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Diet quality mediates the effect of multiple mating on female *Gryllus vocalis* vocal field cricket lifetime reproductive success

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ABSTRACT

Questions: Is there a trade-off between reproduction and survival for female *Gryllus vocalis* field crickets? Does an experimental reduction in diet quality have an effect on the relationship between reproduction and survival? If females are experimentally manipulated to mate large numbers of times, what is the effect on female reproductive success and survival? Is there an interaction between diet quality and large numbers of matings on female lifetime reproductive success?

Organism: Laboratory colony of *Gryllus vocalis* vocal field crickets.

Methods: Females were fed either a high- or low-quality diet, and assigned to mate 5, 10 or 15 times. Fecundity, fertility, and longevity were recorded.

Results: Although females fed the high-quality diet gained fecundity and fertility benefits from mating at least 10 times, females fed the low-quality diet did not receive any reproductive benefits from multiple mating. Females that mated more times were more likely to die within 3 weeks of adult eclosion than females that mated fewer times. However, females that mated more times had better late-life survival than females that mated fewer times. Overall, mating did not have major negative effects on female survival, and thus female crickets did not experience a trade-off between reproduction and survival. However, a low-quality diet can prevent females from realizing the benefits of multiple mating.

Keywords: diet quality, fecundity, fertility, *Gryllus vocalis*, multiple mating, polyandry, survival.

INTRODUCTION

Trade-offs between reproduction and survival have been observed in many taxa (Roff, 1992), and can influence the benefit that females receive from mating multiple times. The trade-off between survival and reproduction can occur because survival and reproduction are competing for the same nutrient resources, as described by de Jong and van Noordwijk's (1992) Y-model. The Y-model depicts a system in which two life-history traits such as reproduction and somatic maintenance draw from a common pool of resources. Individuals

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may vary in both the total resources introduced into the system (acquisition) and/or in the relative distribution of the acquired resources devoted to competing life-history traits (allocation) (Zera and Harshman, 2001). Although the Y-model describes one way in which reproduction and survival can be functionally linked, an alternative functional relationship between reproduction and survival is possible. For females, mating can cause physical damage (Crudgington and Siva-Jothy, 2000), and toxic male accessory gland products transferred from males can shorten female lifespan (Fowler and Partridge, 1989). If reproduction inflicts a direct assault on somatic function, there will be a negative correlation between the traits. This negative relationship is predicted to persist even when acquired resources are experimentally increased (Tatar and Carey, 1995).

Female field crickets have the potential to suffer from reproductive costs, due to either physiological competition for resources or direct harm via interactions with males or male chemical contributions. Although female field crickets cannot be physically coerced to mate by males, and female behaviour affects both the length of copulation and the quantity of male ejaculate transferred (Simmons, 2001), male field crickets have the capacity to affect female behaviour and longevity via the transfer of spermatophores. Male field crickets have arguably the most complex accessory glands of any insect (Kaulenas, 1992). The male spermatophore (sperm packet) contains no nutritive spermatophylax, but delivers both sperm and a variety of known and unidentified accessory gland products that have demonstrated effects on female oviposition, locomotion, and phonotaxis (Khalifa, 1949; Loher and Dambach, 1989). These male accessory gland products have the potential to either benefit females as nuptial gifts, or harm females as a byproduct of male–male sperm competition.

Most studies examining the relationship between reproduction and survival in female insects use only small numbers of matings (Arnqvist and Nilsson, 2000), despite the fact that female insects, including field crickets, commonly mate numerous times. Estimates of field-based paternity in *Gryllus bimaculatus* based on molecular analysis of field-caught females indicates that females can mate as many as seven times in a lifetime (Bretman and Tregenza, 2005). In enclosure studies, *Gryllodes sigillatus* decorated cricket females mated as many as 15 times in a lifetime (Sakaluk *et al.*, 2002). Females of most insect species gain fecundity benefits from mating more than once (Ridley, 1988). If mating has negative effects on female health, the effect of a small number of matings may be too slight to be observed. However, if an increase in daily fecundity reduces longevity (Preziosi and Fairbairn, 1997), it is possible that although mating many times can increase daily fecundity, there may be a concurrent decrease in lifespan. If this happens, there is predicted to be a number of matings at which any negative consequences of mating outweigh the daily fecundity benefits, and cause a female to have an overall reduced lifetime reproductive success.

