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Precedence: Antecedents to the Evolution of a Courtship Food Gift**

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## FEMALE CONTROL OF SPERM TRANSFER AND INTRASPECIFIC VARIATION IN SPERM PRECEDENCE: ANTECEDENTS TO THE EVOLUTION OF A COURTSHIP FOOD GIFT

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**Abstract.**—Manipulation of ejaculates is believed to be an important avenue of female choice throughout the animal kingdom, but evidence of its importance to sexual selection remains scarce. In crickets, such manipulation is manifest in the premature removal of the externally attached spermatophore, which may afford females an important means of postcopulatory mate choice. We tested the hypothesis that premature spermatophore removal contributes significantly to intraspecific variation in sperm precedence by (1) experimentally manipulating spermatophore attachment durations of competing male *Grylloides sigillatus* and (2) employing protein electrophoresis to determine the paternity of doubly mated females. The relative spermatophore attachment durations of competing males had a significant influence on male paternity, but the pattern of sperm precedence deviated significantly from the predictions of an ideal lottery. Instead, paternity data and morphological evidence accorded best with a model of partial sperm displacement derived here. Our model is similar to a displacement model of Parker et al. in that sperm of the second male mixes instantaneously with that of the first throughout the displacement process, but the novel feature of our model is that the number of sperm displaced is only a fraction of the number of sperm transferred by the second male. Regardless of the underlying mechanism, female *G. sigillatus* can clearly alter the paternity of their offspring through their spermatophore-removal behavior, and employ such cryptic choice in favoring larger males and those providing larger courtship food gifts. We discuss how female control of sperm transfer and intraspecific variation in sperm precedence may be important precursors to the evolution of gift giving in insects.

**Key words.**—Courtship feeding, crickets, *Grylloides sigillatus*, mate choice, sexual selection, sperm competition, spermatophore.

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In many insects, females mated to more than one male may actively select the paternity of their offspring by shunting sperm to specialized compartments of the sperm storage organ or by employing the associated spermathecal musculature to expel unwanted sperm (Thornhill and Alcock 1983; Smith 1984; Eberhard 1985; Ward 1993). Although manipulation of ejaculates is thought to be an important avenue of female choice throughout the animal kingdom (Walker 1980; Thornhill and Alcock 1983; Smith 1984; Eberhard 1985; Birkhead and Møller 1992), its contribution to sexual selection on males, relative to intrasexual competition and precopulatory mate choice, remains obscure. Pertinent studies are scarce (e.g., Sakaluk 1984, 1985; Simmons 1986, 1987; LaMunyon and Eisner 1993, 1994), perhaps because in most species, ejaculate manipulation is likely to occur internally and thus may be difficult to observe or investigate directly (but see Eberhard 1993). Crickets are ideal subjects for such investigations because ejaculate manipulation, manifest in the removal by females of the externally attached spermatophore, is readily observed and quantified. Premature spermatophore removal may be an important avenue through which mating preferences are exerted (Sakaluk 1985) and, because females control the extent to which they are inseminated (Sakaluk 1991), may provide a mechanism whose consequences can be unambiguously distinguished from those arising through male-male competition. Sakaluk (1984, 1985) demonstrated that female decorated crickets, *Grylloides sigillatus*, employ spermatophore removal to discriminate among males on the basis of material benefits received from their mates. Similarly, Simmons (1986) showed that female *Gryllus bimaculatus* remove the spermatophores of smaller males before

complete sperm transfer has occurred, and significantly earlier than those of larger males.

The hypothesis that spermatophore removal affords females an effective means of postcopulatory choice predicts that male fitness should be strongly correlated with the duration of spermatophore attachment. In support of this prediction, previous studies have shown that the number of sperm transferred by a male is determined by the time at which the female removes the spermatophore (Sakaluk 1984; Simmons 1986). Even with a shortened spermatophore attachment duration, however, a male may still transfer sufficient sperm to fertilize all of a female's eggs. Nonetheless, a male's fitness may be decreased by a reduction in the number of sperm transferred if his sperm have to compete with the sperm of a female's other mates for the fertilization of her eggs (Parker 1970, 1984). Indeed, sperm competition is likely to be a common occurrence in crickets, because females routinely mate with many different males (French and Cade 1987; Rost and Honegger 1987) and stored sperm remain viable over extended periods (Sakaluk 1986).

Two general kinds of mechanisms have been identified as the primary determinants of interspecific variation in sperm precedence in insects, random sperm mixing, and sperm displacement, the latter of which can arise either through the volumetric displacement or physical removal of previously stored sperm (Parker 1970, 1984; Walker 1980). Parker et al. (1990) recently developed a series of linear models that show how putative mechanisms of sperm precedence can be distinguished by experimentally varying the number of sperm transferred at mating (see Table 1). They identified two patterns of sperm precedence that can arise through simple mix-

ing of ejaculates, ideal lotteries, and loaded lotteries. In an ideal lottery, sperm of competing males are recruited for fertilizations in direct proportion to their relative abundance, whereas in a loaded lottery, the numerical effect is moderated by a bias arising from a mating order advantage. Parker et al. (1990) also formalized two types of displacement models, displacement in which some mixing of ejaculates occurs during sperm transfer and displacement in which no sperm mixing occurs until sperm transfer has been completed.

To date, patterns of sperm precedence have been examined in three grylline cricket species, each of which showed that females mated to two males use the sperm of both males to varying degrees (Sakaluk 1986; Backus and Cade 1986; Simmons 1987). Sakaluk (1986) found equivocal evidence of a relationship between the duration of spermatophore attachment and paternity in *G. sigillatus*, reporting a weak effect in only one of two experimental series. In contrast, Parker et al. (1990) reanalyzed Simmons' (1987) data for *G. bimaculatus* and found them strongly consistent with the predictions of an ideal lottery and inconsistent with alternative mechanisms. The discordance between the two studies may reflect interspecific variation in the mechanisms of sperm precedence or a more complex mechanism of sperm competition than suggested by the ideal lottery.

