

Size dependence of courtship effort may promote male choice and strong assortative mating in soldier beetles

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Abstract Large males of the soldier beetle, *Chauliognathus pennsylvanicus* (Cantharidae), exercise choice for larger females in the field and laboratory. The length of copulation limits the maximum mating rate to once per day. This may afford more competitive males the opportunity to reject females early in the day without significantly reducing their mating rate. Males copulate if they secure evasive females. Body size correlates with the abilities of males to secure females, and of females to evade males. Thus, agonistic courtship gives larger males a mating advantage and may ensure the availability of larger females late into the daily courtship period. Also, larger males spend more time searching for mates and courting than do smaller males which could increase their likelihood of encountering and mating a large female, even after rejecting a smaller one. Stochastic simulations of agonistic courtship indicate that the benefits of male choice are limited to larger males, who are more likely to successfully court a female after having rejected one. Simulations also indicate that strong assortative mating, as observed in the field, requires male choice in combination with agonistic courtship. Both males and females benefit from larger mates, as the fecundity of females is a function of both their own size and the size of their mates. Thus, strong assortative mating magnifies the fecundity advantage of large females through mate effects on fecundity.

Keywords Male choice · Material rewards · Stochastic simulation · Assortative mating

Introduction

Theory suggests that male mate choice can be favored on the basis of direct benefits that females provide (Servedio and Lande 2006; South et al. 2012). For example, males could choose females on the basis of fecundity if fecundity varies greatly among females (Johnstone et al. 1996; Bonduriansky 2001; Edward and Chapman 2011). Males could also use the threat of sperm competition as a basis of choice (MacLeod and Andrade 2014). Yet, male mate choice is rare in polygynous species (Darwin 1871; Andersson 1994; Johnstone et al. 1996) although taxonomically widespread (Myhre et al. 2012). The rarity of male choice may be a consequence of its effect on the mating rate which can be reduced when potential mates are rejected in favor of searching for mates of more preferred phenotypes (Barry and Kokko 2010). Consequently, male choice may limit the total number of matings, which is typically the major determinant of male fitness (Arnold and Duvall 1994; Bonduriansky 2001).

Males are expected to be increasingly unlikely to reject a potential mate with increases in the operational sex ratio (OSR), the number of mating-ready males to mating-ready females (Emlen and Oring 1972). This is because competition between males for mates intensifies with the OSR, making the replacement of a rejected mate ever more unlikely (Bonduriansky 2001; Barry and Kokko 2010). The OSR reflects sex differences in the costs of successive reproductive episodes (Clutton-Brock and Vincent 1991; Clutton-Brock and Parker 1992; Kokko and Johnstone 2002). Thus, the sex investing more will be underrepresented among mating-ready individuals because a longer recovery period is required

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between episodes (Emlen and Oring 1972; Gwynne and Simmons 1990; Kokko and Monaghan 2001). Consequently, members of the overrepresented sex must compete for mating partners (Emlen and Oring 1972; Kvarnemo and Ahnesjö 1996; 2002).

In species with conventional sex roles (Kokko and Johnstone 2002; Myhre et al. 2012), the OSR is male-biased (Clutton-Brock and Parker 1992; Emlen and Oring 1972), males invest less in offspring production and care, and male fitness is primarily a function of the number of females mated (Bateman 1948; Trivers 1972). Yet, male choice occurs in some such species (Myhre et al. 2012).

Male choice can be favored by high parental investment (Johnstone et al. 1996; Kokko and Monaghan 2001; Edward and Chapman 2012). In insects, this often includes energy provided via a nutritional spermatophore or sperm-associated fluids (Thornhill 1976; Gwynne 1984, 1990; Simmons 1988; Fairn et al. 2007; South and Lewis 2011) which results in enhanced fecundity (South and Lewis 2011). Such investment by males raises the cost of mating and lowers their potential reproductive rate. As the potential reproductive rate decreases, the value of choosing among potential mates increases (Edward and Chapman 2012).

Theoretical investigations indicate that male choice could also be favored via a positive genetic correlation between male choosiness and courtship (Servedio and Lande 2006). While this is considered unrealistic (Servedio and Lande 2006), it suggests that selection could favor an allele causing facultative mate choice. In this case, expression of the allele would be limited to males in good condition who would be able to court more frequently or with more effort than males in poor condition (Edward and Chapman 2011; Bertram and Rook 2012). Condition-dependent male choice could also be favored if females prefer males who court more vigorously (Edward and Chapman 2011; South et al. 2012). Condition-dependent male mate choice would reduce the cost of being a choosy male. This is because males more likely to reject a female are also those males more likely to successfully court another female (e.g., Amundsen and Forsgren 2003).

In insects, the basis of condition-dependent mate choice could be body size. Body size can reflect courtship vigor (Kence and Bryant 1978; McCauley 1981) and is determined by one or more of a variety of non-genetic factors. Factors include the quality of the diet (Kelly et al. 2014; Vijendravarma et al. 2011; Jiménez-Cortés et al. 2012), exposure to diseases (Kelly et al. 2014), thermal and desiccation stresses during juvenile stages, and foraging ability (Bertram and Rook 2012).

In this study, we investigate male and female choice in the soldier beetle, *Chauliognathus pennsylvanicus* Hentz (Coleoptera: Cantharidae) in the laboratory and field. We examine whether the fecundity advantage of male choice is a function of male body size, a common reflection of male

condition (Kelly et al. 2014). We predict male choice will be more likely in larger males when courtship is agonistic because larger males will have greater opportunity to successfully court larger, more fecund females. Also, we use stochastic simulations to elucidate both the circumstances favorable to male choice and the impact of male choice on assortative mating.

