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Small-male mating advantage in a species of Jerusalem cricket (Orthoptera: Stenopelmatinae: *Stenopelmatus*)

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Abstract

Scientific literature often touts the many advantages of large body size, but seldom addresses the value of small body size. Yet selection for large size must be counterbalanced by selection for small size, otherwise, all animals would be large. In this paper, we demonstrate female-biased size dimorphism and a strong copulatory advantage for small males in a Jerusalem cricket (JC) (*Stenopelmatus*) from central California. We selectively paired male and female JCs of diverse body sizes and recorded their ability to copulate. All copulations were successful for males smaller or equal in size to females. In contrast, when the male was 6.1 mm longer than the female, copulation had only a 50% chance of occurring successfully. In general, as the difference between male and female body length increased (*i.e.*, as males became longer than their mates), the probability of successful copulation decreased. These patterns of mating resulted in net selection for small male size and large female size. We also detected positive linear direct selection on male hind leg length, which may explain why male JCs have longer legs than females. The copulatory disadvantage of large males derives from the odd mating behavior of this group, in which males must contort and precisely align their bodies to couple. We believe that this is the first example of small-male advantage based solely on the physical aspects of copulation. In this species, small, not large, males have a copulatory advantage.

Key words

Orthoptera, *Stenopelmatus*, Jerusalem cricket, sexual selection, mating position, copulation, population structure, small-male mating advantage, sexual size dimorphism

Introduction

The idea that morphological and other phenotypic traits are under conflicting selection pressures is a central concept in evolutionary theory (Schluter *et al.* 1991, Futuyma 2005). As such, insect body size is thought to be a compromise between competing selective factors, which are usually grouped into three major categories (Blanckenhorn 2000): both fecundity selection in females (larger females can produce more eggs) and sexual selection in males (via male-male competition or female choice) should result in increased body size, whereas adult and juvenile viability selection in both sexes should counterbalance this by selecting for smaller individuals. Food availability, weather conditions, predator avoidance, shelter opportunities, and maturation rates are factors, among others, subsumed under viability selection. That such a balance occurs is suggested by the simple observation that all insects are not large.

Yet, the vast majority of literature on insect body size discusses the advantages of large size for increasing fecundity, homeostasis, dispersal, and interspecific, intraspecific, and sexual competitiveness,

etc., and seldom documents the advantages of small size (Thompson & Fincke 2002). Indeed, Blanckenhorn (2000) remarks, "... (direct) evidence for viability or any other form of selection favoring small body size is relatively scant".

However, a few notable examples of small-size advantage in arthropods include: i) the improved ability of small male *Drosophila* to track the female during courtship dances (Steele & Partridge 1988); ii) the enhanced ability of small adult bruchid beetles to escape from indehiscent fruits relative to larger individuals (Ott & Lampo 1991); iii) accelerated maturation by small male spiders, as well as an enhanced capacity to climb in search of sedentary females (references in Ramos *et al.* 2005); iv) delayed sexual cannibalism of small male spiders compared to larger conspecifics (references in Prenter *et al.* 2006); v) the greater agility of small male damselflies during courtship (Serrano-Meneses *et al.* 2007); and vi) the increased antipredatory survival and opportunity for oviposition of small Lepidoptera (Berger *et al.* 2006, Gotthard *et al.* 2007).

To our knowledge, however, there has been no work to date showing that smaller male insects may have greater mating success than larger males, based solely on the physical aspects of actual copulation. We present here such findings for a species of Jerusalem cricket (JC), a common name that we use to refer to any species in the genera *Stenopelmatus* Burmeister, *Ammopelmatus* Tinkham, *Viscainopelmatus* Tinkham, and *Stenopelmatopterus* Gorochov. These four genera comprise the subfamily Stenopelmatinae, in the family Stenopelmatidae.

Successful copulation in all JC species follows a stereotypic pattern (Weissman 2001b): the male usually initiates mating (Fig. 1a) by rolling on his side (Fig. 1b) or pouncing on the female. If she submits and positions herself on her side or back, then the male orients himself in the opposite direction (Fig. 1c), bites either hind tibia (he may change which tibia he is holding during the initial adjustment period), positions the tarsi of his hind legs on her coxae, and curls his abdomen (Fig. 1d) between his hind legs and her hind legs (Fig. 1e) towards her genital area (Fig. 1f). At this time, the male's incurved, chitinous genital hooks (Fig. 1g) actively shift angle and raise and lower while apparently searching for their proper attachment. Weissman (2001b) showed the importance of the male's two hooks for successful mating: removing one hook caused maneuvering to take longer, but coupling was usually successful. Removing both hooks rendered males incapable of mating. However, even to correctly place one hook, the male needs to align himself properly, necessitating that he place one leg on each side of the female. After anchoring his genital hooks under the posterior edge of the female's abdominal sternite 6 (Figs 1h, i), the male everts

Fig. 1. Mating sequence for *Stenopelmatus* species 19.

a) Shorter male (upper) approaches female.



b) Male rolls onto his side.



