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TIBIAL SPUR FEEDING IN GROUND CRICKETS: LARGER MALES CONTRIBUTE LARGER GIFTS (ORTHOPTERA: GRYLLIDAE)

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ABSTRACT

Many male insects provide somatic nuptial gifts that may strongly influence reproductive fitness by insuring an effective copulation or by increasing paternal investment. In the striped ground cricket, *Allonemobius socius* (Scudder), females receive a nuptial gift by chewing on a specialized spur on the male's hind tibia during copulation. Using a series of no-choice trials, we attempted to quantify gift magnitude and to determine the relationships between male size, gift contribution, and male mating success. Tibial spur chewing duration was a significant predictor of gift contribution ($F_{1,17} = 17.02$, $P < 0.001$) and the magnitude of the gift ranged between 0.2% and 8% of the male's body mass, implying that females receive mostly hemolymph. Large males produced bigger gifts than small males (2.52 ± 0.59 mg vs. 1.33 ± 0.28 mg, $t_{17} = 1.88$, $P < 0.05$, respectively) and females were more likely to mate with larger males ($F_{1,39} = 4.76$, $P < 0.05$). If gift size is shown to influence female reproductive fitness, then nuptial gifts may play a large role in the evolution of male body size.

Key Words: nuptial gift, tibial spur, body size, *Allonemobius socius*

RESUMEN

El macho en muchos insectos provee un regalo nupcial somático que puede influenciar fuertemente la adaptabilidad óptima reproductiva (fitness) al asegurar una cópula eficaz o al incrementar la inversión paternal. En el grillo *Allonemobius socius*, las hembras reciben un regalo nupcial al morder un espolón especializado en la tibia posterior del macho durante la cópula. Utilizando una serie de pruebas de no alternativas, tratamos de cuantificar la magnitud del regalo y determinar la relación entre el tamaño del macho, la contribución del regalo, y el éxito de la cópula del macho. La duración de las mordidas del espolón de la tibia fué un predictor significativo de la contribución del regalo ($F_{1,17}$ - 17.02, $P < 0.001$) y la magnitud del regalo abarcó entre el 0.2% y el 8% del peso del cuerpo del macho, indicando que las hembras reciben principalmente hemolinfa. Los machos grandes produjeron regalos más grandes que los machos pequeños (2.52 ± 0.59 mg vs 1.33 ± 0.28 mg, $t_{17} = 1.88$, $P < 0.05$) y era más probable que las hembras copularan con los machos más grandes. Si el tamaño del regalo influencia la adaptabilidad óptima reproductiva de las hembras, entonces los regalos nupciales pueden actuar un papel importante en la evolución del tamaño del cuerpo de los machos.

In many birds and insects, males offer nuptial gifts to females prior to and/or during copulation (Wiggins and Morris 1986; Gwynne and Brown 1994; Simmons 1995; Neuman et al. 1998). These offerings include captured prey, somatic tissue, synthesized secretions and suicidal food transfers (see Andersson 1994 and references therein). The function of these gifts may vary, serving as a form of male mating effort by increasing fertilization success (Alexander & Borgia 1979; Sakaluk 1984) and/or as paternal investment by increasing reproductive fitness (e.g., increasing egg size, offspring number or offspring viability; Gwynne 1984; Reinhold 1999). For instance, in the hangingfly, *Hylobittacus apicalis* (Byers), nuptial prey functions to increase mating effort by increasing copulation duration, which is in turn associated with the volume of sperm transferred (Thornhill 1976). In contrast, nuptial feeding in the osprey, *Pandion haliaetus* (Linnaeus), acts as paternal investment since it was positively associated with offspring growth rate (Green and Krebs 1995). Regardless of the precise functional significance, these associations suggest that variation in nuptial gift mass may have strong fitness implications for both sexes.