Mutual mate choice, the concurrence of male and female choice, may explain some examples of size assortative mating (Crespi 1989; Hoefler 2007; Ludwig and Becker 2008; Pryke and Griffith 2007). This is of interest, even if size lacks significant heritability, because assortative mating could (1) increase the variance in reproductive success, (2) impact the strength of selection on the current mating system, (3) reduce the effective population size, (4) affect the distribution of maternal benefits, and (5) promote disequilibrium with respect to alleles underlying male and female mate preferences.

Laboratory experiments (McLain 2005) and mark-recapture studies (McLain 1986) reveal that male and female soldier beetles mate approximately daily during the peak of their reproductive season, which extends from September to early October. At our field site in northern Georgia, agonistic courtship occurs during the afternoon, primarily on flowers of goldenrod (*Solidago* spp.; McLain 1988). Males engage in short flights to search for foraging females. After a male lands near a female, a chase may ensue in which the male uses his antennae and forelegs in an attempt to capture the female (Mason 1980). Once a female is captured, some wrestling often follows as the male attempts to mount the female, who may kick at him, shake violently in an apparent attempt to dislodge him, or curl her abdomen away to avoid genital contact. The same evasive manoeuvres of females have been observed in some other insects with agonistic courtship (e.g., Kence and Bryant 1978; McLain 1992; Weall and Gilburn 2000; Dunn et al. 2001).

In soldier beetles (Mason 1980; McCauley and Wade 1978), as in other species exhibiting similar courtship (e.g., Teder 2005; Fairn et al. 2007), females evade some suitors but copulate with those capable of capturing and maintaining hold of them. Evasive behavior by female soldier beetles biases copulations toward males who are relatively large (McCauley and Wade 1978; McCauley 1981; McLain 1982). We address if a mating advantage by size could promote size-dependent male choice.

Material and methods

Field site, observations, and measurements

The study was conducted in late September to early October of 2006–2012. The field site was a 3-ha field near Cornelia, GA (USA), in the foothills of the Blue Ridge Mountains.

Soldier beetles were observed on the leaves, stems, and flowers of goldenrod that grew profusely at the site. Soldier beetles were sexed visually. Each year, mating and non-mating individuals were collected. Elytron length, the index of body size, was measured with an engineering ruler to the nearest 1/8 mm. In most years, we also either observed activities or observed courtship encounters. In these cases, body size was assessed visually and categorized as very small, small, medium, large, or very large. These categories refer, respectively, to elytron lengths in the following size ranges (mm): ≤ 7.500 , $7.625\text{--}7.750$, $7.875\text{--}8.125$, $8.250\text{--}8.375$, and ≥ 8.500 . Throughout, ascription of size as very small, small, medium, large, or very large refers to these size ranges while the terms smaller and larger refer to all size ranges below or above the medium size range of $7.875\text{--}8.125$ mm.

Mate choice in the laboratory

A laboratory study investigated male mate choice as a function of male size. Single males were transferred to 1-l mason jars filled with goldenrod flowers and stems and containing two females, one very large (≥ 8.500) and one small ($7.625\text{--}7.750$ mm). Males were either of small ($7.625\text{--}7.875$ mm; $N=50$) or very large size (≥ 8.500 mm; $N=50$). After 6 h, mating pairs were removed and the size of the mating females was determined. Due to the abundance of plant material in jars, males did not encounter females simultaneously (confirmed by observation). Experimental males were only able to mate once because of the long duration of copulation (see result on copulation duration). Males had not been kept in the laboratory prior to their use in experiments. Experimental females had not been exposed to males for four days to ensure their readiness to mate. A preliminary study had indicated that isolation from males caused both small and very large females to relax their resistance to courtship. In the preliminary study, 30 small and 30 very large females were housed individually in jars and kept without a male for 0, 1, 2, 3, or 4 days since their last mating. A single male, either small or very large, was then introduced into each jar and given 6 hours to initiate copulation. The number of small males mating (out of six) was one, three, five, six, and six after 0, 1, 2, 3, and 4 days of female isolation ($\chi^2=12.804$, $DF=1$, $P<0.001$ comparing 0–1 days of isolation to 2–4 days of isolation). The number of large males mating (out of six) was four, four, six, six, and six after 0, 1, 2, 3, and 4 days of female isolation. Thus, all females became receptive to both small and very large males after 3–4 days without mating.

Mating in the field

Each year, from 1800 to 1900 hours, mating pairs and singletons (non-mating individuals) were plucked from goldenrod flowers, leaves, and stems and measured. At this time, the

proportion of mating individuals peaked. At approximately 1800 hours, mate search flights by unmated males ceased. At approximately 1900 hours, individuals moved from the tops of plants to overnighting positions nearer the ground. Thus, collections from 1800 to 1900 hours provide the least biased survey of mating success during the daily courtship period, provided that copulations initiated earlier in the day were still ongoing (see results in “Copulation duration”).

Copulation duration

In 2006, collections of mating pairs were made to determine if the duration of copulation limits the number of matings to a maximum of one per daily courtship period. We collected a dozen mating pairs at noon and another dozen pairs at 1830 hours. Each pair was sequestered in its own 1-l mason jar containing a goldenrod branch. Subsequently, from the time of collection until 1000 hours the next morning, each pair was checked to determine mating status. All pairs were collected from the same 4-m^2 patch of goldenrod. The patch contained no mating pairs prior to 1100 hours and none immediately after the noon collection. As soldier beetles do not fly while copulating, we are confident that all pairs collected initiated copulation between 1100 and 1830 hours.