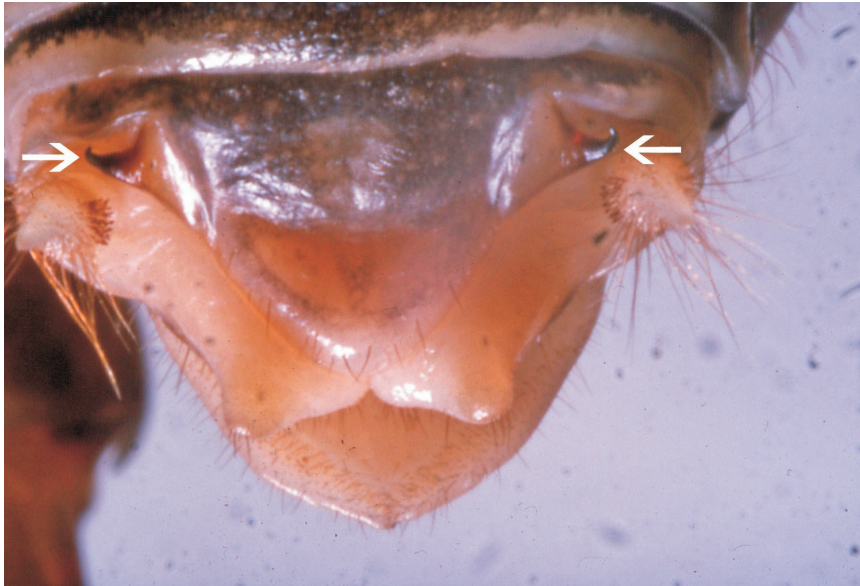
c) Female (lower) now on her side; male bites female right hind tibia.

d) Male (top) starting to curl abdomen; his rear tarsi in contact with her 3rd coxae.

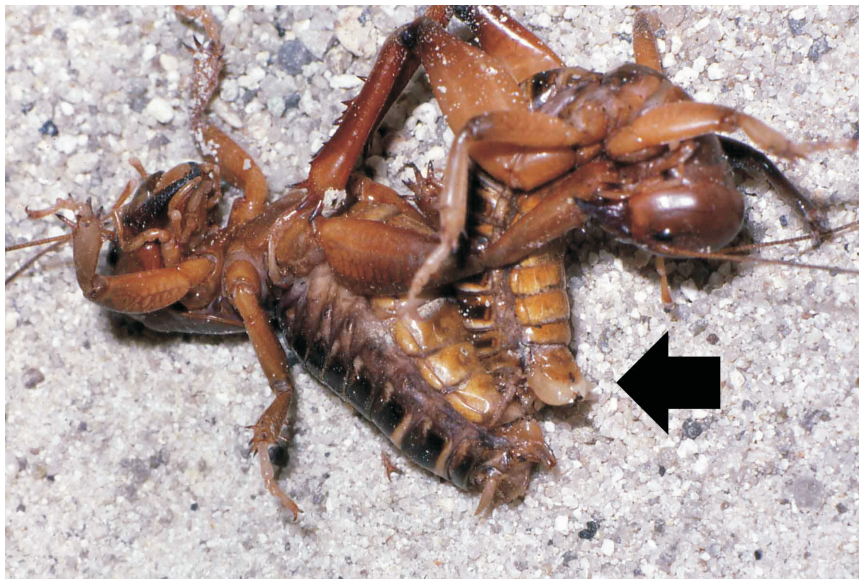
e) Male continues to curl; his anchoring ringlet of six spines at the tibia/tarsi junction now in contact with her coxa.



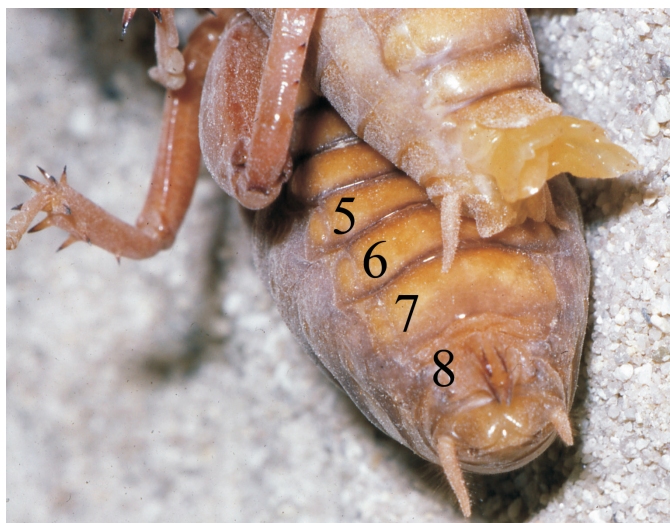
f) Male's abdomen reaches almost to female's subgenital plate.



g) Dorsal view of abdomen tip of adult male *Stenopelmatus* species 18, showing location of hooks (arrows) on each side of the supra-anal plate just medial to each cercus.



h) Male species 19 maximally telescoped, assuming a "bite-back" orientation (where he bites her rear tibia and curls back his abdomen); his hooks anchored on female's penultimate abdominal segment; he starting to evert his phallic lobes (arrow).



i) Male species 2 with hooks almost positioned on distal edge of abdominal segment plate 6 (between labeled plates 6 and 7) and with phallic lobes everted.



j) Spermatophore (arrow) passed from male (top), consisting of whitish bilobed ampulla and clear bilobed spermatophylax.