Nuptial gifts are generally transferred to females via external, intermediate packages such as prey items or self-contained somatic secretions (Andersson, 1994), permitting an easy quantification of their mass. However, in some animal genera the gift is internally transferred making the magnitude and the fitness implications of such gifts difficult to assess. For instance, in the cricket genus *Allonemobius* (Orthoptera: Gryllidae), males internally deliver a nuptial gift through a specialized spur on each hind tibia that is chewed by the female during copulation (Fig. 1). Although chewing damages the spur, males can mate multiple times and females do not discriminate among males based on the spur's condition (unpublished data). This somatic gift has previously been described as a limited glandular contribu-

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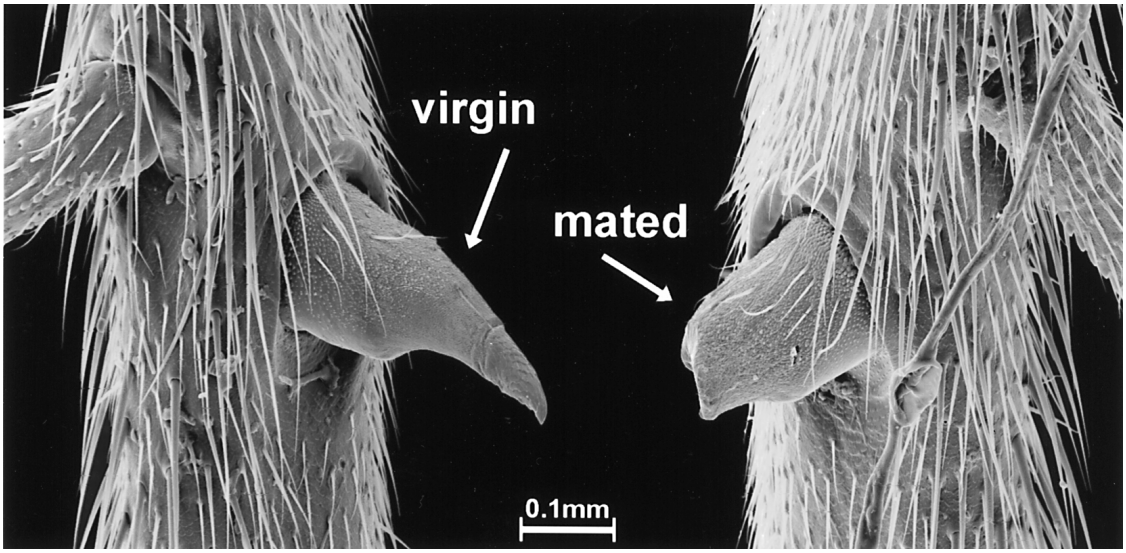


Fig. 1. The tibial spur. This specialized spur delivers a somatic nuptial gift directly to the female through courtship feeding. The spur on the right has been chewed by a female whereas the left is still intact indicating a male's previous mating success.

tion contained within the spur that is exuded once the tip is removed (Fulton 1931; Mays 1971; Forrest 1991). However, a preliminary study suggested that, when the spur tip is artificially amputated and a capillary tube attached, the volume of the extract exceeds the volume of the spur (unpublished data). Thus, the spur may provide females with direct access to the male's hemolymph, making male mass a potential limiting factor in gift contribution. This is important since the evolutionary trajectory of male body size and sexual size dimorphism may be modified if positive selection on the gift exists, coupled with a genetic correlation between body and gift size. Unfortunately, no mass measure of this or any other internally transferred nuptial gift exists.

Using the striped ground cricket,*Allonemobius socius* (Scudder), we attempted to quantify the magnitude of an internally transferred gift. We predicted that male *A. socius* donate more than a limited glandular contribution, and may offer females a continuous supply of hemolymph. Furthermore, we predicted that male contribution is constrained by male mass, with the largest males capable of offering the largest gift. Therefore, females should prefer large males if gift mass is positively related to male mass and to female fitness.

Materials and Methods

A. socius is a small chirping ground cricket found throughout the southeastern United States, with closely related sister taxa ranging throughout North America (Alexander & Thomas 1959; Howard & Furth 1986; Mousseau & Roff 1989). All crickets used in this experiment were second-generation lab-reared individuals originating from a single population near Asheville, North Carolina. Crickets were maintained in 10× 10 × 8 cm plastic cages containing ground cat food, a carrot slice, water vial and strips of brown paper towel for cover. Every three days the food, carrot and paper towel were replaced. Cages were kept in a constant environment at 28°C and a 12:12 [L:D] photoperiod provided by a Percival incubator. The age of all experimental crickets was held constant at 12 ± 2 days post eclosion.