Courtship rate versus body size

To determine if size affects the likelihood of engaging in vigorous activity, we noted the activities of individuals across the period of daytime activity. Beetles were observed in 2 years (2008 and 2010). These behavioral categories were noted: (1) inactive (alone and not moving, on a stem or leaf), (2) foraging (feeding on pollen or ambulating between flower clusters), (3) mate searching (repeating the sequence: fly, land, run), and (4) courting (male mounts or attempts to mount the female) or mating (copulating). The data was analyzed with a log-linear model with year, body size (five categories, see above), time of day (1000–1430 or 1430–1900 hours) and activity as levels. Activity assays were conducted while moving through the field site to eliminate the possibility of counting the same individual twice.

Courtship persistence and male choice

Courtship persistence was assessed in 2011 via the responses of males after a female had been contacted. Male courtship effort was considered persistent if the male did either of these: (a) reengaged the female once dislodged or kicked away or (b) chased after a fleeing female. Courtship was not considered persistent if the male did neither. Male and female sizes were categorized visually as described previously. Courtships ($N=314$) were observed in the early afternoon (1200–1400 hours).

Some observed courtships were terminated after the male secured the female but then apparently chose to abandon her. We ask if abandonment was associated with particular combinations of male and female size category (see above). Size categories were ranked as follows: very small=1, small=2, medium=3, large=4, and very large=5. The difference, rank in male size category–rank in female size category, was tested for its effect on the likelihood of abandonment.

Stochastic simulations

Stochastic simulations of courtship encounters and mate pairing were run using modules in Systat 10.2 (SYSTAT Software, Inc., Richmond, CA). Simulations were used to examine when male choice is beneficial and to evaluate the impact of evasive courtship and male choice on assortative mating. Simulations used 1026 females and either, 1026, 1539, 2052, 2565, or 3078 males. Thus, the OSR ranged from 1.0 to 3.0 in increments of 0.5. Each sex had a mean size of 8.000 mm (range 6.500–9.500 mm, in 0.125-mm increments) and was normally distributed with a SD=0.500 mm. This closely approximated typical field conditions (see below).

To simulate courtship via female evasion, male elytron lengths, arrayed in one column, were randomized then placed adjacent to female elytron lengths arrayed in another column. A mating was considered to have occurred if the male size in a row equaled or exceeded the female size. Thus, the largest female that a male of given size can mate is a function of his size, which accords with field observations (McCauley 1981). Mating pairs were removed from the population. Then, the order of unmated males was re-randomized, followed by another round of encounter and possible mating. Every unmated female encountered a single male in an encounter round. However, as the number of males often exceeded that of females (i.e., when OSR > 1), in any given round, some unmated males failed to encounter females.

In some cases, male choice was simulated by not permitting a mating if male size–female size > 1.000 mm. This approximates field results of the current study. For instance, when male size–female size was 0.63 mm or less, only 7.2 % of males rejected females but when the difference was 0.88 or more, 70.8 % were rejected. In simulations, if a female was rejected, each individual remained in the subset of individuals engaged in the next round of random pairing. Thus, sometimes the choosy male was faced with the decision to accept a female with whom he could mate or to reject her in favor of searching for another female. Should the male accept the female, his fitness would be F_{current} , the fecundity the female would realize were she to mate the male. Should the male reject the female in favor of searching for another, his fitness would be pF_{future} , where p is the probability of encountering another female with whom he could mate and F_{future} is

the fecundity of that female were the male to mate her. Thus, rejecting a female is favored when $pF_{\text{future}} > F_{\text{current}}$, or when $p > F_{\text{current}}/F_{\text{future}}$. Fecundities are determined from the statistical model derived from laboratory matings (see below). Simulations provide insight into both (1) how the size (and size-dependent fecundity) of yet-to-be mated females changes over a daily courtship period, and (2) the probability that a male will mate after rejecting a female.

Also, there were cases in which we simulated the amount of mate search effort as a function of male size. In these cases, a male was included in the subset of courting males in any given round only if the sum of his size plus that of a random number (with equal likelihood, either 0, 0.5, 1, 1.5, 2.0, or 2.5) was ≥ 9.000 . Five simulations were run for each combination of OSR, male type (choosy or not), and whether or not male size determined search effort. Pooled results are presented for each combination as there was very little variation between simulations sharing the same parameter set.

In preliminary studies, the number of rounds of encounter was varied from 1 to 50. However, little was gained in terms of number of matings beyond 12 rounds. Therefore, we present results for 12 rounds. By having all unmated females encounter a male in each round, we assume that densities and male search behaviors are sufficient to ensure courtship encounters. This assumption is justified below.

Fecundity and mate size

A laboratory experiment explored the effect of mate size on the fitness component, fecundity. Seventy-five females of differing size were individually isolated into mason jars and supplied daily with a fresh single flowering stem of goldenrod. Females were held for 1 week without a male. Then, a single male, chosen at random with respect to size, was introduced. The male was removed after a single copulation and reintroduced for a single copulation in each of the next 3 weeks. Egg production was tallied over 4 weeks for 71 females who survived. The multiple contributions to fecundity (= sum of all eggs produced) of male and female size was tested with linear regression.

Results

Male choice in the laboratory

In the laboratory, small and large males differed significantly in the females they mated ($\chi^2=7.875$, DF=1, $P=0.005$). Smaller males mated females at random with respect to size ($\chi^2=0.091$, DF=1, $P=0.763$), mating with the larger female in 21 of 44 cases. In contrast, large males appeared to exercise a preference, mating with the larger female in 31 of 40 cases ($\chi^2=12.100$, DF=1, $P=0.001$).

