Journal of Insect Behavior, Vol. 4, No. 4, 1991

The Adaptive Significance of Mate Guarding in the Soapberry Bug, *Jadera haematoloma* (Hemiptera: Rhopalidae)

Scott P. Carroll[1,2]

Accepted December 6, 1990; revised February 2, 1991

*Male soapberry bugs (*Jadera haematoloma*) face severe mating competition at the northern edge of their range due to male-biased adult sex ratios. Copulations lasting up to 11 days may serve a mate guarding function (encompassing four or more ovipositions), but copulation duration is highly variable, with some pairings lasting as little as 10 min. Data were gathered to describe factors that influence the reproductive costs and benefits of prolonged copulation. Estimated copulation durations (mean ± SD) were 20 ± 23 h in the lab and 50 ± 8 h in the field and were only weakly affected by sex ratio. Females mated for 5 min produced as many fertile eggs as those mated for 600 min laid; they became depleted of fertile sperm after about 25 days. In twice-mated females, the first male's paternity was reduced by about 60%, and all females (*N = 13*) whose mates were removed experimentally mated again within an average of 6 min. The outcome of sperm competition on a per-clutch basis was not highly predictable. The possibility of increased sperm displacement in longer copulations was not tested. Males often guarded females during oviposition and successfully defended them from intruding single males by recopulating. Such intrusions occurred in the majority of oviposition attempts observed in nature. Even though most females mated promiscuously, in a focal aggregation with a mean sex ratio of 2.2 ± 0.4 males/female, the interval between matings by males was commonly several days. Males appeared to respond facultatively to several aspects of the distribution and availability of females. The intensities of mating competition and sperm competition indicate that monogamous mate guarding should be favored over nonguarding in nature. Unpredicted brief*

[1] Department of Biology, University of Utah, Salt Lake City, Utah 84112.
[2] Present address: Center for Population Biology, University of California, Davis, California 95616.

pairings may result from assessment by males of female reproductive value or of their own physical condition, or from female resistance.

KEY WORDS: assessment; *Jadera haematoloma;* Hemiptera; mate guarding; mate searching; prolonged copulation; sex ratio; sexual selection; soapberry bug; sperm competition; sperm transfer.

INTRODUCTION

Males of various animal species behave in ways that reduce the probability that a female they have inseminated will be inseminated by others (e.g., Parker, 1974). One of the interesting features of copulation in many insect species is that its duration is often greater than is required for the transmission of seminal fluids and sperm (reviewed by Thornhill and Alcock, 1983). Such prolonged postinsemination copulation may function to prevent other males from gaining access to females, the guarder's genitalia acting as plugs. Guarders lose opportunities to inseminate other females, so defense is likely to be adaptive only when there is either a high probability of losing fertilizations through sperm competition if females are not guarded (Parker, 1970a,b) or a low probability of finding additional females even if a male searches instead of guards (Parker, 1974).

Prolonged copulation appears to be particularly common in the order Hemiptera (Sweet, 1964), in which (a) species often form dense host-associated aggregations with high encounter rates among individuals, (b) oviposition often occurs within these aggregations, and (c) male biased adult sex ratios may be common (Carroll, 1988; Carroll and Loye, 1990). Copulations lasting several hours or days are known in many species of the cotton stainer *Dysdercus* [Pyrrhocoridae (Meyers, 1927; Van Doesburg, 1968; Carroll and Loye, 1990)], in *Lygaeus equestris* [Lygaeidae (Sillen-Tullberg 1981)], in *Nezara viridula* [Pentatomidae (Harris and Todd, 1980; McLain, 1980)], in the water striders *Gerris remigis* and *G. lateralis* [Gerridae (Clark, 1988; Arnqvist, 1988)], and in the soapberry bug, *Jadera haematoloma* [Rhopalidae (Carroll, 1988)]. In most of these species copulation terminates when the male departs near the time of oviposition, indicating that guarding functions to protect the sperm for immediate fertilization opportunities, rather than as long-term mate monopolization. The soapberry bug is unusual among these bugs in that the male remains with the female during oviposition and is likely to recopulate with her afterwards (Carroll, 1988). Such mate fidelity suggests that, in addition to guarding the ejaculate, the mate may also be guarded for future insemination.

In populations of the soapberry bug near the northern edge of the species' geographic range (e.g., Oklahoma), disproportionate female mortality leads to male-biased adult sex ratios in aggregations during the breeding season [mean ± SD = 2.73 ± 0.95 (Carroll, 1988)]. Further, most males are single in any given period, while most females are mated, leading to a very high operational sex ratio (the ratio of sexually active males to sexually active females). One factor leading to the rarity of single females is that many copulations are prolonged, lasting for several days and including up to four oviposition bouts (Carroll 1988). Some copulations are brief, however, lasting for as little as 10 min.

Prolonged copulation may serve a mate guarding function, but also reduces the time a male has available for inseminating additional females. This study investigates some of the factors that influence the fitness payoffs to mate guarding versus mate searching in this species and, perhaps, explain the great variation observed in copulation duration. Data include observations of mating and mate searching behavior of marked individuals in the field and in captive arenas and the results of experiments investigating sperm transfer, sperm utilization, and sperm competition.

The Study Insect. The genus *Jadera* is specialized on seeds of plants in the family Sapindaceae (Carroll and Loye, 1987). In Oklahoma, adult *J. haematoloma* emerge from overwintering shelters and colonize two tree species as seeds mature in midsummer: *Koelreuteria paniculata*, the introduced and partially naturalized golden rain tree, and *Sapindus saponaria* (v. *drummondii*), the western soapberry tree. Reproductive adults may live for as long as 2 months (this paper). Females are capable of laying several hundred eggs in numerous clutches, laid at 1- to 2-day intervals (Carroll, 1988). About 70% of the females in an aggregation are mating in any given sample. The copulation posture is posterior to posterior. Eggs are usually laid beneath host trees, in dry, silty soil in which the female digs a hole about 1 cm deep. Her mate withdraws his genitalia while she is digging and clings to her dorsum or side, keeping his genitalia near hers and recopulating when she begins to cover the eggs with soil. Both sexes mate with multiple partners. Aggregations grow in size until early autumn, when reproduction ceases and an adult diapause of several months in duration begins. Only adults overwinter, among stones and leaf litter near the host trees, and there is substantial overwintering mortality in both sexes (Carroll 1988).

METHODS

Study Sites and Seasons. Most field observations were made of bugs in aggregations on six golden rain trees on or near the campus of the University of Oklahoma, Norman, between April 1981 and August 1983, in August 1984, and in August–September 1986. The trees were 5–12 m in height, with canopy spreads of 4–8 m, and had short lawn grass and packed dirt beneath. Sites frequented by humans were fenced to reduce traffic. Aggregations were defined as consisting of the individuals in the canopy, on the trunk, and on the ground beneath the canopy. The sparse vegetation on the ground, small size of the trees, and openness of their canopies and foliage made accurate censusing possible.

