

## FEMALES RECEIVE A LIFE-SPAN BENEFIT FROM MALE EJACULATES IN A FIELD CRICKET

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**Abstract.**—Mating has been found to be costly for females of some species because of toxic products that males transfer to females in their seminal fluid. Such mating costs seem paradoxical, particularly for species in which females mate more frequently than is necessary to fertilize their eggs. Indeed, some studies suggest that females may benefit from mating more frequently. The effect of male ejaculates on female life span and lifetime fecundity was experimentally tested in the variable field cricket, *Gryllus lineaticeps*. In field crickets, females will mate repeatedly with a given male and mate with multiple males. Females that were experimentally mated either repeatedly or multiply lived more than 32% longer than singly mated females. In addition, multiply mated females produced 98% more eggs than singly mated females. Because females received only sperm and seminal fluid from males in the experimental matings, these life-span and fecundity benefits may result from beneficial seminal fluid products that males transfer to females during mating. Mating benefits rather than mating costs may be common in many animals, particularly in species where female mate choice has a larger effect on male reproductive success than does the outcome of sperm competition.

**Key words.**—Ejaculates, female life span, female mating preferences, field crickets, *Gryllus lineaticeps*, multiple mating, repeated mating.

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Males and females maximize their reproductive success through different pathways (Bateman 1948; Trivers 1972). The number of female eggs available for fertilization limits the reproductive success of males, and selection favors traits in males that increase fertilization success. The amount of resources that can be converted into viable offspring limits the reproductive success of females, and selection favors traits in females that increase fecundity and offspring quality. Because traits that increase reproductive success in individuals of one sex may reduce the reproductive success of individuals of the opposite sex, there may often be a conflict of interest between the sexes (Parker 1979, 1984). For example, in *Drosophila melanogaster* mating reduces female life span (Fowler and Partridge 1989). This mating cost results from toxic peptides transferred to females in male seminal fluid (Chapman et al. 1993, 1995). These peptides increase a male's success in mating and sperm competition (Harshman and Prout 1994; Clarke et al. 1995) and, as a side effect, they increase female mortality.

The transfer of toxic seminal fluid products by males to females during mating should favor traits in females that reduce this cost. For example, females could evolve higher thresholds for responding to male mating signals, thereby reducing the number of males with which they mate (Rice and Holland 1997; Holland and Rice 1998). Females could also evolve mechanisms to detoxify male seminal fluid products (Rice 1996; Holland and Rice 1999). The evolutionary consequence of mating costs for females may be antagonistic coevolution; males may continually evolve traits that increase their fertilization success, to the detriment of females, and females may continually evolve behavioral, morphological and physiological counter-responses to these male traits (Rice 1996; Holland and Rice 1999).

Female mating costs potentially can arise either as a by-product of male-male competition or from male manipulation of female reproduction. Such costs may be common in animals with internal fertilization because females in these spe-

cies regularly expose their physiology to male seminal fluid products (Rice and Holland 1999). In many insects, for example, products contained in male seminal fluids reduce female receptivity to other males and stimulate rapid egg laying by females (Riemann et al. 1967; Baumann 1974; Stanley-Samuelson and Loher 1986). Less is known about the effects of male seminal fluid products on female reproduction in other animals.

In contrast to the hypothesis of antagonistic coevolution, a number of evolutionary processes may favor the transfer of beneficial products to females during mating. For example, if females can discriminate between males that will provide them with harmful or beneficial substances, selection will favor the evolution of female preferences for males that provide benefits to females, which in turn will favor males that provide these benefits (Eberhard and Cordero 1995). Female choice based on benefits is widespread (reviewed by Andersson 1994), and some of the benefits that females receive from males, such as better paternal care of offspring and good genes for offspring, do not accrue until after mating has occurred and the female's eggs have been fertilized. If female preferences favor the transfer of beneficial substances by males, the result may be mutualistic coevolution; females benefit from their mate choices and males that transfer beneficial substances benefit from doing so (see also Eberhard 1998).

