

NUPTIAL GIFTS AND THE EVOLUTION OF MALE BODY SIZE

KENNETH M. FEDORKA¹ AND TIMOTHY A. MOUSSEAU
Department of Biological Sciences, University of South Carolina,
Columbia, South Carolina 29208
¹E-mail: fedorka@sc.edu

Abstract.—In many insect systems, males donate nuptial gifts to insure an effective copulation or as a form of paternal investment. However, if gift magnitude is both body size-limited and positively related to fitness, then the opportunity exists for the gift to promote the evolution of large male size. In the striped ground cricket, *Allonemobius socius*, males transfer a body size-limited, somatic nuptial gift that is comprised primarily of hemolymph. To address the implications of this gift on male size evolution, we quantified the intensity and direction of natural (fecundity) and sexual (mating success) selection over multiple generations. We found that male size was under strong positive sexual selection throughout the breeding season. This pattern of selection was similar in successive generations spanning multiple years. Male size was also under strong natural selection, with the largest males siring the most offspring. However, multivariate selection gradients indicated that gift size, and not male size, was the best predictor of female fecundity. In other words, direct fecundity selection for larger gifts placed indirect positive selection on male body size, supporting the hypothesis that nuptial gifts can influence the evolution of male body size in this system. Although female size was also under strong selection due to a size related fecundity advantage, it did not exceed selection on male size. The implications of these results with regard to the maintenance of the female-biased size dimorphic system are discussed.

Key words.—Body size, fecundity selection, nuptial gift, sexual selection, tibial spur.

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In many insect systems, males offer females nuptial gifts (e.g., captured prey or synthesized secretions) to insure an effective mating or as a form of paternal investment (Thornhill and Alcock 1983; Andersson 1994). This is accomplished by increasing sperm transfer or by increasing the number and fitness of the gift giver's own offspring, respectively (for review, see Vahed 1998). Moreover, the magnitude of the gift can positively covary with the degree of reproductive fitness (e.g., Gwynne 1984; Sakaluk 1984), providing the opportunity for strong selection on gift size. However, if gift size is also limited by male size, then nuptial gifts may have an indirect, positive affect on male body size evolution.

To address the hypothesis that nuptial gifts indirectly promote the evolution of large male size, we used the striped ground cricket, *Allonemobius socius*. In this system, *A. socius* males possess a specialized tibial spur that delivers a somatic nuptial gift to the female during copulation (Mays 1971; Forrest et al. 1991). This gift is comprised primarily of hemolymph that is ingested by the female once the tip of the spur is removed. Males can mate multiple times and females do not discriminate among males based on the condition of the spur (unpublished data). Most importantly, the magnitude of hemolymph transferred is limited by male size, with the largest males offering the largest gifts (Fedorka and Mousseau 2002a). This relationship has been suggested to drive female choice for larger males in other ground cricket species (Forrest et al. 1991). In addition, male size is not associated with the size of the sperm containing spermatophore that is transferred along with the gift, suggesting that ejaculate contribution is similar among males (Fedorka and Mousseau 2002a).

The binary condition of the spur (mated or virgin) also serves as a simple, unambiguous measure of male fitness (Fig. 1), allowing us to estimate the magnitude and direction of sexual selection on male size due to mating success. Snedden and Sakaluk (1992) have used a similar technique in the

sagebrush cricket, *Cyphoderris strepitans*, where mated males can be identified by the condition of their hind wings, which the females chew upon during copulation. This method of assaying success is conservative in that it does not include variance due to multiple mating. However, it is likely that the variance in reproductive fitness between mated and virgin males is greater than the variance within multiply mated males. Furthermore, our method provides an advantage over commonly used techniques. Many field studies of mating success compare copulating males with solitary males to estimate sexual selection pressures (e.g., Wilkinson and Reillo 1994; Simmons 1995; Abell et al. 1999). Unfortunately, this standard method is unable to detect if a solitary male has previously been successful at acquiring a mate. The benefit of the tibial spur is that previously mated males are accurately identified, likely capturing a larger portion of the variance in male mating success.