Marked Individuals in the Focal Aggregation. The aggregation on one small (4-m-high) tree served as the site for observations of marked individuals. Newly molted (virgin) adults were removed to the laboratory, weighed to the nearest 0.1 mg, uniquely color marked on the pronotum and scutellum with Tek-Pen inks (applied to the surface of the exoskeleton with a syringe and needle with a bevelled tip), and returned to the field within 6 h.

This aggregation was censured daily from June to October 1981. The number, location (canopy, trunk, or ground), and mating state (single or copulating) of marked and unmarked individuals were recorded. On a daily basis, more bugs were recorded in censuses between 1400 and 1800 than at other times (bug activity being positively correlated with ambient temperature), and only data from censuses conducted during this time interval are reported. Bugs were least active at night.

Copulation Duration and Weight Change. Of the individuals marked for daily sampling in the focal aggregation, 67 males and 17 females were observed at least eight times, and only these individuals were used for analyses of mating frequency and copulation duration. The mean number of observations per male was 14.5 ± 6.6 (range, 8–38); the mean number of observations per female was 11.1 ± 3.2 (range, 8–19). Because it was not possible to mark all individuals in the aggregation, I was not able to estimate the total number of different mates possessed by marked males and females. In addition, the once-a-day sampling regimen means that some brief pairings may not have been observed and that the estimated durations of those observed are coarse.

A subset of individuals was removed to the laboratory for weighing every 3–4 days. All individuals were single when collected and were returned to the aggregation within 2 h of collection. Data are reported for 27 males and 7 females for which multiple measures were obtained.

Copulation duration was also examined in two laboratory experiments in which the mating status of individually marked, like-aged adults was recorded more frequently. Each experimental group consisted of 24 adults housed in arenas. In Experiment 1, one group was at a 2:1 sex ratio (16 males and 8 females), and the other a 3:1 sex ratio (18 males and 6 females). These ratios bracket those found in most aggregations in nature (Carroll, 1988). The bugs were initially collected in the penultimate instar in central Oklahoma (Cleveland Co.), then reared to adulthood and held in single sex groups in captivity for about a week. Virgin adults were then placed and observed in 60 × 25 × 6-cm (high) enamel pans under local light and temperature conditions (13.5L:10.5D, "daylight" fluorescent tubes; 33°C average in daytime, 27°C average at night). The pans had hard plaster-of-paris floors containing ground charcoal to absorb waste and provide traction. The pan floors were marked with lines in a grid at 5-cm intervals. Sigmacote silicon coating, from the Sigma Chemical Co., was brushed on the inside walls of the pans to prevent the bugs from walking out. Unlimited food (golden rain tree seeds) and water (in cotton stoppered 2-dram vials) were provided. Bugs did not attempt to fly from the pans.

Observations of each individual were recorded at 2-h intervals, six times each day during the daylight period, for 12 days. Reproductive condition was measured as the mating status (copulating or single) of all individuals, and the relative egg load of females (on a 0–4 scale of increasing abdominal expansion). Because a male's need to feed could compete with time for mating effort, the presence or absence of feeding behavior was also recorded. In addition, male activity rates were recorded as the number of grid lines crossed and the number of mounts on single males, single females and mating pairs by each male in 1-min focal samples every 2 h. Individuals that died during the study were replaced with sexually mature virgins of the same sex.

Oviposition was either observed directly or detected indirectly as a decline in the gravidness of a female from one sample period to the next. Eighty-three ovipositions were identified in this way.

In Experiment 2, the possible effect of sex ratio on mating behavior was further investigated with observations of 24 adults in each of three groups at sex ratios of 1 : 1, 2 : 1, and 3 : 1, respectively. Observations were made once per day (at 1600 h) for 18 days. These bugs were from second-generation lab stocks descended from aggregations in central Oklahoma (Cleveland Co.) and western Oklahoma (Woodward Co.) and were housed and treated in the same manner as those in Experiment 1.

Mate Searching Activity of Males. Male activity rates were recorded in two ways. Focal samples of 180-s duration were made of 117 individual males in the field over 3 days in September 1986 (the mean air temperature during observations was 24°C). Males were marked with a dot of paint at the end of each sample to prevent resampling of the same individuals. The duration of sexual mountings by males on other single adults and on mating pairs was also recorded on these days. Instantaneous scan samples of locomotion in 108 males on the ground and 110 males on host tree trunks were made over 3 days in August 1986 (mean air temperature, 35°C).

Time Until Mating by Females with Their Male Removed. The probability that an unguarded female would remate before using an initial male's sperm was estimated in the field by manually separating 13 pairs and measuring the interval until the females remated. This experiment was conducted in August 1986.

Sperm Transfer and Sperm Depletion. Prolonged copulation could result simply from the need for a long period to transfer the ejaculate. In addition, the rate at which females deplete the sperm transferred by a male could strongly influence the costs and benefits of mate guarding for a male. To assess rates of sperm transfer and sperm depletion (or sperm mortality), 20 pairs of virgin males and females from second generation lab stocks originally from Woodward Oklahoma were isolated from one another and allowed to mate for periods of 5, 30, 200, or 600 min (four pairs at each duration). Some pairs that separated by themselves but that mated for times close to the desired experimental durations were included in the analysis and are indicated under Results. After separation, each female was isolated with food and water. Eggs were collected daily, until oviposition ceased or a clutch consisting of greater than 75% collapsed (unfertilized) eggs was laid. All such clutches immediately followed clutches in which more than half of the eggs were fertile. Hatchlings were removed daily to prevent egg cannibalism. The number of hatchlings, plus any partially developed, dead embryos, was totaled for each female and used to give an estimate of the relative number of sperm transferred as a function of copulation duration. These data also provide an estimate of the number of days for which a female can lay fertile eggs after just one mating. The proportion of fertile eggs was also calculated, including only those eggs laid before a largely infertile clutch was produced.

To test whether infertility in the previous experiment resulted from depletion or deterioration of a male contributed substance or from declining female vitality, some females were mated again after 5 days of not laying eggs or of producing infertile eggs. Because females normally produced clutches of fertile eggs every 1–2 days, 5 days was chosen as the laying interruption indicative of sperm depletion or deterioration. All second matings were of about 120-min duration. The number and fertility of all subsequent eggs laid by these females and by females not mated again were recorded, as were the intervals between the females' last clutches and their deaths.

