

**Sperm Competition and the Evolution of Nuptial Feeding Behavior in the Cricket, *Gryllobates supplicans* (Walker)**



Scott K. Sakaluk

*Evolution*, Volume 40, Issue 3 (May, 1986), 584-593.

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

*Evolution* is published by Society for the Study of Evolution. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/ssevol.html>.

---

*Evolution*  
©1986 Society for the Study of Evolution

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact [jstor-info@umich.edu](mailto:jstor-info@umich.edu).

©2001 JSTOR

## SPERM COMPETITION AND THE EVOLUTION OF NUPTIAL FEEDING BEHAVIOR IN THE CRICKET, *GRYLLODES SUPPLICANS* (WALKER)

SCOTT K. SAKALUK

Department of Entomology, University of Arizona, Tucson, AZ 85721

*Abstract.*—The pattern of sperm predominance in doubly mated female crickets, *Grylloides supplicans*, was investigated using a radiation-sterility technique. Female *G. supplicans* made significant use of sperm from both males in fertilizing eggs; overall, first males to mate enjoyed a small advantage, fertilizing about 60% of the offspring produced subsequent to the second mating. The combined use of the sperm of both males in fertilizing eggs occurred soon after the second mating; evidently, mixing of ejaculates within a female's spermatheca does occur.

Male *G. supplicans* provide females with a nuptial gift, the spermatophylax, which influences the time at which a female removes the externally attached sperm-ampulla; this in turn determines the quantity of sperm that is transferred. Moreover, the degree of sperm precedence achieved by a male may be positively related to the time at which the female removes his sperm ampulla. Thus males, by feeding females, ensure not only that a sufficient number of sperm are transferred to fertilize all of a female's eggs, but also may increase the certainty of their paternity. In mating systems in which females control sperm transfer and paternity is influenced by numbers of sperm (i.e., numerical sperm competition), an increase in prezygotic investment in females may be an adaptive male response.

Received February 4, 1985. Accepted December 9, 1985

Sexual selection is greater on males than females in species in which the male contribution to the survival of offspring is small relative to that of the female (Trivers, 1972). The intensity of selection on males largely reflects the variance in the number of mates that bear males' progeny (Wade, 1979; Wade and Arnold, 1980); ultimately this differential mating success is mediated by competition between males and by female preference (Darwin, 1871). In addition to males competing directly for mates, competition between males' sperm for the fertilization of a female's eggs may also occur, influencing the intensity of sexual selection on males (Wade and Arnold, 1980). Sperm competition is of widespread importance in insects, because females often mate with more than one male and store sperm over extended periods of time (Parker, 1970a). Sperm competition leads to two opposing selective forces: selection on males to preempt sperm from previous matings and selection on males to prevent further insemination of their mates (Parker, 1970a, 1984). The pattern of sperm predominance (i.e., the sequence in which the sperm of two or more males are utilized and the relative proportion of each male's sperm that is used to fertilize eggs) will represent, to some extent, a compromise between the relative

costs associated with the evolution of these tactics (Parker, 1970a, 1970b).

Sexual selection has been intensively studied in a variety of cricket species (Orthoptera: Gryllidae). These studies have addressed both male competition (Alexander, 1961; Boake and Capranica, 1982; Cade, 1975, 1979, 1981a, 1981b, Walker, 1980, 1983a) and female choice (Bell, 1980; Burk, 1983; Crankshaw, 1979; Walker, 1983b). However, with one exception (Backus, 1985), the importance of sperm competition in cricket mating systems has not been investigated. Here, I present data on the pattern of sperm predominance in the decorated cricket (*Grylloides supplicans* Walker: Gryllidae). In this species, copulation lasts 2-3 min (Alexander and Otte, 1967a; Sakaluk, unpubl.) and ends with the transfer of the spermatophore which is attached externally to the female. In most crickets, the spermatophore consists solely of a small sperm-containing ampulla; in *G. supplicans*, a larger gelatinous spermatophylax, devoid of sperm, adheres to the ampulla and is removed by the female within a few seconds of dismounting the male (Alexander and Otte, 1967a; Sakaluk, 1984). The female subsequently eats this nuptial "meal," and recent evidence indicates that its provision functions to deter the female

from removing the sperm ampulla before complete sperm transfer has occurred (Sakaluk, 1984).

Gwynne (1984) suggested that when males provide material benefits to females or their offspring, selection should favor increased investment by the male in mechanisms that enhance the probability of his sperm fertilizing a female's eggs. However, Parker's (1984) models show that such selection will operate only in mating systems in which the female's ability to find a mate is significantly reduced. Even in these mating systems, selection for increased expenditure on paternity assurance will be further weakened if the female decreases investment in her offspring in response to the benefits supplied by the male (Parker, 1984). Nonetheless, some evidence suggests a positive correlation between the degree of male investment and the percentage of eggs fertilized by the last male to mate, at least in insect mating systems (Gwynne, 1984). Here, I examine the role of sperm competition in the evolution of nuptial feeding behavior in *G. supplicans*.