Nuptial gifts may also have a profound impact on sexual size dimorphism (SSD). Most insect systems are female size biased (females larger than males), and this pattern of SSD is often explained through the reproductive advantages of large female size (Darwin 1871; Shine 1988). However, although selection for larger body size-correlated gifts, male reproductive investment may eventually surpass female reproductive investment, modifying the degree of size dimorphism (e.g., Leimar et al. 1994).

Male gift related fitness gains may be due to female choice for larger investments and increased reproductive output. Therefore, we addressed the evolution of male size through two main avenues, sexual and natural (fecundity) selection, over multiple years. Considering the body size and gift relationship previously established in this female size-biased system, we predicted that there would be positive sexual selection on male size due to large male mating success. Furthermore, we predicted that there would be indirect selection on male size due to direct fecundity selection on the

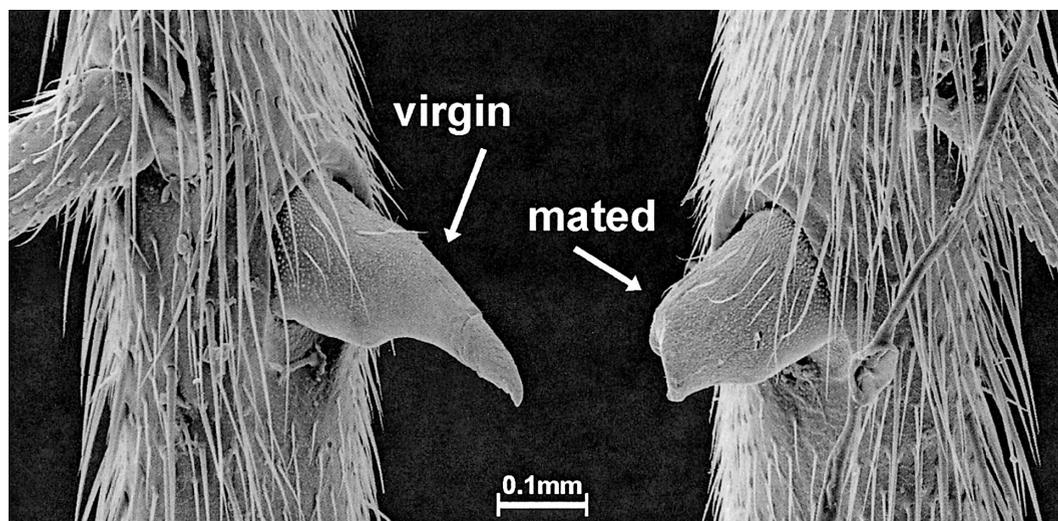


FIG. 1. The tibial spur as a measure of male fitness. This specialized spur not only delivers a somatic nuptial gift (hemolymph) through female courtship feeding, but also indicates a male's mating history. The spur on the right has been chewed by the female (mated) whereas the left is intact (virgin).

nuptial gift, allowing gifts to indirectly influence the evolution of male size.

MATERIALS AND METHODS

Study System

Allonemobius socius is a small chirping ground cricket found throughout the southeastern United States, with closely related sister taxa ranging throughout North America (Alexander and Thomas 1959; Howard and Furth 1986; Mousseau and Roff 1989; Weibel and Howard 2000). In the wild, male *A. socius* attract distant females through a species specific calling song that is switched to a ritualized courtship song and dance once a potential mate is encountered. If the female is receptive, she will briefly mount the male in a momentary "mock copulation," causing the male to discontinue his courtship and form a spermatophore. When complete, he will renew his courtship behavior, again enticing the female to mount. As the female mounts, the male adheres the spermatophore to the female's genitalia. Within seconds, the male will bring his hind tibia forward allowing the female to chew on his spur, which may last upwards of 30 min, until the couple separates (Alexander and Thomas 1959; Mays 1971). Due to the simultaneous nature of spermatophore attachment and spur chewing, sperm and gift transfer are rarely uncoupled (pers. obs.).

