



Female choice and manipulations of forceps size and symmetry in the earwig *Forficula auricularia* L.

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ABSTRACT

The size and asymmetry of male secondary sexual traits are believed to convey reliable information to females concerning the quality of potential mates. Experimental manipulations of male sexual traits provide a powerful approach to the study of preference evolution. Nevertheless, the majority of studies rely on correlational evidence for selection acting on secondary sexual traits. Here we report that in three of four populations of the European earwig, *Forficula auricularia*, females mated sooner with males with longer forceps although there was no female preference based on forceps asymmetry. We isolated the potentially confounding influences of forceps length and asymmetry by independently manipulating each trait. Manipulations of forceps length confirmed that females preferred males with longer forceps. However, manipulations of asymmetry revealed that although females pay attention to forceps condition, they show no preferences based on asymmetry. No relationships were found between the length and asymmetry of forceps in field populations, and there were no differences in condition between symmetrical and asymmetrical males. Our results are consistent with the notion that female choice has contributed to the sexual dimorphism in earwig forceps. However, they refute the notion that fluctuating asymmetry plays a role in sexual selection.

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A growing body of evidence supports the notion that female mate choice does occur and that mate choice decisions are based on secondary sexual traits (Andersson 1994). However, identifying the properties of particular secondary sexual traits that are the focus of female choice can be difficult (Halliday 1983). Correlations between secondary sexual traits and reproductive success are informative, although they can be influenced by other factors such as male dominance, female copying or male behaviour (Halliday 1983; Balmford 1991).

To isolate the specific secondary sexual trait or feature of a trait that females are using to make mate choice decisions, the trait has to be manipulated independently of other potentially confounding effects. The manipulation of tail ornament length in the widow bird, *Euplectes progne* (Andersson 1982) and barn swallow, *Hirundo rustica* (Møller 1988) led to very similar results: compared with controls, males with elongated tail ornaments had an increased mating success, but the mating success of males with shortened tails was reduced (Andersson 1982; Møller 1988). Similarly, male satin bowerbirds,

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Ptilonorhynchus violaceus, with an artificially depleted number of bower decorations gained fewer mates than males with unmanipulated bowers (Borgia 1985; see also Andersson 1991). Manipulations of secondary sexual traits of invertebrates have not been made although enlarging the sexually selected leg tufts in video images of the displaying lycosid spider, *Schizocosa oreata*, elicited a higher frequency of female receptivity postures in females, than when the leg tufts were made smaller (McClintock & Uetz 1996). Acoustic manipulations have demonstrated that in field crickets, *Gryllus campestris*, it is the female's preference for carrier frequency and the degree of frequency modulation in the male call (Simmons & Ritchie 1996) that make large symmetrical males more attractive.

Møller (1993a, d) has argued that patterns of fluctuating asymmetry with respect to trait size may be good predictors of the underlying quality of individuals. Since sexual selection is directional, it is predicted to impose genomic stress that results in an increase in the degree of fluctuating asymmetry in sexually selected traits (Møller 1993a; Møller & Pomiankowski 1993). Furthermore, where secondary sexual traits are costly to produce, individuals of high quality should be in a position to

produce both large and symmetrical traits while small asymmetrical traits should characterize low-quality individuals (Møller 1993a; Møller & Pomiankowski 1993). Thus, a negative relationship between trait fluctuating asymmetry and size is predicted, although evidence for such relationships is equivocal (Møller 1990, 1992b; Manning & Hartley 1991; Manning & Chamberlain 1993; Tomkins & Simmons 1995; Mateos & Carranza 1996; Hunt & Simmons 1997).

By paying attention to the symmetry of secondary sexual traits, females may gain information about the trait bearer's genetic quality; indeed a number of studies have shown that females prefer males with the most symmetrical secondary sexual traits (Møller 1992a, 1993b; Swaddle & Cuthill 1994a; Simmons & Ritchie 1996). However, only a few studies have explored further the correlation between male symmetry and female preference (Markow & Sawka 1992; Møller 1992a, 1993b; Oakes & Barnard 1994; Swaddle & Cuthill 1994a, b). Females may be choosing males on the basis of traits that are correlates of symmetry, rather than symmetry per se. Hence, only by manipulating the symmetry of secondary sexual traits can studies of female choice and asymmetry go beyond correlational support.

Møller (1992a, 1993b) simultaneously manipulated both streamer size (and apparent size) and symmetry (and apparent symmetry) of the outer tail streamers of male barn swallows. Female swallows formed pairs earlier with males that had lengthened and symmetrically manipulated tails and later with males that had shortened and asymmetrical manipulated tails (Møller 1992a, 1993b). The females' preference for males with both longer and more symmetrical tails supports the notion that female swallows are seeking genetic benefits; low asymmetry in males is associated with returning early from migration, high mating success and survivorship (Møller 1994).