#### MATERIALS AND METHODS

*Grylloides supplicans* occurs worldwide in tropical and subtropical regions, where it often is associated with human habitation (Vickery and Kevan, 1983). Crickets used in the present study were descendants of individuals collected at the University of Florida, Gainesville in June 1981. All crickets were housed in glass terraria containing ample food (Purina® cat chow). Two-liter plastic margarine containers filled with moistened vermiculite served both as a source of water and as an oviposition substrate, and cardboard egg cartons were added for shelter. These terraria, as well as subsequent experimental containers, were kept in a controlled-environment room (Constant Temperature Control Ltd., Toronto) maintained at  $28 \pm 2^\circ\text{C}$  and 30% relative humidity, on a 12 hr light : 12 hr dark photoperiod. Virgin females for later experimentation were obtained by isolating late-instar females in a separate terrarium.

A radiation-sterility technique was used to investigate the pattern of sperm predominance in *G. supplicans* (this technique and others for determining paternity of offspring

are reviewed by Parker, 1970a). The method involves mating a virgin female with two different males, one of which has been sterilized by irradiation. Generally, eggs that hatch are fathered by the normal male (N male), those that do not, by the radiation-sterilized male (R male). Because sperm from R males may not be as competitive as those from N males, it is necessary to reverse the order of mating of the two male types as a control. Boorman and Parker (1976) have developed a method which corrects for eggs that are fertilized by an N male but that fail to hatch due to other causes of infertility and for eggs fertilized by R males that do hatch; the expected proportions of these two egg types are generated by singly mating virgin females to individual R and N males.

In the present study, R males were irradiated with a Co gamma-ray source (Gammacell 220) at a dosage of 20 krad (3 krad/min). All experimental R and N males were sexually mature but of an unknown age. Virgin females were first mated 5–10 days after their imaginal molt. Four mating combinations utilizing a total of 30 virgin females were arranged: 1) R matings (female mated once to an R male;  $N = 5$ ), 2) N matings (female mated once to an N male;  $N = 5$ ), 3) NR matings (female mated first to an N male and remated to an R male;  $N = 10$ ), and 4) RN matings (female mated first to an R male and remated to an N male;  $N = 10$ ). Seventeen different males (12 R and 5 N) accounted for all matings; more R males were required because none lived more than 6 days following irradiation. Two NR matings involved the same two males, as was the case with two RN matings; the remaining 16 matings involved unique male combinations. The use of a male in more than one mating violates the principle of statistical independence to some extent. However, this flaw is partly a consequence of theory underlying experiments of this type; the fertility of singly mated N and R females is used in estimating the proportion of eggs fertilized by N and R males in double matings. These estimates are most accurate when males used to obtain the control values are the same males used in the double matings. Observed differences between NR and RN groups cannot be due to the characteristics

of individual males, because the same N and R males are used in both first and second matings.

Females were permitted to mate only once within a 4-hr observation period (8 hr into the dark portion of the photoperiod) on any given day. Once mated, females of NR and RN groups were offered the opportunity to remate the next day, or each day thereafter until they mated a second time. The duration of ampulla attachment was recorded for all matings, as was the interval between matings for all doubly mated females. Experimental females were housed in individually marked, 2-liter plastic margarine tubs (15 cm diameter) covered with screened lids. Cat chow, a small test tube filled with water and plugged with a cotton wick, and a petri dish (5.5 cm diameter) filled with moistened vermiculite to serve as an oviposition substrate, were placed in each container. For each doubly mated female, the oviposition dish was changed immediately after the second mating and at 4-day intervals thereafter, up to the 20th day subsequent to the second mating. Following this period, dishes were changed at 10-day intervals until the female died. Oviposition dishes removed from females' containers were placed in separate containers, identical to those used to house experimental females and marked to identify the particular female and to specify the given oviposition period. Changes in the pattern of sperm precedence with respect to time can be readily detected with this protocol; up to 12 oviposition containers, representing discrete portions of the entire duration over which a female oviposits, were accumulated for a given female.

A vaseline barrier was placed around the top of the inner wall of each container to prevent the escape of nymphs through the screened lid. Adequate levels of moisture in oviposition dishes were maintained by lightly spraying them daily. At about the same time each day, containers were examined for the presence of nymphs; offspring emerging within the previous 24 hr were subsequently mouth-aspirated and counted. This procedure was maintained for each container for about 60 days. This interval allowed ample time for all viable eggs to hatch and generally exceeded the time at which offspring were last found in a con-

tainer by at least 21 days. Oviposition dishes were left to dry for 24 hr before they were examined for unhatched eggs. Vermiculite contained in an oviposition dish was spread evenly over the bottom of a large petri dish (15 cm diameter) equipped with a grid to facilitate egg counting. Counts were performed with a Wild M3 dissecting microscope at 160 $\times$  magnification.

The number of mature eggs remaining in the ovaries was determined upon the death of each female. Additionally, the spermatheca was removed and measured for length (distance from the point where the spermathecal duct enters the spermatheca to its most distal end) and width (widest dimension perpendicular to the length), using a dissecting microscope fitted with an ocular micrometer. Subsequently, the spermatheca was examined for the presence of sperm using a Zeiss photomicroscope. These observations were used to confirm successful transfer of sperm in single and double matings.

Results were analyzed with a Hewlett-Packard Statistical Analysis package. All values are means  $\pm$  SE. Data are normally distributed and variances are homogeneous unless otherwise stated.

