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## Do female leaf beetles *Galerucella nymphaeae* choose their mates and does it matter?

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**Abstract** The role of active female choice in sexual selection is frequently difficult to ascertain, and this is particularly the case for many insect species. Also, it is uncertain whether choosing between males would affect offspring viability. We designed an experiment to investigate the presence of female choice in a Coleoptera species (*Galerucella nymphaeae*). We also estimated whether mate choice would have any effect on offspring performance. Females were first placed with two males in a test arena to see which of the males copulated with the virgin female, and how quickly. Subsequently the loser male was offered a new virgin female to test for any change in latency time until mating. The two-male tests indicated that males with wider upper prothoraxes were more likely to mate with the female, and the latency time until mating was shorter when the winner male had relatively long wings. When the loser males were placed singly with females the latency time was not correlated with male size, and was the same as when two males were used. These results suggest that male-male competition is the most likely cause of sexual selection on size, and if females have any preferences they are not very strong. The seemingly passive female strategy may be sufficient to ensure that females mate with the most vigorous males, since in the field several males usually compete for access to each female. Finally, the benefits of female choosiness were estimated to be low and non-significant. The eggs of the winner males were no more likely to hatch, offspring survival into adulthood was no greater among descendants of winner males, and the offspring did not differ in adult size.

**Key words** *Galerucella nymphaeae* · Leaf beetle · Male size · Offspring viability · Sexual selection

### Introduction

Sexual selection has for many years been one of the most widely studied areas of evolutionary ecology (Balmford and Read 1991; Kirkpatrick and Ryan 1991; Maynard Smith 1991; Andersson 1994). Most research in this area has concentrated on strongly dimorphic species with exaggerated male ornaments or elaborate male display behaviour. It would also be interesting to study mate choice in species that do not show such obvious results of sexual evolution. The question is, how important sexual selection can be in species such as many of the insects, where males often meet females at emergence, feeding or oviposition sites and females often copulate repeatedly (Thornhill and Alcock 1983). It seems that in these cases females do not tolerate any major costs of being choosy, which raises the question of whether the benefits of choosiness are sufficiently high.

Benefits of choosiness can be either direct, influencing immediate female reproductive success, or indirect, influencing offspring performance (Maynard Smith 1991; Andersson 1994). If benefits are immediate, as with courtship feeding (Thornhill 1976; Gwynne 1984), female choice may well evolve. Recent studies in vertebrates have indicated that choosy females also benefit from increased viability among their offspring (e.g. Reynolds and Gross 1992; Norris 1993; Møller 1994; Petrie 1994; von Schantz et al. 1994; Hasselquist et al. 1996). Previous studies in insects have either supported the existence of indirect benefits (Partridge 1980; Watt et al. 1986; Crocker and Day 1987; Simmons 1987a; Gilburn et al. 1993; Wilcockson et al. 1995) or they have found no indication of any such benefits (Shaeffer et al. 1984; Boake 1985; Whittier and Kaneshiro 1995).

Following the Darwinian tradition, sexual selection is usually separated into two parts; intersexual and intra-sexual selection. In much of the work concerning sexual selection the main difficulty has been in separating these two forms from each other. This is particularly the case for insects, where females frequently appear to be rela-

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tively passive (Parker 1983; Thornhill and Alcock 1983; Bradbury 1985). However, active female preferences are obvious in several insect species (see for example Gilburn et al. 1992; Eiriksson 1993; Tuckerman et al. 1993; Boake and Hoikkala 1995) and in some of the lekking insects (Shelly and Whittier 1997). Females could receive future-generation benefits simply by allowing males to compete between themselves. Thus, they would not need to choose males on criteria other than male competitive ability. Indeed, among vertebrates, for example seals, females seem to actively incite males to compete for access to matings (Cox and LeBoeuf 1977). In lekking grouse females actively choose males that are most vigorous in male-male territorial combats (Alatalo et al. 1991; Hovi et al. 1995). Through this kind of relatively passive choice behaviour females might be able to obtain benefits similar to those that could be achieved by active selection behaviour.