Male earwigs use their forceps in both intrasexual competition (Knabke & Grigarick 1971; Eberhard & Gutierrez 1991; Moore & Wilson 1993; Radesäter & Halldórsdóttir 1993; Briceno & Eberhard 1995), and courtship (Moore & Wilson 1993; Briceno & Eberhard 1995), supporting the idea that sexual dimorphism in forceps has arisen through sexual selection. Radesäter & Halldórsdóttir (1993) showed that there is directional sexual selection acting on forceps length in *F. auricularia*, males with longer forceps having a mating advantage in competitive situations. In addition they reported selection for forceps symmetry; in noncompetitive situations symmetrical males gained copulations sooner (Radesäter & Halldórsdóttir 1993). In accordance with the theory that fluctuating asymmetry in secondary sexual traits signals male quality, Radesäter & Halldórsdóttir (1993) also found a negative relationship between male forceps length and forceps asymmetry and that relatively heavy males for their body size (in better condition) were more symmetrical. However, they found no evidence of female choice (Radesäter & Halldórsdóttir 1993). In the present study, we manipulated male forceps length and asymmetry in *F. auricularia*, to investigate female choice based on forceps characteristics. We discuss the relationships between female choice, forceps length and fluctuating

asymmetry in the context of previously reported studies and the honest signalling hypothesis of Møller (1993d) and Møller & Pomiankowski (1993).

EXPERIMENT 1: COURTSHIP SUCCESS

Study Population

We collected adult earwigs from four U.K. populations: Neston (Cheshire), Girton (Cambridgeshire), and Brownsman and West Wideopen islands in the Farne Islands group (Northumbria). In some populations of *F. auricularia* males are dimorphic with macrolabic males having elongated forceps and brachylabic males having short forceps (Tomkins & Simmons 1996). As is typical of mainland populations, macrolabic males were rare or absent in Neston and Girton, but they occurred at a frequency of 25 and 35% on Brownsman and West Wideopen, respectively (Tomkins & Simmons 1996). We examined the behaviour and mating success of the more common brachylabic morph.

Morphological Traits

For each population we collected and measured all the males seen. We measured the pronotum width and left and right forceps lengths of the males under a binocular microscope, and also weighed males from the Girton and the Brownsman populations. Forceps asymmetry was calculated as the left minus right value. Measurement of forceps asymmetry is highly and significantly repeatable in this species ($R=0.92 \pm 0.022$, repeated measures ANOVA: $F_{43,44}=23.46$, $P<0.0001$; Tomkins & Simmons 1995). Measurement error, calculated as the proportion of total variation in fluctuating asymmetry that is found in the within-individual repeated measures, was also low (8.16%).

To be accepted as showing true fluctuating asymmetry, trait asymmetry should be normally distributed about a mean of zero (Palmer & Strobeck 1986). The mean forceps asymmetry of the males in the four populations did not differ significantly from zero. All populations showed significant leptokurtosis (Table 1), which may arise through developmental canalization as the trait grows (Swaddle & Witter 1997; J. L. Tomkins, unpublished data) or through selection acting against asymmetric individuals (Møller 1993c; Naugler & Leech 1994; Ueno 1994). Thus the hypothesis of fluctuating asymmetry was not rejected because of leptokurtosis. Palmer (1994) suggested that extreme outlying values of asymmetry result from processes other than developmental instability and should be removed from analyses of fluctuating asymmetry. We removed four outliers (>0.2 mm) from the Girton population and one (0.4) from the Neston population following the procedure of Grubbs (1969). The distributions of fluctuating asymmetry were not significantly skewed (Table 1).

Behavioural Observations

The earwigs were maintained under a reversed light:dark cycle and observations of courtship behaviour

Table 1. Mean left–right asymmetry of forceps of brachylabic male earwigs from four populations and kurtosis and skewness (\pm SE) of the asymmetry frequency distributions

Population	N	Mean asymmetry	Kurtosis	Skewness
Girton	135	-0.008 \pm 0.005	2.55 \pm 0.42*	-0.30 \pm 0.21
Neston	73	0.001 \pm 0.012	6.50 \pm 1.74*	-0.43 \pm 0.29
Brownsman	199	-0.004 \pm 0.006	3.86 \pm 0.34*	-0.30 \pm 0.17
West Wideopen	147	-0.006 \pm 0.007	1.24 \pm 0.40*	0.28 \pm 0.20

* $P < 0.0001$.**Table 2.** Least squares regression coefficients \pm SE and Spearman rank coefficients of the duration of courtship up until the female solicited or copulated and the length, residual length and asymmetry of males' forceps

Population	Least squares regression slope \pm SE				Spearman rank	
	N	Forceps length versus courtship time	N	Residual forceps length versus courtship time	N	FA versus courtship time
Girton†	49	-13.04 \pm 6.34*	49	-13.64 \pm 6.46*	49	0.173
Neston‡	45	-18.45 \pm 6.57*	45	-18.47 \pm 8.7*	45	-0.040
Brownsman‡	12	-61.45 \pm 22.0*	12	-80.02 \pm 33.8*	11	0.080
West Wideopen†	28	2.97 \pm 5.66	28	88.09 \pm 83.18	28	0.039

FA: fluctuating asymmetry.