Sperm Competition. Sperm competition was studied by mating virgin females twice, once to normal males and once to males irradiated with 12 krad of X rays. I assumed that sperm are released from the spermatheca at the time of oviposition, as is typical of insects (Chapman, 1971, p. 345). For each pairing a female and male were held together in isolation for 24 h (approximating the average mating duration). At the end of the first 24-h pairing, each male was removed and a second male added. Only females copulating in 75% or greater of observations taken at 6-h intervals over the 2-day period and that laid no eggs before the conclusion of the second mating period were included in analyses. No males were used more than once. Preliminary studies showed 12 krad to be the minimum dosage necessary to cause 100% embryonic mortality. Thus, sperm from irradiated males could presumably compete for fertilizations with the sperm from normal males, but only normal males would sire viable offspring. The minimum dosage was used to minimize any impact of irradiation on the competitive ability of sperm, and subsets of the females were mated first to either normal males ($N = 10$) or irradiated males ($N = 8$) as a check for differences in such ability. Eggs were collected once per day from females isolated in cups with food and water.

Paternity was subsequently assigned to eggs on the basis of hatching success, modified for a 7% average failure rate for eggs from control normal males. Thus, in the case of matings of normal, and then irradiated males, the proportion of fertilizations attributed to the second male (P_2) equals one minus the proportion of eggs hatching divided by the fertility rate (0.93), and in the case of matings to irradiated and then normal males, P_2 equals the proportion of eggs hatching divided by the fertility rate. Paternity was analyzed both for the total egg production of each female and on a daily basis, to search for any temporal changes in patterns of sperm storage and utilization within females.

Because the shape of the spermatheca may influence the outcome of sperm competition (reviewed by Thornhill and Alcock, 1983), the spermathecae of five females were dissected and mounted on glass slides. Their size and shape were measured under a light microscope.

RESULTS

Copulation Duration

Pairs in the two captive groups that were observed six times daily (Experiment 1) frequently copulated for long periods, but durations were highly variable (Fig. 1). Brief copulations were most common with virgin females, particularly at the 2 : 1 sex ratio. In this group, the average duration of copulations with virgins was 5.6 ± 5.3 h ($N = 10$), significantly shorter than that for the same females during each of their subsequent five copulations (mean ± SD of copulations 2–5 = 21.2 ± 20.1 h, $N = 38$; Wilcoxon signed-rank z values ≥ 2.0, P values ≤ 0.05 for all four comparisons). Similarly, in the 3 : 1 sex ratio group the average duration of copulations with virgins was 9.8 ± 11.5 h ($N = 8$), briefer than the 30.0 ± 31.7 h for copulations 2–5 ($N = 22$), but not significantly shorter than those in each of their subsequent five copulations (Wilcoxon signed-rank z values, 1.1–1.8; all NS). Mean durations of copulations 2–5 were more uniform and did not differ significantly from one another in either the 2 : 1 or the 3 : 1 sex-ratio group (Friedman's test statistic $T = 1.83$, $P = 0.61$, and $T = 1.80$, $P = 0.62$, respectively).

Mean copulation durations tended to be greater in the captive groups in which the sex ratios were more male biased. In Experiment 1 the effect was not significant (Fig. 1) (2 : 1 group, 17.9 ± 19.2 h; 3 : 1 group, 24.6 ± 29.0 h; $U = 639.5$, $z = 0.83$, $P = 0.20$, $n_1 = 48$ and $n_2 = 30$ copulations, respectively).

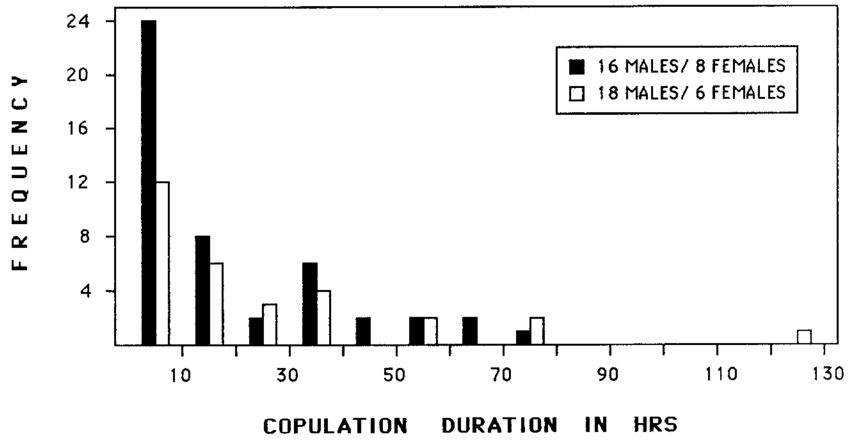

Fig. 1. Frequencies of copulation durations measured for captive bugs at two sex ratios. Solid bars are for a group of 16 males and 8 females; hatched bars are for a group of 18 males and 6 females. Mean ± SD for the 2 : 1 sex ratio 18.0 ± 19.2 h, and for the 3 : 1 sex ratio 24.6 ± 29.0 h.

Significant and near-significant effects of sex ratio were found in Experiment 2 (Table I). A stronger effect is seen in comparing durations at 1 : 1 with those at 2 : 1 and 3 : 1 than between those at 2 : 1 and 3 : 1.

High variance in copulation duration resulted both from variation in duration among the successive copulations of individual males and from differences among males. In the 2 : 1 group, some of the males consistently mated for shorter periods, and analysis of variance suggests differences among the males (Kruskal-Wallis $H = 16.2$, $P = 0.06$, $N = 16$). No difference was found among males in the 3 : 1 sex-ratio group ($H = 3.33$, $P > 0.10$, $N = 18$).

Eighty-three ovipositions were detected in Experiment 1 either by direct observation or by noting a decline in the gravidness from one sample period to the next. In 60 (72%) of these 83 ovipositions, the guarding male recopulated with his mate, and in 23 (28%), he departed, either immediately after oviposition or before the next observation period (2 h later) or before the next morning (in 15 nocturnal ovipositions detected indirectly). Females were never observed to resist recoupling after ovipositing. Departed males remained sexually active, often mounting the next individual adult encountered.

In 42 (70%) of the 60 ovipositions in which the pair remated after eggs were laid (*in copula* 2 h later), the male departed before the 4-h observation period. In 13 of the 60 pairings (22%), pairs remained together for two ovipositions, and in five of these matings the male recoupled for a third, brief period before departing. Four of 60 pairs stayed together for three ovipositions, with a brief fourth mating in one of these. Only one pair remained together for four ovipositions.

Mating Histories in Nature

Marked males and females were observed within the focal aggregation for an average of 3–4 weeks (Table II). The individual females were *in copula* about 2.2 times more frequently than were males ($U = 103$, $P < 0.0001$,

Table I. Mean (±SD) Number of Consecutive Observations (One per Day) for Each Mating by Pairs of *Jadera haematoloma* in Captive Arenas at Three Sex Ratios (M : F), for Two Oklahoma Populations

	Sex ratio		
Population	1 : 1	2 : 1	3 : 1
Cleveland Co.			
No. of obs./mating	1.5 ± 0.92	2.2 ± 1.9	1.8 ± 1.2
No. of matings	73	54	47
U^a and P values			
1 : 1 vs. 2 : 1, 2 : 1 vs. 3 : 1	1611, 0.04		1208.5, 0.34
1 : 1 vs. 3 : 1		1456.5, 0.08	
Woodward Co.			
No. of obs./mating	1.3 ± 0.78	1.5 ± 1.1	1.6 ± 1.0
No. of matings	73	81	52
U and P values			
1 : 1 vs. 2 : 1, 2 : 1 vs. 3 : 1	2544.5, 0.06		2091, 0.47
1 : 1 vs. 3 : 1		1697, 0.13	

[a] Values from Mann-Whitney U tests. These and P values are for the comparisons between sex-ratio treatments.

