

Reproductive Success and Body Size in the Cricket *Gryllus firmus*

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Abstract Male body size influences mate choice and sexual selection in many animal species. Here we investigate the role of male body size in the reproductive success of the field cricket *Gryllus firmus*. This species hybridizes with a close smaller relative, *G. pennsylvanicus*, and it is thought that this size difference may affect reproductive isolation between these species. We paired large and small *G. firmus* males with a single *G. firmus* female and genotyped the resulting offspring. Overall, larger males sired a greater proportion of offspring and in a majority of the crosses the larger male sired all of the offspring. For crosses in which both males sired offspring, there was no difference in the proportion of offspring sired by small and large males. Intrasexual competition, female choice, and differences in ejaculates between males could all influence the patterns we observe. We discuss the implications of our findings within the context of reproductive isolation between *G. firmus* and *G. pennsylvanicus*.

Keywords *Gryllus* · mate choice · body size · speciation · sexual selection

Introduction

Body size can have a profound influence on individual fitness (Roff 1981) and has often been observed to play an important role in mate choice and sexual selection (Andersson and Iwasa 1996). Indeed, the importance of body size in reproductive success has been documented across a wide variety of taxa (Calder 1996; Peters 1986;

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Kingsolver and Huey 2008; Blanckenhorn 2000). In many insects, large male body size has been correlated with increased mating success (Whitman 2008). Larger size is generally thought to provide an advantage in male-male competition (Simmons 1995; Partridge and Farquhar 1983), but females may also show strong preference for larger males (Simmons 1987, 1992). Larger males may transfer more sperm or provide a larger nuptial gift (Vahed 1998; Fedorka and Mousseau 2002a, b). However, body size may also represent a tradeoff, with larger males experiencing greater energetic and developmental costs (Roff 1992). Small males may, for example, reach adulthood faster than larger males and avoid intense competition for mates or other resources (Blanckenhorn 2000).

In this study, we explore the role of male body size in the reproductive success of the eastern North American field cricket, *Gryllus firmus*. *Gryllus firmus* forms an extensive hybrid zone with a close relative, *Gryllus pennsylvanicus*, a cricket that is generally smaller in size (Harrison 1985). Therefore, the influence of body size on mating in *G. firmus* is of particular relevance. Previous studies of the field cricket hybrid zone have found *G. firmus* females to be choosy, mating more readily with conspecifics rather than heterospecifics (Maroja et al. 2009). However, the basis of female preference for conspecifics remains obscure. Traits used for conspecific mate choice have been shown to affect reproductive isolation between related species in a number of cases (Blows and Allan 1998; Ryan and Rand 1993; Wiernasz and Kingsolver 1992). If differences in mating success or mate choice are partially a result of body size differences, this may represent a barrier to gene exchange between the two species and contribute to the observed preference of *G. firmus* females for conspecific males.

This study differs from earlier studies of cricket mate choice in that the effect of body size on mating success is quantified through assessment of paternity. Thus, the influence of body size variation on male reproductive success (due to male-male competition, mate choice, differences in spermatophore or ejaculate size, or some combination of these) can be measured directly. Previous studies of mate choice in field crickets have either focused on the effect of body size on competitive ability, opportunity to mate, or on possible benefits to females of mate choice (e.g. Simmons 1986a, b; Bateman et al. 2001).

Gryllus firmus

Gryllus firmus occurs along the Atlantic coast of the United States, from Florida to Connecticut. The hybrid zone between *G. pennsylvanicus* and *G. firmus* extends from Virginia to Connecticut and largely follows the eastern slope of the Appalachian and Blue Ridge Mountains (Harrison 1986). In the northern part of the range, *G. firmus* has a single generation a year, with an obligate egg diapause. Adults of both species mate in late summer and fall, and the eggs overwinter and hatch in the spring (Alexander 1968). Males of *G. firmus* can be territorial, competing for available burrows and calling locations (Bertram et al. 2011). Males call from a shelter in order to attract females, which use calling song to locate the male. Once a female is in close proximity, the male switches to courtship song. In order for copulation to occur, the female must mount the male, and the male and female must cooperate to successfully transfer a spermatophore. Although spermatophores of many cricket species include a nutrient-rich spermatophylax (Alexander and Otte 1967), field cricket spermatophores do not appear

to provide substantial nutrient benefit to females (Simmons 1988). Furthermore, spermatophore transfer does not necessarily guarantee fertilization; spermatophore attachment time is correlated with quantity of sperm transferred and can be controlled by females (Simmons 1986b). Transferred sperm is stored in an elastic spermatheca, which is capable of storing sperm from multiple males (Zuk and Simmons 1997). After spermatophore transfer, males may engage in mate guarding near their burrow. This serves primarily to restrict access of other males to the female (Alexander 1961). However, polyandry is widespread among field crickets and has been clearly demonstrated in the field crickets *Tel Gryllus oceanicus*, *Tel Gryllus commodus*, and, *Gryllus bimaculatus* (Bretman and Tregenza 2005; Simmons 2001; Simmons and Beveridge 2010).