If a trade-off between two life-history traits is caused by internal competition for resources, as described by the Y-model, adding resources to the system may eliminate the negative correlation between traits. If a trade-off exists between reproduction and maintenance, this effect may not be apparent when animals are fed a high-quality diet *ad libitum*. In some systems, nutrient limitation may drive the trade-off between reproduction and mortality. Tatar and Carey (1995) demonstrated that when food is increased in *Callosobruchus* beetles, the trade-off between mortality and reproduction is decreased. In other systems in which reproduction has a direct negative effect on survival, the trade-off persists even with the experimental addition of resources. In a study of *Drosophila melanogaster*, experimental limitation of diet reduced reproduction but increased longevity (Chippindale *et al.*, 1993). Similarly, when reproduction was experimentally limited, survival increased (Partridge *et al.*,

1987; Tatar *et al.*, 1993; Ellers *et al.*, 2000). Past research suggests that female field cricket reproductive behaviour can be affected by diet quality. In a study of *Teleogryllus commodus*, females reared on a high-quality diet not only developed faster, were heavier at adult eclosion, and lived longer, but were also more sexually responsive, and had stronger preference functions for male call rate and dominant frequency (Hunt *et al.*, 2005). However, a trade-off between reproductive effort and long-term survival in female crickets has not been demonstrated empirically.

The first goal of this study was to bracket the number of matings that maximizes lifetime reproductive success for female crickets. The second objective was to detect whether there is a trade-off between reproduction and survival for females. A past analysis using *G. vocalis* fed a high-quality diet did not find a significant relationship between female reproductive effort and female survival, even when females mated many times (Gershman, 2007). Trade-offs can be sensitive to the environment in which they are measured, and a reduction in diet quality can potentially reveal that trade-off. Finding an interaction between reproduction and survival across diet treatments would suggest that the trade-off between the two traits is resource-based.

METHODS

The *Gryllus vocalis* vocal field crickets (Weissman *et al.*, 1980) used in these experiments were collected from the University of California, Riverside, Botanic Gardens. The laboratory colony was started in the spring of 2002, and every subsequent spring 30–100 field-caught adults were added to the colony. Crickets were maintained in a growth chamber under simulated summer conditions: 28°C with a daily cycle of 14 h light to 10 h dark. This colony produces an average of 50 adults a week year-round.

The high-quality diet treatment consisted of rabbit chow. Colony crickets fed this diet experience rapid growth, high fecundity, and overall good health with little mortality. The low-quality diet treatment was 50% wheat middlings and 50% soybean meal by weight. Compared with rabbit chow, this diet lacks vitamins A and C and choline, and has been demonstrated to have a sublethal effect on growth and survival in crickets (Patton, 1967; Gray, 1999). In previous studies, this low-quality diet slowed nymphal growth rate (Patton, 1967; Gray and Eckhardt, 2001) and affected fat reserves (Gray and Eckhardt, 2001), but did not have an effect on male and female mating behaviours (Gray, 1999; Gray and Eckhardt, 2001). Although crickets reared on the low-quality diet are on average smaller than crickets reared on the high-quality diet (Patton, 1967), crickets in the two treatments do not differ visibly in morphology or behaviour (S.N. Gershman, personal observation). The low-quality diet was pulverized so that both the soybean meal and wheat middlings components were equal in size because crickets selectively eat smaller particles (Patton, 1967). The rabbit chow diet was also pulverized to approximately the same-sized particles.

Part 1: The effect of diet on development, mating rate, and *ad libitum* fecundity

To test the effects of diet quality on nymphal development and fecundity, nymphs were reared on a high- or low-quality diet and females were subsequently allowed to mate and lay eggs. Two hundred nymphs between 0.1 and 0.2 g (fourth and fifth instar) were randomly assigned to either a low- or high-quality diet treatment. *Gryllus vocalis* crickets eclose into adults after 7–9 nymphal instars. Nymphs were housed individually in plastic 0.2-litre cups

with *ad libitum* food of their assigned diet treatment and water. Every other day, nymphs were weighed. Date of eclosion was noted. Measurements were taken until 90% of the crickets had eclosed.

