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The effect of sexual size dimorphism on mating behaviour in two dung flies with contrasting dimorphism

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ABSTRACT

There is a fundamental conflict between the sexes over the frequency and duration of mating; therefore, control of the mating process is important for both. The relative size of the mates may influence who has greater behavioural control over the outcome of mating. In the yellow dung fly *Scathophaga stercoraria*, males are on average larger, whereas in *Sepsis cynipsea*, males are smaller. We manipulated larval environments to phenotypically reverse the natural sexual size dimorphism of both dung fly species and investigate the effects of sexual size dimorphism on mating behaviour. We expected that reversal of sexual size dimorphism would at least partly lead to a shift in the relative control of the outcome of mating from one sex to the other, as evident in qualitative or quantitative changes in various aspects of mating behaviour and ultimately mating success. As both species have common behaviour components, we also expected this shift to reveal more similarities between the two species, which have otherwise evolved quite different mating systems. We found little evidence for this in either species in our laboratory study. We conclude that reversal of sexual size dimorphism did not lead to a shift in control, perhaps because males and females control the mating process at different levels. Male *Scathophaga stercoraria* exert behavioural control because they are larger, whereas females have some internal control through cryptic choice. In *Sepsis cynipsea*, the larger females have behavioural control over mating, whereas males may control fertilization by internally injuring their mates. Overall, our results suggest that the mating system, and the mating conflict, are long-term, ‘hard-wired’ consequences of evolutionary shifts in sexual size dimorphism.

Keywords: body size, dung flies, mating behaviour, mating system, *Scathophaga stercoraria, Sepsis cynipsea*, sexual conflict, sexual size dimorphism.

INTRODUCTION

Mating is characterized by both cooperation and conflict (Alexander *et al.*, 1997). The cooperative nature of mating behaviour is obvious: one mate needs another to reproduce. However, whereas male fitness generally increases with his number of mates, female fitness

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depends on her copulation frequency to a much lesser extent (Bateman, 1948; Arnqvist and Nilsson, 2000). This leads to a fundamental conflict between the sexes, to a point where a fitness increase for one mate may lead to a decrease for the other (Parker, 1979; Stockley, 1997; Parker and Partridge, 1998; Partridge and Hurst, 1998). An evolutionary arms race is expected to result, in which mates continuously counteract the advantages of one another (Alexander *et al.*, 1997; Holland and Rice, 1998; Partridge and Hurst, 1998). At any point in evolutionary time, therefore, one or the other sex may be more or less in control of the outcome of mating (Holland and Rice, 1998; Parker and Partridge, 1998). This conflict is expressed, for example, in divergence between males and females in mating frequency, copula duration or mate guarding, thus affecting the classical sexual selection processes of female choice and male–male competition (Darwin, 1871; Andersson, 1994). Consequently, mating struggles of the sexes are common and are characterized by persistent male mating attempts and prominent behaviour of females to resist mating (Rowe *et al.*, 1994), although the particular behaviour is often species-specific.

Both the process and outcome of sexual conflict are affected by morphology. For example, abdominal processes in female water striders (Arnqvist and Rowe, 1995) or foreleg spines in the male dung fly *Sepsis cynipsea* (Blanckenhorn *et al.*, 1998) should allow one or the other sex to gain better control over their mating partner, as should specific elaborate and ubiquitous morphological genital structures (Eberhard, 1985, 1996). In the simplest case, control could be effected by mere physical strength or large body size; whichever mating partner is larger may have an advantage (e.g. Weigensberg and Fairbairn, 1994; Jormalainen and Merilaita, 1995; Blanckenhorn *et al.*, 2000; Crean *et al.*, 2000; Jormalainen *et al.*, 2000).

Sexual size dimorphism is widespread among animals (Hedrick and Temeles, 1989; Shine, 1989; Fairbairn, 1997). In most ectotherms females are larger, whereas in many birds and most mammals males are larger, but there is considerable variation in sexual size dimorphism even among closely related species (reviewed in Andersson, 1994; Abouheif and Fairbairn, 1997; Fairbairn, 1997). Sexual selection for large male size has been argued to be the primary force affecting the evolution of sexual size dimorphism in general (Price, 1984; Arak, 1988; Andersson, 1994; Fairbairn and Preziosi, 1994; Fairbairn, 1997; Blanckenhorn, 2000) and of male-biased sexual size dimorphism in particular (Clutton-Brock *et al.*, 1977; Cabana *et al.*, 1982). Conversely, a reversal in sexual size dimorphism in any particular species over evolutionary time should lead to concomitant changes in mating behaviour, the mating system and the potential for controlling the outcome of mating for either sex. This can be inferred from extant patterns. In species with larger females, female choice and male scramble competition dominate, whereas in species in which males are larger, male resource defence polygyny, territoriality and forced copulations are common (Andersson, 1994; Gowaty and Buschhaus, 1998).