Materials and Methods

Cricket Collections

All crickets used were second and third generation descendants of field collected crickets from Guilford, CT ($41^{\circ}16'5''$; $-72^{\circ}40'4''$). We maintained lab populations at 28°C in plastic cages ($55\times 43\times 31$ cm) on a 12 h light/dark schedule. Crickets were provided a mix of cat food and rabbit food, water vials, and egg cartons for shelter. As late instar nymphs, males and females were separated, so that only virgin crickets were used in our experiment. We mated all males within 6–12 days of final eclosion and all females within 6–11 days of final eclosion.

Body Size Measurements

Female and male body sizes were quantified by measuring pronotum width, body length, femur length, and wing length using a single pair of calipers. Each cricket was measured three times by a single individual and each body dimension was averaged across the three measurements. While all measured traits are significantly correlated, pronotum width shows the strongest correlation with each of the other measures of body size (Fig. 1). Furthermore, pronotum width is a strong indicator of body size and weight in *G. firmus* (Larson et al. 2013) and in other field cricket species (Simmons 1986a). Consequently, we chose to make all size comparisons using measurements of pronotum width.

Initially, males were sorted into groups of large and small body size, based simply on visual comparisons. Males in the ‘small male’ group ranged in pronotum width from 4.5 mm to 6.0 mm and averaged 5.27 ± 0.41 mm, while males in the ‘large male’ group ranged in pronotum width from 5.6 mm to 7.7 mm and averaged 6.33 ± 0.43 mm (Fig. 2). Males in the ‘large male’ group were significantly larger than males in the ‘small male’ group (two sample paired *t*-test, $t=-11.81$, $df=30$, $p<0.001$).

Crosses

We performed all crosses in rectangular plastic enclosures ($53\times 33\times 13$ cm) containing two egg cartons, food, and water. Reproductive success was compared between large

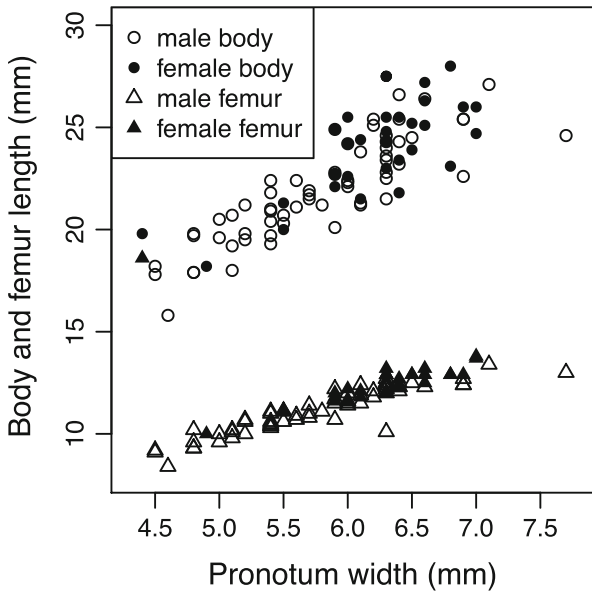


Fig. 1 Relationship between body size measurements for male and female *Gryllus firmus* crickets

and small males. Each group consisted of one large and small male. Each male was randomly chosen from its initial sorting group (large or small). Males were given 24 h to acclimate, after which a female was placed in the enclosure. The enclosure was designed to give both males access to equivalent shelters and food resources, reducing the effect of competition. After a period of 48 h, males were frozen at $-80\text{ }^{\circ}\text{C}$ and females were transferred to individual containers, where they were provided with food,