†Courtship measured up to copulation.

‡Courtship measured up to solicitation.

* $P < 0.05$.

made under red light. We introduced a single male and female into a petri dish 5 cm in diameter 30 min before the beginning of the dark cycle. Observations lasted for the first 60 min of darkness or until copulation occurred. Courtship in *F. auricularia* consists of the male tapping and stroking the female's abdomen with his forceps and presenting his forceps to the female's head. The female nibbles the male's forceps when they are presented to her. Males cannot force copulations (Radesäter & Halldórsdóttir 1993; J. L. Tomkins, personal observation). Rather, females solicit copulations by raising their abdomen with their forceps closed. The male then twists his abdomen through 180° so that the ventral surface is uppermost and genital contact is achieved. We recorded the time that males spent in courtship prior to a solicitation by the female (which is the first cue of female acceptance) or copulation; time of courtship to solicitation correlates strongly with time to copulation ($r_{32} = 0.792$, $P < 0.001$).

Results

The relationship between male forceps asymmetry and mean forceps length in the brachylabic morphs of all four of the populations was flat (Girton: $r_s = 0.151$, $N = 135$; Neston: $r_s = 0.120$, $N = 73$; Brownsman: $r_s = 0.011$, $N = 199$; West Wideopen: $r_s = 0.036$, $N = 147$). The mass of an organism relative to its size is a commonly used measure of condition. Hence, if forceps asymmetry reliably signals male condition, males with asymmetrical forceps should be lighter for their body size than males with symmetrical forceps. There was, however, no relationship between

residual body mass (from a regression of log pronotum width on log body mass) and forceps asymmetry in either the Girton ($r_s = -0.0258$, $N = 135$, NS) or the Brownsman population ($r_s = -0.005$, $N = 76$, NS).

In three of the four populations there was a significant negative relationship between how long a male spent courting a female, before she solicited a copulation (or copulated), and the length of the male's forceps (Table 2). Because body size and forceps length covary, we examined the influence of forceps length on courtship duration using the residual values from a regression of forceps length on pronotum width. The relationship between courtship duration to solicitation and residual forceps length was significantly negative for all but the West Wideopen population (Table 2). Thus in three of the four populations female earwigs solicited copulations from males with long or relatively long forceps sooner than from those with short or relatively short forceps. There was no relationship between the asymmetry of the males' forceps and the courtship duration until solicitation or copulation in any of the populations (Table 2).

EXPERIMENT 2: FORCEPS LENGTH

Methods

We collected fourth-instar nymphs from Neston and measured their forceps. The nymphs were individually reared to adulthood in petri dishes 5 cm in diameter on a diet of pollen and water provided ad libitum. We measured the forceps again when the animals were

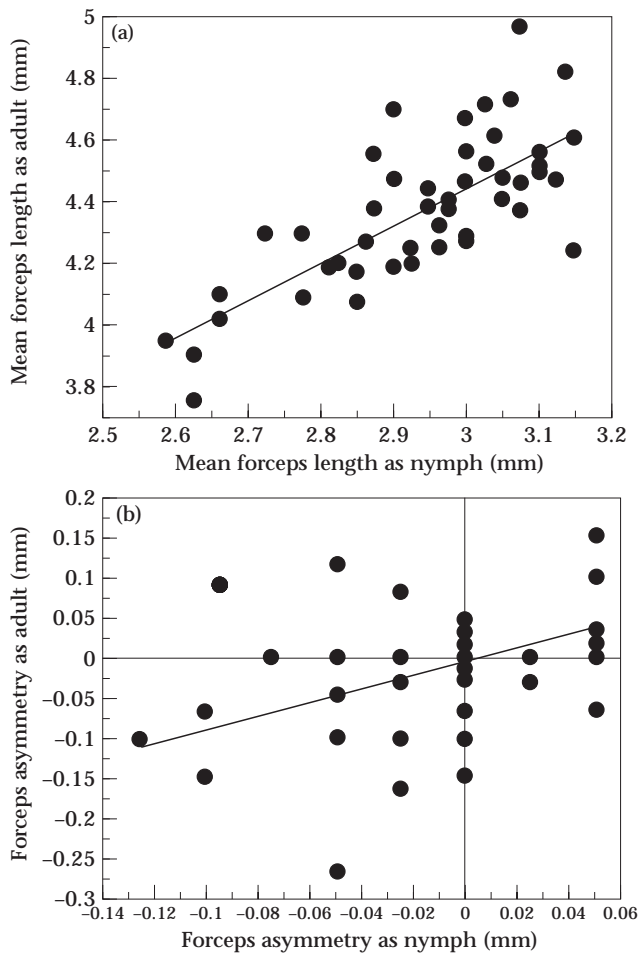


Figure 1. (a) Length and (b) asymmetry of the forceps of adult male earwigs in relation to these measurements when the males were fourth instars (length, $F_{1,46}=60.165$, $r^2=0.567$, $P=0.0001$; asymmetry, $F_{1,46}=11.70$, $r^2=0.203$, $P=0.0013$).