General Maintenance

Laboratory-reared crickets were first or second generation individuals derived from the eggs of wild-caught central South Carolina females. Experimental crickets (both laboratory-reared and wild caught) were maintained in $10 \times 10 \times 8$ cm plastic cages containing ground cat food, a carrot slice, dampened cheesecloth (water source and oviposition material), and strips of brown paper towel for cover. Cages were kept in a constant environment at 28°C and a 12:12 [L:D] photoperiod provided by a Percival (Boone, IA) incubator.

Maintenance was provided twice weekly. The age of all laboratory-reared experimental crickets was 12 ± 2 days post-eclosion (final adult molt).

Measurement of Sexual Selection

To elucidate the contemporary pressures that affect male size, we first examined the direction and intensity of sexual selection over multiple generations. In South Carolina, *A. socius* is bivoltine (two generations per year; Mousseau and Roff 1989), but may be trivoltine under favorable conditions. Adults live approximately four weeks in the wild and there is little or no adult overlap between generations (pers. obs.). Males from central South Carolina were collected throughout the second generation (August through September), weighed to the nearest 0.01 mg, scored for individual mating success via the tibial spur assay, and frozen. Once preserved, two linear body size measures were taken including femur length and wing length using a dissecting scope fitted with an ocular micrometer. These characters were chosen because they represent an overall size estimate (weight) as well as age and condition independent measures of size (wing and femur length). The right femur and overlapping wing were preferentially measured to help control for the potential confounding effects of directional asymmetry. When the right femur or overlapping wing was unmeasurable (e.g., missing or deformed), the left femur was used or no wing measurement was taken.

In the following year, wild males were again assayed for their mating success approximately every two weeks from August to October ($n = 159$; in 1997 October coincided with a brief third generation). This was done both to compare the selective pressures between years and to visualize how male mating success varied according to size within generations of the same year.

We further examined sexual selection on size variation by estimating linear univariate (β'), linear multivariate (β) and nonlinear multivariate (γ) selection gradients (Lande and Ar-

nold 1983; Brodie et al. 1995). Selection gradients were calculated by regressing relative fitness ($\omega_{\text{relative}} = \omega_{\text{individual}} / \omega_{\text{average}}$) against the standardized size characters ($\bar{X} = 0$, $SD = 1$). When compared to β' , β allowed us to disentangle those characters under direct linear selection from those that are indirectly selected. The nonlinear gradient, γ , allowed us to detect potential disruptive or stabilizing selection effects. Because our fitness measure was dichotomous (mated or virgin) and may violate parametric assumptions of normality, we used univariate and multivariate nonparametric logistic regressions to test the significance of the linear model estimates β' and β , respectively (Janzen and Stern 1998). Furthermore, we used a nonparametric fitness function (see below) to provide an additional assessment of the nonlinear model estimate, γ . To compensate for experimentwise Type I error arising from multiple comparisons, sequential Bonferroni corrections (Rice 1989) were performed for each selection gradient type (i.e., β' , β , and γ) within a given year.

Nonparametric fitness functions were also created to help visualize selection. Nonparametric functions need no a priori knowledge of a phenotype's fitness distribution and are therefore a less restrictive representation of the direction and intensity of selection. Employing a FORTRAN program made available by D. Schluter, cubic splines were generated to estimate the fitness probabilities of a given phenotypic distribution. Each spline was bootstrapped 500 times to obtain a measure of confidence around the estimated probability response.

Measurement of Fecundity Selection

In addition to sexual selection on male size, there may also be positive selection on male size due to size-correlated nuptial gifts. Nuptial gifts may influence female reproductive output through either gift quantity or gift quality. For instance, larger gifts may allow more sperm to be transferred (Thornhill 1976), or provide a larger dose of nutrients that help offset oviposition costs or increase offspring viability (Eisner et al. 1996; Reinhold 1999). In 1996, eggs from wild-caught females were collected from the same wild population used for the sexual selection estimates and a laboratory population was established.