A number of lines of evidence suggest that females often benefit from mating. First, females of many species mate more frequently than is necessary to ensure fertilization of their eggs (e.g., Parker 1970; Simmons 1988a; Birkhead and Møller 1992). This includes both repeated mating with a given male and mating with multiple males. These mating patterns are paradoxical if there are high costs of mating for females, and the prevalence of repeated and multiple mating provides indirect support for the hypothesis that females benefit from mating more frequently. Second, direct evidence from a variety of insects suggests that females may receive

life-span or fecundity benefits, rather than incur costs, from products transferred by males during mating (reviewed by Ridley 1988). These direct benefits derive from both courtship feeding (e.g., Gwynne 1984; Wedell and Arak 1989; Brown 1997) and nutrients introduced into the female reproductive tract via internal spermatophores (reviewed by Boggs 1995). Although male insects are known to provide females with a variety of nutrients, the importance of products transferred in male ejaculates has been largely unexplored.

The effect of mating pattern on female fitness may vary depending upon the type of benefit that females receive from males. If females receive direct benefits from males, such as nutrients or products that affect female physiology, females that mate repeatedly and multiply should have a longer life span or a higher fecundity than females that mate singly because repeatedly and multiply mated females will receive more of the beneficial product. In addition, there should be no difference between repeatedly and multiply mated females because both types of females would receive the same quantity of the beneficial product. If females receive only indirect benefits from males (reviewed by Tregenza and Wedell 1998; Yasui 1998; Newcomer et al. 1999), mating pattern should have no effect on female life span. The effect of mating pattern on female fecundity, however, will depend on both the nature of the indirect benefit and female reproductive physiology. For example, if females receive good genes from preferred males and if females exercise cryptic choice through either delayed fertilization or selective use of sperm (Eberhard 1998), multiply mated females may have higher fecundity than both singly and repeatedly mated females. This may occur because multiply mated females are more likely to have mated with at least one high-quality male and will thus more quickly begin using male sperm to fertilize their eggs. If, however, females do not exercise cryptic choice but do receive genetic benefits from mating with preferred males, mating pattern may have no effect on female fecundity. Instead, mating pattern may affect the viability of fertilized eggs or offspring quality.

In the study reported here, we experimentally tested the hypothesis that female variable field crickets, *Gryllus lineaticeps*, benefit from both repeated and multiple mating. First, we examined the frequency of repeated mating by females in the laboratory to determine whether repeated mating by females is common in this species. Second, we examined the effect of mating on female life span and lifetime fecundity by experimentally mating females either singly, repeatedly, or multiply. In the latter two experiments, females received only sperm and seminal fluid from males. As a result, any benefit of repeated or multiple mating is likely the result of products contained in male ejaculates, not nutrients contained in male spermatophores. We report that females of this species engage in extensive repeated mating. In addition, we report that both repeatedly and multiply mated females live longer than singly mated females and that multiply mated females have a higher lifetime fecundity than singly mated females. These results suggest that females benefit from mating more frequently. Because females received only sperm and seminal fluid from males, the life-span benefit appears to result from beneficial products contained in male seminal fluid. The fecundity benefit appears to be at least partially a

consequence of the longer life spans of multiply mated females.

#### *Mating Behavior and Sexual Selection in Field Crickets*

Male field crickets generally sing from the ground within or near burrows (Alexander 1961), and females select mates, in part, based on variation in male calling song (Popov and Shuvalov 1977; Hedrick 1986; Simmons 1988b; Wagner 1996). Once a female approaches a male, the male switches from calling song to courtship song, and the male produces a number of tactile and chemical signals (Loher and Dambach 1989). Both courtship song (Wagner and Reiser 2000) and chemical signals (Tregenza and Wedell 1997) likely affect female mating decisions.