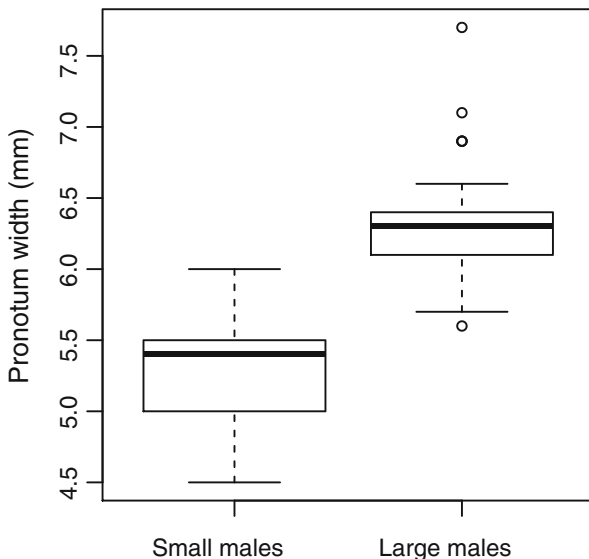


Fig. 2 Boxplot of variation in male pronotum width among small group and large group males. The error bars represent minimum and maximum values within 1.5 interquartile range of the lower and upper quartiles

water, and egg carton, and a soil dish for oviposition. We allowed 10 days for oviposition before freezing the females. The soil dishes were kept at 28 °C for 2 weeks, and then refrigerated (4 °C) for 102 days. Following refrigeration, egg dishes were kept at 28 °C in individual plastic shoeboxes. We collected 23 first instar nymphs as a representative sample from each cross (Larson et al. 2012a). Nymphs were sampled at least 2 days following the first hatching to ensure that the sample of progeny was not biased in favor of rapidly developing hatchlings. A total of 40 crosses were conducted. Thirty-one of these crosses produced at least 23 nymphs and were used for subsequent analysis.

Paternity Analysis

DNA was extracted from whole nymphs with the Agencourt DNAdvance extraction kit (Agencourt, Beverly, MA), following the manufacturer's protocol but with all volumes halved. For adults we extracted DNA from a single femur using the DNeasy Blood and Tissue kit (QIAGEN, Inc, Valencia, CA). Four previously characterized, highly variable microsatellite loci (Larson et al. 2012a, b) were used to assign paternity (Table 1). Locus G28 was substituted for locus Gr116 after the first 96 samples due to lack of polymorphism at Gr116. The Type It II Microsatellite Multiplex PCR Kit (QIAGEN) was used to simultaneously amplify all four microsatellites in 10 µl reactions containing 1 µl of genomic DNA each. We followed the manufacturer's protocol with the addition of a touchdown protocol of 38 cycles of 95 °C for 30s, 59°–53 °C for 90s, and 72 °C for 30s. Forward primers were labeled with fluorescent tags (6-FAM, PET, NED, or VIC). Fluorescent PCR products were then diluted with water to a 1:10 ratio and combined with HiDi formamide and Liz 500 size standard. Fragment sizes were measured with an ABI 3730xl DNA analyzer (Applied Biosystems, Inc, Foster City, CA) at the Cornell University Life Sciences Core Laboratories Center. We identified alleles using GeneMapper (Applied Biosystems) software and determined paternity by visually comparing alleles among parents and offspring.

Table 1 *G. firmus* microsatellite loci amplified for paternity analyses. The annealing temperature is given as T_a and the number of alleles is given as N_a

Locus	Primer Sequence (5'–3')	Repeat	T_a (°C)	Size	N_a	GenBank
PGI	CACACGTGATATACCGACAACACT GCTTTAACCCCTAGCAGAATAAT	ATT ₁₅	56	186–302	35	JN375327
Gr143	CTGCCGCATTCACCAATCATTCAACTAT CAACCAAGGGGCAAAATGAGTCAAACCTT	TG ₁₁	58	152–224	29	JN375328
G3	GCGCGGCGACCGACTATTG CTCGCACCTGTTAACAGTACTAT CAAAAC	TG ₁₆	TD 60–50	157–217	22	JX050157
G28	GCACCGCCCTAAACCCACGAC GGCACGGCAGCTTAAGGACATCAA	TG ₁₁	TD 65–55	261–381	8	JX050156
Gr116	CACACGTGATATACCGACAACACT GCTTTAACCCCTAGCAGAATAAT	A(T) ₃₉	61	186–302	35	JN375327

Statistics

To test whether larger males sired more offspring we compared the mean number of offspring produced by the small and large group males within each mating trial using a paired *t*-test for 1) all crosses, 2) crosses in which all offspring were sired by a single male and 3) crosses in which offspring were sired by both males. The first comparison simply determines whether small or large males sire more offspring. The second comparison allowed us to determine if females who sire offspring from only one male are more likely to have mated with the larger male (either because of female choice or male-male competition), and the third comparison allowed us to determine if larger males sire more offspring when they directly compete for fertilizations (larger ejaculate size, repeated matings). For crosses where a single male sired all offspring, we used a generalized linear model (GLM) with a binomial distribution and logit link function to test whether the magnitude of size difference between the large and small males had an effect on the proportion of offspring sired. In the single paternity crosses we evaluated, using a two-tailed binomial test, whether the number of crosses sired by a large male vs. small male differed significantly from what would be expected as a result of random mating. All statistical analyses were carried out in R version 2.12.0 (R Development Core Team 2010).