Females that eclosed by the end of the study were allowed a single mating opportunity 5 days after eclosion with a male that had been raised on a high-quality diet. Mating trials took place daily at the start of the dark cycle under low light conditions. Females were placed in a clean 0.2-litre cup with a male until mating was observed. Females that did not mate were dropped from the study. Females were then transferred to a 0.2-litre cup that contained food from their assigned diet treatment, and moistened sand that provided both water for drinking and oviposition substrate. After 48 h, the sand was sifted in water to separate eggs, and eggs were counted.

Part 2: The effect of diet and number of matings on female fecundity, fertility, and survival

To test the effect of diet and number of matings on female lifetime reproductive success, female nymphs were fed a high- or low-quality diet, randomly assigned to mate 5, 10 or 15 times, and evaluated for fertility, fecundity, and post-experimental survival.

Crickets used in this experiment were reared from hatching to death on either the high- or low-quality diet. Crickets used in the two diet treatments were reared simultaneously under otherwise identical conditions. One hundred and fifty-four virgin females fed the low-quality diet and 192 virgin females fed the high-quality diet were randomly assigned to mate 5, 10 or 15 times with a novel male each time. Females from the 5, 10, and 15 mating treatment groups were given 7, 14, and 21 days, respectively, to complete their matings, or they were dropped from the study. This was done to control for the possibility that individual variation in female propensity to mate was associated with other measures of condition (Torres-Villa *et al.*, 2004). Thus, females would be equally likely to be dropped from the experiment due to failure to mate their assigned number of matings whether assigned to mate 5, 10 or 15 times. Females from all treatment groups that died before 21 days were eliminated from the study to prevent females from being differentially eliminated from the treatment groups with more matings.

Cheesecloth was used as an oviposition substrate because it is better than sand for use in mass rearing of eggs, egg counting and evaluation. Oviposition pads were collected from each female every other day, and incubated. Eleven days after collection (average hatching time at 28°C), eggs were frozen and counted. The total number of eggs laid per female represents female lifetime fecundity. If eggs had hatched, or contained eyespots or visibly segmented embryos, they were counted as 'fertile'. Eggs that were unfertilized or failed to develop to the eyespot stage were counted as 'not fertile'. It was not possible to visually distinguish unfertilized eggs from fertilized eggs that ceased to develop at the earliest stages, so this measure of fertility is conservative.

For the time following completion of experimental treatments until 21 days, females were transferred daily to a clean cup for 1 h to simulate the handling stress and deprivation of food, water, and oviposition sites experienced by the females that were still receiving mating opportunities. Date of death for each female was noted. In analysis of the effects of experimental treatments, only females who had survived at least 21 days (the maximum length of time of the longest treatment group) were included.

For analysis of the fate of females recruited into the study, females were scored as successful, low mating or died. Females scored as 'successful' successfully mated their

assigned number of times within the time allotted, and also survived 21 days post-adult eclosion. Females scored as 'died' did so before 21 days; some of these females completed their assigned number of matings, whereas others were mating at a sufficiently high rate to complete their assigned mating treatment but died during their mating trials. Females scored as 'low mating' failed to complete their assigned number of matings in the time allotted, but were alive at the time that they were dropped from the study.

RESULTS

Part 1: The effect of diet on development, mating rate, and *ad libitum* fecundity

Of the 100 individuals of each treatment that were initially recruited into the study, 94 of the high-quality diet and 83 of the low-quality diet nymphs survived to adult eclosion. Nymphs reared on the low-quality diet weighed less at adult eclosion (Table 1), although nymphs assigned to each treatment did not differ in their initial weight when recruited to the study ($F_{1,184} = 1.40$, $P = 0.24$). Nymphs reared on the low-quality diet also took longer to eclose into adults (Table 1). Females fed the high-quality diet laid more eggs (Table 1), and had a higher variance in number of eggs laid, than females fed the low-quality diet (Levene $F_{1,74} = 41.5$, $P = 0.0001$).