adults. There was a strong positive relationship between the length of the fourth instars' forceps and the length of the adults' forceps (Fig. 1a). There was also a significant positive relationship between the signed asymmetry of the fourth instars' cerci and the signed asymmetry of the adults' forceps after eclosion (Fig. 1b). These two relationships allow the size and symmetry of the adults' forceps to be predicted at the nymphal stage, thus making it possible to manipulate size and symmetry of the adult.

We collected clutches of earwig eggs and the attending females from burrows under stones and driftwood on Brownsman and West Wideopen islands on 3 April 1996. Females and their eggs were placed in individual soil-filled petri dishes, and the petri dish lids were replaced and secured with an elastic band. The females had returned to tending their eggs when we checked them after a few hours. A week after the nymphs hatched we removed them from their mothers and placed them into a plastic container measuring $30 \times 30 \times 15$ cm. The nymphs were fed on rat chow and water ad libitum. Fourth-instar nymphs were divided randomly into Short and Long treatment groups and one Control group. In

the Short manipulation we removed the distal 25% of the nymphs' forceps, and in the Long manipulation the distal 10% of the forceps. The Control nymphs were anaesthetized and handled in a similar manner to the manipulated nymphs, although they were left unmanipulated. All the manipulations were conducted whilst the earwigs were anaesthetized under carbon dioxide. Subsequent to the removal of the forceps tips, the Short, Long and Control nymphs were reared individually in petri dishes 5 cm in diameter. When the nymphs eclosed as adults the forceps tips showed no signs of damage in the manipulated treatments. The pronotum width and left and right forceps lengths of the adult earwigs were measured under a binocular microscope.

We observed behaviour as in experiment 1. However, in these experiments we tested each female on three occasions so that each female was paired with one male from each of the three treatment groups so that we could compare her responses to each male. The order that females were presented with males from the different treatments was under a random block design and females were presented with a male from each treatment on 3 consecutive days.

Results

We used repeated measures ANOVA to confirm the variance in male morphology within our female subjects; we designed the experiment to ensure that each female was presented with three males differing only in forceps length. Friedman's test was used as a nonparametric alternative to the ANOVA for analysing the fluctuating asymmetry data. There were no significant differences in either pronotum width or forceps asymmetry across the treatment groups (Table 3). However, our manipulations were successful in generating the desired variance in forceps length (Table 3).

Females from West Wideopen and Brownsman differed in their responses to the manipulation of forceps length. For the purpose of experimental clarity, we assumed that the female had to be courted by the male in order to reject him. A female must also have been courted by a male from each of the treatment groups in order to be used in the analysis. For the Brownsman data, we compared the Long and the Short manipulated groups only, because Brownsman Controls rarely courted (four of a possible 19 occasions) and copulated only once. Despite the lack of a control treatment, this analysis is valid since both Long and Short treatments were manipulated as nymphs so that females could not have been discriminating between males on the basis of damage caused by the manipulation. For both islands, there were no differences in how long males from each treatment group had to court before they copulated (Fig. 2). There appeared to be a trend towards longer courtship among Long manipulated males in the Brownsman population. This is, however, strongly influenced by a single Long male that copulated after 31 min of courtship. A better reflection of female preferences can be gauged from whether the female copulated. McNemar's test is appropriate for these data, as it compares the two categories in which the female

Table 3. Mean pronotum widths, forceps lengths and |R-L| asymmetry of the Short forceps, Long forceps and Control groups from Brownsman and West Wideopen islands

	Control	Long	Short	F/χ^2
Brownsman				
Pronotum width	1.97 ±0.02	1.95 ±0.02	1.96 ±0.02	$F_{2,36}=1.816$
Forceps length	4.26 ±0.14†	4.16 ±0.11†	3.87 ±0.07	$F_{2,36}=11.17^*$
Forceps asymmetry	0.050±0.01	0.0916±0.02	0.0983±0.03	$\chi^2_1=2.338$
West Wideopen				
Pronotum width	1.88 ±0.03	1.87 ±0.04	1.86 ±0.06	$F_{2,24}=0.302$
Forceps length	4.21 ±0.92†	4.26 ±0.24†	3.91 ±0.22	$F_{2,24}=22.8^*$
Forceps asymmetry	0.103±0.03	0.069 ±0.02	0.074 ±0.02	$\chi^2_1=1.625$

The F statistic is for repeated measures ANOVA and the χ^2 statistic for Friedman's test.

†Forceps length was not significantly different between these groups (Scheffé's test: $P<0.05$).