First, we tested the hypothesis that male body size is significantly associated with reproductive fitness. To this end, 40 mating trials were conducted using first generation laboratory-reared individuals of controlled age (12 ± 2 days). Randomly chosen virgin male and female pairs were weighed, placed into a mating arena ($10 \times 10 \times 8$ cm plastic cage) and allowed to mate. Females were then isolated to oviposit for two weeks after which time fecundity was measured. Because males and females may mate multiple times throughout their lives, this reproductive fitness measure estimates the fitness gain from a single reproductive bout and is not a measure of lifetime reproductive success.

As with mating success, reproductive success was reexamined in the following year for the same population. We randomly collected adult males from the third generation (3 October–18 October 1997; $n = 78$) and placed each male into a mating arena containing a laboratory-reared virgin fe-

male and allowed to mate. Again, females were isolated for two weeks to oviposit.

To test the hypothesis that selection acts directly on nuptial gift size and not body size, we again assayed reproductive fitness in the fall of 1999. Using the above design, 50 mating trials were conducted and male and female weight and fecundity were measured. In addition, the duration of female spur chewing was recorded as well as oviposition rate (eggs/day). Spur chewing duration is an excellent predictor of nuptial gift magnitude, with longer chewing resulting in larger hemolymph transfer (Fedorka and Mousseau 2002a). Thus, chewing duration was used as our measure of gift size.

For all reproductive assays, females dying before the two-week period ended were removed from the analysis. Univariate selection gradients (β') for males and females were calculated by regressing standardized weight against relative reproductive fitness. Multivariate gradients (β) were estimated to disentangle the direct and indirect effects of weight and gift size on fecundity. In addition, fitness functions were created to help visualize fecundity selection. All data analyses were performed using SAS 1989.

RESULTS

Sexual Selection

Our results indicate that body size is positively associated with male mating success in the wild. In 1996, males with chewed spurs (mated) were on average 46% heavier than males with intact spurs (virgins). The age and condition independent measures of body size (i.e., wing length and femur length) exhibited a similar trend. Hence, a statistically significant morphological difference for each trait was found between males who successfully acquired mates and those who remained unmated (weight: $t_{628} = 14.48$; femur: $t_{562} = 12.18$; wing: $t_{564} = 10.10$; all $P < 0.0001$).

Univariate selection gradients (β') suggested that all three characters were under strong positive selection in the second generation of 1996 (Table 1). Once the confounding effects of correlated characters were removed via multivariate partial regression (β), weight was the only significant predictor of mating success. Cubic spline fitness functions indicated that the nonlinear gradients for weight and wing (Fig. 2; γ , Table 1) were due to a change in the slope of the fitness function and not due to stabilizing selection. (Mitchell-Olds and Shaw 1987).

Analyses of the 1997 data offered the same picture of strong positive selection on male size (Table 1). For consistency, this analysis used only the third generation males allocated for the reproductive assay (second generation results were similar to third generation results). Moreover, the multivariate selection gradient estimates (β) for weight were not significantly different between years ($t_{711} = -0.73$, $P = 0.47$), suggesting that intensity and direction of sexual selection on male body size was consistent over time.

To better visualize the temporal pattern of sexual selection, male weight and mating success were tracked over time in 1997 ($n = 159$). Late August tibial spur assays showed the emergence of a new second generation adult cohort (the first generation was not measured) as indicated by the high proportion of intact spurs (Fig. 3). Here, virginity was probably

TABLE 1. Sexual selection gradients for wild caught males for 1996 ($n = 635$) and 1997 ($n = 78$). Univariate gradients (β') suggested that all characters were under strong linear selection for both years. However, multivariate gradients (β) implied that overall male size (as described by weight) was the best predictor of relative fitness (significance tests for β' and β were provided by nonparametric logistic regressions). Cubic splines suggest that the significant nonlinear gradients (γ) for weight and wing were due to changes in the slope of the fitness functions and not due to stabilizing or disruptive selection. Bolded characters remained significant after a sequential Bonferroni correction. Corrections were done within years for each selection gradient.