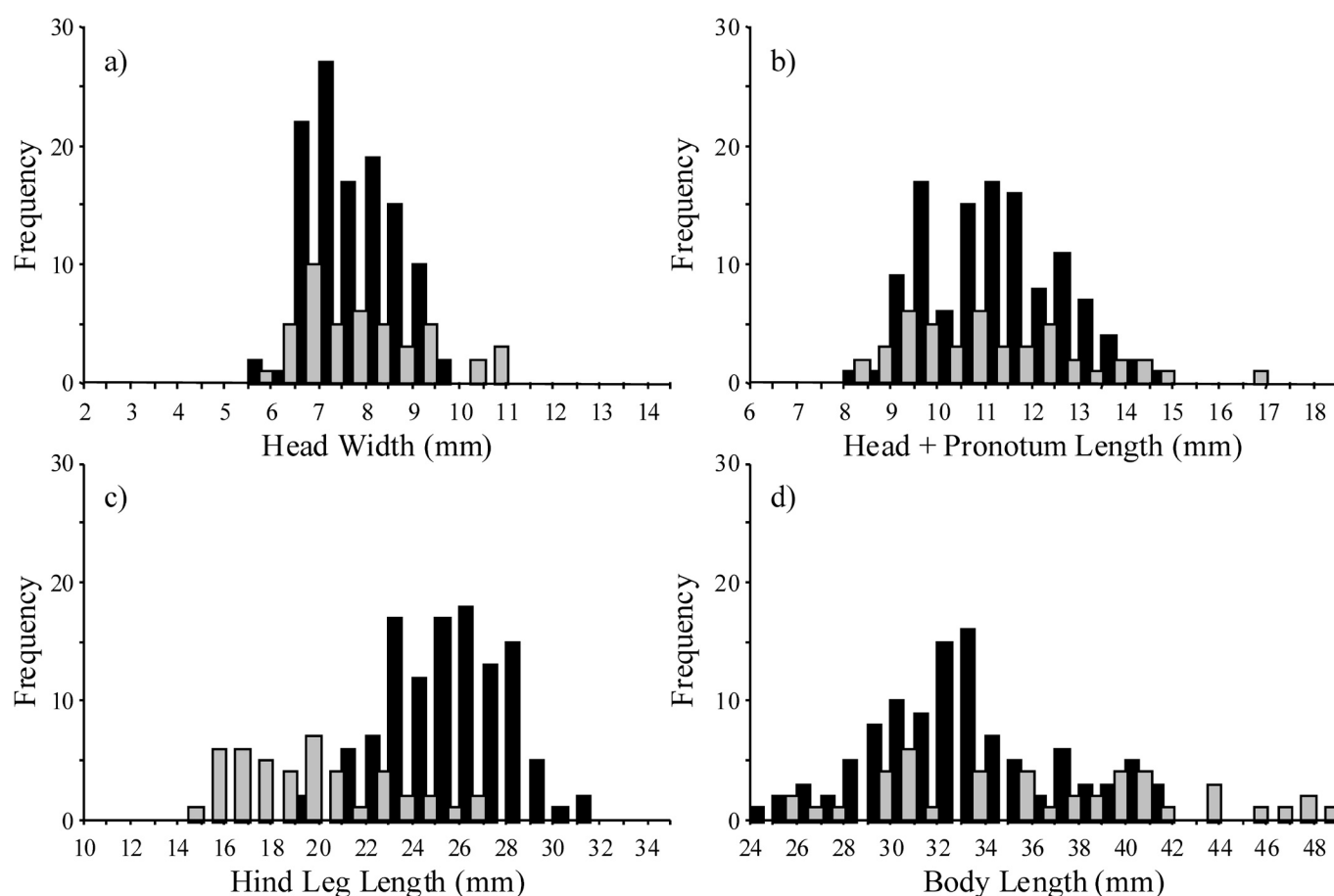


Fig. 2. Frequency distributions of: a) head width, b) head + pronotum length, c) hind-leg length and d) body length for 115 male (black columns) and 45 female (grey columns) *Stenopelmatus* species 18, collected in the wild from Los Gatos, Santa Clara Co., California, USA.

his phallic lobes (Figs 1h, i) and, upon genital coupling, passes a spermatophore (a packet containing the sperm) (Fig. 1j). In cases in which the pair is well matched in size, this whole mating process usually takes less than 10 min.

With only one exception in almost 100 observations of matings (including those reported in this study), after successful copulation females did not eat any part of the spermatophore, which quickly hardened and appears to act as a premating deterrent against subsequent mating for the 2 to 4 days it is visible (Weissman 2001b). During this period, other males display no interest in mating with the female, apparently in response to some olfactory cue/pheromone in the spermatophore. Removal of the spermatophore immediately after copulation results in an almost immediate showing of interest from other males (DBW, pers. obs.), but the mated female remains refractory to such advances for 2 to 3 days. Large males produce larger spermatophores than small males, but since females do not consume the spermatophore, there should be no oral nuptial gift considerations based on male body size, except in those cases where the female may eat the male (Weissman 2001b). In our experience, laboratory-raised virgin females are almost always receptive toward the first male they encounter, regardless of his size. Postmating males generally have a 1-day refractory period, during which they will not attempt mating with a new female (Weissman 2001b).

Three features of JCs make them ideal candidates to examine the relationship between size and mating success. First is that JCs survive well and most mate readily in the laboratory (Weissman

2001a, Weissman & Lightfoot 2007). Second is that most species of JCs exhibit great size variation (DBW unpub. data, this paper), assuring that large and small adults of both sexes are normally present in most populations. Thirdly, all JC species employ a stereotypic mating orientation that is distinctive among insects (Weissman 2001b, contrast with Alexander 1964). In fact, the positions assumed during copulation are so characteristic and unique that they may be used, perhaps for the first time, to delimit an entire subfamily of insects. Copulation in this group requires such mechanical contortions by males that we wondered whether substantial size differences between individuals might physically limit mating.