## RESULTS

### *Female Reproductive Success*

Reproduction of female *G. supplicans* is shown in Table 1. There were no significant differences in mean numbers of eggs produced (eggs laid + mature eggs retained in the ovaries on the death of the female) (ANOVA;  $F = 0.29$ ,  $P > 0.05$ ) or mean numbers of eggs laid ( $F = 0.27$ ,  $P > 0.05$ ) among experimental categories. Additionally, there was no difference in the numbers of eggs laid by NR and RN females before (Mann-Whitney test;  $U = 62$ ,  $P > 0.05$ ) or after the second mating ( $F = 0.49$ ,  $P > 0.05$ ). The  $U$  statistic was used to test for difference in eggs laid before the second mating because of unequal variances (Bartlett's test;  $X^2 = 6.28$ ,  $0.01 < P < 0.025$ ). For N females, 68.0% (1,363/2,004) of all eggs laid hatched. These data, combined with the number of eggs laid by NR females before the second mating, showed that 67.3% (1,663/2,470) of all eggs fertilized by N

TABLE 1. Reproduction of female *Gryllobates supplicans* in all experimental groups.

Group	N	Mean number of eggs produced (±SE)	Mean number of eggs laid (±SE)	% of all eggs laid that hatched
R	5	442.4 ± 199.9	399.0 ± 203.6	0.05 (1/1,995)
N	5	468.4 ± 137.8	400.8 ± 148.3	68.0 (1,363/2,004)
RN				
Before	10	—	13.8 ± 6.8	3.6 (5/138)
After	10	—	349.2 ± 121.0	34.3 (1,197/3,492)
Total	10	401.4 ± 119.4	363.0 ± 119.7	—
NR				
Before	10	—	46.6 ± 17.1	64.4 (300/466)
After	10	—	463.7 ± 109.9	54.0 (2,504/4,637)
Total	10	557.5 ± 124.5	510.3 ± 117.6	—

sperm hatched (control N hatching frequency). For R females, 0.05% (1/1,995) of all eggs laid hatched. These data, combined with the number of eggs laid by RN females before the second mating, showed that only 0.28% (6/2,133) of all eggs fertilized by R sperm hatched (control R hatching frequency).

#### Male Reproductive Success

The observed numbers of offspring produced by NR and RN females after the second mating were compared with the numbers of offspring females were expected to produce if all eggs were fertilized by either the first or second male to mate. Data from singly mated control females were used to generate expected frequencies of offspring production in doubly mated females. If, for example, the first male to mate fertilizes all eggs subsequent to the second mating, then in the NR group, the number of offspring a female is expected to produce is the product of the total number of eggs she lays and the percentage of eggs fertilized by control N sperm that hatch (total eggs laid × 0.673). The results of this analysis are shown in Table 2. Twelve of the 19 females that laid eggs apparently utilized the sperm of both males in fertilizing eggs, five females showed evidence of first-male sperm predominance, and two females showed evidence of last-male sperm predominance.

To examine changes in the temporal pattern of sperm predominance, I used Boorman and Parker's (1976) method to estimate the number of eggs fertilized by N and R males. If  $p_R$  is the proportion of eggs fer-

tilized by the R male,  $x$  is the proportion of eggs hatching after a double mating,  $z$  is the proportion of eggs hatching after single R matings (0.0028), and  $p$  is the proportion of eggs hatching after single N matings (0.673), then:

$$p_R = \left(1 - \frac{x}{p}\right) + \frac{\frac{z}{p} \left(1 - \frac{x}{p}\right)}{1 - \frac{z}{p}}$$

This formula was applied to results obtained from individual oviposition dishes. Thus, the number of eggs fertilized by each male could be estimated for each NR and RN female for a given period of egg laying. Group totals (total number of eggs fertilized by R and N males over a given oviposition interval) were obtained by adding the results of individual females for that period. Note that when the observed hatching percentage exceeds the control N value or is less than the control R value, a negative  $p_R$  value or one greater than 1.0 is obtained, respectively. When this occurred, the paternity of all eggs from a particular oviposition dish was attributed to the N male ( $x > 0.673$ ) or to the R male ( $x < 0.0028$ ).

The results of this analysis are shown in Figure 1. Overall, 64.6% of the total eggs laid by NR females after the second mating were fertilized by the first male to mate ( $p_{NR1}$ ); 59.2% of all eggs deposited by RN females were fertilized by the first male ( $p_{RN1}$ ). This gives an overall  $p_1$  value ( $[p_{NR1} + p_{RN1}]/2$ ) of 61.9. Oviposition periods 2–

TABLE 2. Observed numbers of offspring produced after the second mating by NR and RN females, and expected number if all eggs were fertilized by either the first or second male to mate.

Female code	Number of offspring produced		
	Observed (total eggs laid)	Expected (if all eggs fertilized by 1st male)	Expected (if all eggs fertilized by 2nd male)
<u>NR</u>			
1	73 (286)	192	<1
2	90 (167)	112	<1
3	68 (103)	69 <sup>1</sup>	<1
4	649 (816)	549 <sup>1</sup>	2
5	311 (926)	623	3
6	743 (972)	500 <sup>1</sup>	3
7	142 (483)	325	1
8	137 (554)	373	2
9	291 (330)	220 <sup>1</sup>	1
10	0 (0)	—	—
<u>RN</u>			
1	381 (420)	1	282 <sup>2</sup>
2	238 (402)	1	270
3	108 (294)	1	197
4	44 (136)	<1	91
5	2 (55)	<1 <sup>1</sup>	37
6	33 (62)	<1	42
7	71 (112)	<1	75 <sup>2</sup>
8	55 (357)	1	240
9	204 (289)	1	194
10	61 (1,365)	4	918

<sup>1</sup> First-male sperm predominance.