Z_i	$\beta' \pm SE$	P	$\beta \pm SE$	P	$\gamma \pm SE$	P
1996						
Weight	0.80 \pm 0.06	0.0001	0.29 \pm 0.07	0.0001	-0.17 \pm 0.06	0.0094
Femur	0.77 \pm 0.06	0.0001	0.02 \pm 0.06	0.5330	0.02 \pm 0.05	0.6806
Wing	0.65 \pm 0.65	0.0001	-0.02 \pm 0.09	0.3478	0.10 \pm 0.04	0.0157
1997						
Weight	0.73 \pm 0.11	0.0001	0.44 \pm 0.14	0.0001	-0.27 \pm 0.14	0.0606
Femur	0.67 \pm 0.11	0.0001	-0.15 \pm 0.15	0.5330	-0.13 \pm 0.15	0.3825
Wing	0.61 \pm 0.12	0.0001	0.01 \pm 0.09	0.3478	0.06 \pm 0.08	0.4027

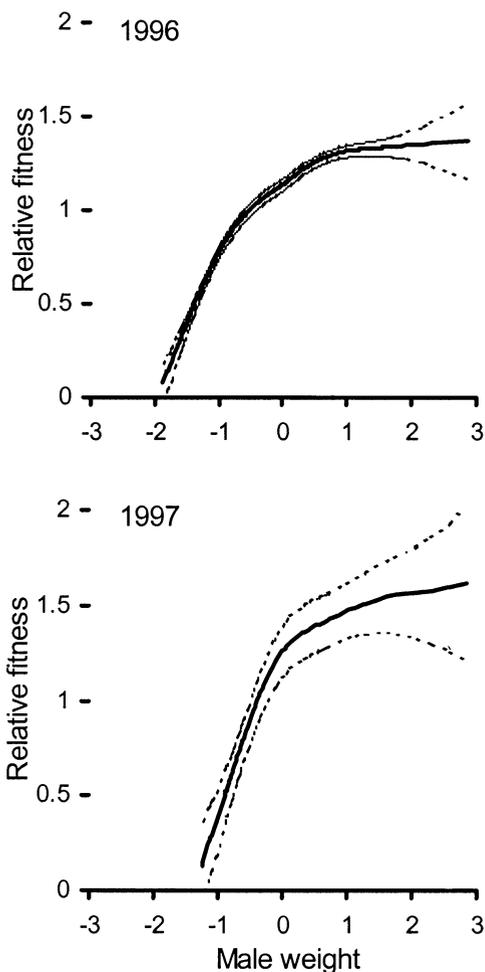


FIG. 2. Male sexual selection fitness functions. The relationship between male weight and fitness reveals strong positive selection on male body size for both years (1996 $n = 635$; 1997 $n = 78$). However, as male weight increases past the mean of the size distribution, the slope of the function decreases. Functions were bootstrapped 500 times. Size characters were standardized to unit variance.

due to sexual incompetence in early adulthood, thus selection on size was weak or nonexistent (newly eclosed adult males may take five to 10 days before they actively court females; K. M. Fedorka, pers. obs.). As males began to mature and mate (September), the proportion of virginity sharply declined and positive selection on male size became apparent. By early October, a short-lived third generation of adults had begun to emerge, again as indicated by the sharp increase in virginity and the associated weak selection for large males. As this third cohort matured, the expected morphological divergence between mated and virgin males returned, suggesting that sexual selection on male size was positive and stable within generations.