Here we test the hypothesis that premature spermatophore removal contributes significantly to intraspecific variation in sperm precedence by (1) experimentally manipulating spermatophore attachment durations of competing male *G. sigillatus* and (2) employing protein electrophoresis to determine the paternity of offspring produced by doubly mated females. One potential difficulty with using allozymes to ascertain paternity is that when pairings are established with randomly chosen individuals, paternity of offspring may remain ambiguous even after several enzyme systems have been screened. In such cases, paternity must be inferred probabilistically on the basis of a maximum-likelihood function (e.g., Dickinson 1986; Price et al. 1989; Watson 1991). However, the advantage to using allozymes in the present study was that the inferred genotype of each male could be determined prior to experimental pairings; a single mesothoracic leg from an adult *G. sigillatus* contains sufficient material for electrophoretic analysis, and crickets with missing legs are easily able to complete matings (pers. obs.). Hence, by using the appropriate combination of genotypes (i.e., homozygotes for alternate alleles), it is possible to resolve unambiguously the paternity of offspring (see also Gwynne 1988a).

## MATERIALS AND METHODS

### General Methods

Experimental *G. sigillatus* were derived from a stock colony, maintained according to standard procedures (details in Sakaluk 1991). Late-instar males and females were housed separately, which ensured their virginity upon adult eclosion. Following initial electrophoretic screening (see below), virgin females and males were assigned to experimental pairings based on their allozyme phenotypes. Each female was mated twice, once to each of two males. No male was used in more than one mating to avoid pseudoreplication of data. Crickets used in experimental matings were at least 6-d-old adult age

(range = 6–26) to ensure their sexual maturity (Sakaluk 1987). Whenever possible, we attempted to use males of a similar age in double matings (median age difference = 2 d, range = 0–12), to minimize any effects of age on the number of sperm transferred. Females were given the opportunity to remate 1 d after their first mating or each subsequent day until remated, corresponding to the typical female intercopulatory interval observed under natural conditions (S. K. Sakaluk, A.-K. Eggert, and W. A. Snedden, unpubl. data); only six of 31 doubly mated females used in paternity analyses failed to remate at their first opportunity (median intercopulatory interval = 1 d, range = 1–3). Females were given no oviposition substrate between matings, to prevent any loss of first males' sperm that would occur upon oviposition by females prior to the completion of the mating sequence.

Spermatophore attachment durations were experimentally manipulated by confining each mated female to a narrow vial, thereby preventing the female from bending backward to remove the spermatophore; the spermatophore was subsequently removed with forceps at a predetermined interval. In accordance with the protocol prescribed by Parker et al. (1990), the spermatophore of the first male was permitted to remain attached for 50 min, the time required for the spermatophore to be completely evacuated of sperm (Sakaluk 1984), whereas the spermatophore attachment duration of the second male was permitted to vary from 5–50 min, in 5-min increments. In five double matings, the spermatophore of the first male was inadvertently dislodged prior to its complete evacuation (spermatophore attachment duration: 22–47 min). We include data from these females in measures of central tendency but exclude them from assessment of models of sperm precedence because they violate a basic assumption of the models, namely, that the first male transfers a complete ejaculate.

Following their second mating, females were held individually in 1-liter plastic containers and allowed to oviposit in plastic weigh boats, filled with an equal mixture of sand and vermiculite, and moistened daily. Offspring were reared in plastic shoe boxes (16.5 × 30.5 × 8.5 cm) provisioned with ample food (Purina® cricket chow), water, and sections of egg carton for shelter.

### Electrophoretic Determination of Paternity

We employed cellulose acetate electrophoresis to determine the paternity of offspring produced by doubly mated females (Hebert and Beaton 1989). A preliminary screening of allozymes revealed three polymorphic loci, *phosphoglucosyltransferase* (*PGM*) and two *esterase* (*EST*) loci, one anodally and the other cathodally migrating. All three loci were diallelic. We chose *PGM* because of the excellent resolution it afforded, and because the two alleles occurred at roughly equal frequencies, maximizing the potential number of homozygotes for use in experimental crosses. Because *PGM* is a monomer, homozygous individuals can be recognized by a single band, whereas heterozygous individuals have a double-banded phenotype. An initial screening of adults revealed that *PGM* is sex-linked in *G. sigillatus*, as it is in other Orthoptera (Hebert 1984); males, because they are XO, exhibit only a single fast or slow band, whereas females (XX) can

exhibit either one or two bands. Hence, only the paternity of female offspring could be resolved on the basis of this allozyme. This necessitated rearing the offspring until at least their final instar so that their sex could be unambiguously ascertained; only female progeny of doubly mated females were subjected to electrophoretic analysis. This protocol assumes that the pattern of sperm precedence revealed in female progeny holds for male progeny as well.

When the sex linkage of *PGM* was taken into account, allomorph frequencies, based on electrophoretic screening of 336 adult males and 312 adult females, did not deviate significantly from the frequencies that would be expected if the alleles were in Hardy-Weinberg equilibrium (relative frequency of alleles: S [slow]: 0.508, F [fast]: 0.492; frequency of phenotypes: single slow band [observed: 245, expected: 251.204], slow and fast band [observed: 176, expected: 155.96], single fast band [observed: 227, expected: 240.836],  $\chi^2 = 3.519$ ,  $P > 0.05$ ). We also established three test crosses involving single females paired permanently to single males (cross 1: female [F/F]  $\times$  male [S/O]; cross 2: female [F/S]  $\times$  male [S/O]; cross 3: female [F/S]  $\times$  male [F/O]); in no instance did offspring phenotype frequencies deviate from those expected based on Mendelian inheritance (number of offspring screened = 11–28,  $\chi^2 = 0.00$ –2.571, all  $P > 0.05$ ). Moreover, only two of more than 1800 offspring screened in our laboratory had phenotypes incompatible with the presumed genotypes of their parents based on Mendelian inheritance, and these presumably were the result of cross-contamination of rearing containers. Collectively, these results support the underlying assumption of our paternity analyses, namely that allozyme phenotype is indicative of underlying genotype.

