mass, number of sperm and, in the case of *G. sigillatus,* spermatophylax mass, are shown in Table 3. Because male body mass was only measured once, we first determined the mean sperm number and mean spermatophore mass across the male's three matings and used these means in correlations involving male body mass. Ampulla mass and sperm number were positively correlated in *G. veletis* ($p < .0001$) and *G. sigillatus* ($p = .012$), but not in *G. texensis* ($p > .05$). In *G. sigillatus,* the mass of the spermatophylax was positively correlated with the mass of the ampulla ($p < .001$), but not with the number of sperm contained in the ampulla ($p = .12$). Male body mass had no consistent relationship with sperm number across species. In *G. sigillatus,* male body mass was positively correlated with the mass of the spermatophylax ($p = .028$) and the ampulla ($p = .012$), but not with sperm number ($p = .58$). In *G. veletis,* male body mass was positively correlated both with the mass of the ampulla ($p = .031$) and sperm number ($p = .0024$). In *G. texensis,* male body mass was positively correlated with ampulla mass ($p = .02$), but not with sperm number ($p = .50$).

DISCUSSION

Of the three cricket species subject to varying risk and intensity of sperm competition, only *G. veletis* behaved according to the predictions of recent evolutionarily stable strategy models (Parker et al., 1996). With an increased risk of sperm competition, male *G. veletis* showed the expected increase in the number of sperm allocated to the sperm ampulla, whereas with an increased intensity of sperm competition, males showed the expected decrease in the number of sperm allocated. Male *G. texensis* showed no significant response to either varying risk or varying intensity of sperm competition. There was a significant interaction between treatment density and the order in which males experienced the three treatments on sperm allocation in *G. sigillatus.* Although the interaction suggests that both variables had an influence on sperm allocation in this species, the effects are not explicable within the context of recent game theory.