During mating, males transfer a small spermatophore consisting of an ampulla containing the ejaculate. This spermatophore is attached externally to a female's genital pore, and sperm and seminal fluid enter the female's reproductive tract. Approximately 30–90 min after attachment, the female often removes the spermatophore and consumes it. Some evidence suggests that spermatophore consumption influences female fitness (Simmons 1988a; Burpee and Sakaluk 1993), but little is known about the effect of seminal fluid products on female fitness. However, the seminal fluids of male field crickets are known to contain a number of physiologically important substances that increase oviposition and reduce remating by females (e.g., Stanley-Samuels and Loher 1986).

Female field crickets mate both repeatedly and multiply, and the number of matings appears to be greater than is necessary to ensure fertilization of a female's eggs (Alexander and Otte 1967; Simmons 1988a; Zuk and Simmons 1997; Tregenza and Wedell 1998). When females mate with multiple males, there appears to be extensive sperm mixing in the spermatheca, the sperm storage organ. As a result, there is not a pronounced directional pattern of sperm precedence (Sakaluk 1986; Simmons 1987; Parker et al. 1990; Sakaluk and Eggert 1996). In *Gryllus bimaculatus*, females that mate more frequently have higher lifetime fecundity and produce eggs that have a higher hatching success (Simmons 1988a), and the fecundity benefit of mating more frequently is similar for repeatedly and multiply mated females (Tregenza and Wedell 1998). Similarly, female *G. velitidis* that were allowed to mate more frequently lived longer and produced more offspring, particularly under conditions of food stress (Burpee and Sakaluk 1993). In these previous studies, females were allowed to consume spermatophores; thus, it is not clear whether these benefits result from nutrients obtained through spermatophore consumption, products contained in the ejaculate, or both.

#### MATERIALS AND METHODS

##### *Repeated Mating by Females*

We examined the frequency of repeated mating by females in 1992 by pairing virgin females with virgin males for a 6-h period. All crickets used were the offspring of field-inseminated females collected from Tucker's Grove Park, Santa Barbara, California. We reared the crickets in a mass culture

in a 113-L plastic container provisioned with cat chow, water vials, moist vermiculite for oviposition, and cardboard egg cartons for shelter. We removed all experimental crickets from the culture prior to adult eclosion and housed them individually in  $9 \times 16 \times 11$  cm plastic containers provisioned with cat chow, a water vial, and a cardboard shelter. All males and all females used were between 7 and 21 days past adult eclosion.

To examine the frequency of repeated mating, we placed a male and female in a  $16 \times 26 \times 17$  cm plastic container with a sand substrate. We observed each pair for a 6-h period using a 40-W red light, and we counted the number of successful matings by each female. A mating was counted as successful only if a spermatophore was transferred to the female and remained attached for at least 2 min. We also counted the number of spermatophores removed and consumed by each female. We observed 17 pairs of males and females. Three additional pairings were aborted before the end of the 6-h observation period because of problems with the males; one male was unable to produce calls because of deformed wings, one male produced aberrant calls, and one male appeared to be incapable of transferring a spermatophore despite being mounted five times by the female.

#### *Effect of Mating on Female Life Span and Fecundity*

We examined the effect of mating pattern on female life span and fecundity in 1997 and 1998 by randomly assigning three females that reached adult eclosion on the same day to one of three mating groups: (1) a single mating with a randomly chosen male (single mating group); (2) three matings with a randomly chosen male (repeated mating group); and (3) one mating with each of three different randomly chosen males (multiple mating group). In total, we mated 19 trios of females. All of the females that we used were the first- or second-generation offspring of field-inseminated females collected from Tucker's Grove Park, Santa Barbara, California. We actively managed all of the matings used to produce the test crickets to prevent inbreeding, and as a result, we knew the genealogies of all of the crickets from the time inseminated females were collected in the field. We raised all of the crickets in family containers, and we removed individuals from the family containers and isolated them in individual containers prior to adult eclosion. Ten days after adult eclosion, we randomly assigned three females that matured on the same day to the three mating groups. Each female of a trio was drawn from a different family. We measured female weight to the nearest 0.0001 g on the day prior to a female's first mating. We mated the females to unrelated males that had reached adult eclosion a minimum of seven days and a maximum of 21 days prior to the first mating.