To determine the allozyme phenotype of an individual cricket, a single mesothoracic limb was removed and the femur crushed in 13  $\mu$ liters Tris Glycine buffer (pH 8.5). Isozymes were separated and stained for *PGM* using techniques adapted from Hebert and Beaton (1989). Only females homozygous for the slow (S/S) or fast (F/F) allele were used in experimental pairings and these were mated twice, once each to an F/O male and an S/O male. An equal number of F/F and S/S females was used, and the order in which these were mated to S/O and F/O males was reversed in half of all double matings, to control for the possibility that sperm precedence is influenced by the *PGM* phenotype of either males or females. All daughters produced by doubly mated females were frozen at  $-70^\circ\text{C}$  for subsequent electrophoretic analysis. Determination of the paternity of daughters was unambiguous on the basis of banding patterns (see Fig. 1). Daughters of F/F females that have been sired by F/O males exhibit a single fast band, whereas those sired by S/O males exhibit two bands; daughters of S/S females sired by F/O males exhibit two bands, whereas those sired by S/O males exhibit a single slow band.

The relationship between sperm precedence and the relative spermatophore attachment durations of competing males was assessed using the linear models developed by Parker et al. (1990), and two new models developed here involving partial displacement of sperm. All of these models require that both males in double matings succeed in transferring sperm to the female. This requirement can be violated in

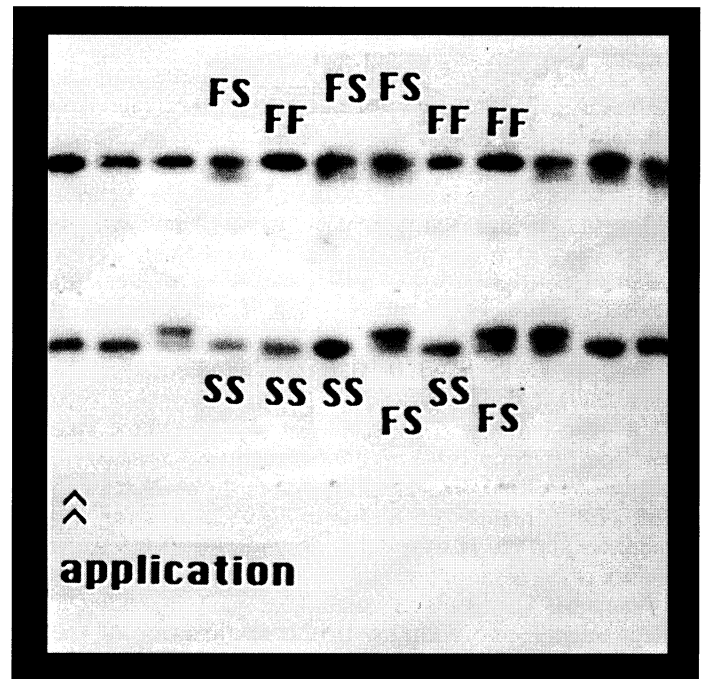


FIG. 1. Cellulose-acetate gel, stained for *PGM*, revealing paternity of daughters produced by two doubly mated females. The 12 offspring in the top row were produced by a female homozygous for the fast allele (FF), and sired by an SO (double band), or FO (single band) male. The 12 offspring in the bottom row were produced by a female homozygous for the slow allele (SS), and sired by an SO (single band), or FO (double band) male.

cricket matings if, as often happens, the narrow spermatophoric tube is not threaded correctly into the female's receptacular duct (Loher and Rence 1978); in such cases, the male fails to transfer any sperm regardless of the duration of spermatophore attachment (Sakaluk and Cade 1980, 1983). To control for this possibility, we include for analysis only those cases for which there is genetic evidence of sperm transfer by both males. We also include only those families for which more than 15 offspring were available for paternity determination.

## RESULTS

### *Variation in $P_2$*

Paternity determinations are based on the electrophoretic analysis of an average of  $55 \pm 5.96$  ( $\pm$ SE) female offspring reared per female ( $N = 31$  sibships, range = 16–153). The proportion of offspring sired by the second male ( $P_2$ ) varied widely, ranging from 0.04 to 0.94 (mean  $\pm$  SE =  $0.46 \pm 0.04$ ). These data include the five double matings in which the spermatophore of the first male was inadvertently dislodged prior to its complete evacuation; when these sibships were excluded from the analysis, the average  $P_2$  was  $0.42 \pm 0.04$  ( $N = 26$ , range = 0.04–0.88). The effect of premature spermatophore removal on male fitness is best illustrated by a regression of the second male's paternity ( $P_2$ ) on his relative spermatophore attachment duration ( $S_2/[S_1 + S_2]$ ) (Fig. 2). The results reveal that as the spermatophore attachment duration of the second male is increased relative to that of the