* $P=0.0001$.

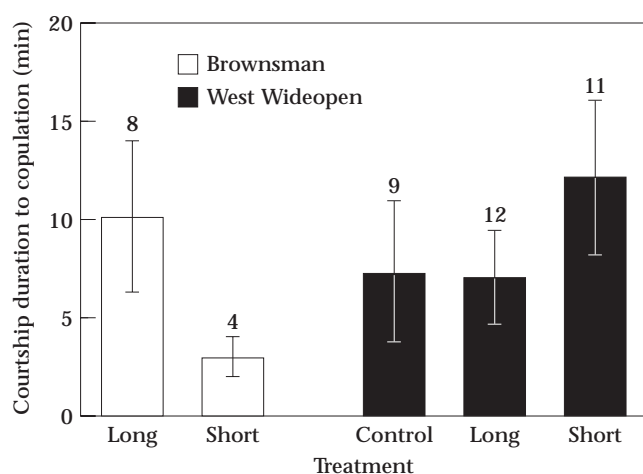


Figure 2. The mean duration of courtship (\pm SE) up to solicitation from the female for the treatment males of Brownsman (unpaired t test: $t_{10}=1.269$, $P>0.233$) and West Wideopen ($F_{2,26}=0.529$, $P=0.519$). The males' forceps were manipulated to be long or short or were nonmanipulated (controls). Sample sizes are given above the bars.

made active decisions, that is, the number of times females copulated with Short and rejected Long males compared to the number that copulated with Long and rejected Short males. Of the 10 occasions that a Brownsman female was courted by both Short and Long males, the female copulated with the Long and rejected the Short significantly more often than expected by chance (Fig. 3).

There was no effect of treatment in the West Wideopen population where females accepted equal numbers of copulations from males in each treatment (Cochran Q : Control=9, Long=12, Short=11, $Q=4.8$, $v=2$, NS). The difference in female preference for forceps length between West Wideopen and Brownsman island populations is consistent with that observed in unmanipulated mating trials reported in experiment 1 (Table 2). West Wideopen females copulated with 74% (41 of 55) of the males that courted whereas Brownsman females copulated with only 43% (13 of 30) of the males that courted them ($\chi^2_1=8.168$, $P<0.01$) further supporting the notion that West Wideopen females were less choosy.

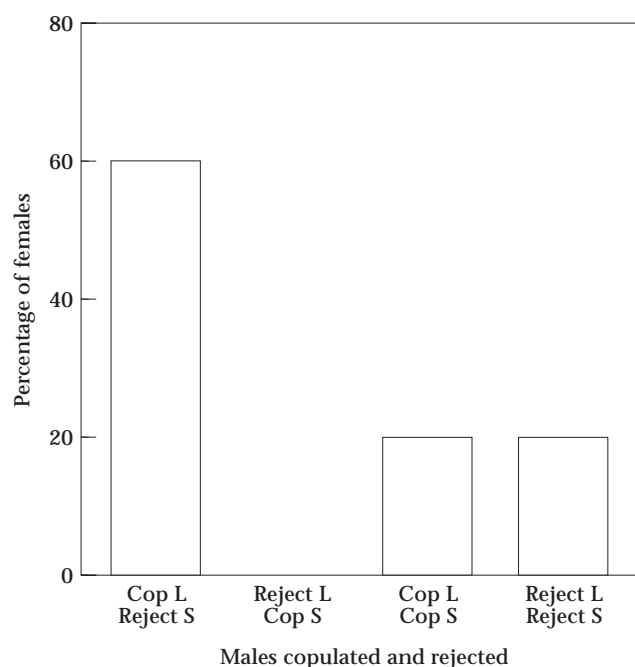


Figure 3. The percentage of Brownsman females, courted by both Long (L) and Short (S) treatment males (i.e. males with long or short forceps) that either copulated (cop) with or rejected them (McNemar's test: $\chi^2_1=5$, $P=0.03$).

EXPERIMENT 3: FORCEPS SYMMETRY

Methods

We manipulated symmetry first on adult earwigs from Neston. Males were separated into symmetrical and asymmetrical based on whether their forceps asymmetry was $\pm 1\%$ of their forceps length, and then further divided into unmanipulated controls and manipulated treatments. Manipulations involved the unilateral removal of the forceps tips in order to make symmetrical animals asymmetrical, and asymmetrical animals symmetrical. Thus, there were four experimental groups: symmetrical (S) and asymmetrical (A) unmanipulated controls, and symmetrical-made-asymmetrical (S-a) and asymmetrical-made-symmetrical (A-s) manipulations. The manipulations were carried out under carbon dioxide anaesthesia,

Table 4. Mean pronotum widths, forceps lengths and asymmetry of the treatment and control groups after the manipulation of forceps lengths as adults

	S	S-a	A	A-s	
Pronotum width	1.66 ±0.04	1.69 ±0.06	1.66 ±0.02	1.64 ±0.06	$F_{3,18} = 0.233$
Forceps length	3.48 ±0.03	3.36 ±0.12	3.38 ±0.09	3.35 ±0.10	$F_{3,18} = 0.435$
Forceps asymmetry	0.006±0.00	0.204±0.06	0.146±0.05	0.078±0.01	$\chi^2_1 = 11.09^*$

S: symmetrical unmanipulated; A: asymmetrical unmanipulated; S-a: symmetrical made asymmetrical; A-s: asymmetrical made symmetrical. The F statistic is for repeated measures ANOVA and the χ^2 statistic for Friedman's test.