Only one other study has examined sperm allocation of

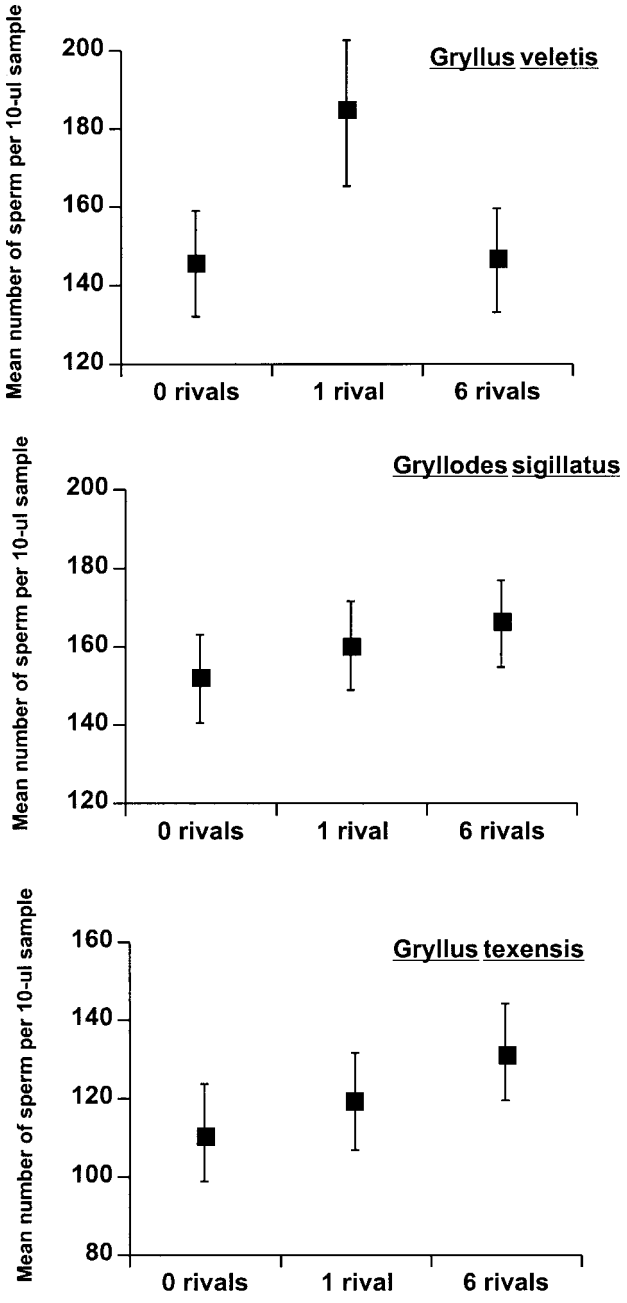

Figure 1
Mean number of sperm (and 95% confidence interval) allocated by males of three cricket species held under each of three levels of apparent inter-rival competition. The number of rivals had a significant effect on the number of sperm allocated by male *Gryllus veletis* ($p = .0079$), but there were no differences in sperm allocation across treatments in either *Gryllodes sigillatus* or *Gryllus texensis* ($p > .05$).

male crickets under varying conditions of sperm competition risk and intensity. Gage and Barnard (1996) examined sperm allocation in *G. sigillatus* and *Acheta domesticus* at treatment densities comparable to those established here. In both species, males' sperm allocation increased with the number of competitors. Males held with no rivals allocated fewer sperm than males held with one rival, consistent with the predicted response to varying sperm competition risk, but males held with one rival transferred fewer sperm than males held with seven rivals, opposite to the predicted response to increasing sperm competition intensity.

Table 3
Pearson product-moment correlations (*r*) between male body mass, spermatophore mass, and number of sperm in three cricket species

	Ampulla mass	Sperm number	Spermatophylax mass
Gryllus veletis			
Body mass	0.44* (24)	0.59** (24)	—
Ampulla mass		0.60*** (67)	—
Gryllus texensis			
Body mass	0.47* (24)	0.05 (24)	—
Ampulla mass		0.04 (68)	—
Gryllodes sigillatus			
Body mass	0.50* (24)	0.12 (24)	0.45* (24)
Ampulla mass		0.30* (68)	0.46*** (57)
Sperm number			0.20 (61)

Sample sizes in parentheses.
* $p < .05$; ** $p < .01$; *** $p < .001$.

The effect of treatment on sperm allocation in *G. sigillatus* was much more apparent in Gage and Barnard's (1996) study than in the present study. We can offer no clear explanation for this difference, except that there are some subtle differences in methodology between the two studies that merit consideration. In Gage and Barnard's (1996) study, comparisons between treatments may have been confounded by male mating status because males were virgins when assigned to their first treatment density, but they were sexually experienced at subsequent treatment densities. A more serious problem with Gage and Barnard's (1996) study, one that they explicitly acknowledge, is that many of the males assigned to their first treatment density would have already possessed fully formed spermatophores and hence would have already been committed to a particular ejaculate expenditure. This would tend to weaken or even eliminate any effect of male competition on male ejaculate expenditures in the first treatments.

Why do males of some species respond as predicted to varying sperm competition intensity while others apparently do not? Parker (1998), in a review of recent models, identified three key variables expected to influence sperm allocation strategies of males: (1) the fairness of the sperm raffle (i.e., the extent to which fertilizations are determined by the relative abundance of males' sperm versus a mating-order advantage), (2) the information available to the male regarding the anticipated risk of sperm competition, and (3) the male's mating role and knowledge of that role (i.e., any mating advantage accruing to the male by virtue of his position in the mating sequence or via his dominance of other males). Of these three variables, only the last two offer any promise to account for the observed differences in sperm allocation across cricket species. In all gryllids studied to date, fertilizations appear to be determined chiefly by lottery (Backus and Cade, 1986; Sakaluk, 1986; Sakaluk and Eggert, 1996; Simmons, 1987), so fundamental differences in the pattern of sperm precedence are unlikely to explain the observed variation in sperm allocation patterns.