Here we investigate the presence of intrasexual and intersexual selection and its consequences for the offspring in a leaf beetle, *Galerucella nymphaeae* L. (Coleoptera, Chrysomelidae). The species is nearly monomorphic and matings take place in aggregations at the oviposition sites. Firstly, we tested whether the final mate choice in this species is solely a result of competition between males, or whether the females choose certain kinds of males as mates. Secondly, we estimated the benefits that females might obtain by being choosy by raising the offspring of both sexually successful and unsuccessful males.

## Materials and methods

### The study animal

The leaf beetle species under study (*Galerucella nymphaeae*) is an aquatic herbivore of Nymphaeaceae water lilies. Although there is a significant difference in female and male width (mean  $\pm$  SD width for males =  $2.45 \pm 0.09$  mm and for females  $2.35 \pm 0.09$  mm;  $t = 6.19$ ,  $n = 120$ ,  $P < 0.001$ ) the differences in morphological traits are so small that the sexes are not distinguishable by size. Body length did not differ between the sexes (mean elytra length for males  $4.72 \pm 0.18$  mm, and for females  $4.68 \pm 0.17$  mm;  $t = 1.14$ ,  $n = 113$ ,  $P > 0.1$ ). Neither are there any obvious external differences in their sexual organs. Adult beetles overwinter on shore in ground litter (Almkvist 1984) or under pine bark (Kouki 1991) and move from shore vegetation to floating leaves of water lilies as soon as the leaves emerge in May (Almkvist 1984; Mappes and Mäkelä 1993). The adults mate on the leaves, females lay egg clutches on them, and the hatching larvae feed, and after three larval stages pupate, on the same leaves (Almkvist 1984). The early life-cycle of the beetles is thus restricted to the same leaves where the females lay eggs.

We collected the beetles used in this study at the end of May 1992 from the shore vegetation of Lake Väärä and Lake Kopru, Konnevesi (62°37'N, 26°20'E), Central Finland, before emergence of *Nuphar lutea*. This is the main water lily in these lakes. The beetles were placed individually in test tubes and sexed in the laboratory. To slow down their metabolism males and females were kept in cold storage room (temperature 5°C) separately until the experiments. The time beetles were stored before the experiments varied from a few days up to 2 weeks. Since no matings have been observed before beetles have moved to water lilies from the shore

vegetation, we could assume the animals collected from the shore were unmated. The unmated females do not start egg laying before they are allowed to mate in the laboratory, after which they lay an egg clutch every day.

### Experiments on intrasexual versus intersexual selection

The mate choice experiment had two phases, the first allowing male-male competition and the second allowing no interactions between males. Initially we tested two males with a virgin female to see which male copulated with the female, and how quickly. We then placed the "loser" male (the one that did not mate) with a new virgin female to see if the latency time until the beginning of mating was longer when only the less successful male was present than when both males were present. These two setups allowed us also to see if sexual selection appears only through intrasexual selection in the two-male trials, or whether females would also show particular avoidance of single loser males.

For each two-phased trial, we chose new beetles randomly and marked the males individually with silver paint pen on their covering wing (elytra). The two males and the randomly chosen female were put to the test arena (a plastic box  $12 \times 8 \times 4$  cm) with a piece of fresh *N. lutea* leaf on the bottom as food. We observed these groups regularly until copulation between the female and one of the males (the "winner") took place. The observation intervals were short enough to allow us to observe the copulations (the mean duration of copulation was 3 h 29 min,  $n = 14$ ); each set of beetles was checked every second hour in daytime and every third hour during the night. When copulation between the female and one of the males was observed, the other male (loser) was carefully removed from the arena and the pair (winner male and the female) was allowed to continue copulation undisturbed.

We weighed all the males to the nearest 0.1 mg before entering them in trials. Further morphological measurements were made with a stereomicroscope after the experiments. The measurements included the width of the upper prothorax and the length of both the covering (elytra) and flying wings, which we measured to 0.05 mm. Because of a high correlation between the length of covering and flying wings (for winners  $r_s = 0.83$ ,  $n = 35$ ,  $P < 0.001$  and for losers  $r_s = 0.72$ ,  $n = 34$ ,  $P < 0.001$ ) we used only the measurements of covering wings. For this paired character we calculated mean values of right and left covering wing measures. The three male morphological characters included in the analyses were correlated with each other but with small correlation coefficients (width and weight  $r_s = 0.310$ ,  $n = 67$ ,  $P < 0.05$ ; width and length of elytra  $r_s = 0.225$ ,  $n = 69$ ,  $P > 0.05$ ; length of elytra and weight  $r_s = 0.418$ ,  $n = 67$ ,  $P < 0.01$ ).