A. socius males perform a calling song used to attract distant females. Once a potential mate is encountered, males switch to a courtship song and dance that culminates with the male orienting his abdomen toward the stationary female. If the female is receptive, she will briefly mount the male in a "mock copulation" lasting only a few seconds. Once an effective mock copulation is achieved (this may take several attempts) the male will cease courting and begin to form a spermatophore (approximately 20 min). When complete, he will renew his courtship behavior, again enticing the female to mount. At this time, the couple will adjoin abdomens as the male adheres the spermatophore to the female's genitalia. The male will then bring his hind tibia forward allowing the female to chew on his spur until the couple separates (upwards of 30 min). Once apart, the female will remove and consume the spermatophore. If a spermatophore is formed but not attached, no spur chewing will take place and the spermatophore will be removed and consumed by the male (Alexander & Thomas 1959; Mays 1971).

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Virgin males and females were randomly paired (n = 41 pairs), placed into a mating arena (6 cm diameter petri dish) and allowed to mate once. Although crickets mate multiply in the wild (Walker 1980; Sakaluk and Cade 1983), only one mating bout is needed to detect the mass changes used in estimating the size of the nuptial gift. Two groups were created depending on the outcome of the mating trial. Males who attached their spermatophore to the female were grouped as successful. Males who formed a spermatophore, but failed to re-attract a female for copulation were grouped as unsuccessful. In both cases, spermatophores were collected after removal to avoid consumption. Male, female and petri dish mass were recorded before and after each mating trial. The mass gain in the petri dish gave us a measure of mass loss due to defecation. In addition, spermatophore mass, trial duration, spermatophore attachment duration, tibial spur chewing duration, and post-chewing spermatophore attachment duration (i.e., the amount of time it takes the female to remove the spermatophore after chewing the tibial spur) were recorded. Since by nature of the mating ritual, a positive association between chewing duration and spermatophore attachment seems inherent, post-chewing spermatophore attachment duration was examined to assess whether larger gifts satiate females to where they will postpone removal and consumption of the spermatophore. Mass was measured using a Sartorius scale (Bohemia, NY) accurate to 0.01 mg. Trial duration was defined as the time elapsed from the onset of male courtship to the removal of the spermatophore by the female (successful) or the male (unsuccessful).

The mass of the gift contribution was estimated for each successful trial by taking the total change in male mass (Δm) and subtracting out the mass lost to defecation (Δp), spermatophore mass (s), and respiration (r), such that,

$$G_{[m]} = |\Delta m| - (\Delta p/2) - s - r \qquad \text{(eq. 1)}$$

The term Δp was halved since we assumed that the rate of defecation was equal between the sexes. To estimate r, we first estimated the average mass lost per minute, R, from the unsuccessful male data while controlling for defecation and spermatophore production,

$$R = \frac{\sum_{1}^{n} (|\Delta m| - (\Delta p/2) - s)/t}{n} \qquad \text{(eq. 2)}$$

where t is the duration of the trial. We assumed that R was equal for successful and unsuccessful males. Thus, for each successful trial, r was estimated by multiplying R by the duration of the mating trial, t. A second independent estimate of the nuptial gift, $G_{[f]}$, was based on female mass gain and obtained by substituting the change in female mass, (Δf), for (Δm) into equations one and two and dropping s. All data analyses were performed using SAS 8.1.

Results

Since the ejaculate contained within the spermatophore that is transferred directly to the female genitalia may confound our estimate of gift mass, we compared the mass of the successful male's depleted spermatophore (mean ± se: 1.03 ± 0.01 mg; n = 19) with the unsuccessful male's intact spermatophore (0.99 ± 0.07 mg; n = 22) to estimate ejaculate contribution. No difference existed between these two groups (one tailed t-test: $t_{39} = -0.93$, NS), suggesting that the ejaculate mass was negligible. There was no effect of male body size on spermatophore mass ($F_{1,39} = 2.07$, NS) or estimated respiratory mass loss ($F_{1,17} = 0.17$, NS). Average male mass was 77.55 ± 1.24 mg and the average $G_{[m]}$ was 1.89 ± 0.33 mg. Thus, the average nuptial gift was approximately 2.44% of the male's initial body mass. When coupled with average spermatophore size (1.03 ± 0.01 mg) males invested approximately 3.77% of their total mass into a single copulation. This is a large investment considering that males are promiscuous and that a substantial proportion of their mass is attributable to exoskeleton.