This paper reports the preliminary findings of our study investigating the effect of body size on mating success in JCs. We show that small male JCs can mate with almost any female they encounter, whereas the largest (=longest) males are unable to mate with small females due to physical constraints arising from the body positions required for copulation. Overall, our study suggests a selective pressure for small body size in male JCs: small males, not large males, appear to have a selective copulatory advantage.

Materials and Methods

Study animals.—Adults of an undescribed species of *Stenopelmatus* (see Weissman 2001b) from Los Gatos, Santa Clara Co., California, were used in all size-mating trials in this study. This taxon will be formally described elsewhere (Weissman in prep.), but in this

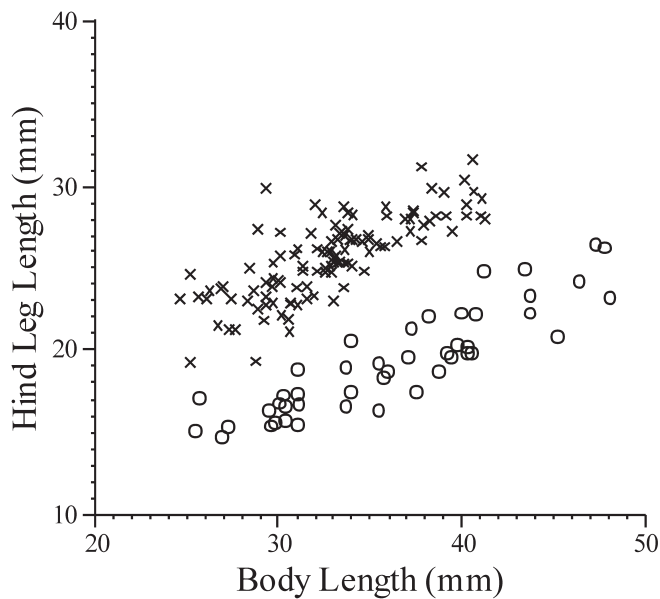


Fig. 3. Relationship between hind-leg length and body length for 115 male (X) and 45 female (O) *Stenopelmatus* species 18.

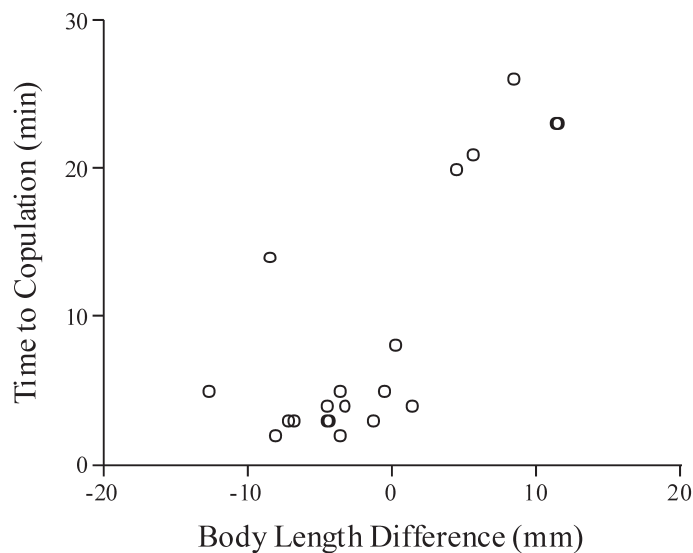


Fig. 5. Relationship between time to copulate and body-size difference (male body length– female body length).

current paper is designated as “species 18”. Individuals are known from five contiguous southeastern San Francisco Bay-area counties. In addition to species 18, we also include photographs of two other undescribed, closely related *Stenopelmatus* species because they are the best available to illustrate copulation in this genus. Species 2 inhabits the San Jacinto Mountains, Riverside Co., CA; and species 19 is from Mountain View, Santa Clara Co., CA. All study specimens were identified by species-specific morphological features and/or calling-song drums (Weissman 2001b; DBW, unpub. data), and were subsequently preserved in 75% ethanol. Twenty-two years of laboratory and field study indicate that omnivorous species 18 (and probably most *Stenopelmatus* spp.) has a two-year life cycle. Eggs are apparently laid in clutches in underground chambers dug by females (Weissman 2001a). The nymphal stage is approximately 21 months