Scathophaga stercoraria and *Sepsis cynipsea* are two common dung flies with similar ecology (Blanckenhorn, 1997), but which differ in natural sexual size dimorphism. Male *Scath. stercoraria* are on average larger, whereas male *S. cynipsea* are smaller, than females. Both species show struggle behaviour during mating, although it is much more pronounced in *S. cynipsea* (for *Scath. stercoraria*, see Parker, 1970a,b; Meile, 1996; for *S. cynipsea*, see Parker, 1972a; Ward *et al.*, 1992). Furthermore, in *Scath. stercoraria*, post-copulatory shaking has been described (Meile, 1996), whereas *S. cynipsea* males perform abdominal strokes and temporary genital contacts (see Parker, 1972a, for a full description), while females bend their abdomen down to avoid matings (cf. Crean and Gilburn, 1998; Crean *et al.*, 2000). Another important difference between these two species is the sequence of mating behaviour: oviposition takes place before copulation in *S. cynipsea* (i.e. there is pre-copulatory guarding: Parker, 1972b), whereas in *Scath. stercoraria* copulation occurs before oviposition (post-copulatory guarding: Parker, 1970a,b).

In this study, we examine how sexual size dimorphism influences mating behaviour in both fly species. Evolutionary shifts in sexual size dimorphism leading to concomitant shifts in mating behaviour cannot be observed directly. However, ectotherms typically show a high degree of phenotypic variation in body size primarily related to variation in environmental variables such as temperature and juvenile food availability (e.g. Amano, 1983; Blanckenhorn, 1997). We thus manipulate sexual size dimorphism and investigate whether, in the extreme, reversal of dimorphism in both species changes their mating behaviour and, in particular, the relative degree of behavioural control by males or females. If both species have retained some behavioural flexibility to respond in nature to untypical but not entirely absent sexual size dimorphism, we expect our manipulation to reveal similarities between these species, which have otherwise evolved quite different mating systems, ultimately relating to their contrasting sexual size dimorphism. The mating system of *Scath. stercoraria* is dominated by male contest and scramble competition, little behavioural female choice, strong sperm competition, cryptic female choice and nearly certain (forced) copulation (Parker, 1970a,b, 1979; Borgia, 1981, 1982; Sigurjónsdóttir and Parker, 1981; Ward, 2000). That of *S. cynipsea* is dominated by male scramble competition, behavioural female choice, strong female reluctance to mate with any male due to mortality costs of copulation expressed in extended and vigorous pre-copulatory shaking, and low copulation rates (Parker, 1972a; Ward *et al.*, 1992; Blanckenhorn *et al.*, 2000, in press); the extent of sperm competition and cryptic female choice is unknown. The results of this study should ultimately further our understanding of patterns of mating behaviour relating to sexual size dimorphism in general.

Mating by definition is a complex interaction between the sexes. It is thus generally difficult to assess objectively who is in control and who ‘wins’ the mating conflict, and an operational definition of control independent of the eventual outcome of mating is clearly lacking (cf. Parker and Partridge, 1998). We therefore assess the effect of our manipulation of sexual size dimorphism on several behavioural variables previously described in both species (Parker, 1970a,b, 1972a,b, 1979; Meile, 1996; Ward *et al.*, 1992; Blanckenhorn *et al.*, 2000), in an attempt to identify shifts in behaviour even if subtle. Very generally, we expect qualitative changes in the resolution of conflict between the sexes, in that the normally smaller sex will gain more behavioural control over the outcome of mating in both species when it is larger (due to manipulation).