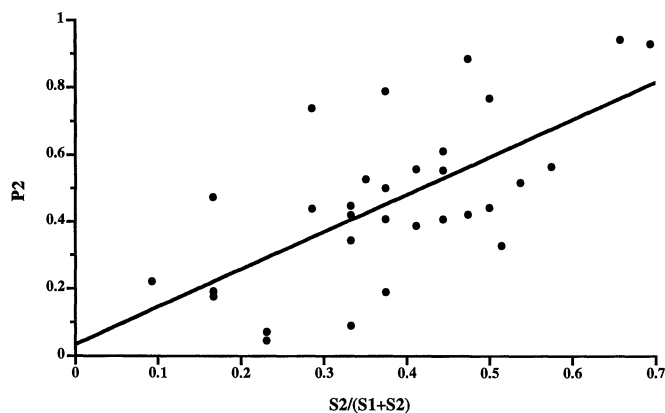


FIG. 2. The relationship between the proportion of offspring sired by the second male ( $P_2$ ) and his relative spermatophore attachment duration [ $S_2/(S_1 + S_2)$ ]. The regression is highly significant ( $b = 1.12$ ,  $r^2 = 0.43$ ,  $df = 29$ ,  $P < 0.0001$ ).

first, so too does the proportion of offspring sired by the second male increase ( $b = 1.12$ ,  $r^2 = 0.43$ ,  $df = 29$ ,  $P < 0.0001$ ). Hence, male paternity is strongly dependent on the duration of spermatophore attachment, regardless of the underlying mechanism of sperm precedence.  $P_2$  was not influenced by the allozyme phenotype of the female (S/S or F/F) or the order in which males of alternative phenotypes (S/O or F/O) were presented to females. An analysis of covariance (ANCOVA) in which mating combination (four levels, corresponding to the four different mating combinations) was entered as the main effect, and the relative spermatophore attachment duration of the second male ( $S_2/[S_1 + S_2]$ ) as the covariate, revealed no significant effect of allozyme phenotype on male paternity ( $F = 1.39$ ,  $P = 0.269$ ). Hence, in testing models of sperm precedence, data from different allozyme mating combinations were pooled in paternity analyses.

#### Models of Sperm Precedence—Parker et al. (1990)

The linear models of sperm precedence developed by Parker et al. (1990) are assessed in Table 1. In fitting our data to the models, we assumed that the number of sperm transferred increases linearly with the duration of spermatophore attachment, based on Sakaluk (1984). In assessing the sperm-displacement models, the size of the sperm store was set to the size of the first male's ejaculate as in Parker et al. (1990). The paternity data for *G. sigillatus* do not accord well with either a sperm lottery (ideal or loaded), or the form of sperm displacement in which no mixing of sperm occurs until displacement is completed. The data show a highly significant fit to the model of sperm displacement with instantaneous mixing of ejaculates during displacement (Fig. 3, slope =  $1.02 \pm 0.34$ ,  $t = 2.99$ ,  $P = 0.006$ ; intercept =  $0.08 \pm 0.21$ ,  $t = 0.37$ ,  $P = 0.71$ ).

The fit of the linear models of Parker et al. (1990) can be influenced by assumptions regarding the trajectory of sperm delivery. For example, in the above analysis we assumed a linear increase in the number of sperm transferred with increasing spermatophore attachment duration, whereas Parker et al. (1990), in reanalyzing Simmons' (1987) data, assumed a curvilinear trajectory. Accordingly, we reanalyzed our data

using a curvilinear trajectory based on a regression of the number of sperm transferred on spermatophore attachment duration, using the data of Sakaluk (1984) ( $S = 5.72 \ln[t] - 8.45$ ,  $r^2 = 0.70$ ,  $P < 0.0001$ ). The fit of the models of sperm precedence was not appreciably altered by varying the sperm-delivery trajectory; Parker et al.'s (1990) model of sperm displacement with instantaneous mixing still afforded the only statistically significant fit to our paternity data (slope =  $1.02 \pm 0.38$ ,  $t = 2.71$ ,  $P = 0.012$ ; intercept =  $-0.07 \pm 0.28$ ,  $t = -0.24$ ,  $P = 0.81$ ).

#### Partial Sperm Displacement—Two New Models

The spermatheca of *G. sigillatus* is an elastic structure that expands upon the introduction of additional ejaculates (Sakaluk 1986), a property that has been noted for other gryllines as well (Loher and Rence 1978; Simmons 1986). This observation creates something of a paradox, because the model that best fits the paternity data for *G. sigillatus* (sperm displacement with instantaneous mixing) assumes that the sperm store is fixed to the size of the first male's ejaculate. The paradox is more apparent than real, however, because different processes can yield the same pattern of paternity. We show below that when the size of the sperm store is not fixed but still allows partial displacement of the first male's sperm, the resultant pattern may be difficult to distinguish empirically from a model assuming a fixed sperm store.

The models of Parker et al. (1990) assume that the female's sperm store is either fixed in size (sperm displacement) or perfectly expandable (sperm lotteries); using their notation,  $S_{total}$  is set either at  $S_1$  (sperm displacement) or  $S_1 + S_2$  (lottery), where  $S_{total}$  equals the number of sperm that can be accommodated in the sperm store, and  $S_1$  and  $S_2$  represent the number of sperm transferred by the first and second males, respectively. However, this situation represents only two ends of a continuum, in which less-than-perfectly expandable sperm stores constitute structures intermediate to these two extremes. We envisage a spermatheca that stretches to accommodate additional ejaculates, but whose elasticity offers some resistance such that some displacement occurs. What distinguishes our models from those of Parker et al. (1990) is that the sperm store ( $S_{total}$ ) accommodates more than  $S_1$  (the number of sperm in a full ejaculate of the first male) but less than  $S_1 + S_2$  (total number of sperm transferred by both males).