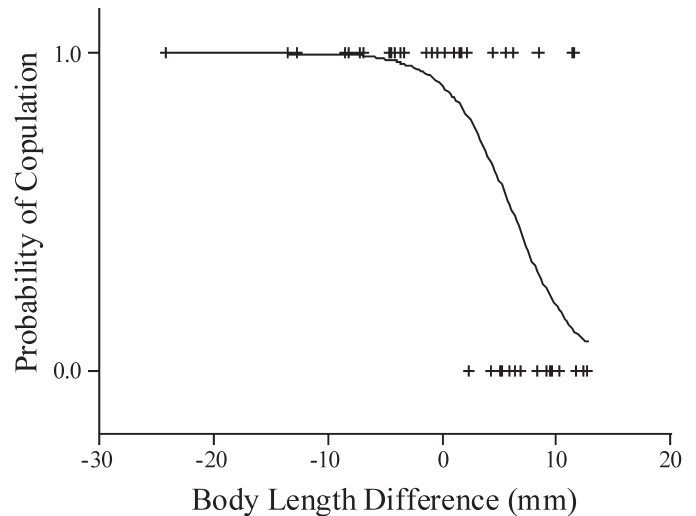


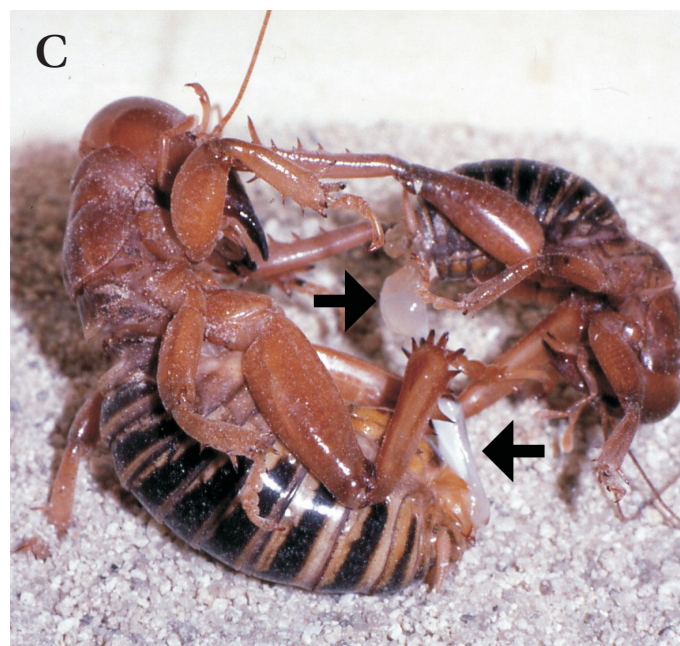
Fig. 4. Probability that a given pairing would result in a successful copulation vs the difference in body size between male and female (male body length– female body length).

long (Weissman 2001a). The adult molt occurs between mid-August and mid-October, and mating occurs soon after. Except for mating, individuals are solitary and generally subterranean. Once fall rains begin in Santa Clara County’s Mediterranean climate, adults of both sexes undertake above-ground nocturnal wanderings, during which time they advertise by drumming their abdomens against the substrate (Weissman 2001b). Females answer the male call, and it is believed that males then orient to the stationary females. Although we have reared thousands of individuals of various JC species, we have not observed protandry. Field collecting of nymphs generally reveals a 1:1 sex ratio. Laboratory-reared adult female JCs live up to eight months and laboratory-reared adult males may survive for up to six months. We believe females also outlive males in nature. Body size does not seem to vary from year-to-year, or to be associated with any particular weather conditions, such as drought, possibly because their ~1.75-year nymphal development period and subterranean habitat transcends short-term weather fluctuations.

Morphometrics.—We measured 115 adult males and 45 adult females of *Stenopelmatus* species 18 using Mitutoyo Model No. CD-6” CS Absolute Digimatic calipers. Most specimens were collected between 1986 and 1990 after drowning in DBW’s swimming pool. Bloated or decomposed specimens were discarded. Additional live specimens for mating trials were collected from under rocks and logs in Los Gatos, CA. Megacephalic individuals of either sex of species 18 are unknown (DBW, pers. obs.). The following characters were measured on each specimen to identify those whose dimensions best correlated with overall body size: **body length** (from vertical face to end of abdomen, exclusive of ovipositor); **hind-leg length** (from the proximal end of the femur to the distal end of the tibia with the leg extended), **head width** (at the widest part), and **head + pronotum length** (dorsally from vertical face to posterior edge of pronotum). We included body lengths of gravid females with extended abdomens.

Mating trials and copulation behavior.—Preliminary observations indicated that the relative sizes of copulating males and females influenced copulation success (DBW, pers. obs.). To test this hypothesis, we conducted mating trials as per Weissman (2001b),

Fig. 6. Example of a mating in species 18 in which the female is 13.5 mm longer than the male. A. Pair consists of small male (top) and large female (bottom). B. Male on top of female, as opposed to more typical position with both on their sides; male's hind legs fully extended trying to find anchorage on female (compare with Fig. 1f). C. Spermatophore (arrows) passed but dislodged despite the male still biting the female's left hind tibia.



using a wide range of body sizes. We paired individuals in 16-cm diameter containers with sandy floors and carefully recorded the resulting activities. In all cases, a pairing was only considered a "trial" if both individuals were obviously receptive, resulting in either successful or multiple and continuous attempts at copulation. JCs mate readily in captivity under moderate light levels, which allows visual observation. In pairings where we desired to use one or both individuals multiple times, coitus was interrupted after the male was properly aligned with hooks set, but before spermatophore transfer

could occur. Such trials were scored as successful. We initially left unmated pairs together overnight, and frequently the male was still attempting copulation 8 to 10 h later. However, after a large male cannibalized a particularly small female during the night, we shortened trials to 1 to 2 h. One hour exceeds the total of 2 to 20 min normally required by a size-compatible pair to mate (Weissman 2001b). Overall, we observed ~90 matings in species 18, and for 46 of these we collected morphological measurements of both male and female for use in selection analyses (see below).

Fig. 7. Example of a mating in species 18 in which the male is longer than the female. **A.** Female (middle) is 5.4 mm shorter than the male on her right, and 1.7 mm shorter than the male on her left. **B.** Shorter female (right) shows her receptivity by rolling onto her side. **C.** Longer male (top) unable to initiate curling since he cannot properly position his hind legs to get anchorage.



Statistical Analysis.—We tested for differences between wild-caught male and female *Stenopelmatus* species 18 in four morphological measurements (see above) using Student's *t*-tests for unequal variances. To further explore sexual dimorphism, we used discriminant function analysis (DFA) to identify a linear combination of the four morphological variables (*i.e.*, the discriminant function) that separated males from females.