When we replaced Δm with Δf in equations one and two, average $G_{[f]}$ was estimated to be 1.01 ± 0.45 mg, providing a second, independent measure of gift size. Although this estimate is lower than the male estimate, they are not significantly different (two tailed t-test: $t_{36} = 1.53$, NS). Six $G_{[f]}$ estimates were negative (Fig. 2), and were most likely the result of the error inherent in the methodology used to estimate the mass lost to respiration, r. All six negative $G_{[f]}$ estimates were well within one standard deviation in r away from a positive estimate. As a consequence, our estimate of the average $G_{[f]}$ is conservative.

Since no difference existed between the successful and unsuccessful groups with regard to spermatophore mass (s), mass lost to defecation (0.58 ± 0.02 mg and 0.67 ± 0.02 mg, respectively; Δp two tailed t-test: $t_{39} = 0.52$, NS), and the duration of the trial (two tailed t-test: $t_{39} = -0.72$, NS), we calculated two additional estimates of gift mass, $G_{[lm]}$ and $G_{[lf]}$, using the least squares means difference in Δm and Δf between the two groups, respectively. These estimates were calculated because they are free of the error attributed to estimating mass lost to respiration and defecation. Since initial male mass was significantly associated with Δm ($F_{1,39} = 4.41$, $P < 0.05$), we used an analysis of covariance with initial male mass as the covariate (ANCOVA: $F_{2,38} = 14.75$, $P < 0.001$;

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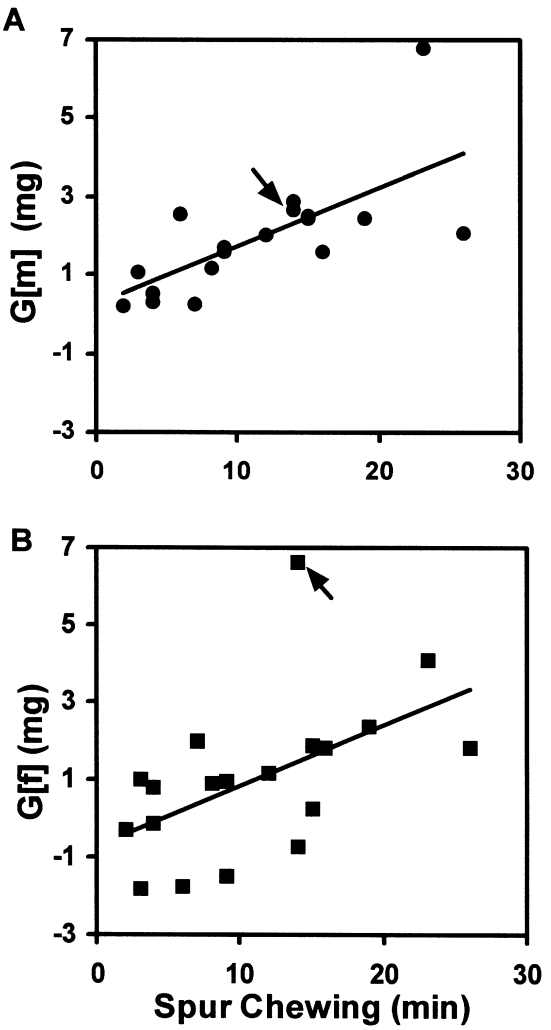


Fig. 2. Nuptial gift contribution as a function of spur chewing duration. A) As females chewed on the tibial spur, male gift contribution increased ($y = 0.1496x + 0.2444$, $R^2 = 0.50$). B) The relationship between female mass gain and courtship feeding also provided a rate of male contribution ($y = 0.1547x - 0.6922$, $R^2 = 0.28$). Both male ($G_{[m]}$) and female ($G_{[f]}$) estimates of the nuptial gift were controlled for mass lost to defecation, respiration and spermatophore production. The arrows indicate a potential outlier in the female $G_{[f]}$ estimate and the corresponding $G_{[m]}$ estimate.

no interaction between covariate and group). Using this method $G_{[lm]}$ was estimated to be 1.75 mg. Likewise, $G_{[lf]}$ was estimated to be 1.28 mg. Considering that the tibial spur weighs less than 0.001 mg, these estimates suggest that the gift far exceeds the capacity of the spur. Moreover, these gift estimates exceed the weight of the entire male tibia (0.75 ± 0.05 mg), implying that the gift is comprised mostly or entirely of hemolymph.