In our Model 1—Partial Sperm Displacement, the number of first male's sperm displaced is a constant proportion of the number of sperm that the second male transfers, mixing of ejaculates does not occur until displacement is complete, and fertilizations are determined by lottery after displacement has occurred. Biologically, this means that the second male always displaces some of the first male's sperm but that he displaces fewer of the first male's sperm the smaller his own ejaculate. If  $b$  represents the displacement efficacy of the second male, equal to the probability that a sperm of the second male entering the sperm store displaces a sperm of the first male, then the total number of sperm remaining in the female's spermatheca following the second mating is

$$S_1 + (1 - b)S_2,$$

and the paternity of the second male can be determined as

TABLE 1. Tests of hypotheses concerning the mechanism of sperm competition in *G. sigillatus*. Linear models adapted from Parker et al. (1990).  $P_1$  and  $P_2$  designate the proportions of eggs fertilized by the first and second males, respectively.  $S_1$  and  $S_2$  designate the ampulla attachment durations of the first and second males, respectively.

Hypothesis	Lottery (ideal and loaded)	Sperm displacement	
		(1) With instantaneous mixing	(2) No mixing until displacement complete
Linear model	$1/P_2 = b(S_1/S_2) + a$	$-\ln(P_1) = b(S_2/S_1) + a$	$P_2 = b(S_2/S_1) + a$
<b>Slope</b>			
Predicted slope	$b > 0$	$b > 0$	$b = 1$
Observed slope ( $\pm$ SE)	$0.638 \pm 0.497$	$1.022 \pm 0.341$	$0.499 \pm 0.147$
Model supported?	No	Yes	No
Rationale	$b$ not different from 0	$b > 0$	$b < 1$
$t$ -test	$t = 1.285, P = 0.211$	$t = 2.994, P = 0.0062$	$t = -3.410, P < 0.003$
<b>Intercept</b>			
Predicted intercept	$a = 1$	$a = 0$	$a = 0$
Observed intercept ( $\pm$ SE)	$2.559 \pm 1.539$	$0.079 \pm 0.210$	$0.145 \pm 0.090$
Model supported?	Yes	Yes	Yes
Rationale	$a$ not different from 1	$a$ not different from 0	$a$ not different from 0
$t$ -test	$t = 1.013, P > 0.2$	$t = 0.079, P > 0.3$	$t = 1.602, P = 0.122$

$$P_2 = S_2/(S_1 + (1 - b)S_2). \quad (1)$$

A linear version of this model is given by rearranging Equation 1 into the following form:

$$(S_1 + S_2)/S_2 = 1/P_2 + b. \quad (2)$$

Hence, if we regress  $x = 1/P_2$  against  $y = (S_1 + S_2)/S_2$ , we should obtain a line with a slope of +1.0 and an intercept  $b$ , where  $b$  is greater than 0 but less than 1. When regressed in this fashion, however, the paternity data for *G. sigillatus* do not accord with the predictions of the model (slope =  $0.10 \pm 0.07$ ,  $t = 1.28$ ,  $P = 0.21$ ; intercept =  $3.04 \pm 0.49$ ,  $t = 6.15$ ,  $P < 0.001$ ).

Equation 1 was also used to generate a series of 10  $P_2$  values, with  $b$  set to a value of 0.2,  $S_1$  set to 50 min (the spermatophore attachment duration required for the transfer of one complete ejaculate), and  $S_2$  allowed to vary from 5 min to 50 min, in 5-min increments. The simulated data, when regressed as per Equation 2, show a perfect fit with slope = 1 and intercept = 0.2, thereby confirming the derivation of our model. More interesting, however, is the fit of the sim-

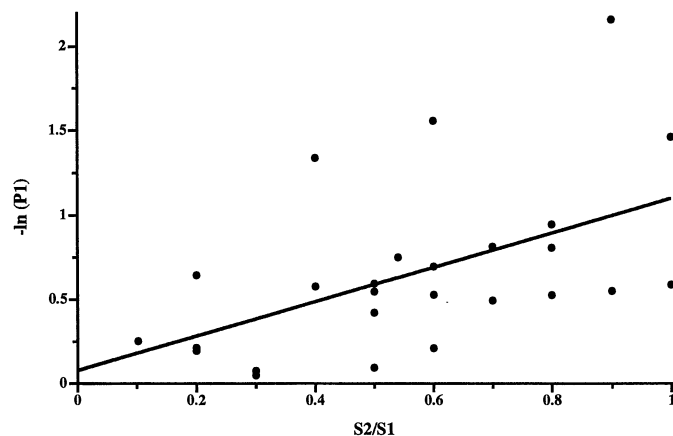


FIG. 3. Paternity data fitted to Parker et al.'s (1990) model of sperm displacement with instantaneous mixing ( $b = 1.02 \pm 0.34$ ,  $t = 2.99$ ,  $df = 24$ ,  $P = 0.006$ ; intercept =  $0.08 \pm 0.21$ ,  $t = 0.37$ , NS).

ulated data set to Parker et al.'s (1990) model of sperm displacement with instantaneous mixing; when  $S_{total}$  is assumed to be fixed and equal to  $S_1$ , the simulated data produce an almost perfect fit to the model (slope =  $0.79 \pm 0.01$ ,  $t = 65.0$ ,  $P < 0.0001$ ; intercept =  $0.036 \pm 0.007$ ,  $t = 4.81$ ,  $P = 0.0013$ ). Although in this case the analysis reveals that the intercept is significantly greater than zero in apparent violation of the model, its value is so low as to be virtually obscured in an actual empirical study with a realistic sampling error. The above analysis illustrates the difficulty of inferring process from pattern, and underscores the requirement made explicit by Parker et al. (1990) that some knowledge of constraints on the sperm stores be obtained in concert with paternity analyses.