There are a number of reasons that information available to males concerning their anticipated risk of sperm competition, or knowledge of their mating roles, might differ across cricket species. One possibility is that rearing conditions may mitigate against a facultative response in ejaculate expenditures. Male *G. sigillatus* and *G. texensis* used in this study were from long-standing communal colonies (3+ years), whereas

male *G. veletis* were F_1 offspring of crickets collected locally. In our laboratory, crickets are normally reared at high densities, and, consequently, males of both *G. sigillatus* and *G. texensis* would have been subject to high sperm competition risk and intensity for about 10–15 generations. Assuming that plasticity in ejaculate expenditures comes at a cost, the laboratory rearing environment may have inadvertently selected against this ability in laboratory-reared male *G. sigillatus* and *G. texensis,* whereas male *G. veletis,* having been spared this breeding regimen, retained the ability to make facultative adjustments in sperm allocation. Arguing against this proposition, however, is the fact that the male *A. domesticus* and *G. sigillatus* used in Gage and Barnard's (1996) study came from even older cultures, but nevertheless showed a clear response to increased sperm competition risk.

A second possibility to account for the observed interspecific variation in facultative sperm allocation is that ecological factors may favor such plasticity in some species, but conspire against it in others. A prime candidate in this regard would be population density because population density should covary both with sperm competition risk and intensity. In species subject to historically high population densities, the risk and intensity of sperm competition might be uniformly high and fluctuate little temporally; under such circumstances, selection for facultative sperm allocation might be relaxed. In contrast, in low-density populations, where the risk and intensity of sperm competition might fluctuate according to variation in local abundance, the ability to adjust sperm allocation in response to varying sperm competition risk and intensity might be selectively advantageous. Population densities of each of the three species as they have been observed in nature provide some support for this hypothesis. *G. texensis* frequently occur in dense populations, whereas *G. veletis* occur in populations of much lower density (Alexander and Meral, 1967; Cade, 1979b, 1981; Cade and Cade, 1992). In Tucson, Arizona, where our *G. sigillatus* stock originated, population densities have shown a marked increase from the late 1970s to the early 1980s, resulting in the species becoming a widespread urban pest (Smith and Thomas, 1988; Thomas, 1985). Moreover, recent studies of *G. sigillatus* conducted in a seminatural outdoor enclosure at the University of New Mexico, Albuquerque (USA), have revealed that even when there is a preponderance of shelters, individuals of both sexes typically aggregate in large clusters under one or two shelters (Sakaluk SK, Eggert A-K, and Snedden WA, unpublished data). Such behavior would tend to promote high levels of sperm competition and risk even in the face of temporal fluctuations in overall population density. However, a definitive causal link between any one ecological factor and plasticity in sperm allocation must await studies of other species whose natural history has been equally well established.

A final factor that could account for differences between species in sperm allocation is interspecific differences in female mating behavior. Our experimental design assumed that the number of nearby rivals is an accurate gauge of the intensity of sperm competition. However, the validity of this assumption depends on whether females arriving in a local cluster of males mate with most or all of them. If, instead, females mate with only one male before departing the local area, then the actual intensity of sperm competition may be less than is apparent. A further complicating issue in *G. texensis* is that some males behave as satellites, males who surreptitiously intercept the females attracted to territorial calling males (Cade, 1975, 1979a). Recent models suggest that in a fair raffle, sneaks should always allocate more sperm to females than guarding males (Parker, 1998). In the present study, male *G. texensis* were assigned to treatments without regard to their prospective mating roles (i.e., sneaks vs. territorial callers), and so a greater allocation of sperm by sneak males may have obscured any attempt to detect significant treatment differences. There may also be differences between species in the propensity of females to mate with multiple males. If, for example, females mate repeatedly with the same male, as occurs in some cricket species (Hissmann, 1990; Loher and Rence, 1978; Rost and Honegger, 1987; Zuk, 1987), males may adjust their sperm allocation not by varying the number of sperm contained in the spermatophore but by varying the number of spermatophores transferred. This possibility was not addressed in the present study, but remains an obvious candidate to explain why sperm allocation in two of the three species did not conform to theoretical expectations.