Part 2: The effect of diet and number of matings on female fecundity, fertility, and survival

Results for all crickets recruited into the study

Mortality prior to the completion of the study (21 days after adult eclosion) among low-quality diet females was very high (42%), and many low-quality diet females were dropped from the study because they failed to make their assigned number of matings (31%). Consequently, *post hoc* analysis was performed to determine whether diet and mating treatments caused differences in female fate (whether females successfully completed their treatment, failed to complete their treatment due to a low mating rate, or died before the end of the experiment). Diet quality was related to female fate ($\chi^2 = 18.9$, d.f. = 2, $P < 0.0001$): females on the low-quality diet were more likely to die before the end of the

Table 1. Results of analysis of variance for the effects of the high- versus low-quality diet

	High-quality diet (mean (SE))	Low-quality diet (mean (SE))	d.f.	*F*	*P*
Proportion surviving to eclosion	0.94	0.83	1,199	6.07	0.0146**
Weight at adult eclosion (g)	0.34 (0.0085)	0.27 (0.0085)	1,184	32.9*	0.0001**
Time to eclosion (days)	22.0 (0.46)	23.7 (0.49)	1,154	5.95*	0.0158**
Female fecundity	192.1 (22.8)	55.3 (10.1)	1,57	30.1*	0.0001**

Note: For 'proportion surviving to eclosion', proportion surviving females out of 100 are presented, and logistic regression was used for the analysis. For other summary data, means and standard errors (SE) are shown. For *F*-values indicated by one asterisk, data were normally distributed but heteroscedastic among diet treatments, thus were analysed with Welch ANOVAs. The *P*-values indicated by two asterisks are statistically significant with a sequential Bonferroni correction for multiple comparisons.

experiment, and be less likely to complete their mating treatments, than females fed the high-quality diet. There was also a relationship between assigned mating treatment and female fate ($\chi^2 = 27.7$, d.f. = 4, $P < 0.0001$): females assigned to mate more times were more likely to die, and not complete their matings, than females assigned to mate fewer times. Moreover, females that mated 5 times were less likely to die ($\chi^2 = 9.8$) and females that mated 15 times were more likely to die ($\chi^2 = 8.95$) than would be expected by chance. When diet treatments were considered separately, relationships were observed between assigned mating treatment and female fate for both females reared on the high-quality diet ($\chi^2 = 13.9$, d.f. = 4, $P = 0.0075$) and females reared on the low-quality diet ($\chi^2 = 18.3$, d.f. = 4, $P = 0.001$).

Results for females that successfully completed their mating treatments

For crickets that successfully completed their assigned numbers of matings, females reared and maintained on the low-quality diet laid four-fold fewer eggs than females fed the high-quality diet (Table 2, Fig. 1a). Furthermore, although a previous analysis which included only females fed the high-quality diet indicated that females that mated more times had higher fecundity (Gershman, 2007), females fed the low-quality diet that mated more times did not lay more eggs (ANOVA: $F_{2,38} = 0.13$, $P = 0.88$; Fig. 1a).

Females fed the low-quality diet did not differ from females fed the high-quality diet in terms of fertility (Table 2, Figs. 1b and 1c). In addition, the number of times that low-quality diet females mated did not have an effect on the proportion of laid eggs that were fertilized (ANOVA: $F_{2,38} = 0.53$, $P = 0.60$; Fig. 1b).

Females fed the low-quality diet survived for fewer days after the end of the 21-day experiment than females fed the high-quality diet (Table 2, Fig. 1d). Females fed the

Table 2. Results of MANOVA and full factorial ANOVA for the effect of diet, number of matings, and the interaction between diet and number of matings on female *G. vocalis* fecundity, fertility, and post-experimental survival

		F	d.f.	*P*
Diet	Wilks' λ	31.6	3	<0.0001*
	fecundity	87.2	1	<0.0001*
	fertility	0.23	1	0.64
	survival	22.6	1	<0.0001*
Matings	Wilks' λ	2.85	6	0.011*
	fecundity	3.82	2	0.024*
	fertility	1.78	2	0.17
	survival	4.75	2	0.010*
Diet × Matings	Wilks' λ	1.33	6	0.25
	fecundity	3.09	2	0.049
	fertility	0.50	2	0.61
	survival	1.08	2	0.34

Note: The *P*-values indicated by asterisks are statistically significant with a sequential Bonferroni correction for multiple comparisons.