Chewing duration covaried with both the male estimate (Fig. 2a; $G_{[m]}$: $F_{1,17} = 17.02$, $P < 0.001$) and the female estimate (Fig. 2b; $G_{[f]}$: $F_{1,17} = 6.67$, $P < 0.05$) of the nuptial gift implying that females who chewed longer received a larger gift contribution. The size of the gift ranged from 0.2% to 8% of initial male mass. Although, the rate of male gift contribution and female gift gain (Fig. 2) were not significantly different ($F_{1,16} = 2.12$, NS), $G_{[f]}$ exceeded $G_{[m]}$ in four trials. In three of these trials the differences were small and, as with the negative estimates of $G_{[f]}$, fell well within 1 standard deviation of our estimate of *r*. The remaining trial discrepancy showed female mass gain to be 3.94 mg greater than the male contribution, and cannot be reconciled with the previous argument suggesting that it may be the result of measurement error. However, when this observation was removed, the relationship between chewing duration and $G_{[m]}$ and $G_{[f]}$ remained unchanged ($F_{1,17} = 15.68$, $P < 0.001$, $R^2 = 0.50$ and $F_{1,17} = 10.21$, $P < 0.01$, $R^2 = 0.40$, respectively).

In addition, male mass was significantly associated with spur chewing duration (Fig. 3: $F_{1,17} = 4.24$, $P = 0.05$) implying that larger males provide a larger gift. In turn, spur chewing duration was significantly associated with spermatophore attachment duration ($F_{1,17} = 4.51$, $P < 0.05$), which is expected since the spermatophore is attached at the onset of spur chewing. However, chewing duration was not associated with post-chewing spermatophore attachment duration ($F_{1,17} = 0.06$, NS), implying that females do not delay removal of the spermatophore if a larger gift is received.

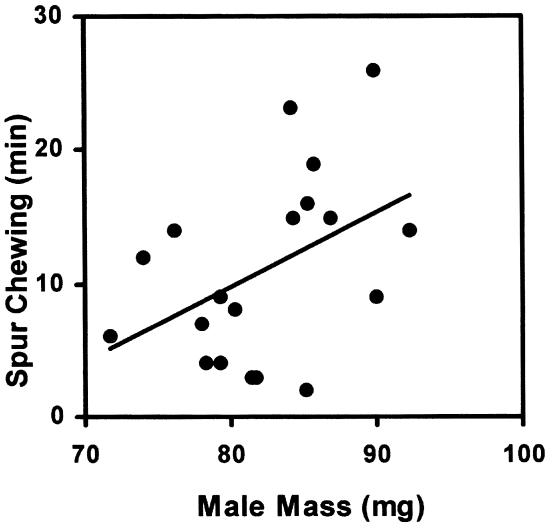


Fig. 3. Spur chewing duration as a function of male mass. Large males were chewed longer than small males ($y = 564.18x - 35.419$, $R^2 = 0.20$) suggesting that male size may ultimately constrain gift size.

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Successful males were significantly larger than unsuccessful males ($F_{1,39} = 4.76$, $P < 0.05$). This may be the result of female choice or a mechanical constraint of small male size. In crickets, copulation may be impeded if the size difference of a mating pair is too great, making proper genitalic alignment and spermatophore transfer difficult (Sakaluk, pers. comm.). However, there was no distinction between successful and unsuccessful males with regard to male and female size differences ($F_{1,39} = 1.28$, NS), suggesting that large male success was not due to small male inability in passing a spermatophore, but perhaps to female preference for larger mates.