Fecundity Selection

In 1996 only 36 females survived the two-week oviposition period and were included in the analysis. Here, β' for male weight indicated that the direction and intensity of selection

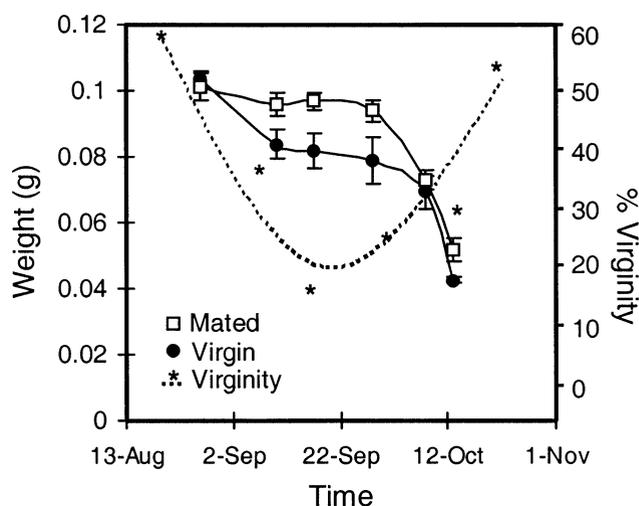


FIG. 3. Male mating success as a function of weight over time. As males matured throughout the 1997 breeding season, size (weight \pm SE) became a significant, consistent predictor of mating success (see text for full description). October signifies the emergence of a third adult generation. Mated males were significantly larger than virgins for all dates except for 27 August and 3 October ($P < 0.05$).

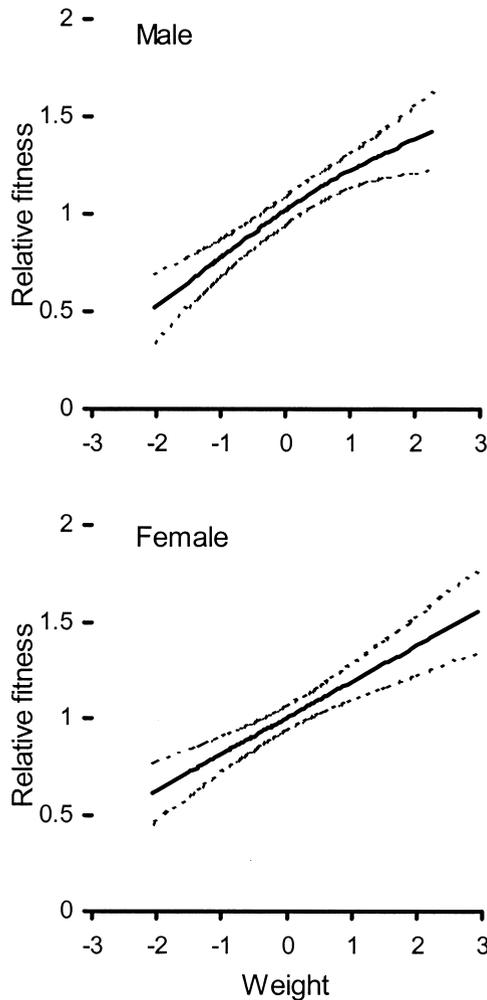


FIG. 4. Fecundity selection fitness functions. Pooled data from 1996 and 1997 revealed significant positive selection on both male and female size. However, these slopes were not significantly different, suggesting that selection pressure on female size is similar to male size. In both cases, a one standard deviation increase in size increased fitness by 15%. Functions were bootstrapped 500 times. Characters standardized to unit variance.

were both strong and positive ($\beta' \pm \text{SE}$: 0.39 ± 0.14 , $P < 0.01$). Hence, a standard deviation increase in male weight was associated with a 39% increase in relative fitness, suggesting an adaptive advantage for females who mate with larger individuals. Female weight was not significantly associated with reproductive fitness ($\beta' \pm \text{SE}$: 0.16 ± 0.17 , $P = 0.37$).

In 1997 neither male nor female weight were significantly associated with reproductive success. However, male weight was positively associated with mating success ($F_{1,75} = 49.49$, $P < 0.0001$), which was in turn associated with reproductive success ($F_{1,75} = 5.08$, $P < 0.05$). Considering this, the yearly reproductive data were pooled, under the assumption that our inconsistent results were the product of low sample sizes and not of shifting selective pressures between years.