Results

Because the microsatellite loci have very high levels of polymorphism (Table 1), we could assign paternity by eye without ambiguity. Only four of the 713 nymphs collected could not be assigned unambiguously due to amplification failure and were excluded from the analyses. While the Gr116 locus was found to be largely uninformative in the first 96 samples, information from the three other loci was sufficient to assign paternity with confidence.

Overall, larger males sired a greater proportion of the sampled offspring than small males (Fig. 3a; paired *t*-test, $t=-2.699$, $df=30$, $p=0.011$). In a little over half the crosses ($N=17$) a single male sired all of the offspring. Of the crosses sired by a single male, 14 were sired by large males and only three were sired by small males (Fig. 3b; paired *t*-test, $t=-3.386$, $df=16$, $p=0.004$). This differed significantly from the 50/50 distribution expected if mating were random with respect to size (two-tailed binomial test: $p=0.013$).



Fig. 3 Mean number of offspring (SE) sired by small versus large males within **a** all crosses ($N=31$), **b** crosses where only one male sired offspring ($N=17$), and **c** crosses where both males sired offspring ($N=14$)

However, in crosses where both males sired one or more offspring ($N=14$) there was no difference in the proportion of offspring sired by the large and small males (Fig. 3c; $t=-0.146$, $df=13$, $p=0.886$). For the crosses sired by a single male, we found that the magnitude of the size difference between the large and small males that were paired had no effect on paternity (GLM: $z=-0.255$, $df=16$, $p=0.779$).

Discussion

Previous studies have shown that larger body size in male crickets confers potential advantages in gaining access to females (Simmons 1986a, b; Hack 1997; Rodríguez-Muñoz et al. 2010). Here, we show that body size also influences paternity when female crickets are housed with both large and small males. Overall, larger males sired a greater proportion of offspring, but this pattern was driven by larger males being the sole sires in a greater number of crosses. There were no differences in the proportion of offspring sired by large and small males for crosses in which females produced offspring sired by both males. Male mating success was also not directly correlated with the magnitude of body size differences between competing males. This suggests that being the larger of the two males, regardless of the magnitude of size difference, is what counts.

Effects of Body Size on Male-Male Competition

Studies of the field crickets *G. bimaculatus* and *Acheta domesticus* have revealed that larger males are more successful in male-male competition (Simmons 1986a; Hack 1997). In addition, observations of *G. bimaculatus* have shown that males assess each other prior to fighting and make judgments about whether to fight or flee. In cases where large and small males are paired and when males do compete, the majority of these fights are won by the larger male (Brown et al. 2006; Rillich et al. 2007). It is possible that the large number of single paternity crosses we observe (Fig. 3B) could be the result of male-male interactions similar to those in other field crickets. If smaller males judge that they are likely to lose an aggressive encounter, they may not engage the larger male, which would then have no competition for the female. The exceptions could be cases where variation in aggressiveness, health, endurance, or other factors, enable smaller males to win encounters (Alexander 1961).

Our results differ from other studies in that the magnitude of difference in body size between competing males showed no correlation with mating success. Differences in experimental design may be important; in particular, in our experiment males competed pairwise (rather than in groups) and calling sites were not a limiting resource. However, studies methodologically similar to ours, in which crickets were paired, have found that the degree of difference in body size is important in competitive success (Hack 1997; Hofmann and Schildberger 2001). Although larger males show higher fitness in *G. firmus*, this does not seem tied to the degree of difference in size between crickets. It might be that larger size in *G. firmus* results in greater competitive ability and thus greater fitness. It could also be that male-male competition, while a contributing factor, is not the primary mechanism responsible for the increased fitness of large males.