### Progeny of successful and unsuccessful males

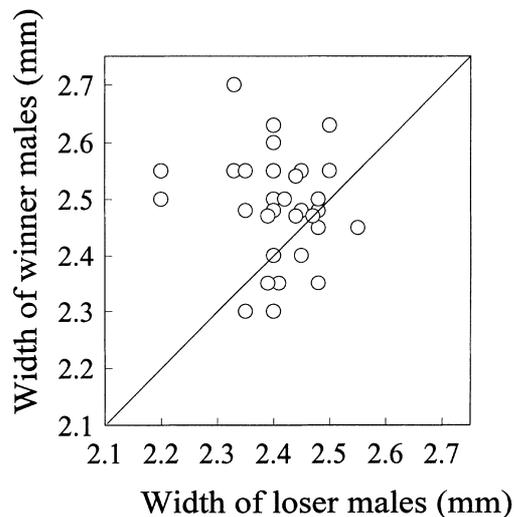
When the winner of the first phase of the experiment and the female had finished copulation, the male was taken from the arena and the female was allowed to lay two egg clutches. Likewise, the females that copulated with the loser males in the second phase of the mate choice experiment were allowed to lay two egg clutches each. Thus we could compare the subsequent breeding success of the females that mated with the winner males with that of the females that mated with the loser males, and estimate any resemblance in size-traits between the offspring and the male parent. All the hatched progeny of both types of males were reared to adulthood under similar laboratory conditions, and fed on fresh leaves of *Nuphar lutea*. The rearing conditions were not particularly favourable for the larvae, but, most importantly, all the offspring were kept in the same conditions. The adults used in the trials and the consequent progeny were stored in 70% alcohol for morphological measurements. The progeny were stored after they had passed the final larval stage, and the width of their upper prothorax and the length of their elytra were measured similarly to those of adults. All the measurements were done by one person (S.P.) to minimise measurement error.

## Results

### Two-male trials

In the first phase of the experiment, where two males were allowed to compete with each other for access to a female, males seemed to be active in attempting copulations and the females seemed to try to escape all the copulation attempts. In many cases we saw males physically competing over the female. This behaviour included attempts to get the other male away from the female's back. Males were even seen trying to copulate with each other. There was one clear difference in the morphological traits between winner and loser males. The winner males, (the first ones to copulate with the female), had wider upper prothoraxes than loser males (Fig. 1, Table 1). The difference represents 74.7% of the standard deviation in male traits, and thus directional selection for males with wider prothoraxes is very clear. There were no significant differences in body weight or elytra length, nor did the variances of these characters differ (Table 1), and thus there was no sign of strong stabilising selection.

Among the winner males there was a negative relationship between the length of the elytra and the time until copulation, i.e. males which had longer elytra



**Fig. 1** The body width of winner and loser males. Each dot represents one pair of males. When the dot is above the line, the winner male was wider than the loser, and when it is below the line the loser was wider than the winner

**Table 1** Size measures of winner males (from phase 1 of the experiment) and loser males (from phase 2 of the experiment) and the pairwise comparisons. *F*-values for pairwise comparisons of variances

		Mean	SD	<i>n</i>	<i>t</i>	<i>P</i>	<i>F</i>	<i>P</i>
Body weight (mg)	Phase 1	1.28	1.4	35	0.06	0.952	1.50	0.121
	Phase 2	1.28	1.7					
Body width (mm)	Phase 1	2.48	0.10	33	3.05	0.0034	1.57	0.100
	Phase 2	2.42	0.08					
Wing length (mm)	Phase 1	4.73	0.18	34	0.55	0.584	1.17	0.325
	Phase 2	4.71	0.19					