<sup>2</sup> Second-male sperm predominance.

6 represent consecutive egg-laying intervals of 4 days each and periods 7–11 represent intervals of 10 days each. During the first 20 days of oviposition (periods 2–6), females of the NR and RN groups deposited 68.8% and 68.2% of all eggs laid after the second mating, respectively. The proportion of eggs fertilized by the first male remained fairly constant over this interval for both groups. Corresponding estimates for the last three oviposition periods (9–11) are somewhat problematic. For the NR group, the results suggest that virtually all of the eggs laid by females within this period were fertilized by the second male, whereas for the RN group, the results indicate that almost all of the eggs laid (426/430) were fertilized by the first male to mate. A sharp decrease in the natural fertility of females at the end of the oviposition phase would account for this disparity; in any event, even if this portion of the total egg-laying period is ignored, the effects on the  $p_{NR1}$  and  $p_{RN1}$  estimates cancel out each other, leaving the

overall  $p_1$  value unaffected. Additionally, assumptions regarding changes in the level of natural infertility can be circumvented if Boorman and Parker's (1976) formula is applied directly to individual totals (i.e., as opposed to summing values obtained from analyzing discrete portions of the entire oviposition phase). Values obtained in this manner differ only slightly from those reported above ( $p_{NR1} = 53.9$ ;  $p_{NR1} = 71.6$ ;  $p_1 = 62.7$ ).

#### *Duration of Ampulla Attachment and Intercopulatory Interval*

Are there any differences between NR and RN females that might account for the disparity in predominance values, other than differential competitiveness of R and N sperm? One possible factor is the duration of sperm-ampulla attachment, a strong predictor of the number of sperm transferred. Previously, I demonstrated that the time after mating at which a female removes the ampulla determines the quantity of sperm transferred to the female (Sakaluk, 1984). The ampulla must be attached for about 55 min to allow the complete transfer of sperm; longer durations of ampulla attachment do not result in an increase in the number of sperm transferred. Therefore, I have used an arbitrary but conservative maximum value of 65 min in calculating mean durations of ampulla attachment. Eighty-eight percent (44/50) of all observed attachment times fell within the interval, bounded by this cutoff; a value of 65 min was assigned to the six remaining ampulla attachment durations (69, 69, 78, 81, 88, and 90 min). Ampulla-attachment data remained normally distributed subsequent to truncation (D'Agostino's test;  $D = 0.2853$ ,  $P > 0.05$ ). The mean ampulla attachment duration for all matings was  $38.8 \pm 2.4$  min. Ampulla attachment durations of first and second matings did not differ significantly for NR (paired  $t$  test,  $t = 0.73$ ,  $P > 0.05$ ) or RN groups ( $t = 1.63$ ,  $P > 0.05$ ). A comparison of NR first matings with RN first matings also showed no significant difference ( $F = 0.17$ ,  $P > 0.05$ ), as was the case with NR and RN second matings ( $F = 0.48$ ,  $P > 0.05$ ).

Another possible factor affecting estimates of the level of sperm predominance

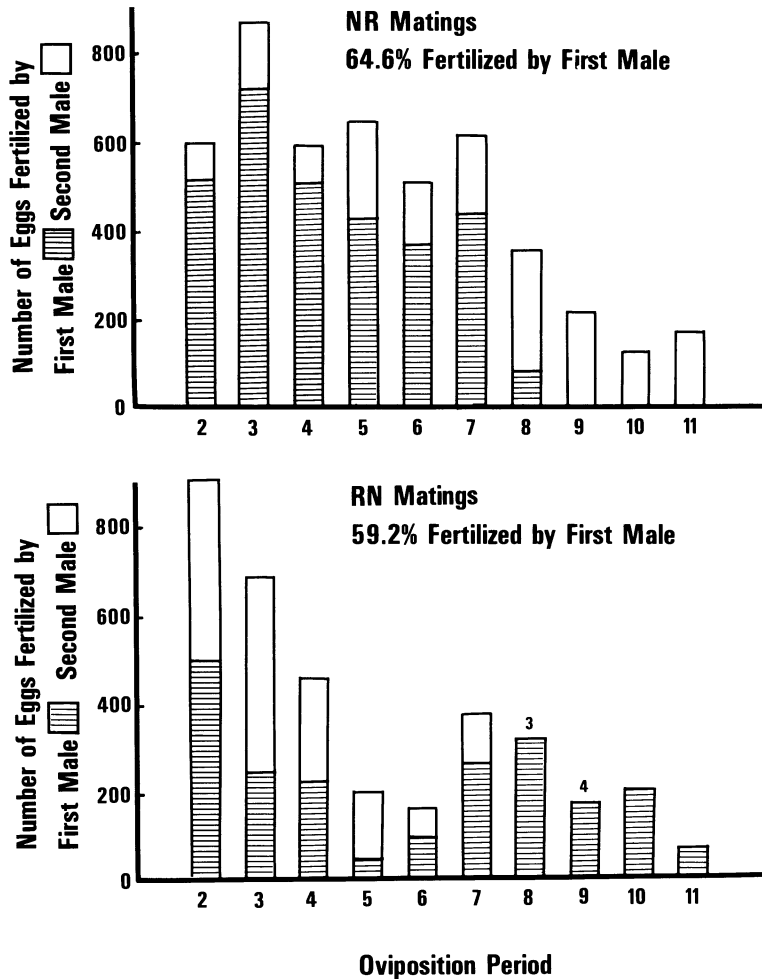


FIG. 1. Temporal pattern of sperm precedence in doubly mated female *Gryllobates supplicans*. The numbers of eggs fertilized by first and second males to mate were estimated from observed hatching frequencies (see text). Oviposition periods 2–6 represent consecutive egg-laying intervals of four days each. Periods 7–11 represent consecutive intervals of ten days each. Superscripts over bars 8 and 9 in the RN group each denote the number of eggs fertilized by the second male to mate in those intervals.