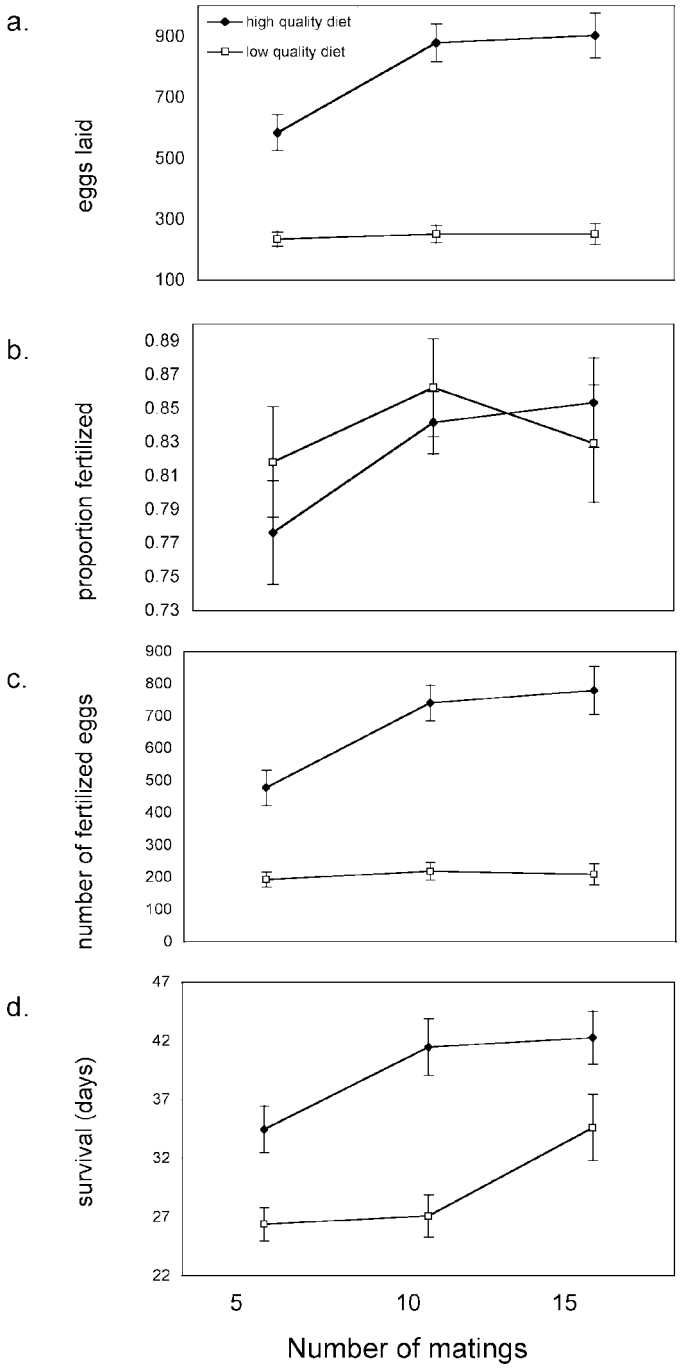

Fig. 1. (a) Eggs laid per female, (b) proportion of laid eggs that were fertilized, (c) numbers of fertilized eggs, and (d) post-experimental days survived by females fed a high-quality diet (black diamonds) or low-quality diet (open squares) and assigned to mate 5, 10 or 15 times. For the high-quality diet, $n = 35$, 30, and 24 respectively. For the low-quality diet, $n = 16$, 13, and 10 respectively. Values shown are means and standard errors.