For the 46 mating trials for which we have both male and female morphological measurements, we conducted selection analyses (Lande & Arnold 1983) to examine the relationships between both male and female traits and mating success (*i.e.*, sexual selection on both male and female traits). To calculate selection differentials, which measure net selection on a trait, we conducted univariate ordinary least squares (OLS) regressions between relative mating success and each of the traits. Linear selection gradients, which measure direct selection on each trait, were the partial regression coefficients from multiple regressions of relative mating success on the four morphological traits. Selection differentials and gradients were estimated separately for males and females, and before analysis, traits were standardized to a mean of zero and standard deviation of one. Statistical significance was tested by conducting randomization tests (Legendre & Legendre 1998). First we generated a null distribution for the parameter of interest by shuffling fitness

values relative to trait values, conducting an OLS regression on the shuffled data, and then iterating this procedure 9999 times. Then we calculated the proportion of this null distribution where the *t*-test statistic equaled or exceeded the observed *t* value. Tests were done on the absolute value of the *t*-test statistics so that the test was two-tailed. The resulting proportion is equivalent to a *p* value (Legendre & Legendre 1998).

To test for an effect of the relative size of males and females on the success of copulation, we conducted forward stepwise logistic regression, with the difference in each trait (male dimension – female dimension) as predictors and copulation success (1 = copulated, 0 = did not copulate) as the response variable.

Selection analyses were carried out using the PopTools (Hood 2005) add-in for Microsoft Excel. All other statistical tests used SPSS (version 10, SPSS Inc.), were carried out at $\alpha = 0.05$, and were two-tailed.

Results

Morphometrics.—All four morphometric measurements were highly correlated with each other in both adult male and adult female *Stenopelmatus* species 18 (Table 1). Males had longer hind legs



Fig. 8. Example of a mating in species 18 in which: A, the female (right) is 6.2 mm shorter than the male (left). B. The pair were able to mate successfully, with the male (left) positioning his hind-leg ringlet spines under her mandibles. Contrast with Fig. 1f where male anchors his ringlets on female's hind-leg coxae.



Table 1. Pearson correlation coefficients for four morphometric measurements for 115 male (above the diagonal) and 45 female (below the diagonal) *Stenopelmatus* species 18. All correlations are statistically significant at $p < 0.001$.

Measurement	HW	HPL	HLL	BL
Head Width		0.906	0.920	0.804
Head + Pronotum Length	0.966		0.845	0.847
Hind Leg Length	0.973	0.939		0.770
Body Length	0.843	0.815	0.893	

(mean \pm SE: 25.7 \pm 0.23 mm), but shorter body lengths (32.9 \pm 0.37 mm) than adult females (hind leg length: 19.4 \pm 0.47 mm; body length: 36.3 \pm 0.93 mm; Table 2, Fig. 2). Males and females did not differ in either head width or head + pronotum length (Table 2, Fig. 2). Discriminant function analysis of the four morphological measurements resulted in a discriminant function that accurately distinguished males and females 100% of the time (Wilk's Lambda = 0.075, $\chi^2 = 403.5$, df = 4, $p < 0.001$). Hind-leg length and body length loaded most heavily on the discriminant function, but in opposite directions (Table 1), indicating that the relationship between these two measurements is sexually dimorphic in *Stenopelmatus* species 18 (Fig. 3).

Selection Analysis.—In 46 staged trials (*i.e.*, where both individuals were receptive) involving 21 individual males and 16 individual females, 31 resulted in a successful copulation. Males and females were reused because of the difficulty in obtaining experimental animals, and so selection coefficients should be interpreted with caution. Selection differentials, which measure net selection on a given trait, showed significant negative selection on all four traits in males (Table 3) and positive selection on all four traits in females (Table 3). Furthermore, linear selection gradients indicated

that there was direct negative selection on male head width, but direct positive selection on male hind-leg length. There were no statistically significant linear selection gradients for females (Table 3). The above patterns were similar when we removed duplicate individuals (data not shown); however, we present the analysis of all 46 pairings to facilitate comparisons between selection on males and females.

Effect of relative size on copulation success.—Forward stepwise logistic regression analysis revealed difference in body length to be the strongest predictor of copulation success ($\chi^2 = 24.109$, df = 1, $p < 0.001$, Nagelkerke $R^2 = 0.569$). As males became progressively longer than females, successful copulation became less likely ($B = -0.355$, SE = 0.107, Wald = 10.959, $p = 0.001$; odds ratio = 0.701; Fig. 4). Based on the resulting logistic equation:

$$y = e^{2.159 - 0.355x} / (1 + e^{2.159 - 0.355x})$$

where y is the probability of successful copulation and x is the difference in body size between male and female in millimeters, we can calculate the body-size difference which results in a specified probability of successful copulation. For example, the male–female body length difference that results in a 95% probability that the pair will copulate successfully is –2.21 mm (*i.e.*, the male is 2.21 mm shorter than his mate). The corresponding values for 50% and 5% probabilities of successful copulation are 6.08 mm and 14.37 mm respectively (*i.e.*, the male is 6.08 mm or 14.37 mm longer than his mate).

In a smaller subset of matings ($N = 20$), we were able to record time to actual copulation once both individuals were in physical contact (JCs simultaneously introduced into the arena require 5 to 30 min to begin exploring their enclosure). Time to copulate, after contact, was positively correlated with the difference in male and female body length ($F = 32.673$, $p < 0.001$, Pearson $r = 0.805$; Fig. 5), meaning that as males became progressively longer than their

Table 2. Summary of morphometric measurements for 115 male and 45 female *Stenopelmatus* species 18. Loadings are the correlations between each measurement and the discriminant function separating males and females.