is the interval between first and second matings. As this interval increases, the first male's sperm should contribute less to the fertilization of subsequent eggs, because first-male sperm are utilized in fertilizing eggs that are deposited before the second mating. The mean interval between matings was  $1.1 \pm 0.1$  days for RN females and  $2.6 \pm 0.3$  days for NR females, a statistically significant difference ( $U = 92.5$ ;  $P < 0.001$ ;  $U$  statistic employed because of unequal variances; Bartlett's test,  $X^2 = 8.96$ ,  $P < 0.005$ ). Normally, this difference should lead to more eggs being deposited before the second

mating (and hence, greater utilization of the first male's sperm) by females with the longer interval between matings. As noted earlier, NR females did deposit more eggs than RN females prior to the second mating, but this difference was not significant.

#### *Ampulla Attachment Time and Male Reproductive Success*

The competitive ability of a male's sperm may be related directly to the quantity of sperm (or volume of ejaculate) transferred. Thus, a female's ampulla-removal behavior may affect the pattern of sperm precedence.

This possibility was tested by examining relationships between: 1) ampulla attachment durations of first males to mate and the percentage of eggs later fertilized by them and 2) ampulla attachment durations of second males to mate and the proportion of eggs later fertilized by them. The arcsine of the square root was used to transform each percentage point (Zar, 1984). There was a significantly positive correlation between the ampulla attachment time of the first mating and the percentage of eggs later fertilized by the first male to mate in the NR group ( $r = 0.59$ ;  $t = 1.93$ ;  $P < 0.05$ ) but not in the RN group ( $r = -0.15$ ;  $t = 0.44$ ,  $P > 0.05$ ). There was no significant correlation between second-mating ampulla attachment time and the proportion of eggs fertilized by the second male in either the NR ( $r = -0.04$ ;  $t = 0.12$ ,  $P > 0.05$ ) or the RN groups ( $r = -0.36$ ;  $t = 1.09$ ,  $P > 0.05$ ).

#### *Spermathecal Contents and Female Longevity*

Spermathecae that were examined upon the death of females all contained sperm, with one exception. Because that female (singly mated) left viable offspring, it was assumed that sperm had been successfully transferred but completely utilized. There was a positive and significant correlation between the width and length of spermathecae for all experimental females ( $r = 0.46$ ;  $t = 2.64$ ,  $P < 0.02$ ). The mean width of the spermathecae of doubly mated females was  $0.95 \pm 0.03$  mm, while that of singly mated females was  $0.79 \pm 0.05$  mm, a statistically significant difference ( $F = 6.1$ ,  $P < 0.025$ ). However, the mean lengths of spermathecae were  $1.24 \pm 0.05$  mm for doubly mated females, and  $1.20 \pm 0.06$  for single mated females, a difference that was not statistically significant ( $F = 0.3$ ,  $P > 0.05$ ). The mean longevity of females after the first mating was  $45.4 \pm 4.0$  days. There were no significant differences in longevity among experimental groups ( $F = 1.3$ ,  $P > 0.05$ ).

#### DISCUSSION

The majority of doubly mated female *G. supplicans* made significant use of the sperm of both males in fertilizing eggs; a similar result recently has been reported for another

cricket, *Gryllus integer* (Backus, 1985). The overall  $p_1$  value (percentage of eggs fertilized by the first male) for *G. supplicans* was 61.9%. First males to mate fathered more offspring in both NR and RN groups. However, the reduction in eggs fertilized by the first male was greater when the second male was an N male ( $p_1 = 54\text{--}59\%$ ) as opposed to an R male ( $p_1 = 64\text{--}72\%$ ). This difference in predominance values may have been due to sampling error. Alternatively, irradiation may have reduced the competitiveness of the sperm of R males; this effect has been used to account for similar differences occurring in other studies utilizing the radiation-sterility technique (Proverbs and Newton, 1962; Flint and Kressin, 1968; Parker, 1970b; Katiyar and Ramirez, 1970; Riemann and Thorson, 1974; Parker and Smith, 1975; Fincke, 1984).