Mating in the field

Female size (elytron length) was significantly greater for mating (mean=7.950, SD=0.424; $N=421$) than non-mating individuals (mean=7.833, SD=0.529, $N=288$; $F=6.522$, $DF=1$, 695 ; $P=0.011$). Female size varied between years ($F=15.564$, $DF=6,695$, $P<0.001$) as did the magnitude of the effect of mating status (interaction, mating status \times year: $F=8.968$, $DF=6,695$, $P<0.001$). Similarly, among males, those mating (mean=8.082, SD=0.399, $N=421$) were larger than those not mating (mean=7.700, SD=0.497, $N=432$; $F=66.744$, $DF=1$, 839 , $P<0.001$). Male size also varied between years ($F=12.358$, $DF=6,839$, $P<0.001$). The magnitude of the effect of mating status varied between years (interaction: $F=5.433$, $DF=6,839$, $P<0.001$). In general, the effect of mating status was greater in females when male size was larger relative to female size and greater in males when female size was larger relative to male size.

Mating pairs did not occur at random with respect to the sizes of males and females (Fig. 1; $\chi^2=221.474$, $DF=16$, $P<0.001$).

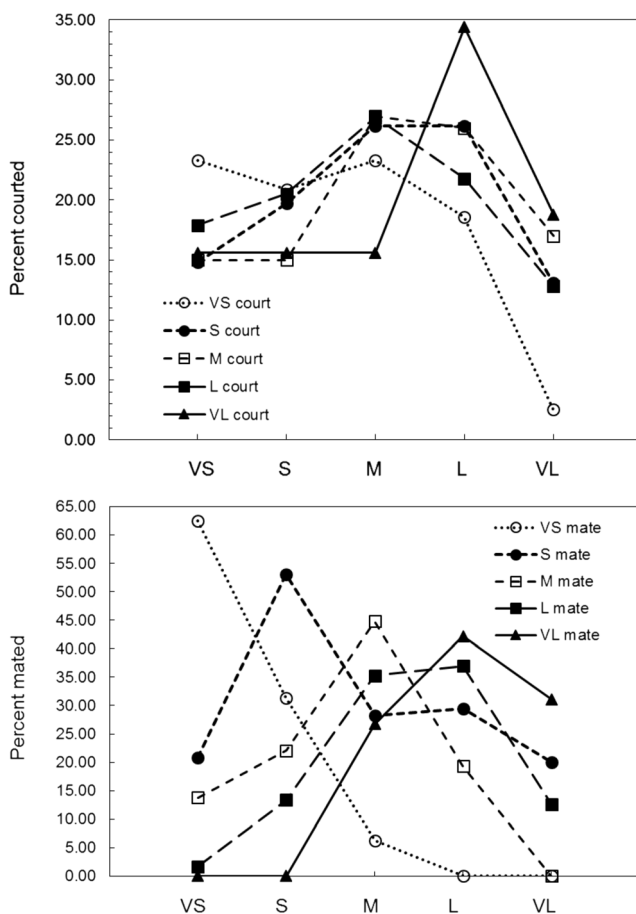


Fig. 1 Percent of females courted (*upper panel*) and mated (*lower panel*) by males of each size category as a function of female size category (X -axis). Size category (associated elytron lengths): *VS* very small (≤ 7.500 mm), *S* small (7.625–7.750 mm), *M* medium (7.875–8.125 mm), *L* large (8.250–8.375 mm), *VL* very large (≥ 8.500 mm)

For example, 34.80 % of courtships of large and very large males were with very small and small females, but only 7.55 % of matings by these males were with very small and small females. Among mating pairs, male and female size was strongly correlated ($r=0.669$, $t=18.437$, $P<0.001$, $N=421$).

Copulation duration

All 24 mating pairs collected in early and late afternoon copulated continuously until at least 1000 hours the next morning. However, none were mating at 1100 hours when they were released into the goldenrod patch where they were collected.

Courtship rate

In the field, the activity of males varied by time of day (Fig. 2; $\chi^2=337.45$, $DF=3$, $P<0.001$), year (Fig. 2; $\chi^2=98.68$, $DF=3$, $P<0.001$), and male size category (Fig. 2; $\chi^2=271.67$, $DF=$