We mated the singly mated females once on day 10. We mated the repeatedly mated females three times to the same male, with the first mating on day 10 and each subsequent mating separated by 48 h. We mated the multiply mated females once each to three different males, with the first mating on day 10 and each subsequent mating separated by 48 h. After the first mating, we housed each female in  $9 \times 16 \times 11$  cm plastic container with a small dish of moist sand for oviposition and a small dish of water. We fed the females

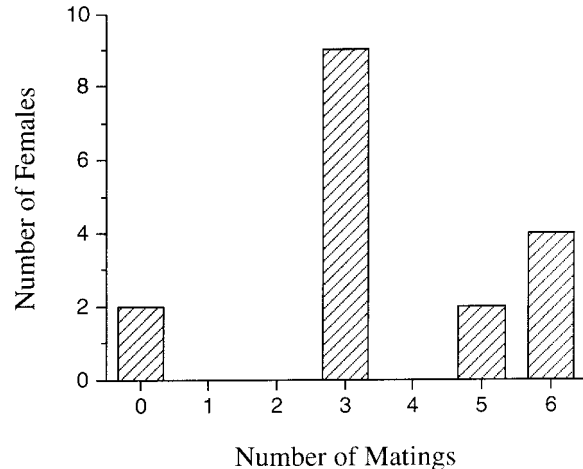


FIG. 1. Frequency distribution of the number of matings by females when housed with a single male for a six-hour period.

cat chow ad libitum throughout their lives. Beginning the day after the first mating, we collected the dishes of sand daily and replaced them with fresh sand. We separated the eggs from the sand by submerging the sand in a salt-water solution, thus causing the eggs to float to the surface. We then collected and counted the eggs. We started the first trio of females on 16 August 1997 and the last trio of females on 14 October 1998.

To reduce variation in the quantity of sperm and seminal fluids received by females during each mating, we removed all spermatophores 30 min after attachment. We then discarded the spermatophores. Females therefore did not have the opportunity to remove and consume the spermatophores. As a result, any effect of differential sperm and seminal fluid transfer arising from differences between mating groups in the timing of spermatophore removal was precluded. In addition, any effect of spermatophore consumption was precluded. Because different trios of females were mated at different times of the year and because life span and fecundity might be affected by differences in laboratory conditions during different times of the year, all statistical analyses included mating block (i.e., trio) as a blocking factor. There was not a significant difference in female weight between the mating groups (singly mated females:  $\bar{x} = 0.661$  g, SE = 0.038; repeatedly mated females:  $\bar{x} = 0.679$ , SE = 0.030; multiply mated females:  $\bar{x} = 0.700$ , SE = 0.027; ANOVA:  $F_{2,54} = 0.36$ ,  $P = 0.703$ ). Because the variance in lifetime fecundity differed between the mating groups, lifetime fecundity was square-root transformed prior to analysis.

## RESULTS

### *Repeated Mating by Females*

In the observational study of female mating behavior, females engaged in extensive repeated mating when paired with males for a 6-h period (Fig. 1). Of 17 females, only two (11.8%) failed to mate. Of the 15 females that did mate with males, all mated repeatedly with the male with which they were paired; the minimum number of matings was three and the maximum number of matings was six ( $N = 15$ ,  $\bar{x} = 4.07$ ,

TABLE 1. Effect of mating on female life span, daily fecundity, and lifetime fecundity.

Variable	Source	df	MS	F	P
Life span	Mating treatment	2	2372.4	4.21	0.023
	Mating block	18	1082.2	1.92	0.047
	Error	36	563.1		
Daily fecundity	Mating treatment	2	55.8	2.12	0.134
	Mating block	18	32.0	1.22	0.299
	Error	36	26.3		
Lifetime fecundity	Mating treatment	2	419.1	4.20	0.023
	Mating block	18	96.7	0.97	0.511
	Error	36	99.7		

SE = 0.36). Females that mated consumed 88.4% of the spermatophores that they accepted from males ( $N = 15$ ,  $\bar{x} = 3.60$ , SE = 0.41). The remaining spermatophores were dislodged by the females but not consumed.