Table II. Mean and Ranges of Mating History Data of Individually Marked *Jadera haematoloma* in Nature ($N = 67$ Males and 17 Females)

Sex	Days present	Days mating	Mating frequency (%)	Mean interval between matings (days)[a]
Males	23.5 ± 11.7 (8–52)	6.4 ± 1.1 (0–14.6)	28.7 ± 15.7 (0–62)	5.2 (0–24)
Significance[b]	NS	*	*	*
Females	29.1 ± 12.2 (8–59)	18.8 ± 5.8 (8–26.2)	64.4 ± 19.9 (29–90)	2.5 (0–8)

[a] Approximated as the mean number of days not mating divided by the mean number of matings.
[b] Significance levels for differences between values for the sexes.
*$P < 0.01$, Mann-Whitney U test.

Mann–Whitney *U* test). The mean interval between matings was accordingly briefer for females (Table II). These females were observed with up to nine different mates (mean, 4.2 ± 1.8; range, 2–9), and males with up to eight different mates (mean, 3.2 ± 1.9; range, 0–8). The mean mating duration of the bugs described in Table II was estimated to be 2.1 ± 0.3 days (range, 10.5 min to 11 days).

Aggregation Structure

Males and females differed in their distributions within the focal aggregation, leading to different sex ratios in different areas. Most single males were found on the tree trunk or ground, while females were most abundant in the canopy and on the ground (Fig. 2) ($X^2 = 965.9$, df = 2, $P < 0.001$). The density of males appeared to be greatest on the trunk. Mated females were more common on the trunk and in the canopy than were single females ($X^2 = 60.2$, df = 1, $P < 0.001$). Single females were least common in the region of greatest male density.

Weight Change and Feeding Frequencies

Newly molted (prereproductive) males weighed less than newly molted females (41.4 ± 4.8 mg, range 30.2–52.4 mg, $N = 33$, versus 68.8 ± 11.5 mg, range 39.2–90.7 mg, $N = 71$). Males lost weight during at least the first

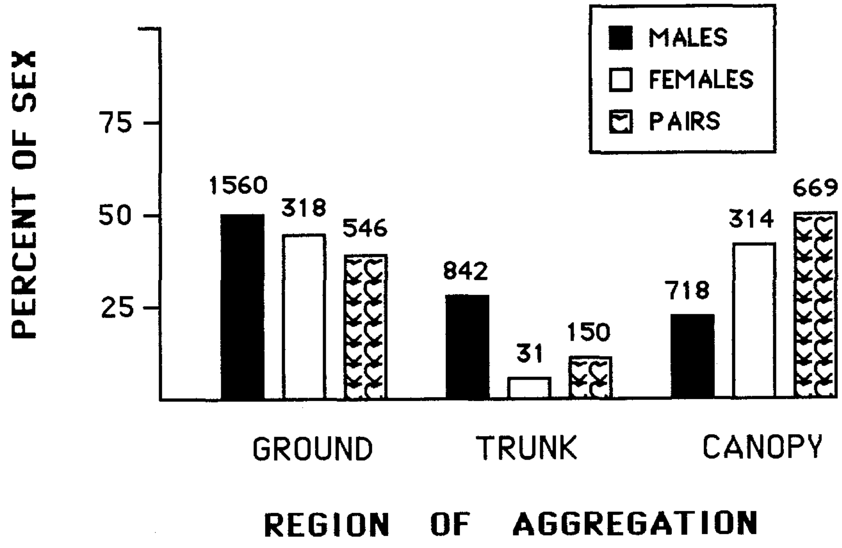

Fig. 2. Numbers of single males, single females, and mating pairs located in the three regions of the focal aggregation. Total numbers observed during all censuses are reported above the columns.
]

2 weeks after maturing: for 27 males weighed on the day of their terminal molt and again two or more times, the average loss was 1.1% of the initial body weight per day. Female weights were more variable over time, as a result of egg production and oviposition, but all females that became reproductive gained weight. Initial, virgin weights for seven females that became reproductive (and for which three or more measures were taken, at approximately 4-day intervals) averaged 73.7 ± 12.0 mg, which was 63% of the mean maximum of these females (115.5 ± 8.5 mg; range, 83.6–139.7 mg).

These sex differences in weight change patterns are related to differences in feeding frequency. In captivity at a 2:1 sex ratio, single males fed in only 4.2% of 775 observations. This is significantly less frequently than in single females (10.8% of 111 observations; $X^2 = 7.3$, df = 1, $P < 0.01$) and mating females (12.7% of 471 observations; $X^2 = 25.5$, df = 1, $P < 0.001$) but significantly more frequently than in mating males, which were often unable to reach the seed upon which their mates were feeding and fed in only 0.6% of 452 observations ($X^2 = 12.4$, $P < 0.001$). At the 3:1 sex ratio, feeding frequencies were similar, except for that of single males (1.6% of 718 observations), which fed significantly less frequently than single males in the 2:1 sex-ratio treatment ($X^2 = 7.4$, df = 1, $P < 0.01$).

Sperm Transfer, Storage, and Utilization

Of 20 females mated once for periods ranging from 5 to 600 min, 14 lived long enough to fully deplete their stores of fertile sperm. These 14 females laid a mean of 150.0 ± 87.8 fertile eggs over a mean of 24.9 ± 8.11 days (Table III); the interval between clutches averaged 1.1 ± 0.2 days. No differences were found among the four mating duration treatments in the total number of eggs laid by the 20 females (Kruskal–Wallis statistic $H = 1.26$, $P = 0.75$), the total number of fertile eggs laid ($H = 1.19$, $P = 0.75$), the percentages of fertile eggs ($H = 0.86$, $P = 0.86$), or the number of days over which eggs were laid ($H = 2.00$, $P = 0.57$). (Statistical results are similar when only the 14 females that survived to fully deplete their stores of fertile sperm are analyzed.)

None of the eight surviving females that were not mated a second time produced additional fertile eggs. All of the six twice-mated females did produce additional eggs, with an average enhancement of lifetime fecundity of 30.0 ± 15.3%. The maximum life span beyond the laying of the last egg for twice-mated females was 6 days. Comparing the number of eggs produced after the initial depletion of fertile sperm, the females allowed to mate again laid more eggs subsequently (mean, 78.1 ± 53.3; range, 16–155), than did the eight females kept in isolation (mean, 12.1 ± 7.5; range, 2–24; all infertile; $U = 1$, $P = 0.001$, Mann–Whitney U test). This result suggests that females reduce oviposition rate in association with the absence of stored or fertile sperm.