low-quality diet that mated more times survived longer than females that mated fewer times (ANOVA: $F_{2,38} = 4.92$, $P = 0.013$). In the previous analysis, which included only high-quality diet females, there was a trend towards females that mated more times surviving longer, but there was not a significant effect of number of matings on female post-experimental survival. However, when high- and low-quality diet females were pooled, females that mated more times had longer post-experimental survival (Table 2). Due to unequal sample sizes for females that mated 5, 10, and 15 times in the low- ($n = 16$, 13, 10) and high-quality ($n = 36$, 30, 24) diet treatments, Box's M-test was performed to assess the robustness of significance tests. Although Box's M was significant at $P < 0.001$, the high-quality diet treatment, which had larger sample sizes, also had higher variances than the low-quality diet treatment. Consequently, the alpha level of significance tests is conservative, and the null hypothesis can be rejected with confidence (Tabachnick and Fidell, 2001).

Because females assigned to mate more times were more likely to die before 21 days post-eclosion, it was valuable to determine whether mating encounters or mating had an effect on the survival of females recruited to the study. Because females were given a single mating opportunity per day, females that lived longer had more matings and mating opportunities, so it is not revealing to correlate either number of matings or mating encounters with survival. However, an alternative *post hoc* analysis was possible. First, many of the females that did not mate their assigned number of times within the required number of mating opportunities continued to have a single mating opportunity per day. All females were maintained until death. Thus, for females that survived beyond 21 days post-eclosion, both retained in the study and dropped, it is possible to examine the relationship between numbers of matings, mating encounters, and survival. Of the females that survived more than 21 days post-eclosion, data were available for 125 females that mated their assigned number of times as well as 65 females that were dropped from the previous analysis due to a low mating rate. Using a general linear model with number of matings, number of mating encounters, and the cross-product as independent variables and survival as the dependent variable, there was an effect of the model on female survival ($F_{3,189} = 3.5$, $P = 0.0167$). Females that mated more times lived longer ($t = 2.37$, $P = 0.019$), although the number of mating encounters, and the interaction between numbers of matings and mating encounters, did not affect female survival ($t = -1.39$, $P = 0.166$ and $t = 1.47$, $P = 0.143$, respectively).

Females in the three mating treatments were given proportionately equivalent opportunities to complete their assigned number of matings to prevent females from being differentially dropped from mating treatments. However, it is possible that females that are capable of mating at a high rate are inherently superior in some way that also confers longer survival. To determine whether mating rate and survival were correlated for females, I used linear regression to determine the correlation between mating rate (number of successful matings divided by total number of encounters) and number of post-experimental days that females survived. This measurement is independent of both the number of times that females mated, and the duration of time over which the encounters took place. Both females that successfully completed their assigned number of matings and females that were dropped from the previous analysis, but survived at least 21 days post-adult eclosion, were included in the analysis. Females that had a higher mating rate survived longer ($n = 309$, $r = 0.36$, $P = 0.0001$).

DISCUSSION

In this study, the effect of number of matings on female cricket fecundity, fertility, and survival was mediated by diet quality. The relationship between number of matings and lifetime egg production was different among females fed a high- versus a low-quality diet. Similar to other studies, females fed the low-quality diet had depressed fecundity compared with females fed the high-quality diet (Roff and Gelinas, 2003; Naya *et al.*, 2007). When fed the high-quality diet, females gained significant fecundity benefits for mating as many as 10 times (Gershman, 2007). Furthermore, the number of matings had no effect on the fecundity of low-quality diet females. This suggests that although mating more times can result in a fecundity benefit, females fed the low-quality diet cannot reap the benefits of mating multiply. Female cricket oviposition is stimulated by male chemical contributions transferred during mating (Loher and Dambach, 1989), and it is possible that females that mate more times gain additional male chemicals to stimulate fecundity. Females reared on a low-quality diet may be limited not by male chemical contributions, but by the number of eggs that they can provision on a reduced diet (Wheeler, 1996; Zera and Larsen, 2001; Ziegler and Van Antwerpen, 2006).

Female insects generally gain a reproductive benefit from mating multiple times (Ridley, 1988; Jennions and Petrie, 2000). In studies manipulating both female resources (diet and water) and numbers of matings, females provided with poorer resources received greater benefits from mating than females with better resources (Ivy *et al.*, 2000; Wagner and Harper, 2003). The results of this study run contrary to this pattern, and highlight that different kinds of direct benefits given by males to females, as well as resource availability and female condition, dictate when females should seek out multiple matings. Moreover, future studies should focus on the quality of diet in the field, as it is likely to affect the significance of laboratory-based studies on the effects of multiple mating for females.