Evidence for Female Preference for Large Bodied Males

Female mate choice may also be a determinant of the patterns we see. In field crickets, the female must mount the male in order to receive a spermatophore; forced copulation is not possible. Moreover, studies of *G. bimaculatus* have found that aggressive male behavior such as mate guarding has little influence over female spermatophore removal or female escape; rather, it serves to limit access of other males to the female (Simmons 1986b). Thus, female choice is undoubtedly important in male reproductive success. Field crickets are highly polyandrous both in natural populations and in the lab (Bretman and Tregenza 2005; Simmons 2001; Rodríguez-Muñoz et al. 2011; Harrison RG unpublished data). It is commonly thought that polyandry provides a way for females to minimize genetic incompatibilities (Simmons 2001). Evidence of this has been found in a variety of species (Zeh and Zeh 2006; Barbosa et al. 2010). Studies of *G. bimaculatus* and *T. oceanicus* have shown that females that mate with at least two males have a higher egg hatching rate than females that mate with equal frequency to a single male (Simmons 2001; Tregenza and Wedell 1998). In this context, the high proportion of single paternity crosses in our data is unexpected. However, if *G. firmus* females show a strong preference for larger males the benefit of mating exclusively with a large male may outweigh the benefits of multiple mating.

Female preferences are often tied to male traits exhibiting high heritability (Jennions and Petrie 1997), and several morphological traits corresponding to body size in *G. firmus* are highly heritable (Webb and Roff 1992). It therefore seems plausible that female *G. firmus* may use body size as a metric to judge male quality. A strong female preference for large male body size could explain the frequent occurrence of crosses in which only one of the males sired offspring. *Gryllus bimaculatus* females remove spermatophores received from small males at a higher rate than those transferred by large males, and females stay longer with larger males post-mating, allowing for a higher probability of complete sperm transfer (Simmons 1986b). In addition, larger *G. bimaculatus* males are more frequently found paired with females in the wild than smaller males (Simmons 1992). However, while female preference for larger males has been documented in *G. bimaculatus*, this preference appears to be absent in *G. pennsylvanicus* and *G. veletis*, suggesting that female preference may vary among species within the genus *Gryllus* (Zuk 1987).

Influence of Body Size on Ejaculate Volume and Sperm Precedence

Studies across a variety of field cricket species suggest that sperm precedence, the differential use of sperm for fertilization, does not occur in field crickets (reviewed in Larson et al. 2012a). Female field crickets mated sequentially with two males usually produce approximately equal numbers of offspring sired by the two males. Indeed, it has been suggested that sperm are simply utilized in proportion to their numbers inside the spermatheca (Simmons 1987; Zuk and Simmons 1997). Consequently, males can influence the proportion of offspring sired through sperm competition avoidance (mate guarding and sperm loading via repeated matings) or ejaculate volume (i.e. spermatophore size). While some Orthopterans show an increase in spermatophore size with body size, this does not appear to be the case in field crickets (Sakaluk 1985; Simmons 1988). In *G. bimaculatus*, spermatophore size does not vary with body size. However,

it appears that smaller males may pay a larger energetic cost to achieve a spermatophore size equivalent to that of larger males. As a result of this differential investment, smaller males have a longer refractory time and generally mate at a lower frequency than larger males (Simmons 1988). In our study, there were no differences in the proportion of offspring sired by large and small males in crosses with mixed paternity. This suggests that the overall greater number of offspring sired by larger males is not a result of either sperm loading or ejaculate volume. Instead, larger males appear to gain access to females more often than smaller males. Whether this is entirely due to male-male competition, female choice, or some combination of the two is still unclear.

Potential Impacts of Male Body Size on Assortative Mating Within the Hybrid Zone

We have shown that larger relative body size results in increased reproductive success in *G. firmus* males. While it remains difficult to completely disentangle the individual contributions of male-male competition and female choice, both of these components, which are not mutually exclusive, may play some role in determining observed patterns. It is possible that females prefer larger males because of differences in overall quality and actively choose males based on this trait. Furthermore, even if larger males usually win competitive interactions with smaller males, females must still choose to mount and accept the spermatophore of larger males. Strong pre-mating, behavioral barriers have been demonstrated to exist between *G. firmus* and *G. pennsylvanicus* (Maroja et al. 2009). There is some evidence that *G. pennsylvanicus* females are less likely to mate with heterospecific males, whereas *G. firmus* females show a strong preference for mating with conspecifics (Maroja et al. 2009). Previous study of *G. pennsylvanicus* has shown that females do not seem to show significant preference for differences in male body size (Zuk 1987). While further crosses between heterospecifics are needed to clarify the role of body size in reproductive isolation, female preference for larger males (or lack thereof) in *G. firmus* and *G. pennsylvanicus* could have its basis in body size differences between the species.

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