Table III. Oviposition and Fertility of 20 Female *Jadera haematoloma* Mated for Different Periods of Time

First mating					Second mating				
Mating duration[a]	No. eggs laid	% fert.	No. of days laid[b]	Died in <5 days?[c]	Mating again?[d]	No. eggs laid	% fert.	No. of days laid	Days last egg until dead[e]
5	45	89	7	Y	—	—	—	—	—
5	134	86	17	Y	—	—	—	—	—
5	197	93	24	N	N	21	0	7	3
5	212	91	36	N	Y	25	92	15	4
5	225	89	28	N	N	6	0	7	12
30	18	56	14	N	N	2	0	1	25
30	70	94	10	Y	—	—	—	—	—
30	123	81	15	Y	—	—	—	—	—
30	154	96	21	N	N	11	0	7	5
30	324	92	32	N	Y	44	91	10	6
175	23	78	9	N	Y	16	94	5	5
190	110	90	19	N	N	7	0	7	11
200	189	95	27	N	Y	101	87	17	4
200	256	96	41	Y	—	—	—	—	—
200	257	93	37	N	N	12	0	9	2
600	145	88	20	N	Y	90	88	11	5
505	166	90	21	N	N	24	0	25	0
600	178	98	32	N	Y	155	83	14	3
600	189	90	27	Y	—	—	—	—	—
600	241	83	28	N	N	14	0	13	7

[a] In minutes.
[b] Interval during which fertile eggs were produced.
[c] Did the female die between the cessation of laying fertile eggs and the time for remating (5 days)? Y, yes; N, no.
[d] Determined by the experimenter.
[e] How long did the female live after ceasing egg production? No twice-mated female laid more than five collapsed eggs after ceasing to produce fertile eggs.

Sperm Competition

Dissections showed that the single spermatheca of *J. haematoloma* is a spherical sac about 0.25 mm in diameter, at the distal end of a long and narrow (1.3 × 0.04-mm) coiled tube.

About 93% of the eggs laid by females mated to normal (N) males hatched, and none hatched for females mated to irradiated (R) males (Table IV). Comparing hatch rates for the eggs of females mated twice, to one male of each type, shows that substantial fertilization competition was common but that the pattern was also highly variable (Table IV). The second male most frequently fertilized either about 30% or about 80% of the progeny. The order of mating

Table IV. Hatching of Eggs from Virgin Females Mated Once to Normal Males (N) or Irradiated Males (R) or Mated Twice, Once to Each Type of Male

Mating type	Number of eggs	% hatching	% fertilized by second male[a]
	Controls		
N	58	91	
N	272	87	
N	239	93	
N	266	95	
N	17	100	
R	253	0	
R	23	0	
R	10	0	
R	50	0	
R	87	0	
R	123	0	
	Experiments		
N–R	59	71.2	23.4
N–R	150	17.4	81.4
N–R	92	6.5	93.0
N–R	137	65.0	30.2
N–R	114	57.9	37.8
N–R	178	50.6	45.6
N–R	99	63.6	31.6
N–R	82	19.5	79.0
N–R	104	11.5	87.6
N–R	159	17.0	81.7
Grand mean ± SD			59.1 ± 27.6
R–N	87	4.6	4.9
R–N	143	37.8	40.6
R–N	109	74.3	79.9
R–N	80	0.0	0.0[b]
R–N	128	64.1	68.9
R–N	116	68.1	73.2
R–N	72	80.6	86.7
R–N	100	88.0	94.6
Grand mean ± SD			64.1 ± 31.2

[a] Assuming 93% fertility for eggs fertilized by normal (N) sperm.

[b] Excluded from calculation of mean percentage fertilized by second male because it probably indicates that the normal male transferred no viable sperm.

(N–R or R–N) did not affect the overall outcome of sperm competition, suggesting that the gametes of all males competed equally well for fertilizations.

Sperm competition patterns as a function of the time after mating were only weakly predictable (Table V). For R–N matings a reduction in the proportion of eggs fertilized by the second male was most common, with a nearly

Table V. Spearman Rank Correlations Between the Proportion of Fertilizations by the Second Male in Each Clutch as a Function of Clutch Rank (the First Clutch Laid = Clutch 1, the Second = Clutch 2, Etc.)[a]

Mating sequence	No. of clutches	Correlation	z value	P value[b]
N-R	16	0.31	1.20	NS
N-R	15	0.26	0.97	NS
N-R	21	−0.05	0.22	NS
N-R	19	0.26	1.10	NS
N-R	24	0.26	1.25	NS
N-R	29	0.61	3.23	0.001
N-R	21	0.58	2.59	0.01
N-R	15	0.44	1.65	NS
N-R	26	−0.09	0.45	NS
N-R	22	0.81	3.71	0.0002
All N-R	208	0.37	5.32	0.00001
R-N	16	0.04	0.16	NS
R-N	25	−0.58	2.84	0.004
R-N	18	−0.03	0.12	NS
R-N	18	0.56	2.31	0.02
R-N	18	−0.23	0.95	NS
R-N	15	−0.56	2.10	0.036
R-N	23	−0.03	0.14	NS
All R-N	133	−0.12	1.38	NS

[a] Values for individual females are in the same order as in Table IV. Proportions were calculated as in Table IV.

[b] Listed are two-tailed probabilities, because no direction of deviation from the null hypothesis was specified.

significant, weak negative relation overall. In contrast, N–R matings commonly showed a minor *increase* in the proportion of fertilizations by the second male, with a significant positive relation overall. In general, these results are consistent with the hypothesis that sperm mortality is high during storage. High correlation values for certain females may indicate either that the sperm of the males has been segregated within the spermathecae or that sperm mortality rates differ between males.

Mate Searching in Nature

Male *J. haematoloma* searched for females in any of three ways: "active searching," "sit-and-wait searching," and rarely, "pair riding."

Active searching occurred mainly on the ground beneath the canopy and in the canopy itself. In this behavior, males walked in a general direction for several seconds, then stopped for several seconds, and then resumed walking whether or not any other individuals were detected, sometimes changing direction between movement bouts. Such males appeared to detect moving individuals most readily, particularly when they (the searchers) were stationary. Other adults, mating pairs, and large nymphs were approached upon detection and mounted. In instantaneous scan samples 57 of 108 (52%) of males were in motion on the ground. In 180-s focal samples of males on the ground, locomotion occurred during an average of 69 ± 39 s (39% of sample period; range, 4–161 s; $N = 117$ males).