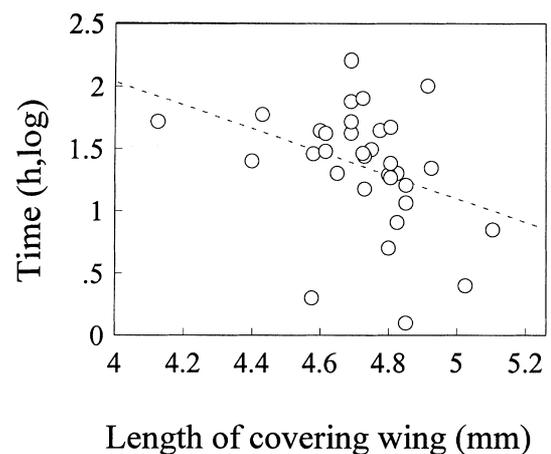
copulated sooner than winner males which had shorter wings (Fig. 2, Table 2).

### Trials with loser males

In the second phase of the experiment the loser males were given a new unmated female and these pairs were observed as in the first phase. The latency time until copulation did not differ from that in the first part of the experiment (phase 1, winners: 26 h 30 min  $\pm$  32 h 25 min, median  $\pm$  SD, *n* = 33; phase 2, losers: 24 h 30 min  $\pm$  41 h 55 min, *n* = 25; Mann-Whitney *U*-test, *z* = 0.24, *n*<sub>1</sub> = 33, *n*<sub>2</sub> = 25, *P* > 0.1). The distributions of these times did not differ from each other (Fig. 3). There was no indication that females would have delayed the start of copulation in the presence of only the previously unsuccessful male. In this setup male morphology did not have any significant effect on latency times (Table 2).

### Offspring viability

The number of eggs laid by females did not differ between successful and unsuccessful males (mean  $\pm$  SD for females mated to winner males 19.7  $\pm$  8.0, *n* = 32, for females mated to loser males 21.9  $\pm$  7.1, *n* = 29, *t* = 1.13, *df* = 59, *P* > 0.1). Neither were there any differences in the proportion of eggs that hatched; 53%  $\pm$  35% (mean  $\pm$  SD) of the eggs laid by females



**Fig. 2** The correlation between the length of elytra (covering wings) and the latency time until copulation among winner males

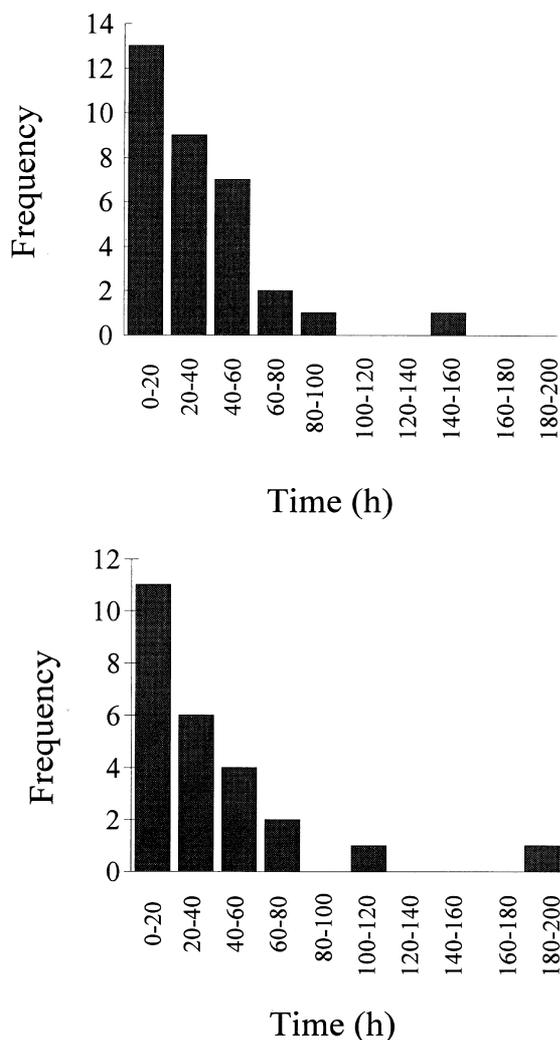


Fig. 3 The distribution of latency times until copulation in a two-male trials, **b** trials with loser male only