In our Model 2—Partial Sperm Displacement, the total number of sperm displaced is a constant proportion of the number of sperm that the second male transfers, as in the previous model. Unlike the previous model, however, sperm transferred by the second male mix instantaneously with those of the first, such that the second male actually displaces some of his own sperm, as in Parker et al. (1990). As the number of sperm transferred by the second male increases, so too does the number of his own sperm that he displaces. Fertilizations are determined by lottery after displacement has occurred. As in our previous model,  $b$  represents the displacement efficacy of the second male and is equal to the probability that a sperm of the second male that enters the spermatheca displaces a sperm already present in the spermatheca. Again, the total number of sperm remaining in the female's spermatheca following the second mating is

$$S_1 + (1 - b)S_2.$$

As in Parker et al. (1990), the paternity of the second male is a function of the number of second-male sperm remaining in the fertilization set ( $s_2$ ) after  $S_2$  sperm have been transferred. Unlike Parker et al. (1990), however, both the number of second-male sperm and the total number of sperm remaining in the set are influenced by  $b$ , the displacement efficacy of the second male's sperm. Here the rate of change

of  $s_2$  (number of second-male sperm remaining in the spermatheca) with respect to  $S_2$  (number of sperm originally transferred by the second male) is given as

$$ds_2 / dS_2 = 1 - bs_2/[S_1 + (1 - b)S_2]. \quad (3)$$

We now require a function  $s_2(S_2)$  that satisfies Equation 3. The appropriate function is

$$s_2(S_2) = [S_1 + (1 - b)S_2] - S_1^{1/(1-b)}[(1 - b)S_2 + S_1]^{b/(b-1)}. \quad (4)$$

*Proof.* If

$$s_2(S_2) = [S_1 + (1 - b)S_2] - S_1^{1/(1-b)}[(1 - b)S_2 + S_1]^{b/(b-1)},$$

then

$$\begin{aligned} ds_2 / dS_2 &= (1 - b) - S_1^{1/(1-b)}(1 - b)[b/(b - 1)] \\ &\quad [(1 - b)S_2 + S_1]^{1/(b-1)} \\ &= (1 - b) + S_1^{1/(1-b)}b[(1 - b)S_2 + S_1]^{1/(b-1)}. \end{aligned}$$

Inserting Equation 4 into Equation 3 gives

$$\begin{aligned} ds_2 / dS_2 &= 1 - [b/(S_1 + (1 - b)S_2)][(S_1 + (1 - b)S_2) - \\ &\quad S_1^{1/(1-b)}[(1 - b)S_2 + S_1]^{b/(b-1)}] \\ &= 1 - b + S_1^{1/(1-b)}b[(1 - b)S_2 + S_1]^{1/(b-1)}. \end{aligned}$$

Function  $s_2(S_2)$  therefore satisfies Equation 3 and the requirements that  $s_2(0) = 0$  and  $ds_2 / dS_2 = 1$  for  $S_2 = 0$ . The paternity of the second male can be determined as

$$P_2 = s_2(S_2)/(S_1 + (1 - b)S_2). \quad (5)$$

Substituting Equation 4 for  $s_2(S_2)$  in Equation 5 yields

$$P_2 = 1 - S_1^{1/(1-b)}[(1 - b)S_2 + S_1]^{-1/(1-b)}. \quad (6)$$

The paternity of the first male is therefore determined as

$$P_1 = 1 - P_2 = S_1^{1/(1-b)}[(1 - b)S_2 + S_1]^{-1/(1-b)}. \quad (7)$$

A linear version of this model is given by rearranging Equation 7 into the following form:

$$P_1^{b-1} = [(1 - b)/S_1]S_2 + 1. \quad (8)$$

Hence, if we regress  $x = S_2$ , against  $y = P_1^{b-1}$ , we should obtain a line with a slope of  $(1 - b)/S_1$  and an intercept of  $+ 1.0$ .

The model described by Equation 8 can be assessed only when  $b$ , the displacement efficacy of the second male's sperm, is known. An estimate of  $b$  can be derived either by volumetric measurements of the spermathecae of once- and twice-mated females, or by counting the number of sperm in the spermathecae. For volumetric measurements,  $b$  is determined as

$$b = 2 - V_2/V_1, \quad (9)$$

where  $V_2$  equals the volume of the spermatheca after two matings, and  $V_1$  equals the volume of the spermatheca after one mating (for sperm counts, substitute numbers of sperm for  $V_1$  and  $V_2$ , respectively). Hence, for a perfectly elastic spermatheca,  $V_2$  should be twice that of  $V_1$  and  $b$  will be 0; for a perfectly rigid spermatheca,  $V_2$  should be the same as  $V_1$  and  $b$  will be 1.

We derived a crude estimate of  $b$  for *G. sigillatus* using

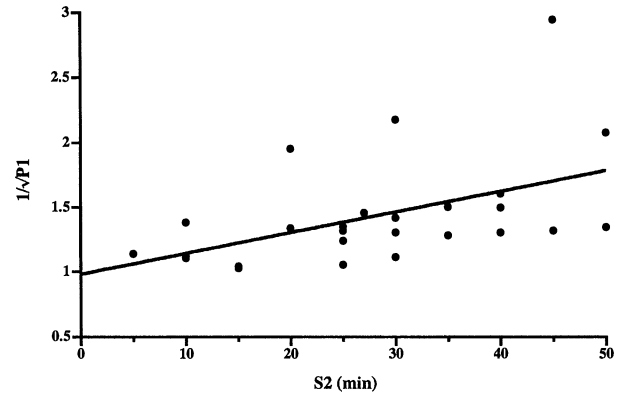


FIG. 4. Paternity data fitted to a model involving partial displacement of the first male's sperm (Model 2—see text for derivation) ( $b = 0.016 \pm 0.006$ ,  $t = 2.69$ ,  $df = 24$ ,  $P = 0.013$ ; intercept =  $0.98 \pm 0.18$ ,  $t = 5.31$ ,  $P < 0.001$ ).

linear measurements of the length and width of the spermathecae of single- and twice-mated females presented in Sakaluk (1986). Spermathecal volume was calculated according to the formula for a rotational ellipsoid,  $4/3\pi a^2b$ , where  $a$  and  $b$  are one-half the short and long axes of the spermatheca, respectively. The spermathecae of twice-mated females ( $0.586 \text{ mm}^3$ ) were 1.49 times the volume of once-mated females ( $0.392 \text{ mm}^3$ ); hence, we estimate the displacement efficacy,  $b$ , as 0.5.