Sit-and-wait searching occurred mainly on the tree trunk, where males often greatly outnumbered females. Waiting males remained stationary until they detected movement by another individual, at which time they approached and mounted. Densities were as high as 100 males/m^2 of trunk, and mounting attempts on other males occurred very frequently, with a cascade effect as progressively more males were attracted to the vicinity of an initial mounting. Males approached other individuals from distances of up to 15 cm and mounted. After dismounting from an unproductive target, males resumed a stationary pose until again advancing upon a nearby individual that moved. In a newly formed aggregation on a tree with immature seeds and no females, almost no movement was observed in the total of 16 males in four scan samples taken over 20 min (6%; 4 of 64 observations). In contrast, in a dense reproductive aggregation, instantaneous scan samples of sit-and-wait searching showed a movement frequency of 50% (55 of 110 males, at the same air temperature), similar to that for active searching.

Pair riding was a rare form of mate searching, or perhaps interference, in which a single male remained on the female of a copulating pair for a prolonged period with his genitalia near the female's, occasionally attempting to displace the copulating male. In captivity, pair riding, defined as males remaining on a pair for the entirety of a 1-min observation period, was more common in the group with a sex ratio of 3:1 (19 of 474 mounts) than in the group with a sex ratio of 2:1 (5 of 575 mounts, $G = 14.94$, $\mathrm{df} = 1$, $P < 0.01$). Such mounts may last for several hrs.

The frequencies of active searching males and sit-and-wait searching males were approximately proportional to their respective frequencies on the ground plus in the canopy versus on the trunk (73 vs 27%; Fig. 2). Pair riding probably occupied <5% of males at any given time.

Mate Discrimination by Searching Males

In the field, both the duration and the frequency of unsuccessful mounting attempts by males varied significantly with the sex and mating status of the mounted individuals. The average duration of attempts on single females was 12.7 ± 11.5 s ($N = 17$); on mating pairs 5.5 ± 5.4 s ($N = 31$); and on single males, 1.1 ± 0.4 s ($N = 29$). Sex of the mounted individual had a significant effect on the duration of the copulation attempt [$F_{(2,76)} = 4.95$, $P < 0.01$, ANOVA], and the duration of the copulation attempt differed significantly among the three classes of mounted individuals [$P < 0.05$, Duncan's multiple-range test; no instances of ''pair riding'' (see below), or of successful mating with a single female, were included in this analysis].

Captive males did not mount other adults at random. The average number of mounts per min was 0.58 ± 0.38 on other single males, 0.46 ± 0.26 on mating pairs, and 0.07 ± 0.07 on single females ($N = 34$ males, mean sex ratio = 2.5 males per female, mean number of observation periods/male = 65 ± 6). Based upon their proportional abundance, other males were mounted 13% less frequently than expected, while mating pairs and single females were mounted more frequently than expected (16 and 12%, respectively; $X^2 = 24.6$, df = 2, $P < 0.001$, N = a total of 537 mounts on males, 476 mounts on mating pairs, and 83 mounts on single females, with expected frequencies of 613, 409, and 74, respectively). These males traveled a mean of 0.40 ± 0.20 m per 1-min observation period.

Intrusions and Guarding During Oviposition

In 27 ovipositions observed from start to finish in the focal aggregation (mean duration, 9.2 ± 7.5 min), single males that attempted to copulate interrupted 21 of them. Six pairs experienced intrusions by two different males, one by three, and one by four. In all cases the guarding male retained his mate.

Of four mate takeovers observed, three occurred while the female was ovipositing and the guarder was standing on her dorsum. In each case the intruder displaced the guarder even though the guarder recopulated when the intruder approached. After each takeover, the female resumed oviposition shortly. The durations of these copulations (i.e., the times until the new male withdrew, standing guard on the female's dorsum, permitting oviposition) were comparatively brief: 10.5, 14, and 20 min.

Rate of Remating by Experimentally Deserted Females

All females of the 13 manually separated pairs remated within 15 min (range, 1 min 9 s–14 min 53 s). The mean remating time was 6 min 12 s ± 3 min 35 s. This period is far briefer than the average interval of sperm utilization.

DISCUSSION

Copulation Duration and Guarding

Multiple lines of evidence from this study show that many soapberry bug copulations are longer than needed for sperm transfer alone and indicate that prolonged copulation serves a postinsemination guarding function. First, copulations interrupted after 5 min resulted in the production of as many fertile eggs as those lasting 600 min. This indicates both rapid transfer of sperm and of any nutrients affecting fecundity. Second, most females in nature mated with several males, and females with their mates manually removed recopulated in an average of 6 min, a period much briefer than the average period over which sperm from a single insemination were used (about 25 days for females mated once). Third, the average paternity loss incurred by a male whose mate copulated with another was approximately 60%. Fourth, females were subject to intrusions by searching males in most of the ovipositions observed from start to finish, but the paired males prevented takeovers by recopulating. These conditions of demography, remating rates, and sperm competition are consistent with those modeled by Yamamura (1986) to promote mate guarding (versus mate searching) in insects.

Single males were in motion about 50% of the time in diel observations, and much of this motion appears to function in mate searching. Captive individuals traveled about 40 body lengths/min and mounted other individuals at a rate of > 1 per min. Males made several types of decisions, both during searching and during copulation. They distributed themselves nonrandomly within aggregations, being least common in the canopy, where the high frequency of females already paired and at branch tips (where the seeds are) makes searching relatively expensive. Active searching was most common on the surface of the ground, where many females feed and where oviposition normally occurs. The greatest male density occurred at the physical bottleneck of the aggregation, on the trunk, over which pairs and single females passed in transit between feeding in the canopy and ovipositing on the ground. Here sit-and-wait searching predominated. Pair riding occurred mainly when operational sex ratios were strongly male biased (i.e., encounters with single females were very rare). Male-biased sex ratios may also lead to an increase in mean copulation duration, which may indicate an increase in allocation to mate guarding versus mate searching, as found for other hemipterans by McLain (1980), Sillen-Tullberg (1981), and Clark (1988). In addition, shorter mount durations and lower mount frequencies on males and paired females versus single females [probably resulting from the detection of chemical cues (Aldrich *et al.*, 1990)] reduced the amount of time spent with unproductive targets. Wilcox (1984) found some similar patterns in the water strider *Gerris remigis*.

Factors Affecting the Evolution of Mate Guarding in the Soapberry Bug

Departure of a male after a prolonged copulation, but before oviposition, is clearly ejaculate guarding rather than defense of the mate for future insemination. Such male behavior is found in the hemipterans *Lygaeus equestris*, in which the last male to mate fertilizes about 90% of the subsequent ova (Sillen-

Tullberg 1981), *Nezara viridula*, in which the last fertilizes about 50% of the ova (McLain 1980), and *Dysdercus bimaculatus* [(Carroll and Loye, 1990) Harwalkar and Rahalkar (1973) found the last male fertilization rate to be about 65% in a congener]. Compared with these bugs, *J. haematoloma* exhibits the innovation of guarding the female through oviposition, instead of departing just before the eggs are laid. Thus the ejaculate may be better defended from competitors, even though the risk of sperm displacement is not as great as in, for example, *L. equestris*.