Eggs laid within the first four days following the second mating were fertilized by both first and second males (Fig. 1). Thereafter, the relative proportion of eggs fertilized by each male remained the same over most of the entire oviposition period. This indicates that the sperm of both males is used soon after the second mating, as opposed to the case in which one male's sperm is used only after the other male's sperm has been completely utilized. Thus, significant mixing of ejaculates likely occurs within the female's spermatheca. Walker (1980) suggested that the morphology of females' sperm storage organs was an important factor in the evolution of patterns of sperm predominance in insects. In species in which females possess elongate or tubular spermathecae, displacement of the first male's sperm may occur, resulting in a "first sperm in, last sperm out" phenomenon (Schlager, 1960; Riemann and Thorson, 1974; Brower, 1975; Vardell and Brower, 1978). Spheroid or ovoid spermathecae are expected to mitigate against displacement of the first male's sperm; they often are associated with first-male sperm predominance (Walker, 1980). The spermatheca of a female *Gryllodes* is ovoid but becomes more ovoid and increases in volume after the female remates. Spermathecal volume in females of another gryllid, *Teleogryllus commodus* (Walker), also increases with additional matings (Lohrer and Rence, 1978). These results suggest



that spermathecal shape may be an incidental effect of mating frequency, rather than a cause of patterns of sperm predominance, at least in some species.

When the sperm of two or more males are in competition for a female's eggs, the total number of sperm transferred by a male may determine, per se, the probability of his obtaining fertilizations (Parker, 1970*a*, 1984). The results presented here showed a positive correlation between first-male ampulla attachment time (a strong predictor of the number of sperm that a male transfers; Sakaluk, 1984) and the percentage of eggs fertilized by the first male to mate, but only for the NR females. This relationship would be affected if, in a given mating, no sperm were transferred (due perhaps to some ampullar dysfunction). While doubly mated females each had at least one successful mating (sperm were found in the spermathecae of all doubly mated females), we cannot know with certainty that both matings were successful for each female. Given the possibility of this confounding factor, my data nonetheless are suggestive that the number of sperm transferred by a male influences the extent to which his sperm are successful in competing for fertilizations.

A model developed by Werren et al. (1980) showed that paternity would influence the evolution of paternal care only in species in which caring males sacrificed at least some promiscuous matings. Alternatively, increased parental investment by the male would favor increased expenditure by the male on paternity assurance, but only in mating systems in which the female's ability to find mates consequently was reduced (Parker, 1984). In insects for which the degree of sperm predominance is known, only one species apparently meets these criteria, the giant water bug, *Abedus herberti* (Belostomatidae). Male *A. herberti* brood eggs on their backs and always copulate with females before receiving their eggs. The limited amount of back space severely curtails the number of females with which a male can mate; conversely, females may find it difficult to find an unencumbered male, at least at low population densities (Smith, 1979*a*). Experiments using a genetic marker in double matings showed that the last male to mate sired, on the average, 99% of the

offspring subsequently produced (Smith, 1979*b*).

Generally, models such as these consider only those situations in which certainty of paternity is independent of the degree of male parental investment. In *G. supplicans*, a male provides the female with a nuptial meal, the spermathecal phylax, whose size influences the time at which the female removes the sperm-containing ampulla (Sakaluk, 1985). The duration of ampulla attachment, in turn, determines the number of sperm that are transferred to the female's spermatheca (Sakaluk, 1984). The data here suggest that the success of a male's sperm in competing for fertilizations depends, at least partly, on the number of sperm he has transferred. Thus males, by feeding females, not only ensure that they provide enough sperm to fertilize a female's eggs, but also increase the overall competitiveness of their ejaculate relative to that of other males.

When the ejaculates of two or more males overlap temporally in the reproductive system of a female and fertilization is essentially by lottery, then such conditions will select for adaptations that serve to maximize sperm transfer (Parker, 1970*a*). Examples of such adaptations include excessive sperm loads in cockroaches (Woodhead, 1985), repeated copulations with the same mate in bighorn sheep (Hogg, 1984), and large testis size in some primates (Harvey and Harcourt, 1984). Numerical sperm competition also may have influenced the evolution of nuptial provisioning in the Orthoptera. Provision of spermathecal phylaxes occurs in other crickets (Boldyrev, 1927; Alexander and Otte, 1967*a*; Otte and Cade, 1983, 1984) and most katydids (Gwynne, 1983); courtship feeding of female crickets occurs in other forms including provision of additional spermathecal phylaxes (Mays, 1971; Loher and Rence, 1978), glandular secretions from a tibial spur (Mays, 1971; Bidochka and Snedden, 1985) or metanotal gland (Fulton, 1915; Alexander and Otte, 1967*a*; Walker, 1978; Bell, 1980), and consumption of a male's wings (Alexander and Otte, 1967*b*; Dodson et al., 1983). In these species, females likely control sperm transfer through their spermathecal-removal behavior. My study suggests that in species in which females control sperm transfer and

fertilization success is determined numerically, one adaptive male response is to increase prezygotic investment in females.

#### ACKNOWLEDGMENTS

This study was supported by a National Sciences and Engineering Research Council of Canada postgraduate scholarship to S.K.S. and an NSERC operating grant (4946) to Dr. Glenn K. Morris. I thank Andrew Snedden for his assistance in the lab and Dr. Alan Rawlinson of the Princess Margaret Hospital at Toronto, Ontario for irradiating the crickets. I thank W. H. Cade, J. H. Fullard, D. Sherry, and W. G. Sprules for helpful discussions of this material and R. L. Baker, D. T. Gwynne, G. K. Morris, P. J. Pointing, J. S. Quinn, S. S. Tobe, and D. W. Zeh for critical comments on the manuscript. This work represents a portion of a thesis submitted to the University of Toronto in partial fulfillment of the requirements for the Ph.D. degree.