* $P < 0.01$.

Table 5. Adult mean pronotum widths, forceps lengths and forceps asymmetry of the treatment and control groups after forceps symmetry manipulation as nymphs

	S	A	S-a	S-s	A-a	A-s	F/χ^2
Pronotum width	1.638±0.03	1.666±0.03	1.638±0.03	1.663±0.04	1.616±0.03	1.737±0.02	$F_{5,45} = 1.585$
Forceps length	3.288±0.06	3.260±0.05	3.136±0.07	3.076±0.04	3.105±0.08	3.130±0.05	$F_{5,45} = 0.183$
Forceps asymmetry	0.002±0.00	0.177±0.06	0.182±0.02	0.042±0.02	0.165±0.03	0.072±0.04	$\chi^2_1 = 32.514^*$

The F statistic is for repeated measures ANOVA and the χ^2 statistic for Friedman's test.

* $P = 0.0001$.

and the males were left to recover in petri dishes 5 cm in diameter for a week with pollen and water provided ad libitum. Males in each treatment did not differ in either pronotum width or forceps length, but did differ significantly with respect to forceps asymmetry (Table 4). Again we used repeated measures ANOVA to test the variance generated within subject females, that is, the test was designed to ensure that each individual female was presented with males differing only in forceps asymmetry.

In the second manipulation of asymmetry we manipulated the forceps of fourth-instar nymphs. Nymphs from Neston were separated into symmetrical and asymmetrical based on whether their forceps asymmetry was ± 0.02 mm (1% of mean cercus length). One control group from each class (Symmetrical and Asymmetrical) was reared to adulthood without forceps manipulation. One treatment group from each class had the tips of their forceps bilaterally removed to leave them symmetrical, the other treatment group had the tips of their forceps bilaterally removed to leave them asymmetrical. These animals were reared to adulthood. This gave six groups: symmetrical (S), symmetrical made symmetrical (S-s), symmetrical made asymmetrical (S-a), Asymmetrical (A), asymmetrical made symmetrical (A-s) and asymmetrical made asymmetrical (A-a). For the mate choice trial we chose adults whose forceps showed the least signs of damage from the manipulations and whose forceps best met the criteria of their treatment. Forceps asymmetry differed significantly between the groups but forceps length and pronotum width did not (Table 5). Behavioural observations followed the protocol of previous experiments.

Results

There was no effect of the symmetry manipulation of the adult males' forceps on the courtship duration up to

copulation ($F_{3,49} = 0.5$, $P = 0.683$). However, analysis of how the copulations were distributed among the males that courted the females revealed that there was a significant difference between the treatments (S=12; S-a=4; A=9; A-s=3; $\chi^2_3 = 8.29$, $P = 0.04$). Nevertheless, this result does not support the hypothesis that females are paying attention to symmetry. Rather it shows that females discriminate against males with forceps manipulated in adulthood (matings with unmanipulated, but not manipulated males=16; matings with manipulated but not unmanipulated males=2; McNemar's test: $\chi^2_1 = 13.47$, $P = 0.001$). There were no differences between the unmanipulated treatments (matings with S but not A=3; matings with A but not S=0; McNemar's test: $\chi^2_1 = 1.33$, NS).

When forceps asymmetry had been manipulated at the fourth instar, there were no differences in the females' decision to copulate with the males from the different treatment groups (Fig. 4a). There was also no difference between the unmanipulated symmetrical and asymmetrical treatments when they were compared separately (matings with S but not A=6; matings with A but not S=1, McNemar's test: $\chi^2_1 = 2.28$, NS). The amount of time that males from the different treatment groups had to spend in courtship before they were solicited by a female was no greater between than within the groups (Fig. 4b).