Although chewing duration was related to both male mass and estimated gift mass, male mass and gift mass were not directly related. To further investigate the relationship between body and gift mass, we separated the successful males into two groups, large and small, based on their mass relative to the mean (82.30 ± 1.27 mg). The ten males who fell below the mean were placed into the 'small male' group, and the nine males who fell above the mean were placed into the 'large male' group. On average, larger males were chewed upon twice as long and provided nearly twice as much gift as did smaller males (chewing duration: 15.46 ± 2.38 min vs. 7.01 ± 1.20 min, $t_{17} = -3.27$, $P < 0.01$; gift donation: 2.52 ± 0.59 mg vs. 1.33 ± 0.28 mg, $t_{17} = 1.88$, $P < 0.05$, respectively. T-tests were one tailed). Using this analysis, male mass was significantly associated with gift mass, suggesting that the magnitude of the nuptial gift may be constrained by male size.

Discussion

In ground crickets (Neonemobius sp.), females are attracted to larger males and this preference was previously speculated to be based on the male's ability to provide a larger nuptial gift (Forrest et al. 1991). In this study, we have shown that larger males are more successful at attracting and copulating with females. More importantly, we have shown that male mass was positively associated with the magnitude of gift contribution, providing a mechanism for the maintenance of female preference. This body size and gift size relationship coupled with sexual selection on gift size via female choice may have profound evolutionary implications.

In insects, the common pattern of female-biased size dimorphism is usually attributed to the reproductive advantages of being large (Shine 1988). However, if gift mass is related to female fitness, then the strength of size selection on males may surpass females, eventually increasing male size and modifying degree of dimorphism (e.g., Leimar et al. 1994). An association between gift mass and female fitness is common in Orthoptera (Gwynne 1983, 1984; Brown 1997; Calos & Sakaluk 1998; Reinhold 1999). However, an association between male mass and gift mass is not (Wedell 1997), though an association between male mass and a spermatophylax gift/sperm ampulla complex has also been shown in some species (Gwynne 1982; Sakaluk 1985). To elucidate the implications of the nuptial gift on male size evolution in this system, we are presently examining the impact of gift mass on female fitness along with the selective pressures and underlying genetic architecture surrounding these traits.

Currently, it is unknown whether gift mass is shaped through male mating effort (e.g., by increasing sperm transfer) or paternal investment (i.e., by increasing the number and fitness of the gift givers offspring). Our data suggest that mating effort is a plausible hypothesis since gift size (i.e., chewing duration) was highly associated with spermatophore attachment duration. These results run contrary to a previous study by Bidochka and Snedden (1985) that examined mating behavior in a closely related sister species, *Allonemobius. fasciatus*. In this study female access to the tibial spur was manipulated through three treatments (spur covered, surrounding spur area covered—spur uncovered, and spur uncovered) and subsequent copulation duration (an approximation of chewing duration and hence nuptial gift size) and spermatophore attachment duration recorded. They found that females who were denied access to the spur had a significantly shorter copulation duration than the other two treatments. In addition, they concluded no association between treatment and spermatophore attachment duration. However, if we compare the published summary statistics for the covered (16.72 ± 3.59 min, n = 30) and uncovered treatments (29.26 ± 5.35 min, n = 19) only, they are significantly different (two tailed t-test: $t_{47} = -2.023$, $P < 0.05$), suggesting that spermatophore attachment duration may be related to copulation duration in *A. fasciatus*, supporting our results.

In the wild, male and female ground crickets are promiscuous and mate with numerous individuals throughout the breeding season, exceeding the mating rate necessary to continually produce offspring prior to senescence. Promiscuous behavior often carries associated costs including increased time and energy expenditure (Thornhill & Alcock 1983), increased predation risk (Arnqvist 1989), increased disease susceptibility (Hurst et al. 1995), and/or caustic seminal fluids that potentially reduce fitness (Fowler & Partridge 1989; Rice 1996). The large size of the nuptial gift in *A. socius* described here provides the opportunity for these costs to be offset by increasing female fitness through increasing reproductive rate, reproductive longevity or fecundity. Associations between gift size and female reproductive fitness components are common in insects (Gwynne 1984; Andersson 1994).

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Currently, the contents of the gift in *A. socius* are unclear though our data suggest it is mostly hemolymph and not simply a limited glandular secretion. Other systems have shown that nuptial gifts may contain oviposition inducing hormones (Friedel & Gilliot, 1977), or act as indicators of important male chemical resources that may affect offspring fitness (Eisner et al. 1996). Considering the relationship between gift size, male size and large male mating success in our data, gift quantity may be more important than gift quality.

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