#### LITERATURE CITED

- ALEXANDER, R. D. 1961. Aggressiveness, territoriality, and sexual behavior in field crickets (Orthoptera: Gryllidae). *Behaviour* 17:130-223.
- ALEXANDER, R. D., AND D. OTTE. 1967a. The evolution of genitalia and mating behavior in crickets (Gryllidae) and other Orthoptera. *Misc. Publ. Mus. Zool. Univ. Mich.* 133:1-62.
- . 1967b. Cannibalism during copulation in the brown bush cricket, *Hapithus agitator* (Gryllidae). *Florida Entomol.* 50:79-87.
- BACKUS, V. L. 1985. Sperm utilization patterns in *Gryllus integer* (Orthoptera: Gryllidae). M.S. Thesis. Brock Univ., St. Catharines, ON.
- BELL, P. D. 1980. Multimodal communication by the black-horned tree cricket, *Oecanthus nigricornis* (Walker) (Orthoptera: Gryllidae). *Can. J. Zool.* 58:1861-1868.
- BIDOCHKA, M. J., AND W. A. SNEDDEN. 1985. Effect of nuptial feeding on the mating behaviour of female ground crickets. *Can. J. Zool.* 63:207-208.
- BOAKE, C. R. B., AND R. R. CAPRANICA. 1982. Aggressive signals in "courtship" chirps of a gregarious cricket. *Science* 218:580-582.
- BOLDYREV, B. T. 1927. Copulation and spermatophores of *Gryllomorpha dalmatina* (Ocsk.) (Orthoptera: Gryllidae). *Eos* 3:279-288.
- BOORMAN, E. B., AND G. A. PARKER. 1976. Sperm (ejaculate) competition in *Drosophila melanogaster*, and the reproductive value of females to males in relation to female age and mating status. *Ecol. Entomol.* 1:145-155.
- BROWER, J. H. 1975. Sperm precedence in the Indian meal moth, *Plodia interpunctella*. *Ann. Entomol. Soc. Amer.* 68:78-80.
- BURK, T. 1983. Male aggression and female choice in a field cricket (*Teleogryllus oceanicus*): The importance of courtship song, pp. 97-119. *In* D. T. Gwynne and G. K. Morris (eds.), *Orthopteran Mating Systems: Sexual Competition in a Diverse Group of Insects*. Westview, Boulder, CO.
- CADE, W. H. 1975. Acoustically orienting parasitoids: Fly phonotaxis to cricket song. *Science* 190:1312-1313.
- . 1979. The evolution of alternative male reproductive strategies in field crickets, pp. 343-379. *In* M. S. Blum and N. A. Blum (eds.), *Sexual Selection and Reproductive Competition in Insects*. Academic Press, N.Y.
- . 1981a. Field cricket spacing, and the phonotaxis of crickets and parasitoid flies to clumped and isolated cricket songs. *Z. Tierpsychol.* 55:365-375.
- . 1981b. Alternative male strategies: Genetic differences in crickets. *Science* 212:563-564.
- CRANKSHAW, O. S. 1979. Female choice in relation to calling and courtship songs in *Acheta domesticus*. *Anim. Behav.* 27:1274-1275.
- DARWIN, C. 1871. *The Descent of Man and Selection in Relation to Sex*. Murray, London, U.K.
- DODSON, G. N., G. K. MORRIS, AND D. T. GWYNNE. 1983. Mating behavior of the primitive Orthopteran genus *Cyphoderris* (Haglidae), pp. 305-318. *In* D. T. Gwynne and G. K. Morris (eds.), *Orthopteran Mating Systems: Sexual Competition in a Diverse Group of Insects*. Westview, Boulder, CO.
- FINCKE, O. M. 1984. Sperm competition in the damselfly *Enallagma hageni* Walsh (Odonata: Coenagrionidae): Benefits of multiple mating to males and females. *Behav. Ecol. Sociobiol.* 14:235-240.
- FLINT, H. M., AND E. L. KRESSIN. 1968. Gamma irradiation of the tobacco budworm: Sterilization, competitiveness, and observations on reproductive biology. *J. Econ. Entomol.* 61:477-483.
- FULTON, B. B. 1915. *The tree crickets of New York: Life history and bionomics*. Tech. Bull. No. 42. N.Y. Agric. Exp. Sta., Geneva, NY.
- GWYNNE, D. T. 1983. Male nutritional investment and the evolution of sexual differences in Tettigoniidae and other Orthoptera, pp. 337-366. *In* D. T. Gwynne and G. K. Morris (eds.), *Orthopteran Mating Systems: Sexual Competition in a Diverse Group of Insects*. Westview, Boulder, CO.
- . 1984. Male mating effort, confidence of paternity and insect sperm competition, pp. 117-149. *In* R. L. Smith (ed.), *Sperm Competition and the Evolution of Animal Mating Systems*. Academic Press, N.Y.
- HARVEY, P. H., AND A. H. HARCOURT. 1984. Sperm competition, testes size, and breeding systems in primates, pp. 589-600. *In* R. L. Smith (ed.), *Sperm Competition and the Evolution of Animal Mating Systems*. Academic Press, N.Y.
- HOGG, J. T. 1984. Mating in bighorn sheep: Multiple creative male strategies. *Science* 225:526-529.
- KATIYAR, K. P., AND E. RAMIREZ. 1970. Mating frequency and fertility of Mediterranean fruit fly females alternately mated with normal and irradiated males. *J. Econ. Entomol.* 63:1247-1250.
- LOHER, W., AND B. RENCE. 1978. The mating behavior of *Teleogryllus commodus* (Walker) and its central and peripheral control. *Z. Tierpsychol.* 46:225-259.