We thank A. Gage for advising us on the preparation of sperm samples, S. Juliano for statistical advice, W. Cade for supplying the *G. texensis* stock, P. Brady for laboratory assistance, and J. Armstrong, S. Loew, and two anonymous reviewers for helpful comments on the manuscript. This research was supported by grants from the Graduate Student Association of Illinois State University and the Phi Sigma Biological Honors Society (Beta Lambda Chapter) to J.M.S. and grants from Illinois State University and the National Science Foundation (IBN-9601042 and REU supplemental award) to S.K.S.

REFERENCES

Alexander RD, Meral GH, 1967. Seasonal and daily chirping cycles in the northern spring and fall field crickets, *Gryllus veletis* and *G. pennsylvanicus*. Ohio J Sci 67:200–209.

Backus VL, Cade WH, 1986. Sperm competition in the field cricket *Gryllus integer* (Orthoptera: Gryllidae). Fla Entomol 69:722–728.

Baker RR, Bellis MA, 1993. Human sperm competition: ejaculate adjustment by males and the function of masturbation. Anim Behav 46:861–885.

Burpee DM, Sakaluk SK, 1993. Repeated matings offset costs of reproduction in female crickets. Evol Ecol 7:240–250.

Cade WH, 1975. Acoustically orienting parasitoids: fly phonotaxis to cricket song. Science 190:1312–1313.

Cade WH, 1979a. The evolution of alternative male reproductive strategies in field crickets. In: Sexual selection and reproductive competition in insects (Blum MS, Blum NA, eds). New York: Academic Press; 343–379.

Cade WH, 1979b. Field cricket dispersal flights measured by crickets landing at lights. Texas J Sci 31:125–130.

Cade WH, 1981. Field cricket spacing, and the phonotaxis of crickets and parasitoid flies to clumped and isolated cricket songs. Z Tierpsychol 55:365–375.

Cade WH, Cade ES, 1992. Male mating success, calling and searching behaviour at high and low densities in the field cricket, *Gryllus integer*. Anim Behav 43:49–56.

Cade WH, Otte D, 2000. *Gryllus texensis* n. sp.: a widely studied field cricket (Orthoptera; Gryllidae) from the southern United States. Trans Am Entomol Soc 126:117–123.

Dewsbury D, 1982. Ejaculate cost and male choice. Am Nat 119:601–610.

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

Gage MJG, 1991. Risk of sperm competition directly affects ejaculate size in the Mediterranean fruit fly. Anim Behav 42:1036–1037.

Gage MJG, 1998. Influences of sex, size, and symmetry on ejaculate expenditure in a moth. Behav Ecol 9:592–597.

Gage MJG, Baker RR, 1991. Ejaculate size varies with socio-sexual situation in an insect. Ecol Entomol 16:331–337.

Harcourt AH, Harvey PH, Larson SG, Short RV, 1981. Testis weight, body weight and breeding system in primates. Nature 293:55–57.

Hissmann K, 1990. Strategies of mate finding in the European field cricket (*Gryllus campestris*) at different population densities: a field study. Ecol Entomol 15:281–291.

Loher W, Dambach M, 1989. Reproductive behavior. In: Cricket behavior and neurobiology (Huber F, Moore TE, Loher W, eds). Ithaca, New York: Cornell University Press; 43–82.