DISCUSSION

Female choice has been demonstrated in a number of acoustic insects (Bailey 1985; Simmons 1986) and in those that advertise using pheromones (Averhoff & Richardson 1974; Moore 1988; Thornhill 1992). There are few examples, however, of a female preference for an exaggerated morphological trait in insects (Wilkinson & Reillo 1994). Our results demonstrate for the first time

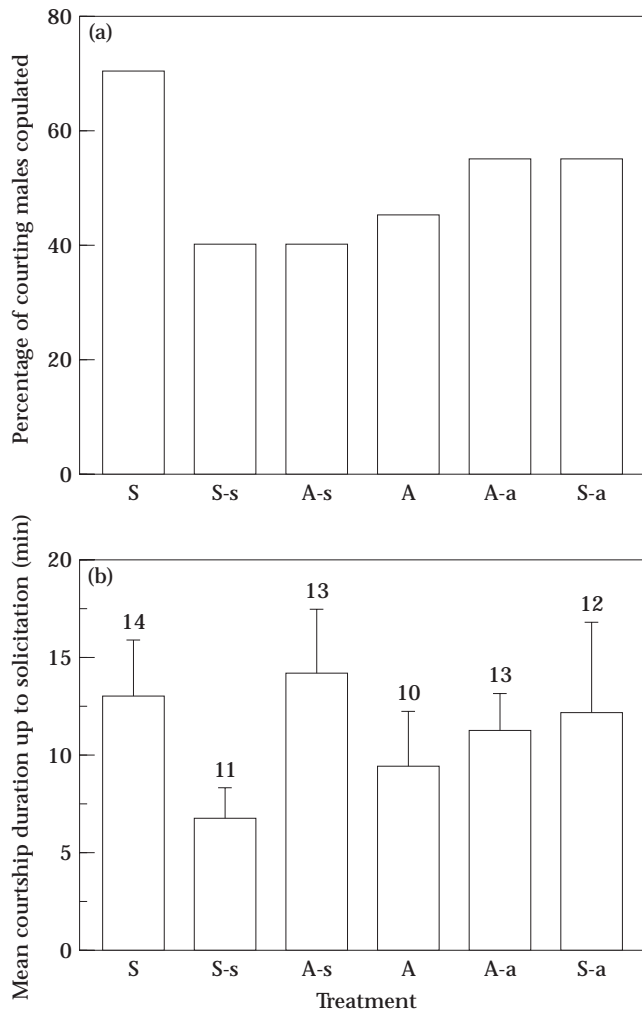


Figure 4. (a) Percentage of copulations gained by males from females that were courted by a male from each treatment group (combined replicates). Cochran Q test: $Q=6.24$, NS. (b) Amount of time males from each treatment group spent courting before a female solicited them (Kruskal–Wallis: $H_5=6.84$, NS). Forceps asymmetry of males was manipulated when they were fourth instars. S: symmetrical; S-s: symmetrical made symmetrical; A-s: asymmetrical made symmetrical; A: asymmetrical; A-a: asymmetrical made asymmetrical; S-a: symmetrical made asymmetrical. Sample sizes are given above the bars.

that female choice occurs in the Dermaptera and is for an exaggerated morphological trait.

There was evidence of female preference for long forceps in three of the four populations that we sampled. These preferences for unmanipulated forceps length are supported by the finding that when forceps were manipulated in length and all other body traits were held constant, matings were biased away from the males with shortened forceps. We manipulated forceps length in only two of the four populations and only Brownsman females showed a preference for the Long treatment males. Nevertheless the Brownsman population may be typical given that the patterns among females for unmanipulated males were the same for this island as for the two mainland populations.

Experimental manipulations of sexually selected traits have revealed female preferences for supernormal stimuli in a number of taxa (Andersson 1982; Borgia 1985; Møller 1988; McClintock & Uetz 1996). However, unlike previous manipulation of secondary sex traits, we could not elongate the forceps of the males, so females were not exposed to ‘supernormal’ forceps. Nevertheless, in common with other manipulations of secondary sex traits, males with the reduced trait suffered the lower mating success.

Nonrandom mating in *F. auricularia* could have evolved through females deriving direct benefits from choosing particular males, for example if males defend or possess resources such as oviposition sites (Thornhill & Alcock 1983) or nutrients such as a salivary mass (Thornhill & Alcock 1983) or nuptial gift (Thornhill 1976). However female *F. auricularia* are unlikely to receive such direct fitness benefits. Earwigs are generalists in their diet (Buxton 1974) and do not have specialized oviposition sites (Lamb 1976), making resource defence unlikely. In addition males do not cooperate in parental care (Lamb 1976) and transfer only free sperm without a nutritious spermatophore (J. L. Tomkins, personal observation). Females may gain direct benefits in other ways that are less easy to dismiss, for example they may increase their fecundity, or avoid sexually transmitted diseases by mating with particular males. However, since forceps length is heritable (Tomkins 1997), nonrandom mating may have evolved through the fitness benefit that the females’ offspring derive from their mothers’ choice, following either the good genes (Hamilton & Zuk 1982) or arbitrary trait (Fisher 1958) models of sexual selection.