*Effect of Mating on Life Span*

In the experimental study of the consequences of repeated and multiple mating, mating pattern had a significant effect on female life span (Table 1). Repeatedly and multiply mated females lived, on average, more than 32% longer than singly mated females (Fig. 2A). There was not, however, a significant difference in the life spans of repeatedly and multiply mated females.

There was significant variation in the survivorship curves of females in the three mating groups (Breslow-Gehan Wilcoxon test [Lee 1992]:  $\chi^2 = 6.55$ ,  $df = 2$ ,  $P = 0.038$ ; Fig. 2B). There was no mortality in any of the mating groups during the first three weeks following mating. After three weeks, survivorship declined more rapidly for singly mated females than for repeatedly and multiply mated females. Most of the divergence in mortality between the mating groups occurred between weeks 4 and 8; 47.4% of the singly mated females died by the end of week 8, whereas 26.3% of the repeatedly and 15.8% of the multiply mated females died by the end of week 8.

*Effect of Mating on Daily Fecundity*

Daily fecundity was estimated as the mean number of eggs produced per day from the time of a female's first mating until the time the female died. Mating pattern did not have a significant overall effect on daily fecundity (Table 1). In addition, there was not a significant difference in daily fecundity between singly and repeatedly mated females (Tukey HSD multiple comparisons:  $P = 0.709$ ), singly and multiply mated females ( $P = 0.117$ ), or repeatedly and multiply mated females ( $P = 0.433$ ).

*Effect of Mating on Lifetime Fecundity*

Mating pattern had a significant effect on lifetime fecundity (Table 1). Multiply mated females had significantly higher fecundity than singly mated females, but there was not a significant difference in fecundity between singly and repeatedly mated females or between repeatedly and multiply mated females (Fig. 3). On average, multiply mated females produced nearly twice as many eggs as singly mated females.