- MAYS, D. L. 1971. Mating behavior of nemobiine crickets *Hygronemobius*, *Nemobius* and *Pteronemobius* (Orthoptera: Gryllidae). Florida Entomol. 54:113-126.
- OTTE, D., AND W. CADE. 1983. African crickets (Gryllidae). 3. On the African species of *Velarifictorus* Randell (Gryllinae, Modicogryllini). Proc. Acad. Nat. Sci. Phil. 135:241-253.
- . 1984. African crickets (Gryllidae). 5. East and South African species of *Modicogryllus* and several related genera (Gryllinae, Modicogryllini). Proc. Acad. Nat. Sci. Phil. 136:67-97.
- PARKER, G. A. 1970a. Sperm competition and its evolutionary consequences in the insects. Biol. Rev. 45:525-567.
- . 1970b. Sperm competition and its evolutionary effect on copula duration in the fly *Scatophaga stercoraria*. J. Insect Physiol. 16:1301-1328.
- . 1984. Sperm competition and the evolution of animal mating strategies, pp. 1-60. In R. L. Smith (ed.), Sperm Competition and the Evolution of Animal Mating Systems. Academic Press, N.Y.
- PARKER, G. A., AND J. L. SMITH. 1975. Sperm competition and the evolution of the precopulatory passive phase behaviour in *Locusta migratoria migratorioides*. J. Entomol. 49:155-171.
- PROVERBS, M. D., AND J. R. NEWTON. 1962. Some effects of gamma radiation on the reproductive potential of the codling moth, *Carpocapsa pomonella* (L.) (Lepidoptera: Olethreutidae). Can. Entomol. 94:1162-1170.
- RIEMANN, J. G., AND B. J. THORSON. 1974. Viability and use of sperm after irradiation of the large milkweed bug. Ann. Entomol. Soc. Amer. 67:871-876.
- SAKALUK, S. K. 1984. Male crickets feed females to ensure complete sperm transfer. Science 223:609-610.
- . 1985. Spermatophore size and its role in the reproductive behaviour of the cricket, *Gryllodes supplicans* (Orthoptera: Gryllidae). Can. J. Zool. 63:1652-1656.
- SCHLAGER, G. 1960. Sperm precedence in the fertilization of eggs in *Tribolium castaneum*. Ann. Entomol. Soc. Amer. 53:557-560.
- SMITH, R. L. 1979a. Paternity assurance and altered roles in the mating behaviour of a giant water bug, *Abedus herberti* (Heteroptera: Belostomatidae). Anim. Behav. 27:716-725.
- . 1979b. Repeated copulation and sperm precedence: Paternity assurance for a male brooding water bug. Science 205:1029-1031.
- TRIVERS, R. L. 1972. Parental investment and sexual selection, pp. 136-179. In B. Campbell (ed.), Sexual Selection and the Descent of Man: 1871-1971. Aldine, Chicago, IL.
- VARDELL, H. H., AND J. H. BROWER. 1978. Sperm precedence in *Tribolium confusum* (Coleoptera: Tenebrionidae). J. Kansas Entomol. Soc. 51:187-190.
- VICKERY, V. R., AND D. K. MCE. KEVAN. 1983. A monograph of the orthopteroid insects of Canada and adjacent regions. Vol. I. Mem. Lyman Entomol. Mus. Res. Lab. 13:1-679.
- WADE, M. J. 1979. Sexual selection and variance in reproductive success. Amer. Natur. 114:742-747.
- WADE, M. J., AND S. J. ARNOLD. 1980. The intensity of sexual selection in relation to male sexual behaviour, female choice, and sperm precedence. Anim. Behav. 28:446-461.
- WALKER, T. J. 1978. Post-copulatory behavior of the two-spotted tree cricket, *Neoxabea bipunctata*. Florida Entomol. 61:39-40.
- . 1980. Reproductive behavior and mating success of male short-tailed crickets: Differences within and between demes. Evol. Biol. 13:219-260.
- . 1983a. Diel patterns of calling in nocturnal Orthoptera, pp. 45-72. In D. T. Gwynne and G. K. Morris (eds.), Orthopteran Mating Systems: Sexual Competition in a Diverse Group of Insects. Westview, Boulder, CO.
- . 1983b. Mating modes and female choice in short-tailed crickets (*Anurogryllus arboreus*), pp. 240-267. In D. T. Gwynne and G. K. Morris (eds.), Orthopteran Mating Systems: Sexual Competition in a Diverse Group of Insects. Westview, Boulder, CO.
- WALKER, W. F. 1980. Sperm utilization strategies in nonsocial insects. Amer. Natur. 115:780-799.
- WERREN, J. H., M. R. GROSS, AND R. SHINE. 1980. Paternity and the evolution of male parental care. J. Theoret. Biol. 82:619-631.
- WOODHEAD, A. P. 1985. Sperm mixing in the cockroach *Diploptera punctata*. Evolution 39:159-164.
- ZAR, J. H. 1984. Biostatistical Analysis. Prentice-Hall, Englewood Cliffs, NJ.

Corresponding Editor: R. H. Crozier