Measurement (mm)	Males		Females		t^*	p	Loading
	Mean (SE)	Range	Mean (SE)	Range			
Head Width	7.8(0.08)	5.6 - 9.7	7.9(0.20)	5.9 - 10.9	-0.391	0.697	-0.011
Head + Pronotum Length	11.3(0.13)	8.1 - 14.6	11.1(0.29)	8.0 - 16.6	0.649	0.518	0.017
Hind Leg Length	25.7(0.23)	19.3 - 31.5	19.4(0.47)	14.8 - 26.5	12.045	<0.001	0.304
Body Length	32.9(0.37)	24.6 - 41.3 [†]	36.3(0.93)	25.4 - 48.0 [‡]	-3.390	0.001	-0.093

* Student's t -tests for unequal variances.

[†] Maximum recorded male body length = 46.42 mm

[‡] Maximum recorded female body length = 51.30 mm

Table 3. Selection differentials (s) and linear gradients (β) for the four morphological traits in both males and females.

Traits	s (SE)	p	β (SE)	p
Males				
Head Width	-0.295(0.096)	0.005	-1.722(0.736)	0.024
Head + Pronotum Length	-0.285(0.097)	0.006	1.216(0.700)	0.087
Hind Leg Length	-0.235(0.100)	0.025	1.016(0.398)	0.014
Body Length	-0.290(0.097)	0.005	-0.768(0.489)	0.121
Females				
Head Width	0.227(0.100)	0.027	-0.184(0.706)	0.801
Head + Pronotum Length	0.245(0.099)	0.017	0.436(0.665)	0.517
Hind Leg Length	0.228(0.100)	0.028	-0.235(0.657)	0.729
Body Length	0.249(0.099)	0.015	0.228(0.401)	0.574

mates, copulation (when it occurred) took longer to occur (slope \pm SE = 1.020 ± 0.178 min/mm).

Observations of mating behavior when the sexes vary greatly in size.—In contrast to when adults are of similar body size (see Introduction), males that differ greatly in size from females often have difficulty copulating. When the **female is longer than the male**, he may place his hind-leg tarsi on her ventral abdominal surface, posterior to her hind coxae, or he may anchor under the caudal edge of sternal plate 7. This situation was observed in one of our mating pairs, where the female was 13.5 mm longer than the male (Fig. 6a). During mating he initially bit her middle tibia, but switched 15 min later to her hind tibia (Fig. 6b). At 21 min, they mated successfully (Fig. 6c), although most of the spermatophore was dislodged. We have staged other trials in which the female was as much as 24.2 mm longer than the male, and the spermatophore passed without incident.

A different set of problems is observed when the **male is longer than the female**, and the primary obstacle is misalignment. When the male is much longer than the female, he is essentially restricted to using her neck area for tarsal placement, because his hind legs are too long to be positioned on her front coxae. However, the female's neck area may not be wide enough to accommodate both tarsi simultaneously. The male apparently also has limited (if any) ability to angle his hind legs inward while attempting to place both of his tarsi under her neck, because his abdomen physically blocks such movement. Thus, if the male is only able to position one tarsus under her neck, his longitudinal body axis is not parallel with her axis, and neither rear abdominal hook will be aligned. Furthermore, every time he tries to improve his alignment, he moves the female by virtue of his bulk. Because he is biting her hind tibia and she is on her back or side, his actions often result in pivoting the female in a circle.

The following descriptions of the mating attempts of actual pairs of JCs illustrate these problems. We initially attempted to mate a pair where the female was 5.4 mm shorter than the male (Fig. 7a; male on the right, female in the center). They engaged (Fig. 7b) four times in the first 90 min, but he could not position his legs properly, and continually curled his abdomen off to the side of the female. He obtained fair, but not perfect alignment by positioning himself over her (Fig. 7c), but his abdomen and legs were too long to find anchor on any part of her body. The couple remained unsuccessful, and were given the opportunity to mate for 10 h overnight: they were still trying the next morning.

The following evening, we introduced this same female with a different male who was only 1.7 mm longer than her (Fig. 7a, male on the left). They were able to mate, but maneuvering required almost an hour, and the male again had problems placing his hind legs. Her head and the venter of her thorax were almost too narrow for him to anchor to, and once he curled, he had trouble positioning his hooks.

In other trials, another male was paired with females that were 5.8 and 6.4 mm shorter than him. Again, the couples were unable to copulate, despite being together overnight. Each time this particular male tried to maneuver into position, he moved the female out of alignment. In contrast, a pair in which the male was 6.2 mm longer than the female (Fig. 8a), was able to mate, but only because the male positioned his legs under her mandibles (Fig. 8b), while hyperextending her head and neck.

Discussion

There is a pervasive opinion in zoology that larger individuals are more fit, and that larger males can achieve more matings than smaller males. However, these ideas conflict with both evolutionary theory and empirical data (Thompson & Fincke 2002). Evolutionary theory suggests that most traits represent a compromise between conflicting selective pressures (Schluter *et al.* 1991, Futuyma 2005). Hence, for body size, there are both fitness benefits for larger size and fitness benefits for smaller size. Body size in nature may already represent the optimal trait state, given the entirety of selective forces acting on that population. Likewise, empirical observations tell us that in the vast majority of insects and other animal species, males are smaller than females (Andersson 1994, Fairbairn 2005). If large male size was always favored, all males would be large. That they are not is *prima facie* evidence that large males are not always selected for, and that there must be fitness advantages for small size.