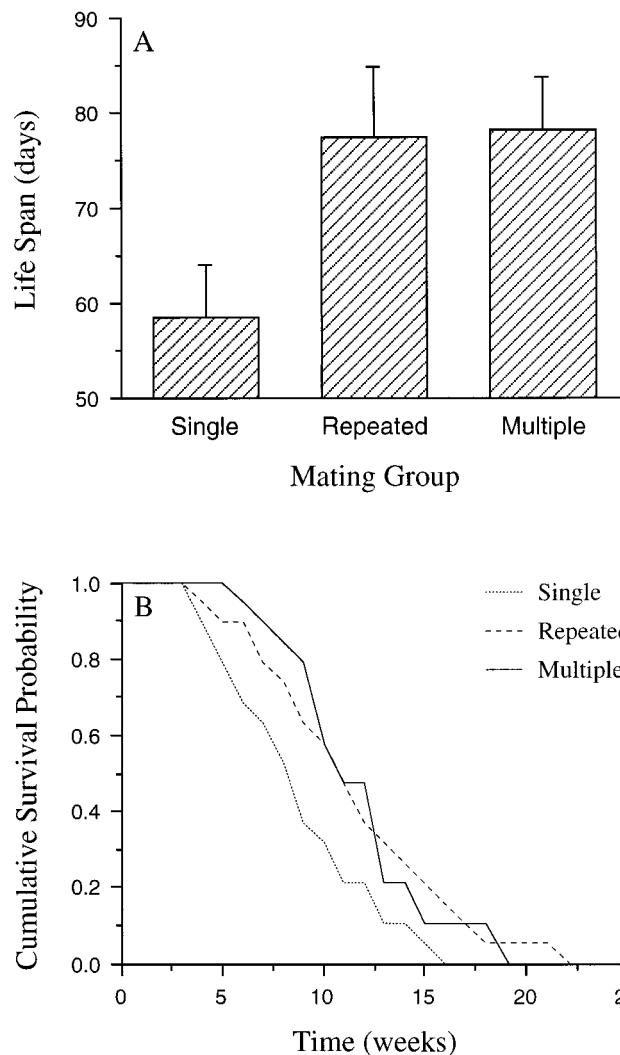


FIG. 2. Effect of mating treatment on female life span. (A) Mean  $\pm$  SE life span of females in the three mating groups. There was a significant difference in life span between singly and repeatedly mated females (Tukey HSD multiple comparisons:  $P = 0.048$ ), between singly and multiply mated females ( $P = 0.038$ ), but not between repeatedly and multiply mated females ( $P = 0.994$ ). (B) Survival curves for females in the three mating groups. Cumulative survival probability is the proportion of females alive at the end of each seven-day period following the first mating.

*Correlation of Life Span and Daily Fecundity with Lifetime Fecundity*

An increase in lifetime fecundity can result from an increase in life span, an increase in daily fecundity, or an increase in both life span and daily fecundity. Partial correlation analysis was used to assess the independent correlations of life span and daily fecundity with lifetime fecundity. Across the mating groups, there was a significant positive correlation between life span and lifetime fecundity when holding daily fecundity constant ( $r = 0.73$ ,  $df = 54$ ,  $P < 0.001$ ). In addition, there was a significant positive correlation between daily fecundity and lifetime fecundity when holding life span constant ( $r = 0.94$ ,  $df = 54$ ,  $P < 0.001$ ). An identical pattern is evident within each of the mating groups as well (Table



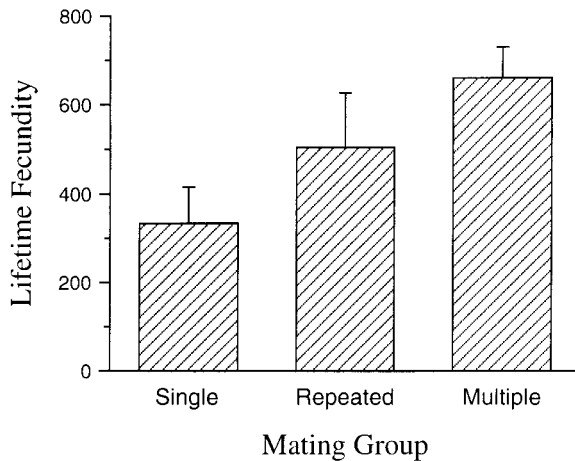


FIG. 3. Effect of mating treatment on lifetime fecundity. Mean  $\pm$  SE lifetime fecundity of females in the three mating groups is shown. Data were square-root transformed prior to statistical analysis because of differences in variance of lifetime fecundity between the mating groups. There was a significant difference in lifetime fecundity between singly and multiply mated (Tukey HSD multiple comparisons:  $P = 0.017$ ), but not between either singly and repeatedly mated females ( $P = 0.394$ ) or repeatedly and multiply mated females ( $P = 0.269$ ).

2). As a result, increased lifetime fecundity appears to have resulted from both increased life span and increased daily fecundity.

#### DISCUSSION

Female *G. lineaticeps* engage in extensive repeated mating. When housed with males, 88.2% of females mated, and all females that mated did so at least three times over the 6-h observation period. More than a quarter of the females that mated did so six times. Male field crickets cannot force females to mate, because the transfer of a spermatophore requires female cooperation; females must move on top of males and remain motionless while the spermatophore is transferred. Females were unable to escape from males in these trials, however, and it is possible that aggressive mate guarding by males, which is common in field crickets (Alexander and Otte 1967; Loher and Rence 1978), coerced females into mating more frequently than they would have if they had been given the opportunity to escape from males. Nonetheless, our results suggest that females often mate repeatedly with males. Other species of field cricket likewise engage in extensive repeated mating (Alexander and Otte 1967; Simmons 1988a; Zuk and Simmons 1997; Tregenza and Wedell 1998). It is not known how frequently *G. lineaticeps* engage in multiple mating, but observations on other species suggest that multiple mating is widespread in field crickets (Zuk and Simmons 1997).