Based on the calculated displacement efficacy of 0.5, our Model 2—Partial Sperm Displacement was assessed by regressing  $y = 1/\sqrt{P_1}$  against  $x = S_2$  as specified by Equation 8. For this displacement efficacy, the model predicts a slope of 0.01 and an intercept of  $+1.0$ . Our data show a highly significant fit to the model (Fig. 4, slope =  $0.016 \pm 0.006$ ,  $t = 2.69$ ,  $P = 0.0128$ ; intercept =  $0.981 \pm 0.185$ ,  $t = 5.313$ ,  $P < 0.001$ ). We conclude, therefore, that the pattern of sperm precedence in *G. sigillatus* is consistent with a model in which only a portion of sperm in the store is displaced, and sperm of the second male mixes instantaneously with that of the first throughout the displacement process.

## DISCUSSION

Studies of sperm competition typically have attempted to determine an average  $P_2$  value, representing the average proportion of offspring sired by the last male to mate with a female (reviews in Gwynne 1984a; Ridley 1989). Such an approach, however, overlooks the substantial variation in  $P_2$  values that can be obtained from experimental pairings within the same species; such intraspecific variation may have important implications for the intensity of sexual selection on males (Siva-Jothy and Tsubaki 1989; Lewis and Austad 1990, 1994; Simmons and Parker 1992; Eady 1994). In the present study,  $P_2$  varied widely, and a significant proportion of the variation (43%) could be attributed to the relative spermatophore attachment durations of the first and second males. Last-male paternity would be expected to vary at least as much under normal circumstances, because the time at which a mated female removes the spermatophore varies considerably (range = 5–130 min in undisturbed matings), and such often occurs before the spermatophore is emptied of sperm

(Sakaluk 1984, 1987). Indeed, an earlier study in which spermatophore attachment durations of competing males were permitted to vary according to the spermatophore-removal behavior of females, revealed considerable variation in  $P_2$  values (Sakaluk 1986). Female *G. sigillatus* can clearly alter the paternity of their offspring through their spermatophore-removal behavior, and hence this behavior provides females with a potent mechanism of postcopulatory mate choice. Because such choice often goes unnoticed in studies equating mere mating success with insemination success, it has been termed cryptic female choice (Thornhill 1983).

The most important factor influencing female spermatophore removal is the spermatophylax, a large, non-sperm-containing, gelatinous mass forming part of the spermatophore and consumed by the female after mating (Sakaluk 1984). Consumption of this courtship food gift keeps the female preoccupied while sperm are evacuated from the remaining portion of the spermatophore (sperm ampulla) into her reproductive tract (Sakaluk 1984). Smaller spermatophylaxes require less time to consume, and males providing such gifts are penalized in the form of premature ampulla removal and reduced sperm transfer (Sakaluk 1985). The postcopulatory preference of females for males providing larger courtship food gifts results in differential reproductive success of males with respect to two other phenotypic traits correlated with the size of the spermatophylax, body size and wing polymorphism. Larger males synthesize larger food gifts, which result in significantly longer spermatophore attachment durations (Sakaluk 1985). Males with long hind wings produce smaller spermatophylaxes than those of the more common wingless morph and consequently are disadvantaged with respect to premature spermatophore removal (Sakaluk, unpubl. data).

It is widely assumed that in species such as *G. sigillatus*, where males provide material resources to females, the benefits of female choice are self-evident: females preferentially mating with those males providing the greatest resources experience enhanced fecundity and/or increased survival of offspring (e.g., Bradbury and Andersson 1987; Kirkpatrick 1987; Ryan and Rand 1993). But this argument holds true only when female assessment takes place before females receive resources from males, and acceptance of a particular mate precludes matings with other males. In *G. sigillatus* and a number of other insect species (see below), females often accept copulations with males without regard to their material investment; discrimination occurs only after copulation has taken place. In these species, it is not at all clear what females gain from discriminating against males once they have accepted the males' material offerings; with or without discrimination, the fitness advantages that can be derived from utilization of the male-provided resource remain the same.

As an alternative to the "direct-benefits" hypothesis of female choice in gift-giving species, it may be that the size of a food gift provides females with a reliable indicator of a male's overall fitness (Zahavi 1975, 1977; Kodric-Brown and Brown 1984). Such a possibility does not conflict with the presumed origin of the spermatophylax, namely, as a device for the protection of the male's ejaculate (Sakaluk 1984; Wedell and Arak 1989; Wedell 1993). If the mass of the spermatophylax synthesized by a male reliably reflects his ability

to secure resources or some other aspect of his viability, females may secure genetic benefits for their offspring by allowing greater sperm transfer of males providing larger food gifts (Thornhill and Alcock 1983; Sauer et al., in press). Such an "honest" indicator of male fitness implies a cost to the provision of a courtship food gift but does not require that females benefit directly through courtship feeding. Indeed, viability-based mate choice may account for the lack of a nutritional benefit to courtship feeding that has been documented in several gift-giving orthopterans (e.g., Wedell and Arak 1989; Wedell 1993; Reinhold and Heller 1993; Will and Sakaluk 1994), which cannot be explained if female choice is based on direct benefits. In an extreme case, males of certain empidid flies transfer empty silken balloons to females, which in other species serve to encapsulate insect prey (Downes 1970; Cumming 1994); if female choice is predicated on the nutritional quality of male food gifts, it is difficult to imagine how such artifice could evolve.