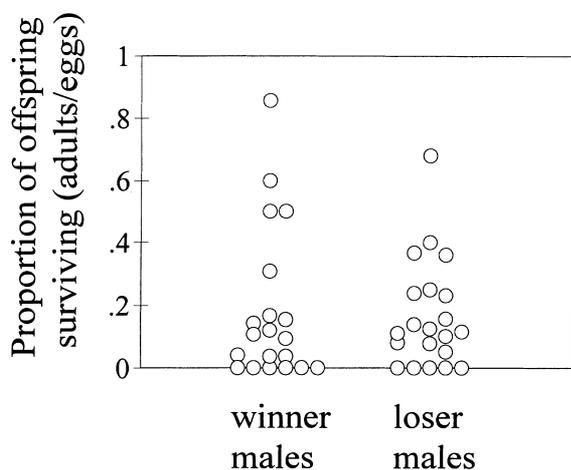


Fig. 4 The proportion of offspring of winner and loser males reaching adulthood (as proportion of eggs laid)

Table 2 Correlations (Spearman correlation  $r_s$ ) between male morphological traits and latency time until copulation for winner and loser males

a Phase 1 of the experiment (winner males)			
	$r$	$n$	$P$
Weight	-0.226	33	0.206
Body width	0.246	32	0.175
Wing length	-0.451	33	0.008
b Phase 2 of the experiment (loser males)			
	$r$	$n$	$P$
Weight	-0.013	25	0.951
Body width	-0.246	25	0.236
Wing length	-0.155	25	0.459

mated to winner males hatched and  $52\% \pm 32\%$  (mean  $\pm$  SD) of the eggs of females of loser males (Mann-Whitney  $U$ -test,  $z = 0.06$ ,  $n_1 = 21$ ,  $n_2 = 22$ ,  $P > 0.1$ ). To obtain a standardised estimate of the difference in offspring performance we describe the effect in terms of standard deviations units. The standardised estimate for offspring hatching difference was  $+0.028$  SD (the upper confidence interval, C.I., estimate with 5% risk  $+0.491$ ). The average absolute number of offspring reaching adulthood for winner males was  $4.28 \pm 5.36$  (mean  $\pm$  SD) and for loser males  $4.83 \pm 4.76$ , and there was no difference between male groups (Mann-Whitney  $U = 139.5$ ,  $n_1 = 18$ ,  $n_2 = 18$ ,  $P > 0.1$ ). Neither was there any difference in the proportional numbers of offspring surviving to adulthood (number of adults as proportion of eggs laid; mean  $\pm$  SD;  $0.203 \pm 0.250$  for winner males and  $0.193 \pm 0.171$  for loser males, Mann-Whitney  $U = 143.0$ ,  $n_1 = 18$ ,  $n_2 = 18$ ; Fig. 4). For the offspring survival the difference estimate is  $+0.048$  SD units with the upper 5% C.I. of  $+0.524$ .

#### Offspring size

Female and male descendants differed slightly in their morphology. However, in contrast to the adults, among the progeny females were wider and had longer elytra than the males (mean  $\pm$  SD for prothorax width of female descendants  $2.24 \pm 0.10$  and for male prothorax  $2.14 \pm 0.09$ , respectively;  $t = 3.64$ ,  $n = 46$ ,  $P < 0.001$ ; mean for length of elytra of female descendants  $4.52 \pm 0.25$  and for male descendants  $4.22 \pm 0.14$ ;  $t = 4.92$ ,  $n = 46$ ,  $P < 0.001$ ). There were no differences in progeny sizes of winner and loser males (females were compared with females and males with males) (Table 3). The heritability of the width of upper prothorax and length of elytra were estimated by mid-parent offspring linear regressions. The heritability estimates were calculated separately for female and male progeny due to the slight differences between female and male progeny morphology. The estimate of heritability,  $h^2$  ( $\pm$  SD), for the width of upper prothorax was  $0.16 \pm 0.29$  ( $n = 22$ ,  $P = 0.60$ ) for female progeny and  $0.14 \pm 0.27$  ( $n = 20$ ,  $P = 0.61$ ) for male progeny. In the case of the length of

**Table 3** Morphological measures of the progeny of phase 1 (winner) and phase 2 (loser) males and the results of paired *t*-tests. Female and male progeny were tested separately