Our results suggest that selection favors repeated and multiple mating by females, at least partially because of a direct life-span benefit that accrues to females that mate more frequently. Females that were mated three times lived more than 32% longer than singly mated females, regardless of whether these mating were with the same male or with different males. In our mating design, males in the repeated mating group

TABLE 2. Partial correlations between life span, daily fecundity, and lifetime fecundity for singly, repeatedly, and multiply mated females (all  $df = 16$ ,  $P < 0.001$ ).

	Life span	Daily fecundity
(A) Singly mated females		
Daily fecundity	-0.86	
Lifetime fecundity	0.88	0.98
(B) Repeatedly mated females		
Daily fecundity	-0.60	
Lifetime fecundity	0.62	0.92
(C) Multiply mated females		
Daily fecundity	-0.74	
Lifetime fecundity	0.71	0.90

were mated to a female three times, whereas males in the multiple mating group were mated to a female only once. This difference in male mating history did not produce a detectable difference in the life spans of repeatedly and multiply mated females. Newcomer et al. (1999) criticized some studies of the direct benefits of multiple mating because these studies did not control for potential genetic benefits. Because an increase in female life span can only result from direct benefits, however, female *G. lineaticeps* appear to receive a direct benefit from both repeated and multiple mating. Other studies on insects have also suggested that females receive life-span benefits from mating more frequently (e.g., Ridley 1988; Fox 1993; Wiklund et al. 1993), although it is often unclear whether these life-span benefits arise from nutrients contained in male spermatophores or from products contained in male ejaculates.

Female field crickets may engage in extensive repeated mating because they can obtain some of the same benefits that they would receive from multiple mating while incurring fewer of the costs. Females moving between males are potentially subject to predation from a number of nocturnal animals, including arachnids, anurans, and small mammals. Although few studies have explicitly examined the costs that females might incur during search for a mate, these costs are likely to be substantial for field crickets, and females are known to alter their mating behavior under conditions of high predation risk (Hedrick and Dill 1992). There are also potential costs of remaining in association with a given male, such as predation from acoustically orienting parasitoid flies that are attracted to male calls (Cade 1975; Walker 1986; Wagner 1996). This cost, however, may be similar for females that spend a given amount of time in association with a single male and for females that partition this time among multiple males.

Because females in our experiment received only sperm and seminal fluids from males during the experimental matings, the life-span benefit of repeated and multiple mating is likely a consequence of either substances transferred in male seminal fluid or the breakdown of male sperm within the female reproductive tract. Male crickets are known to transfer substances in their seminal fluid that reduce female receptivity and that stimulate egg laying (Stanley-Samuelson and Loher 1986). They may transfer other substances in their seminal fluid as well. Although sperm digestion has not been

described for crickets, some hermaphroditic animals obtain nutrients from digesting surplus sperm (Calow et al. 1979; Baur 1998; Michiels 1998), and degradation of sperm within the female reproductive tract has been observed in at least one insect (*Callosobruchus maculatus*: Eady 1994). It seems unlikely that energy derived from nutrients in seminal fluid or from sperm digestion is responsible for the increased life span of repeatedly and multiply mated females; all females in our study were fed ad libitum throughout their lives. It is possible, however, that females receive nutrients from males that are scarce in their normal diets, and that these nutrients affect female life span and fecundity (e.g., Gwynne 1988). In addition, it is possible that the physical process of mating induces physiological changes in females that increase female life span independent of products transferred by males.