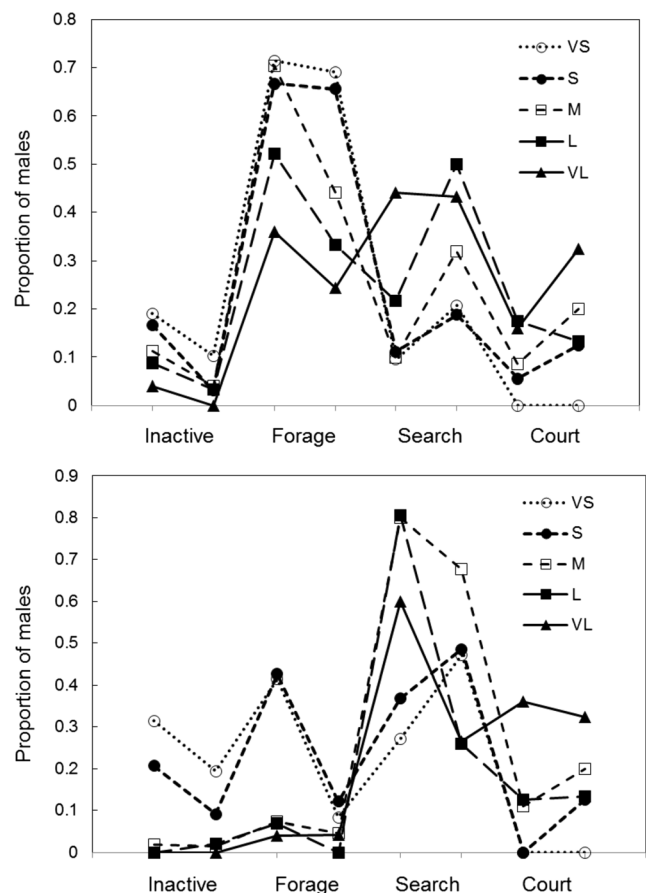


Fig. 2 Proportion of males engaged in various activities as a function of size category early (*upper panel*) and late (*lower panel*) in the daily courtship period. Size category (associated elytron lengths): *VS* very small (≤ 7.500 mm), *S* small (7.625–7.750 mm), *M* medium (7.875–8.125 mm), *L* large (8.250–8.375 mm), *VL* very large (≥ 8.500 mm). For each activity, the left value is for the year 2008 while the right value is for the year 2010. The activity label “court” represents both courting and mating

12, $P < 0.001$). Males were more likely to rest or forage earlier in the day and to search for mates or engage in courtship later in the day. Large and very large males were far more likely to court females than were smaller males. Very small and small males were much more likely than larger males to rest or forage. Variation between years primarily involved the relative number of courtships and matings observed versus the number of mate searches observed.

Courtship persistence

Courtships were initiated at random with regard to body size (Fig. 1). Thus, the frequency with which females of a given size category were courted was independent of the male size category of courting males ($\chi^2 = 7.356$, $DF = 16$, $P = 0.966$). On average, the size category of males who engaged in persistent courtships was larger than for males who engaged in courtships that were not persistent (Kruskal-Wallis test, $\chi^2 = 35.868$, $DF = 1$, $P < 0.001$; Table 1). Male persistence in courtship also varied with female size. Males were less likely to be persistent when courting females of larger size categories ($\chi^2 = 5.269$, $DF = 1$, $P = 0.022$). This weak effect appears to reflect the tendency of smaller males to court larger females less persistently (Table 1). For instance, among very small males, persistent courtships were more likely to involve smaller females (Kruskal-Wallis test, $\chi^2 = 7.392$, $DF = 1$, $P = 0.007$; Table 1).

Males were more likely to abandon a courted female as the difference in rank by size category increased (Kruskal-Wallis test, $\chi^2 = 34.584$, $DF = 1$, $P < 0.001$; Fig. 3). For example, the female was abandoned in only one of 126 courtships in which the male rank was smaller than that of the female. However, the female was abandoned in 49 of 116 courtships in which the male rank was larger. Large and very large males were responsible for 22 of 29 cases of mate abandonment (=75.9 %) although they represented only 33.8 % of courting

Table 1 Number of courtships that were not persistent (left number) and that were persistent (right number) as a function of male and female size category

Females	VS	S	Males	L	VL	Female sum
			M			
VS	3/6	2/3	0/6	0/6	0/0	5/21
S	2/6	5/6	1/12	0/7	0/4	8/35
M	5/5	5/10	6/18	0/19	0/3	16/55
L	5/0	7/7	4/21	2/13	0/7	18/51
VL	6/0	3/5	6/11	2/7	1/5	18/28
Male sum	21/20	22/31	17/68	4/52	1/19	65/190

VS very small (≤ 7.500 mm), S small (7.625–7.750 mm), M medium (7.875–8.125 mm), L large (8.250–8.375 mm), VL very large (≥ 8.500 mm)

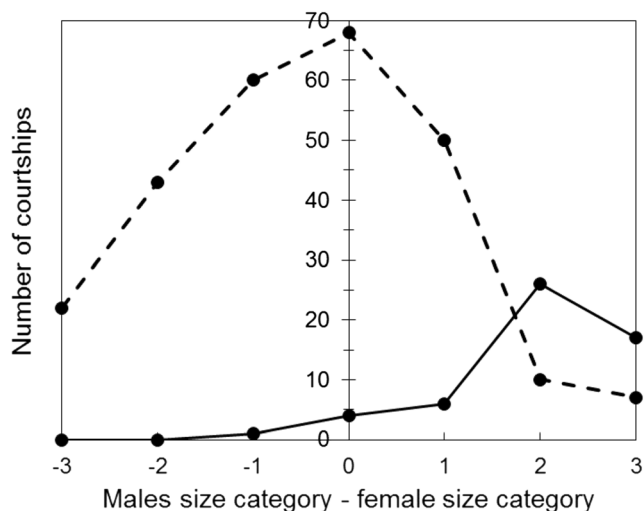


Fig. 3 Number of courtships in which the female was (solid line) or was not (dashed line) abandoned by the male as a function of the difference, rank male size category–rank in female size category. Size category (associated elytron lengths) and rank: very small (VS, ≤ 7.500 mm)=1, small (S, 7.625–7.750 mm)=2, medium (M, 7.875–8.125 mm)=3, large (L, 8.250–8.375 mm)=4, very large (VL, ≥ 8.500 mm)=5

males. Small and very small females were 65.5 % of those abandoned but were only 35.0 % of those courted.

Stochastic simulations

Stochastic simulations revealed that modest positive assortative mating by body size, measured by the correlation between mate sizes, can result when (1) encounters between potential mates are random with respect to body size and (2) the largest female that can be mated is a positive function of male size (Table 2). The correlation increased with the OSR (Table 2). For any OSR, the correlation was reduced when the frequency with which males engaged in courtship (search effort) was determined by body size and was increased when males exercised mate choice (Table 2). Both the size of mating males and females, and female fecundity (based on the equation determined from laboratory results; see below) increased slightly with the OSR (Table 2). The number of females mating increased much with the OSR and slightly with male choice (Table 2).