Diet quality did not affect the proportion of fertilized eggs out of the total eggs that females laid. However, diet quality did affect the relationship between number of matings and fertility. High-quality diet females that mated more times laid a higher proportion of fertilized eggs. For females fed the low-quality diet, number of matings did not affect the proportion of eggs fertilized. This result is consistent with previous fecundity results: for low-quality diet females, reproduction is likely limited by the number of eggs that females can provision (Zera and Larsen, 2001), not the quantity of sperm that they receive. This result is also revealing because females in the low-quality diet treatment had fewer provisioned eggs, so it might be predicted that if sperm number limited fertility, low-quality diet females would lay a higher proportion of fertilized eggs than high-quality diet females, but this was not the case. The fact that females have imperfect fertility when fed either a low- or high-quality diet suggests that factors other than sperm number affect fertilization success (Loher and Dambach, 1989; Snook and Hosken, 2004).

Females that successfully completed their mating treatment and were assigned to mate more times also survived longer. However, this result is mitigated by the fact that females that were assigned to mate more times were less likely to survive the duration of the experiment to be included in the final analysis than females that were assigned to mate fewer times. Additionally, females that tended to mate at a higher rate survived longer than females that mated at a low rate. This implies that females in better condition may be capable of both mating at a high rate and surviving longer. Two conclusions are possible. First, females capable of mating at a higher rate are also capable of surviving longer (Sih *et al.*, 2004), such

that females that were retained in the 15-mating treatment survived longer. To minimize a possible correlation between variation in individual mating rate and fecundity, fertility, and survival, females in all treatments had limited opportunities in which to complete their assigned number of matings. However, the effect of variation in individual mating rate cannot be discounted (Torres-Villa *et al.*, 2004). Alternatively, mating more times may give females a survival benefit. This effect has been demonstrated in *Gryllus lineaticeps* (Wagner *et al.*, 2001). A positive correlation between number of matings and survival could be caused by substances transferred in the male ejaculate, or could be a spurious positive correlation due to the presence of an unknown variable (Roff, 2002). The effect of multiple mating on female survival differs among studies of different field crickets. Bateman *et al.* (2006) found that courtship and copulation had a negative effect on female survival in *Gryllus bimaculatus*. However, Simmons (1988) noted that number of matings did not have a significant effect on survival in *Gryllus bimaculatus*. The mixed results of the experiments in this paper suggest that the time scale over which female survival is measured can influence the effect of mating on female survival.

If females experience a trade-off between reproductive effort and maintenance as described by the Y-model (de Jong and van Noordwijk, 1992), females assigned to mate more times are expected to have reduced survival. Although multiple mating generally confers increased daily fecundity, harm caused by mating may cause females to survive fewer days, and ultimately lay fewer eggs than females that have mated fewer times (Preziosi and Fairbairn, 1997; Arnqvist *et al.*, 2005). However, the results of this experiment demonstrate that females do not suffer a mortality cost from mating, and potentially enjoy a survival benefit. Even with large numbers of matings and reduced diet quality, no trade-off is apparent. Thus, the Y-model does not accurately describe the relationship between reproduction and survival in *G. vocalis* females. The high mortality and reduced fecundity of females in the low-quality diet treatment provides evidence that the diet was of sufficiently low quality to reveal a trade-off between reproduction and survival, if one existed. The fact that reproduction was not constrained by survival suggests that there is the potential for correlational selection to simultaneously maximize both traits unless checked by some additional factor (Roff and Fairbairn, 2006). It is likely that in nature, predation, parasitism, and energetic and time constraints act to limit female mating rate (Hedrick and Dill, 1993; Velez and Brockmann, 2006). This study shows that in the absence of such environmental factors, mating, which includes courtship, copulation, and exposure to the sperm and accessory gland products transferred from the male during mating, does not bear a survival cost for females.

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