Males may derive adaptive benefits through the provision of courtship food gifts in at least three ways, none of which are mutually exclusive. First, the presentation of a food gift may improve a male's prospects of mating. For example, hind-wing feeding in male sagebrush crickets, *Cyphoderris strepitans* (Orthoptera: Haglidae) and tegminal-gland feeding in wood crickets, *Nemobius sylvestris* (Orthoptera: Gryllidae) serve to facilitate spermatophore transfer, but have no obvious effect on the retention of the spermatophore per se (Dombrowski and Dambach 1994; Eggert and Sakaluk 1994). Similarly, male *Drosophila subobscura* provide females with a regurgitated food drop that influences whether mating takes place, but there is no evidence that such influences the number of sperm transferred during copulation (Steele 1986).

A second means by which males may benefit by provisioning females is through an increase in the fitness of offspring sired by investing males. In a katydid, *Requena verticalis*, males provide females with a spermatophylax that is twice as large as necessary to achieve complete insemination; hence, males invariably transfer a full complement of sperm (Gwynne et al. 1984; Gwynne 1986). Female consumption of the spermatophylax results in an increase in the number and mass of eggs produced, ultimately leading to increased offspring survival (Gwynne 1984b, 1988b). Similar effects have been reported in another katydid species, *Kawanaphila nartee* (Simmons 1990).

A third and final means by which males may benefit by offering courtship gifts is through an increase in their certainty of paternity, and it is this benefit that may best explain the evolution of courtship feeding in *G. sigillatus*. Because the spermatophylax is consumed only after copulation has been successfully completed, it seems unlikely that this trait increases a male's probability of mating. Nor is it likely that males benefit through any increase in offspring fitness, because spermatophylax consumption in *G. sigillatus* has no effect on the number and size of eggs produced by females (Will and Sakaluk 1994). Instead, the principal benefit of the spermatophylax appears to be that it mediates an increase in the number of sperm transferred to the female, which in turn greatly enhances the paternity of the male.

Courtship food gifts that function as paternity enhancers are most likely to evolve in species, such as *G. sigillatus*, in



which (1) females, even after they have consented to mating, determine the number of sperm transferred, and (2) male fertilization success is determined primarily by the number of sperm transferred, rather than by mating order per se (cf. Gwynne 1984a). Such species might be expected to exhibit a suite of characteristics exemplified by decorated crickets: (1) females mate with multiple males; (2) the number of sperm transferred at mating is highly variable; (3) the number of sperm transferred is correlated with the size (or quality) of the courtship food gift; (4) sperm precedence is highly variable; and (5) the average  $P_2$  value is intermediate, reflecting a high degree of mixed paternity. Indeed, the mating systems of three other gift-giving species conform reasonably well to this pattern. In a spermatophylax-donating katydid, *Decticus verrucivorus* (Orthoptera: Tettigoniidae), and a saliva-secreting scorpionfly, *Panorpa vulgaris* (Mecoptera: Panorpidae), sperm transfer is subject to female control and influenced by the size of the food gift (Wedell and Arak 1989; Thornhill and Sauer 1991). Sperm precedence in both species is highly variable and contingent on the number of sperm transferred, and average  $P_2$  values are intermediate (Wedell 1991; Thornhill and Sauer 1991). In another katydid, *Poecilimon veluchianus*, sperm transfer is determined by the size of the spermatophylax as in the previous two species, but appears to be an all-or-nothing process which, once initiated, occurs very rapidly (Reinhold and Heller 1993). DNA fingerprinting of the progeny of four doubly mated females revealed little variation in sperm precedence, with the last male fertilizing on the average about 90% of the eggs (Achmann et al. 1992).

Other gift-giving taxa that may conform to the paternity-enhancement model include the prey-donating scorpionflies (Mecoptera: Bittacidae) and dance flies (Diptera: Empididae). In both groups, females determine the number of sperm transferred through their control of copulation duration and the time at which a female terminates a copulation is based primarily on the size of the nuptial prey she receives from the male (Thornhill 1976; Svensson et al. 1990). We predict that an investigation of sperm competition in these taxa is likely to reveal a mixed sperm precedence that is dependent on the number of sperm transferred.

The results of the present study reveal differences among grylline crickets in the pattern of sperm precedence, which may be explicable on the basis of variation in spermathecal elasticity. Previous measurements of the spermatheca of *G. sigillatus* show that the spermatheca of twice-mated females expands to only about 1.5 times its volume in once-mated females (Sakaluk 1986), suggesting a less-than-perfectly expandable spermatheca. The pattern of sperm precedence in this species is consistent with a model in which only a portion of previously stored sperm is displaced, and sperm of the second male mixes instantaneously with that of the first during the displacement process. Spermathecal measurements in *Teleogryllus commodus* reflect even more stringent constraints on the expandability of the spermatheca with successive matings (Loher and Rence 1978), suggesting that displacement of the previous male's sperm in this species may be more severe than in *G. sigillatus*; however, no data are available on the pattern of sperm precedence in *T. commodus*. In contrast, the pattern of sperm precedence in *G.*

*bimaculatus* is consistent with a sperm lottery suggesting no constraints on spermathecal expansion and no displacement of previous males' sperm (Parker et al. 1990). In this species, however, the increase in the number of sperm contained in the spermatheca with successive matings is commensurate with a perfectly expandable spermatheca (Simmons 1986). Such variation within the same subfamily should not be considered surprising; for example, Pitnick and Markow (1994) have recently documented significant variation in both the location of sperm storage and spermathecal morphology in the *Drosophila nanoptera* species group. Variation in spermathecal morphology among closely related species suggests a rapid evolutionary divergence that may underlie diversification of sperm precedence patterns within taxa.

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