We have shown that males and females of *Stenopelmatus* species 18 are sexually dimorphic, with males having shorter bodies and longer hind legs than females (Table 2, Fig. 3). In our behavioral trials, the longest males were usually unable to copulate with the shortest females (Fig. 4), and when they were successful, took longer to complete copulation (Fig. 5). In addition, our selection analysis indicates significant negative net selection for body length in males, but positive net selection for body length in females (Table 3). These results, coupled with detailed observations of the mechanics of copulation, provide a partial explanation for the pattern of sexual dimorphism seen in this species of JC. Males of species 18 may be smaller than females, in part, because of sexual selection for small male size, mediated through a small-male copulatory advantage. In this case, the historic (phylogenetic) mating behavior, shared by the entire subfamily Stenopelmatinae, may act as a powerful constraint against increased male body size.

At the beginning of this study, we intuitively assumed that smaller males would have difficulty mating with normal or large females because their abdomens would be too short to reach the female's genital area, or because small males would not be able to overcome larger and stronger females. However, we were surprised to observe exactly the opposite: males as little as 2 mm longer than a potential and willing female may be unable to copulate, whereas males as much as 24 mm shorter have little or no difficulty. Likewise, we detected almost no effect of male size on female receptivity. Indeed, under laboratory conditions, nearly all females appeared willing to mate with the first male they encountered, although one very small male (body length = 26.9 mm) could not induce three females, 8, 19, and 20 mm longer than him, to mate. He was, however, successful with three other females that were 7, 7, and 8 mm longer. This may indicate that extremely small males are selected against for reasons other than their ability to copulate (*e.g.*, mate attraction or inducement to copulate). This hypothesis could be tested by conducting a selection analysis in the wild and estimating nonlinear selection gradients (which would indicate the presence of intermediate fitness optima).

Our study demonstrates sexual selection against large body size in males, and this selection acts via a mechanical difficulty for large males attempting to copulate with smaller females. But, if a small male-to-female size ratio aids copulation, why aren't all males small and all females large? Again, we suggest the presence of unknown counterbalancing selective factors (*e.g.*, Thompson & Fincke 2002). Large male size may aid locomotion, digging, and dispersal. Large males may be louder drummers and able to contact females over

a wider area. Large males may be able to induce more females to mate. Large males may have greater antipredator defenses, survival or lifespan than small males. Conversely small females could reach sexual maturity quicker, increasing their fecundity (as in Gotthard *et al.* 2007), and they may experience less predation than large females. There could be genetic linkage between male and female body size (Lande & Arnold 1985, Reeve & Fairbairn 1996) such that large males result because of selection for large females.

One problem with JCs is our inadequate knowledge of natural matings. During 22 y of field study on species 18, only four field matings have been observed (Weissman 2001b, DBW pers. obs.). In three cases, pairs were found under objects (a board or a stone), and such locations might assist a large male to properly align with a smaller female if she is wedged in place by the object. The fourth mating occurred on flat ground. Unfortunately we know almost nothing about field matings — they occur at night and are rare, and JCs are extremely sensitive to ground vibrations (*e.g.*, foot steps) (see refs in Weissman 2001b, Strauß & Lakes-Harlan 2008). Hence, a researcher's presence would presumably disrupt calling.

During our study, we observed no evidence of sexual selection for large males in the form of male-male competition. Unlike in crickets (Kortet & Hedrick 2005), and many other insects (Thornhill and Alcock 1983, Andersson 1994), male JCs do not fight with each other when in the presence of females (DBW unpub. data). Some JC species have individuals with megacephalic (large) heads. However, in such species, males appear to use such enlarged heads exclusively for digging in their generally sandy habitat, not for combat (DBW unpub. data). This apparent lack of male-male competition for females is consistent with the absence of male-biased body length size dimorphism (Fisher and Cockburn 2005), although there is clearly male-biased hind leg dimorphism. Relatively larger hind legs in males may aid locomotion (as has recently been found in another orthopteran, the Cook Strait giant weta, *Deinacrida rugosa* Buller [Kelly *et al.* 2008]), digging, defense, and drumming, and is a ubiquitous character state throughout the many species of *Stenopelmatus* that comprise the DNA clade to which species 2, 18, and 19 belong (Vandergast A. & Weissman D.B. unpub.).

There is also no evidence that females choose males of a certain size: a virgin adult female in the presence of two adult males will mate with whichever male is quickest to initiate courtship. Also, females will mate in the laboratory as many as four times in 12 d (Weissman 2001b), suggesting that females are capable of multiple matings in the field.

We suspect that our results are characteristic for other species 18 populations. We observed similar size variation in this same species among 35 individuals collected at Felton, Santa Cruz County, 30 km southwest of Los Gatos in the Santa Cruz Mountains. Also, similar size variability occurs in other species of JCs (DBW unpub. data). Although we believe that ours is the first documentation of small-male advantage based on physical aspects of copulation, we expect that this phenomenon is not rare in nature. Many taxa exhibit both great size variation within sexes, and complicated copulation that relies on correct alignment of various structures (Davey 1965, Rentz 1972, Eberhard 1985). Such groups are good candidates among which to look for copulatory-size incompatibility. Finally, we predict that careful examination will reveal the existence of balancing (stabilizing) selective forces for body size in virtually all animal species (*e.g.*, Thompson & Fincke 2002).

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