When the data were pooled, a significant year effect was detected. Consequently, year was included as a variable in all subsequent selection gradient models to remove any con-

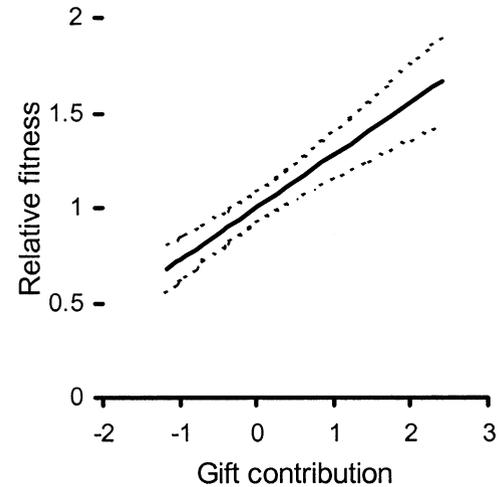


FIG. 5. The effect of the nuptial gift on reproductive fitness. Although male size was significantly associated with fecundity, gift size appeared to be more closely associated, as suggested by the multivariate linear gradients. Here, a standard deviation increase in gift size increased relative fitness by 27%. This is nearly a twofold increase when compared to the male weight function.

founder effects before individual characters were tested. The pooled results indicated that both male and female weight were significant predictors of relative reproductive fitness ($\beta' \pm \text{SE}$: 0.15 ± 0.06 and 0.15 ± 0.06 , respectively; all $P < 0.05$; Fig. 4). Furthermore, these gradients suggest that selection on male and female size was similar.

When male weight and gift size were both included in a multivariate model (fall 1999 data; 41 females survived oviposition period), gift size was the only significant predictor of reproductive fitness (Fig. 5; gift size: $\beta \pm \text{SE}$: 0.27 ± 0.10 , $P < 0.05$ vs. weight: $\beta \pm \text{SE}$: 0.08 ± 0.10 , $P = 0.44$). Gift size was also positively associated with the rate of oviposition ($F_{1,35} = 6.49$, $P < 0.05$).

DISCUSSION

Our present study indicates that both fecundity selection and sexual selection contribute to the evolution of male size in *A. socius*. Wild tibial spur assays revealed that large males are more successful at acquiring mates, implying strong positive sexual selection on male body size in natural populations. This pattern was similar within generations of a single year and between years. The largest males, as described by weight, also sired more offspring once mating was achieved placing additional positive selection on male size. However, multivariate selection analyses revealed that gift magnitude was the best predictor of reproductive fitness. In other words, direct fecundity selection for larger gifts placed indirect positive selection on male body size due to the body size/gift correlation previously established in this system, supporting the hypothesis that nuptial gifts can influence the evolution of male body size.

Theoretically, a correlated response in body size due to directional selection on gift size may occur only if the two traits are genetically correlated (Roff 1997). Although the genetic nature of the gift and body size relationship is currently unknown, it is probably the result of pleiotropy. Thus,

the correlated response to selection depends on the trait's phenotypic variances, heritabilities, and the genetic correlation. Currently, these variables are being investigated.

The relationship between gift magnitude and female fecundity also implies that those females who mate with larger males have higher fitness. Whether females actively discriminate among males based on their gift-giving potential remains to be tested. It is possible that male mating success is based on characters more closely associated with courtship, and that male size and gift size are only correlated with this unknown trait(s). However, the success of large males at acquiring mates found here, coupled with their ability to provide larger gift contributions, suggests that female choice for larger gifts is a plausible hypothesis.