Simulations indicated that, when male size does not impact search effort, male choice is only beneficial for males of size ≥ 8.000 at $OSR = 1$ and for males of size ≥ 8.375 at $OSR = 1.5$. However, when size determines search effort, male choice can be beneficial at for some males up to $OSR = 2.5$. Thus, at $OSR = 1, 1.5, 2,$ and 2.5 male choice is beneficial, respectively, for male sizes of $\geq 8.125, \geq 8.375, \geq 8.750,$ and ≥ 9.000 . Choice was differentially favored for very large males because of high probabilities of mating after rejecting a female. Fecundity gains ($F_{future} - F_{current}$) varied less by male size than did p .

Table 2 Simulation results for the Pearson's correlation (r) between mate sizes, the mean sizes of mating males and females, and mean fecundity versus the OSR, the presence or absence of male choice, and whether or not male size determines the likelihood of courtship

OSR	Male choice	Size effect on courtship rate	r	Male size	Female size	Fecundity	Number
1.0	No	No	0.430	8.222	7.776	118.247	3570
1.0	Yes	No	0.732	8.185	7.183	118.734	3795
1.0	No	Yes	0.195	8.264	7.721	117.320	3333
1.0	Yes	Yes	0.675	8.209	7.763	117.699	3607
1.5	No	No	0.493	8.293	7.856	121.493	4185
1.5	Yes	No	0.753	8.251	7.833	121.656	4376
1.5	No	Yes	0.224	8.338	7.815	121.003	4006
1.5	Yes	Yes	0.721	8.278	7.875	121.781	4344
2.0	No	No	0.500	8.330	7.889	122.931	4448
2.0	Yes	No	0.765	8.276	7.910	122.731	4582
2.0	No	Yes	0.438	8.367	7.887	123.429	4447
2.0	Yes	Yes	0.748	8.311	7.921	123.555	4661
2.5	No	No	0.407	8.297	7.992	123.532	4576
2.5	Yes	No	0.769	8.285	7.923	123.229	4668
2.5	No	Yes	0.423	8.389	7.909	124.370	4604
2.5	Yes	Yes	0.754	8.335	7.936	124.307	4757
3.0	No	No	0.554	8.353	7.916	124.024	4629
3.0	Yes	No	0.769	8.279	7.920	123.201	4633
3.0	No	Yes	0.486	8.407	7.927	125.105	4718
3.0	Yes	Yes	0.759	8.341	7.939	124.477	4783

An example of these characteristics is provided for males at OSR=1 (Table 3).

Fecundity and mate size

The fecundity of laboratory females was correlated ($R^2=0.600$) with both their size ($t=8.560$, $N=71$, $P<0.001$) and that of their mates ($t=4.110$, $N=71$, $P<0.001$). The statistical model was $\text{fecundity} = 57.919 + [(\text{female size} - 6.500) \times 27.754] + [(\text{male size} - 6.5) \times 14.470]$. Subtracting 6.500 from sizes converts them to increments above the minimum size observed. Thus, the smallest female, mated to the smallest male, would be expected to oviposit about 58 eggs in 4 weeks. In contrast, the largest female mated to the smallest male would have an expected fecundity of about 141 eggs. The model suggests that, on average, increases in male size result in about half the gain in fecundity as increases in female size (i.e., $14.470/27.754$).

Discussion

Male mate choice

Our laboratory study reveals that in soldier beetles, female fecundity correlates with female body size, as in other insects (Honek 1993; Tammaru and Haukioja 1996; Sokolovska et al.

Table 3 Pooled simulation results for male choice under agonistic courtship at an OSR = 1

Male size	N	Rejections/male	P	Gain	Cost
7.625	385	0.013	0.258	5.317	55.042
7.750	450	0.042	0.291	6.883	55.208
7.875	490	0.031	0.372	9.640	51.057
8.000	510	0.037	0.693	18.677	26.491
8.125	490	0.065	0.912	25.972	8.007
8.250	450	0.120	0.995	21.205	0.538
8.375	385	0.260	1.000	11.823	0.000
8.500	310	0.319	1.000	14.612	0.000
8.625	235	0.583	1.000	13.488	0.000
8.750	165	0.782	1.000	13.933	0.000
8.875	115	1.078	1.000	13.391	0.000
9.000	75	1.213	1.000	20.191	0.000
9.125	40	1.425	1.000	17.194	0.000
9.250	20	2.150	1.000	18.873	0.000
9.375	15	4.067	1.000	14.737	0.000
9.500	10	7.200	0.900	11.540	14.401

Male size = sizes of males able to reject females. N = number of males. Rejections/male = mean number of times a female was rejected across 12 rounds of random encounter. P = proportion of males that mated after rejecting potential mates. Gain = mean of the product of P and the difference in fecundity of accepted and rejected females. Cost = mean of the product of $(1 - P)$ and the fecundity of rejected females

2000). Thus, there is opportunity for selection to favor male choice for larger females (Bonduriansky 2001).

Some field observations are consistent with male choice for larger females in the soldier beetle. First, mating females are larger, on average, than non-mating females. Second, larger males mated smaller females less frequently than expected. Other interpretations are possible for these results. For instance, if smaller females are of poorer condition, they may be less frequently receptive to mating. Or, large males might be less likely to encounter smaller females if body size influences microhabitat use or the timing of courtship activity. However, courtships occur at random with respect to male and female size, suggesting that the low rate of mating between large males and small females reflects male decisions not to mate.