According to current models of fluctuating asymmetry (Møller 1993a; Møller & Pomiankowski 1993) discrimination between good genes (Zahavi 1975; Hamilton & Zuk 1982) and arbitrary trait (Fisher 1958) models might be achieved by scrutinizing the patterns of female choice with respect to the subtle asymmetries found in secondary sexual traits (Møller 1993a; Møller & Pomiankowski 1993). Females choosing males on the basis of their genetic quality should, therefore, pay attention to the symmetry as well as the size of secondary sexual traits (Møller 1993a; Møller & Pomiankowski 1993). Female choice for size and symmetry should generate a negative relationship between the two traits. Alternatively, females choosing purely for the benefits their male offspring will derive from bearing a large trait should pay attention to trait size regardless of its symmetry (Møller & Pomiankowski 1993).

Female *F. auricularia* from four populations showed no preference for field-collected males with symmetrical forceps. These results are contrary to the findings of Radesäter & Halldórsdóttir (1993), who found that males with symmetrical forceps copulated sooner than asymmetrical males. The different results of Radesäter & Halldórsdóttir (1993) are consistent with a population difference in female choice given that other patterns of fluctuating asymmetry and condition were also different from those reported here. However, their data are inconsistent with the general patterns of fluctuating asymmetry and forceps length found across the Dermaptera

(Tomkins & Simmons 1995). Field studies of three species of *Drosophila* (*D. simulans*, *D. mojavensis* and *D. pseudoobscura*) and a study of captive ring-necked pheasants, *Phasianus colchicus*, have demonstrated female preferences that are similarly unrelated to male symmetry (Markow & Ricker 1992; Markow et al. 1996; Mateos & Carranza 1996).

Our experimental manipulation of adult male forceps demonstrated that females are paying attention to their quality, since males whose forceps had been cut at the adult stage were rejected as mates. However, the rejection of cut forceps may have obscured any preferences for symmetry. When we subsequently manipulated forceps when the animals were fourth instars, there were no effects of the forceps asymmetries on either the male's likelihood of mating or the amount of courtship that he had to perform to gain a solicitation. Thus, females appear to assess the size and quality of a male's forceps, although they do not base their mate choice decisions on the symmetry of the forceps.

A disregard for symmetry in female choice has been predicted in situations where female mate preferences have evolved through runaway selection, and male genetic quality is not the target of selection (Møller 1993a; Møller & Pomiankowski 1993). However, it may equally be that females are in search of males with high genetic quality but that forceps asymmetry is not a reliable indicator of condition (Tomkins & Simmons 1995, 1996). Radesäter & Halldórsdóttir (1993) found that asymmetrical *F. auricularia* males were lighter for their body size than symmetrical males and were therefore in poorer condition. Replication of Radesäter & Halldórsdóttir's (1993) procedure for males from Girton and Brownsman Island revealed no such relationship between condition and forceps asymmetry. Females paying attention to symmetry in these populations would thus gain no information about the body condition of their potential mates.

In common with patterns across the Dermaptera (Tomkins & Simmons 1995), there were no negative relationships between forceps length and forceps symmetry in any of the populations. A negative relationship is predicted where traits are costly to produce and only males of high genetic quality can maintain symmetry under the stress associated with the production of a large trait (Møller 1993a; Møller & Pomiankowski 1993). Furthermore, there must also be a cost to the production of an asymmetrical trait, for example through female choice (Møller 1993a). A negative relationship between forceps asymmetry and forceps size is not expected within populations of *F. auricularia* where females pay no attention to symmetry and where symmetry does not reflect condition.

There were differences in the patterns of female choice in the populations we sampled. In particular, females from the West Wideopen population were less choosy than those on Brownsman Island in terms of the proportion of courting males with which they refused to copulate. West Wideopen females did not share the preference for males with long forceps found on Brownsman or the mainland. West Wideopen males

have relatively longer forceps than Brownsman males (Tomkins & Simmons 1996). Hence there is a paradox: the population with no female choice for forceps length has males with more exaggerated forceps. This situation may have arisen as a consequence of past selection through female choice, perhaps eroding the genetic variance among males on West Wideopen to a point where there is no longer an advantage to choice. Equally male-male competition driven by a higher density of earwigs on West Wideopen may also account for the increased forceps length, without selection via female choice. Population differences in female choice warrant further study.

In conclusion, our data suggest that sexual dimorphism in the forceps of *F. auricularia*, and indeed sexual dimorphism in forceps across the Dermaptera, may have arisen, in part, by sexual selection through female choice. Our experiments demonstrate that females choose males on the basis of forceps length and, although they discriminate against males with damaged forceps, they do not pay attention to forceps symmetry. Female disregard for forceps symmetry is consistent with it being a random trait that does not reflect condition (Markow & Ricker 1992; Balmford et al. 1993; Eggert & Sakaluk 1994; Evans et al. 1995; Tomkins & Simmons 1995; Mateos & Carranza 1996; Hunt & Simmons 1997). In contrast, although there is a significant heritable component to forceps length (unpublished data), diet manipulations have demonstrated that forceps length is also dependent upon nutritional condition (Tomkins 1997). By choosing long forceps, females may choose males that are both good competitors as nymphs and have a genetic predisposition towards long forceps that will be expressed in their offspring.

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