It is currently unclear whether the nuptial gift serves as a form of mating effort or paternal investment, although these functions are not mutually exclusive. In many Orthopteran systems, the gift facilitates a longer spermatophore attachment and thus, a higher number of sperm transferred (e.g., Gwynne 1983; Sakaluk 1984; Vahed 1998), supporting the mating effort hypothesis. Likewise, previous work in this system suggests that spermatophore attachment duration and gift size are positively related ($F_{1,58} = 7.37$, $P < 0.01$). However, unlike gift size, spermatophore attachment duration was not associated with fecundity (gift: $F_{1,54} = 7.88$, $P < 0.01$ vs. spermatophore: $F_{1,43} = 0.44$, $P = 0.51$; Fedorka and Mousseau 2002b). Thus, variance in female fecundity seems more likely the result of variance in gift size/content rather than variance in spermatophore attachment duration. This may be due to oviposition-inducing hormones (Friedel and Gilliot 1977) or limited nutrient resources contained within the gift (Eisner et al. 1996). Furthermore, for the gift's influence on reproductive fitness to be fully realized, the rate of incorporation of donated nutrients and subsequent oviposition must be faster than the female's reproductive refractory period (Wedell 1993), otherwise it is improbable that these extra eggs would be fertilized by the gift giver. The positive relationship between gift size and oviposition rate described here implies that an increase in reproductive fitness may be partially realized, especially if female refractory periods are long (e.g., in low-density populations) or if males transfer chemicals (e.g., through the spermatophore) that temporarily arrest a female's receptivity (e.g., Arnqvist and Nilsson 2000).

As previously stated, studies have suggested that female size-biased dimorphic systems are largely maintained through positive fecundity selection (Shine 1988). Although female body size appears to be under positive selection due to a fecundity advantage, the magnitude of male and female selection gradients did not differ significantly, resulting in a reproductive selection balance. Furthermore, there was additional strong, positive sexual selection on male body size. Considering this, why does the female-biased dimorphic pattern persist?

First, the body size implications of sexual selection on females were not examined. Although female sexual selection in crickets is not uncommon (e.g., sex role reversal in Mormon crickets; Gwynne 1981), there is no evidence that it exists in this system. Moreover, in the *A. socius* populations studied here, nearly all wild caught females were gravid in

contrast with a high proportion of virgin males. Thus, the variance in male mating success is far larger than in female mating success, suggesting that female sexual selection alone is an unlikely candidate.

Size-specific adult mortality rates may also differ between the sexes. For instance, a male's continual advertisement of his location through his calling song is necessary to attract a mate (Boake 1983). This signal may also be used by auditory-based predators, which are common in cricket systems (Cade 1975; Sakaluk and Belwood 1984; Zuk et al. 1995). Because larger males usually have lower calling frequencies (e.g., Brown 1997), they create a larger broadcast range, which may ultimately increase their susceptibility to predation. Such differences in survivorship will have large repercussions on individual lifetime reproductive success, potentially modifying the net selective forces described here.

There may also be stronger developmental constraints on male body size. A longer juvenile development period (i.e., more instars) results in a larger adult size (Roff 1992), implying a higher potential fitness. In this species, latitudinal clines are evident where mean body size increases with an increase in mean season length (Mousseau and Roff 1989), suggesting that season length imposes strong selection against developmental overinvestment. Individuals who spend more time in nymphal development to achieve larger body size risk reducing their reproductive success due to an ephemeral breeding season. This trade-off is suggested in the mid-October data of Figure 3. As the last cohort emerged, mean body size dropped by 64%, reflecting a shortened development period to compensate for a diminishing season.

Lande (1980) has suggested that a dimorphic response to selection may be constrained by a high genetic correlation between the sexes for a homologous trait. However, the genetic correlation between sexes for one body size component, femur length, is significantly less than 1 ($r_A = 0.70$, $P < 0.0001$; estimates of other size components are unavailable; K. M. Fedorka, unpubl. data). This, combined with the moderate heritability (h^2) estimate for this character (male $h^2 = 0.55 \pm 0.03$, female $h^2 = 0.55 \pm 0.04$; Mousseau and Roff 1989), suggests that body size and dimorphism could still be strongly influenced by contemporary selection.

Regardless of how SSD is maintained, we have shown that male body size in *A. socius* was significantly associated with mating and reproductive success. Furthermore, the variance in reproductive success seemed to be due directly to the variance of the size-limited nuptial gift. Thus, nuptial gifts appear to play an important role in the evolution of male body size and SSD in this system.

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Corresponding Editor: S. Pitnick