In our study, there were no significant differences in daily fecundity between singly, repeatedly, and multiply mated females. As a result, there is no evidence that selection will act on female mating pattern because of differences in the rate of oviposition. Although some patterns of cryptic female choice, combined with preferences based on characters correlated with genetic quality, might predict a difference in the daily fecundity of repeatedly and multiply mated females, such a pattern was not evident. There was, however, significant variation among the mating groups in lifetime fecundity: Females that were mated multiply produced nearly twice as many eggs as females that were mated singly. Females thus appear to obtain lifetime fecundity benefits from multiple mating. Because multiply mated females lived longer than singly mated females and because lifetime fecundity was positively correlated with life span, this benefit may be partially a consequence of the difference in life span between singly and multiply mated females. This conclusion is supported by the observation that differences between the mating groups in lifetime fecundity disappear when life span is included as a covariate ( $F_{2,18} = 2.37$ ,  $P = 0.108$ ). Similarly, in a study of *G. velitis*, Burpee and Sakaluk (1993) found that an increased rate of repeated mating resulted in higher lifetime fecundity, but that this effect was due primarily to an increase in life spans of females that mated more frequently. The absence of a difference in lifetime fecundity between repeatedly and either singly or multiply mated females may be due to a variety of factors, including a lack of statistical power and the mating design used in our study. Additional work will be necessary to determine if repeatedly mated females differ in their lifetime fecundity from either singly or multiply mated females.

Our results strongly suggest that male field crickets transfer seminal fluid products to females during mating that increase female life span and that this increase in life span results in an increase in lifetime fecundity. There are at least four general hypotheses that can explain why selection might favor males that transfer such products to females. First, females might prefer to mate with males that provide them with beneficial substances. In *G. lineaticeps*, females have strong preferences based on both calling song and courtship song variation (Wagner 1996; Wagner and Reiser 2000). If beneficial seminal fluid products have evolved because of female mating preferences, females that mate with preferred males should live longer or have higher fecundity. Males are known

to provide material resources to females in many species because females prefer to mate with males that provide these resources (reviewed by Andersson 1994), and it is possible that female preferences based on direct benefits also extends to materials provided in seminal fluid. This requires either that females be able to evaluate the quality of the substances that males will transfer before mating occurs through assessment of traits correlated with the quality of the benefit or that females be able to directly assess the quality of the substances that males are transferring during mating and terminate sperm transfer if male substances are not of high quality. If females must assess benefit quality through signals correlated with benefit quality, it also requires a mechanism to constrain the production of deceptive signals by males (e.g., Zahavi 1979; Pomiankowski 1988; Grafen 1990). Second, selection might favor the evolution of substances that increase a male's success in sperm competition, and some of these substances might, as a side effect, be beneficial to females rather than toxic. In *D. melanogaster*, for example, the toxic effect of male seminal fluid products may be a side effect of the functioning of these products in sperm competition. Third, selection might favor the evolution of substances that are beneficial for the offspring sired by a male's sperm (Simmons and Parker 1989), and these substances might, as a side effect, be beneficial to females. Some male insects, for example, are known to transfer substances to females that are incorporated in eggs and protect the eggs from predators (e.g., butterflies: Dussourd et al. 1989). Fourth, selection might favor the evolution of substances that increase female life span because longer-lived females will produce more offspring sired by the male. This hypothesis, however, requires a low rate of multiple mating by females. Because female field crickets may engage in extensive multiple mating, only a fraction of a female's offspring may be sired by any one male.

It has been proposed that mating is generally costly for females, particularly in species where internal fertilization exposes females to male seminal fluids (Rice and Holland 1999). Although it is clear that products transferred by males to females during mating can be a very important source of selection on female mating behavior and that coevolution between the sexes is of fundamental importance to the evolution of traits in both sexes (Rice 1996; Rice and Holland 1997; Holland and Rice 1998, 1999), the outcome of this coevolutionary process may be variable even among species with internal fertilization. In some species, strong selection on male success in intrasexual competition may result in the transfer of products that negatively affect female fitness, resulting in antagonistic coevolution. In other species, strong selection on females to obtain benefits from males may result in the transfer of products that positively affect female fitness. Our data for a field cricket suggest that females mate more frequently at least in part because of the direct benefits that they receive from products transferred in male ejaculates. This benefit may be a consequence of female preferences favoring beneficial seminal fluid products. Rather than antagonistic coevolution, the outcome of sexual selection may often be mutualistic coevolution; females may mate with males from which they derive benefits, and males that provide

such benefits may subsequently benefit from female mating preferences (Eberhard 1998).

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