	Body width (mm)				
	<i>x</i>	SD	<i>n</i>	<i>t</i>	<i>P</i>
Phase 1 (fem.)	2.26	0.10	22	0.77	0.451
Phase 2 (fem.)	2.23	0.10			
Phase 1 (male)	2.14	0.06	22	0.37	0.712
Phase 2 (male)	2.13	0.11			
	Wing length (mm)				
	<i>x</i>	SD	<i>n</i>	<i>t</i>	<i>P</i>
Phase 1 (fem.)	4.54	0.17	22	0.42	0.679
Phase 2 (fem.)	4.50	0.29			
Phase 1 (male)	4.23	0.14	20	0.29	0.776
Phase 2 (male)	4.21	0.14			

elytra  $h^2$  was  $-0.37 \pm 0.45$  ( $n = 22$ ,  $P = 0.43$ ) for female progeny and  $0.03 \pm 0.26$  ( $n = 20$ ,  $P = 0.92$ ) for male progeny. Thus, all the heritability estimates are close to zero.

## Discussion

Studies of sexual selection in species where mating takes place in the same environment where animals emerge, feed or oviposit indicate that intermale competition may in many cases be so strong that the final pairing is a result of male competition only (Thornhill and Alcock 1983). Males and females of our study species *G. nymphaeae* aggregate on the floating leaves of water lilies as soon as the leaves emerge. Subsequent feeding, copulation, oviposition and hatching of a new generation takes place on these leaves. In the early summer when the small number of water lily leaves limits the distribution of beetles the density of animals on single leaves can be very high. In these circumstances the potential for females to select their mates is obviously quite limited. The results of our choice experiment, and the lack of differences in the latency times until copulation in different situations, indicate that female mate choice plays at most a minor role. In male-male competition males larger than their opponents are more likely to succeed in copulating despite female resistance. The difference between winner and loser males in the width of upper prothorax, and the negative correlation between length of elytra and the time until copulation, indicate that male size in general has a role in determining the outcome of male-male interactions. Width of body and length of wings of male beetles can be seen as traits describing male size in general, which has been shown in several other studies to be correlated with male mating success (Partridge and Farquhar 1983; Partridge et al. 1987; Pettersson 1987; Benton 1992; Gilburn et al. 1992; McPeck 1992).

However, some sort of female choice may also operate in this species. This possibility comes from the observation that females tried to avoid practically all copulation attempts until they allowed one of the males to copulate. Females also tried to prevent males copulating when they were with one male only. As our results show, the males which obtained the copulations were larger than the loser males. This might be an outcome of inter male competition, but possibly also of female preference for larger and more competitive males. Thus, by trying to escape all the copulation attempts females might be able to “test” males and their quality, eventually copulating with the most vigorous males. The outcome of this kind of behaviour and proper active female choice would be very similar; females would mate discriminatingly with better quality males.

There were no significant differences between the size traits of progeny of winner and loser males, and the estimated heritability of these size traits was low. Several studies have indicated some additive genetic variance for male body size in insect species where body size is under directional sexual selection (McLain 1987; Simmons 1987a,b; Simmons and Ward 1991; Wilcockson et al. 1995). However, if indirect fitness benefits were essential for female choice we would expect differences in offspring viability. We found no significant difference in the proportion of progeny of females that had mated with winner or loser males that hatched or reached adulthood. Admittedly our sample sizes are not large enough (even if they correspond to the sample sizes of most similar studies) to allow us to discern any small indirect benefits in offspring viability or growth. Lack of statistical power is a general problem in sexual selection studies and therefore there has been a bias towards publishing only significant results (Alatalo et al. 1997). This leads to overestimation of the true effects among the offspring, and thus for the purpose of any meta-analyses we have presented standardised estimates of the differences in offspring performance.

In sum, in the leaf beetle *G. nymphaeae* male-male competition seems to explain most, if not all, of the sexual selection on male upper prothorax width. Female choice might operate through male-male competition and indeed with both mechanisms acting together the final results for the females could be argued to be more or less the same. We found no evidence of indirect benefits of selective behaviour, but we cannot entirely rule out the possibility that they exist.

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