Some field and laboratory evidence more directly indicates that males prefer larger over smaller females. In the field, males are much more likely to abandon relatively small than relatively large females. Male abandonment dramatically contrasts with the more frequent form of failed courtship in which the female escapes by fleeing or by shaking and kicking the male away. In the laboratory, larger males were more likely to mate the larger of two females with whom they were housed. However, in similar circumstances, smaller males exhibited no preference (see also Adams and Morse 2013). The greater tendency of larger males to mate larger females could be caused by a plastic preference that is predicated on prior courtship success in the field (Kasumovic and Brooks 2011; Dingemans and Wolf 2013).

Field results indicate that mating success increases with male size. Thus, smaller males may become conditioned to mate any female they can secure (Fawcett and Johnstone 2003; Fowler-Finn and Rodriguez 2011; Rodríguez et al. 2013). In contrast, the greater mating success of larger males might favor rejecting smaller females because a larger female is likely to be encountered and mated (Rodríguez et al. 2013).

Simulations of agonistic courtship suggest that male choice for larger, more fecund females could be beneficial provided that such choice is restricted with respect to male size (see also Barry and Kokko 2010). Thus, male choice was favored at low OSR (1.0–1.5) for medium- and larger-sized males and at moderate OSR (2.0–2.5) for larger males. Choice was not favored at any OSR (from 1.0 to 3.0) for males of less than average size. Further, simulations indicate that when mate search effort declines with smaller body size, as was observed in the field, choosiness by larger males is more likely to prove beneficial. This is because the absence of some smaller males from the pool of mate-searchers necessarily increases the access to females of the remaining larger males. These results are consistent with theoretical models indicating that choice is favored only for males in good condition when the OSR is male-biased (Candolin and Salesto 2009).

We do not know the OSR in natural populations of the soldier beetle nor do we know if it changes seasonally or across daily courtship periods. However, anecdotal evidence suggests that the OSR is close to parity. For instance, both males and females will mate almost daily in the laboratory. Also, the number of unmated individuals is typically low at the end of daily courtship periods.

Conditions conducive to male choice

Theoretical studies indicate that positive selection for male choice on the basis of female fecundity requires that the variation in fecundity is high and that costs of locating females are low (Johnstone et al. 1996; Kokko and Monaghan 2001; Servedio and Lande 2006; Venner et al. 2010). Our laboratory study shows that fecundity varies greatly with female body size. Also, mate search costs may generally be low in the soldier beetle. For instance, densities can be as high as 500 beetles/m², which result in multiple courtship encounters per minute. However, during the current study, densities were much lower. Yet, it is still likely that mate search costs were low. This is because most beetles (>90 %) occurred at one of several locations in the field where densities were moderate (10–30 beetles/m²). At these densities, mate-searching males could encounter dozens of females in an afternoon (McLain 2005). It should be noted that our simulations of male choice did not include costs for mate searching and mate assessment. If the energetic costs of these are high, it is likely that males searching later in the daily courtship period would suffer a loss of vigor, making them less likely to acquire mates.

Male choice is also favored by high parental investment (Johnstone et al. 1996; Kokko and Monaghan 2001; Edward and Chapman 2012). Males of some soldier beetle species provide energetic nuptial gifts upon mating (Eberhard 2006). Our laboratory data suggests that *Chauliognathus pennsylvanicus* males can provide energetic rewards to females during copulation because the fecundity of females increased with mate size. Of course, it is possible that females mating larger males chose to invest more in reproduction. This could be favored if larger males were more likely to provide greater genetic benefits. However, significant between-year variation in body size suggests that body size is a response to environmental conditions and, therefore, is not a basis for evaluating male genetic quality.

Soldier beetle courtships extend from one afternoon to the next morning, limiting the number of matings a male can achieve to a maximum of one per daily courtship period. This limitation affords a male the opportunity to shop for a mate before committing to copulation without necessarily reducing his mating rate. The willingness of female soldier beetles to mate almost daily (McLain 2005) could also favor male choice by depressing the OSR and, thereby, reducing competition for mates. Reduced competition results in lowered costs

for mate rejection by increasing the subsequent likelihood of successfully courting another female.

In the soldier beetle, larger males appear to be more vigorous than smaller males. This is because increases in size are associated with more time allocated to searching for females or courting while decreases in size are associated with more time allocated to feeding or resting. Perhaps as a consequence of better condition, larger males also court females more persistently than do smaller males. Our field results suggest that male choice is condition-dependent. Thus, compared to smaller males, larger males are more likely to reject smaller females as mates and are, probably as a consequence, less likely to mate smaller females. Also, results of our laboratory study are consistent with condition-dependent male choice for larger females.

The cost of rejecting females, in terms of the potential mating rate, would be further reduced if females preferred as mates males in good condition (Edward and Chapman 2011; South et al. 2012). Consequently, males in good condition would face less competition for females, increasing their odds of mating after rejecting a female (Amundsen and Forsgren 2003). Thus, female preferences could support condition-dependent male mate choice (Clutton-Brock 2007, 2009; Bonduriansky 2009; Edward and Chapman 2012).

Agonistic courtship

The agonistic mating system of the soldier beetle may be a mechanism by which females bias matings toward males in relatively good condition and of relatively high quality, where quality is the ability to provide energetic or other benefits to females (Wiegmann et al. 2013). Copulation occurs when the male possesses sufficient vigor to engage in the persistent pursuit of an evasive female (McCauley 1981; Dunn et al. 2001; Teder 2005). In soldier beetles, agonistic courtship favors larger males who court females more persistently although some bias toward larger males is attributable to the fact that they also spend more time searching for mates and courting than do smaller males. The importance of size in courtship is clear from the field observation that smaller males do not mate larger females, in contrast to the success of larger males with larger females.