Because this ''extra'' guarding is sometimes followed by recopulation, prolonged copulation in *J. haematoloma* may function, in addition to ejaculate guarding, as mate monopolization (i.e., sequestering a female, allowing additional, later transfer of sperm that fertilize an additional proportion of her future egg production). The male-biased adult sex ratios that characterize aggregations of the soapberry bug in Oklahoma (Carroll, 1988) result in intense male–male competition that could favor mate monopolization even in the absence of sperm competition (by extension of Yamamura, 1986).

No males were observed to guard a female for her entire reproductive life span, and they most frequently guarded mates through just one or two ovipositions. For the guarding tactic to be maintained in the population, the fitness increment (i.e., the proportion of eggs fertilized by a guarder/the proportion of eggs fertilized by a searcher) must frequently be greater than the time cost accumulated by the guarding of females in addition to searching for them. This dynamic will depend on (a) the number of ovipositions for which a guarder remains with a single female (the greatest savings in search time would be realized for the male that guarded one female throughout her life span), (b) the effect on the outcome of sperm competition in females as they mate with successive males, and (c) the true average search time.

Based upon the observation that males commonly guard females for some period, the increment in fertilization rate due to guarding a female for a single clutch probably outweighs the costs of time invested in guarding. But it is enigmatic that while most males guard, they mainly guard for just one oviposition, because the time taken to find another female, and guard her until she oviposits, should be greater than that required for the initially guarded female to produce another clutch. The average interval between matings by males in the field is coarsely estimated at about 5 days, and while this estimate almost certainly overlooks some brief matings, it is still much greater than the approximately 1-day interval between ovipositions. Most females continue to produce eggs at a steady rate for 2–3 weeks (Carroll, unpublished data), and so a female is not likely to be of inferior reproductive value following most ovipositions. However, perhaps unguarded females on average oviposit more quickly after being mated by a new male than do continuously guarded females. It is also not clear why matings with virgin females were on average the most brief. They were not typically terminated by oviposition.

Captive pairs recoupled after oviposition in a majority of cases, but only in a minority of such cases did pairings last until the next oviposition, with males remaining for an additional period of ≤4 h, perhaps transferring more sperm. By then departing, they did not guard the ejaculate from other males, but might have fertilized a greater proportion of the female's eggs in the next oviposition than if they had not recoupled. Additional ejaculate might simply refill the female or, perhaps, act to further displace ejaculates of other males already present. Alternatively, the brief postoviposition copulations may last only until males have detected that the female has completed a particular oviposition bout, at which time some males depart and switch to searching behavior. Given the substantial variation in sex ratio among aggregations and within aggregations over time (Carroll, 1988), periodic searching might allow males to assess current levels of reproductive competition.

Copulation duration could vary in response to facultative assessments made by males of the reproductive values of females or of their own mating abilities or physical condition. Given that the majority of females in an aggregation will at any one time be carrying stored sperm, insemination with large amounts of ejaculate may function in sperm displacement (cf. Dickinson, 1986). Thus, the relative brevity of matings with virgin females (as also found for a bug by Sillen-Tullberg, 1981) might result because simple insemination is a faster process than is sperm displacement. However, the pairings after takeovers, preceding ovipositions, were also uniformly brief.

Temporary sperm depletion or physical weakness may occur after single inseminations, at which point a male could continue to copulate with the same female while replenishing supplies or depart to engage in activities that might increase the rate of replenishment such as feeding. Feeding rates were higher in captive single males (4.2%) than in captive mating males (0.6%), perhaps in part because the "tail-to-tail" mating posture often prevents mated males from reaching the seed upon which their mate is feeding. In addition, feeding rates were higher in single males in the less sexually competitive 2 : 1 sex-ratio condition that in the 3 : 1 condition, suggesting that males may reduce allocation to maintenance when females are rarer. However, feeding by males was in general sufficiently rare to suggest that it is not important in terms of temporal allocation. Males in nature suffered only a slow decline in body weight, and, therefore, male nutritional needs probably play only a minor role in the termination of copulations.

Mating durations tended to increase at higher sex ratios, suggesting an increase in allocation to guarding, but durations at the highest sex ratios may have been reduced by interference from pair riding males, whose frequency increased with sex ratio. Intermale variation in time allocated to guarding versus searching, evident at a sex ratio of 2 : 1, may also have been obscured by increased interference at the 3 : 1 ratio.

Further, female mating decisions may influence the duration of some pairings. Mated females resist their mates (by kicking and shaking) in about 5% of observations, resulting in separation within 3 h of about one-third of such pairs, as opposed to separation of only about 5% of pairs in which resistance was not observed (Carroll, unpublished data). Thus females may sometimes terminate pairings in which males are attempting to remain.

Additional ultimate factors may also be involved in the evolution of copulation duration in this species. Variation in the payoff to postinsemination guarding could result if the proportion of eggs fertilized by a given male changed from one oviposition to the next. However, the results of the sperm competition experiment indicate that while proportional paternity does not vary strictly at random among clutches, it probably does not change with sufficient predictability to affect the evolution of male behavior in this mating system, unless males can tell in particular cases how a female is apportioning ejaculates to fertilization. Differential sperm mortality may have played an important role in cases in which a pattern was detected.

Other ultimate factors promoting the evolution of prolonged copulations in insects that were not directly examined in this study include a decrease in the risk of predation or parasitism (Eisner, 1965; McLain, 1980; Sivinski, 1980, 1983; but see Arnqvist, 1989) and a reduction in the rate at which they are harassed by males (Walker, 1980; Fincke, 1984; Wilcox, 1984; Arnqvist, 1988, 1989). Soapberry bugs are protected from predation by toxins (Ribeiro, 1989; Aldrich *et al.*, 1990), but mated female soapberry bugs were less attractive to single males than were single females. Enhanced feeding rates have also been reported for paired females in other species (Rubenstein, 1984; Wilcox, 1984), but there was no indication that feeding rates were affected by pairing in female soapberry bugs.

The plastic response of guarding duration to sex ratio is analogous to the patterns of polymorphic pure strategies predicted under different sex ratio conditions by Yamamura (1986). He predicts a guarder-searcher polymorphism in a zone of intermediate payoff conditions; such conditions could select equally well for conditional responses by individuals provided that the costs of plasticity are not too great. Moreover, the occurrence of both long and short matings in the histories of most captive males may indicate that the payoffs to each tactic are sufficiently similar that males (1) either switch tactical states unconditionally at a rate reflected by the proportions of various mating durations (Brockmann *et al.*, 1979) or (2) closely monitor both internal and external conditions and continually revise tactical decisions accordingly.