Loher W, Rence B, 1978. The mating behavior of *Teleogryllus com-*

modus (Walker) and its central and peripheral control. Z Tierpsychol 46:225–259.
MacDiarmid AB, Butler MA IV, 1999. Sperm economy and limitation in spiny lobsters. Behav Ecol Sociobiol 46:14–24.
Marconato A, Shapiro DY, 1996. Sperm allocation, sperm production and fertilization rates in the bucktooth parrotfish. Anim Behav 52: 971–980.
Maxwell SE, Delaney HD, 1990. Designing experiments and analyzing data: a model comparison perspective. Belmont, California: Wadsworth.
Møller AP, 1991. Sperm competition, sperm depletion, paternal care, and relative testis size in birds. Am Nat 137:882–906.
Nakatsuru K, Kramer DL, 1982. Is sperm cheap? Limited male fertility and female choice in the lemon tetra (Pisces, Characidae). Science 216:753–755.
Parker GA, 1970. Sperm competition and its evolutionary consequences in the insects. Biol Rev 45:525–567.
Parker GA, 1984. Sperm competition and the evolution of animal mating strategies. In: Sperm competition and the evolution of animal mating systems (Smith RL, ed). New York: Academic Press; 1–60.
Parker GA, 1998. Sperm competition and the evolution of ejaculates: towards a theory base. In: Sperm competition and sexual selection (Birkhead TR, Møller AP, eds). San Diego, California: Academic Press; 3–54.
Parker GA, Ball MA, Stockley P, Gage MJG, 1996. Sperm competition games: individual assessment of sperm competition intensity by group spawners. Proc R Soc Lond B 263:1291–1297.
Rost R, Honegger HW, 1987. The timing of premating and mating behavior in a field population of the cricket *Gryllus campestris* L. Behav Ecol Sociobiol 21: 279–289.
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, 1991. Post-copulatory mate guarding in decorated crickets. Anim Behav 41:207–216.
Sakaluk SK, 2000. Sensory exploitation as an evolutionary origin to nuptial food gifts in insects. Proc R Soc Lond B 267:339–343.
Sakaluk SK, Cade WH, 1980. Female mating frequency and progeny production in singly and doubly mated house and field crickets. Can J Zool 58:404–411.
Sakaluk SK, Cade WH, 1983. The adaptive significance of female multiple matings in house and field crickets. In: Orthopteran mating systems: sexual competition in a diverse group of insects. (Gwynne DT, Morris GK, eds). Boulder, Colorado: Westview Press; 319–336.
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.
SAS Institute, 1988. SAS/STAT user's guide, release 6.03 ed. Cary, North Carolina: SAS Institute.
Simmons LW, 1987. Sperm competition as a mechanism of female choice in the field cricket, *Gryllus bimaculatus*. Behav Ecol Sociobiol 21:197–202.
Simmons LW, Kvarnemo C, 1997. Ejaculate expenditure by male bushcrickets decreases with sperm competition intensity. Proc R Soc Lond B 264:1203–1208.
Smith RL, Thomas WB, 1988. Southwestern distribution and habitat ecology of *Gryllodes supplicans*. Bull Entomol Soc Am 34:186–190.
Stockley P, Gage MJG, Parker GA, Møller AP, 1997. Sperm competition in fish: the evolution of testis size and ejaculate characteristics. Am Nat 149:933–954.
Svärd L, Wiklund C, 1989. Mass and production rate of ejaculates in relation to monandry/polyandry in butterflies. Behav Ecol Sociobiol 24:395–402.
Thomas WB, 1985. The distribution, biology, and management of the Indian house cricket *Gryllodes supplicans*. (MS thesis). Tucson: University of Arizona.
Trivers RL, 1972. Parental investment and sexual selection. In: Sexual selection and the descent of man: 1871–1971 (Campbell B, ed). Chicago: Aldine-Atherton; 136–179
von Ende CN, 1993. Repeated-measures analysis: growth and other time-dependent measures. In: Design and analysis of ecological experiments (Scheiner SM, Gurevitch J, eds). New York: Chapman and Hall; 113–137.
Wedell N, Cook PA, 1999. Butterflies tailor their ejaculate in response to sperm competition risk and intensity. Proc R Soc Lond B 266: 1033–1039.
Zuk M, 1987. The effects of gregarine parasites, body size, and time of day on spermatophore production and sexual selection in field crickets. Behav Ecol Sociobiol 21:65–72.
Zuk M, Simmons LW, 1997. Reproductive strategies of the crickets (Orthoptera: Gryllidae). In: The evolution of mating systems in insects and arachnids (Choe JC, Crespi BJ, eds). Cambridge: Cambridge University Press; 89–109.