Agonistic courtship in soldier beetles may be a version of female choice based on a preference for males who court more intensely (Johnstone 1997; South et al. 2012). Such preferences can favor male choice and promote assortative mating even if relevant male phenotypes are entirely determined by the environment (South et al. 2012). Also, agonistic courtship may be an expression of motor performance skills which might reveal health and the energy status of the courting male (Dunn et al. 2001; Irschick 2003; Sisodia and Singh 2004; Irschick et al. 2006; Byers et al. 2010; McGinley et al.

2013), which could correlate with his ability to provide nuptial gifts.

Selection on females favors the mating strategy that optimizes mate quality under current ecological conditions and constraints of cognitive ability, time, the cost of choice, and availability of high quality males (Wiegmann et al. 2013; Castellano 2010; Castellano et al. 2012; Wiegmann et al. 2013). Evasion and agonistic courtship, as a mechanisms for translating a preference for high quality males into a realized choice, would appear to require little time, limited cognitive ability, and little investment in sensory organs or information acquisition. With evasion and agonistic courtship, the ability of a female to exercise choice is a positive function of her own ability to resist males. Our results indicate that medium-sized and larger females are able to use evasion as a basis of mate choice. However, females of smaller size and limited strength may not be able to exercise choice for high quality males. Thus, agonistic courtship is a version of condition-dependent female choice (see Cotton et al. 2006). The plight of smaller females may do little to oppose evasion and attendant agonistic courtship as a mating strategy because smaller females are of lower fecundity and are less preferred by males.

While agonistic courtship and female evasion are common in animals (reviewed in Perry et al. 2009) the interpretation that they constitute a mechanism of mate choice would probably be incorrect in many cases. This is because aggressive courtship can be sexual coercion that is actually costly to females (e.g., Olsson 1995; Clutton-Brock and Langley 1997; McLain and Pratt 1999; Vahed 2002). Thus, the interpretation of female choice for vigor versus a manifestation of sexual conflict (Rowe et al. 1994; Rowe and Day 2006) in which larger males overcome female resistance can be problematic. To address these alternative interpretations we are currently completing a more complete analysis of the costs and benefits of daily mating as well as changes in the behavior of females as a function of their rate of encounter with males.

Assortative mating

Assortative mating is a common outcome of mating preferences (Franceschi et al. 2010) and can be strengthened by male choice (Cézilly 2004; MacLeod and Andrade 2014). When successful courtship entails males securing evasive females, weak assortative mating by body size occurs provided that body size is correlated with both the ability of females to evade, and the ability of males to secure (McCauley 1981). This is because copulatory pairings between small males and large females will not occur. Simulations of pairing without male choice resulted in correlations of approximately 0.20–0.55. The higher correlations occurred with more male-biased sex ratios and when male size did not affect the likelihood of courtship. With more male-biased sex ratios, it was more likely that some large males remained unmated until later

encounter rounds, increasing the odds that large females would encounter large males. Thus, more females mated as the sex ratio increased. When male size affected the likelihood of courtship, smaller-medium-sized females were less likely to encounter smaller-medium-sized males. Consequently, these females encountered and mated larger males at higher rates, reducing the body size correlation. These matings reduced the number of large males remaining available to large females which resulted in fewer total matings and lower mean fecundities.

In the field, the correlation between the sizes of members of mating pairs was relatively high, 0.669. This value may reflect the effects of male choice and of male body size on both courtship persistence and the rate of courtship. Simulations suggest that male choice promotes a high correlation even at low OSR, counteracting the impact of size-dependent courtship rates. Male choice, as modeled in the simulations, reduced pairing between larger males and smaller females. The indirect effects of this are to increase encounter rates between smaller females and smaller males and between larger females and larger males. In the field, these effects would contribute to a moderately high level of assortative mating, as observed.

Moderately strong assortative mating would also be promoted if smaller males in poorer condition chose not to court larger females (Hoefler 2007; Härdling et al. 2008; Venner et al. 2010). This prudent choice strategy would permit smaller males to avoid competition with larger males for larger females, allowing smaller males to focus their efforts on the smaller females who may actually mate them (Bel-Venner et al. 2008; Candolin and Salesto 2009; Wada et al. 2011). Prudent choice is favored under conditions that may apply to soldier beetle populations: (1) a low, but still male-biased OSR, (2) high female-encounter rates for mate-searching males, and (3) matings of prolonged duration (Härdling et al. 2008; Venner et al. 2010). The failure of smaller males to choose larger females in the laboratory is consistent with prudent choice in the soldier beetle as is the tendency of very small males to court smaller females more vigorously than larger females.

Conclusions

The evasive behavior of female soldier beetles biases matings toward larger males who court more frequently and more persistently. The bias is advantageous to females because mate size correlates with female fecundity. The potential reproductive rate of males is probably limited by the high cost of mating, inferred from fecundity enhancement, and by prolonged copulations that reduce the maximum mating rate to once per day. These limitations are conducive to male choice for larger, more fecund females. Male choice is favored

to the extent that a male is likely to encounter and mate a more fecund female after rejecting a less fecund one. Larger males enjoy both higher rates of courtship and higher rates of successful courtship. Moreover, localized population densities are high enough to ensure multiple courtship encounters with apparently little mate-searching effort. Thus, it appears that selection could favor size-dependent male choice. Such choice is indicated by male abandonment of smaller females and by sequential choice for larger females in the laboratory.

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