ACKNOWLEDGMENTS

For support and advice, I thank M. Aide, D. Berrigan, E. Charnov, P. Coley, K. Cramer, O. Cuellar, W. Darwall, D. Davidson, J. Dickinson, V. Eckhart, G. Edmunds, J. Endler, M. Geber, M. McGinley, B. Milstead, D. Mock, J. Quinn, D. Rubenstein, M. L. Salamon, J. Seger, B. Spivey, D. Temme, J. Thompson Jr., B. Vestal, and R. Vickery. J. Loye has been especially generous throughout with gifts of insight and effort in both the field and the lab. W. Robinson, superintendent of Boiling Springs State Park, Woodward, Oklahoma, has greatly facilitated fieldwork.

The ICI Americas Corporation (Wilmington, Delaware) provided Fluon AD-1 for lab work. Financial support has been provided by the Department of Zoology, University of Oklahoma, Department of Biology, University of Utah, Sigma Xi, NIH Training Grant 5 T32 GM07464-08 in Genetics, NSF Grant BSR-8715018, and University of Utah Research Council.

REFERENCES

Aldrich, J. R., Carroll, S. P., Lusby, W. R., Thompson, M. J., Kochansky, J. P., Waters, R. M., and Rudmann, A. A. (1990). Chemical ecology of "scentless" plant bugs (Heteroptera: Rhopalidae): Allelochemics and pheromones. *J. Chem. Ecol.* **16:** 199–210.

Arnqvist, G. (1988). Mate guarding and sperm displacement in the water strider *Gerris lateralis* Schumm. (Heteroptera: Gerridae). *Freshwater Biol.* **19:** 269–274.

Arnqvist, G. (1989). Multiple mating in a water strider: Mutual benefits or intersexual conflict? *Anim. Behav.* **38:** 749–756.

Brockmann, H. J., Grafen, A., and Dawkins, R. (1979). Evolutionarily stable nesting strategy in a digger wasp. *J. Theor. Biol.* **77:** 473–496.

Carroll, S. P. (1988). Contrasts in the reproductive ecology of tropical and temperate populations of *Jadera haematoloma* (Hemiptera: Rhopalidae), a mate-guarding insect. *Ann. Entomol. Soc. Am.* **81:** 54–63.

Carroll, S. P., and Loye, J. E. (1987). Specialization of *Jadera* species (Hemiptera: Rhopalidae) on seeds of the Sapindaceae (Sapindales), and coevolutionary responses of defense and attack. *Ann. Entomol. Soc. Am.* **80:** 373–378.

Carroll, S. P., and Loye, J. E. (1990). Male-biased sex ratios, female promiscuity, and copulatory mate guarding in an aggregating tropical bug, *Dysdercus bimaculatus*. *J. Insect Behav.* **3:** 33–48.

Chapman, R. F. (1971). *The Insects: Structure and Function*, 2nd ed., Elsevier, New York.

Clark, S. J. (1988). The effects of operational sex ratio and food deprivation on copulation duration in the water strider (*Gerris remigis* Say). *Behav. Ecol. Sociobiol.* **23:** 317–322.

Dickinson, J. L. (1986). Prolonged mating in the milkweed leaf beetle *Labidomera clivicollis clivicollis* (Coleoptera: Chrysomelidae): A test of the "sperm-loading" hypothesis. *Behav. Ecol. Sociobiol.* **18:** 331–338.

Eisner, T. E. (1965). Defensive spray in a phasmid insect. *Science* **148:** 966–968.

Fincke, O. M. (1984). Sperm competition in the damselfly *Enallagma hageni* Walsh (Odonata: Coenagriondae): Benefits of multiple mating to males and females. *Behav. Ecol. Sociobiol.* **14:** 235–240.

Harris, V. E., and Todd, J. W. (1980). Temporal and numerical patterns of reproductive behavior in the southern green stink bug, *Nezara viridula* (Hemiptera: Pentatomidae). *Entomol. Exp. Appl.* **27:** 105–116.

Harwalker, M. R., and Rahalkar, G. W. (1973). Sperm utilization in the red cotton bug. *J. Econ. Entomol.* **66:** 805–806.

McLain, D. K. (1980). Female choice and the adaptive significance of prolonged copulation in *Nezara viridula* (Hemiptera: Pentatomidae). *Psyche* **87:** 325–336.

Meyers, J. G. (1927). Ethological observations of some pyrrhocoridae of Cuba. *Ann. Entomol. Soc. Am.* **20:** 279–300.

Parker, G. (1970a). Sperm competition and its evolutionary consequences in the insects. *Biol. Rev.* **45:** 525–567.

Parker, G. (1970b). Sperm competition and its evolutionary effect on copula duration in the fly *Scatophaga stercoraria. J. Insect Physiol.* **16:** 1301–1328.

Parker, G. (1974). Courtship persistence and female-guarding as male time investment strategies. *Behaviour* **48:** 157–184.

Ribeiro, S. T. (1989). Group effects and aposomatism in *Jadera haematoloma* (Hemiptera: Rhopalidae). *Ann. Entomol. Soc. Am.* **82:** 466–475.

Rubenstein, D. I. (1984). Resource acquisition and alternative mating strategies in water striders. *Am. Zool.* **24:** 345–353.

Sillen-Tullberg, B. (1981). Prolonged copulation: A male "post-copulatory" strategy in a promiscuous species, *Lygaeus equestris* (Heteroptera: Lygaeidae). *Behav. Ecol. Sociobiol.* **9:** 283–292.

Sivinski, J. (1980). The effects of mating on predation in the stick insect *Diapheromera veliei* Walsh (Phasmatodea: Heteronemiidae). *Ann. Entomol. Soc. Am.* **73:** 553–556.

Sivinski, J. (1983). Predation and sperm competition in the evolution of coupling durations, particularly in the stick insect *Diapheromera veliei.* In Gwynne, D. T., and Morris, G. K. (eds.), *Orthopteran Mating Systems*, Westview, Boulder, Colo., pp. 147–162.

Sweet, M. H. (1964). The biology and ecology of the rhyparochrominae of New England (Heteroptera, Lygaeidae). Part II. *Entomol. Am.* **43:** 1–124.

Thornhill, R., and Alcock, J. (1983). *The Evolution of Insect Mating Systems*, Harvard University Press, Cambridge, Mass.

Van Doesburg, P. H., Jr. (1968). A revision of the New World species of *Dysdercus* Guerin Meneville (Heteroptera, Pyrrhocoridae). *Zool. Verhandelingen* **97:** 1–215.

Walker, W. F. (1980). Sperm utilization strategies in nonsocial insects. *Am. Nat.* **115:** 780–799.

Wilcox, R. S. (1984). Male copulatory guarding enhances female foraging in a water strider. *Behav. Ecol. Sociobiol.* **15:** 171–174.

Yamamura, N. (1986). An evolutionary stable strategy (ESS) model of postcopulatory guarding in insects. *Theor. Pop. Biol.* **29:** 438–455.