Our expectations are based on the general belief that a female’s optimum mating frequency is expected to be lower than that of males (Bateman, 1948; Arnqvist and Nilsson, 2000). In addition, if sperm competition occurs, the optimal copula duration is largely male determined and can be expected to be shorter for females than males (Parker *et al.*, 1993; Parker and Simmons, 1994; Martin and Hosken, in press). Our expectations for all behavioural variables assessed in both species when sexual size dimorphism is reversed are listed in Table 1; except when the behaviour does not occur in one or the other species, our expectations are symmetrical. Specifically, when females are larger and thus have potentially more control: (1) the time and number of male mountings required before a female is successfully mounted should increase; (2) pre- and post-copulatory female shaking indicating

Table 1. Species-specific expectations of the relative influence of females (F) and males (M) on mating behaviour and outcome, when sexual size dimorphism shifts from a male- to a female-biased situation in *Scath. stercoraria* and from a female- to a male-biased situation in *S. cynipsea*

Behaviour	*Scath. stercoraria*	*S. cynipsea*	Influenced by
Time to first mounting	increased	decreased	F + M
Number of male mountings	increased	decreased	M
Pre-copulatory female shaking	increased	decreased	F + M
Post-copulatory female shaking	increased	—	F + M
Number of male genital strokes	—	increased	M
Temporary genital contacts	—	increased	F + M
Mating frequency	—	increased	F + M
Copula duration	decreased	increased	F + M

her reluctance to mate should increase; and (3) copula duration should decrease. For *S. cynipsea* only, (4) mating frequency should decrease (in *Scath. stercoraria*, mating almost certainly results) and (5) there should be fewer male genital strokes and temporary genital contacts because males cannot force them as easily.

MATERIALS AND METHODS

Rearing conditions

Parents of the experimental *Scath. stercoraria* were collected in April 2000 at Fehraltorf near Zürich, Switzerland (47°23′ N, 8°44′ E). *S. cynipsea* adults were collected at the same site in May 2000; the F1 and F2 for *S. cynipsea* were reared in the laboratory to be used in the mating experiments.

Dung restriction and warm temperatures during the larval stage result in small adults (Amano, 1983; Sigurjónsdóttir, 1984; Blanckenhorn, 1997). Therefore, larvae were grown in two different environments to obtain large and small size classes of males and females. For *Scath. stercoraria*, larval conditions were a photoperiod of 13 h, 60% relative humidity (r.h.) and (a) ~1 g dung per larva and 19°C for small individuals and (b) >2 g (i.e. superabundant: Amano, 1983) dung per larva and 15°C for large individuals. For *S. cynipsea*, larval conditions were a photoperiod of 15 h and (a) ~10 g dung per 25 adults, 27°C and 30–40% r.h. for small individuals and (b) more than 20 g dung per 25 adults, 20°C and 80% r.h. for large individuals. These conditions are well within the natural range of both species (Blanckenhorn, 1997). At emergence, individuals were separated by sex, age, body size class (small or large, corresponding to the larval environment) and family. *Scath. stercoraria* were housed individually, *S. cynipsea en masse*. In both species, hind tibia length was used to estimate body size (Ward, 1983; Parker *et al.*, 1993; Blanckenhorn *et al.*, 1999). Once separated, individuals of both species were maintained under standard laboratory conditions: 17°C, 13 h photoperiod and 60% r.h. with *ad libitum* sugar, water and *Drosophila* spp. as prey for *Scath. stercoraria*; 20°C, 15 h photoperiod and 60% r.h. with *ad libitum* sugar, water, pollen and fresh cow dung for *S. cynipsea* (see Blanckenhorn, 1997, for more details).

The mating experiment

We set up four size class combinations. For both species, the two matching combinations small male/small female (SS) and large male/large female (LL) represent a normal sexual size dimorphism. For *Scath. stercoraria*, the large male/small female (LS) combination represents the extreme but normal sexual size dimorphism and the small male/large female (SL) combination the reversed sexual size dimorphism. For *S. cynipsea*, the large male/small female (LS) combination represents the reversed sexual size dimorphism and the small male/large female (SL) combination the extreme but normal sexual size dimorphism (cf. Table 2).

For *Scath. stercoraria*, a randomly chosen male was introduced in a 200 ml plastic bottle containing a smear of fresh dung on a filter paper for oviposition. The female, also randomly chosen but not from the same family, was added afterwards, as is natural. For *S. cynipsea*, three randomly chosen males from the same holding container were placed in a 50 ml glass tube to increase the likelihood of mating (Blanckenhorn *et al.*, 2000); the female (not from the same container) was introduced afterwards, as is natural. A trial started as soon as the female entered the experimental chamber.

We recorded the variables listed in Table 1: (1) time to first mounting (indicating male readiness to mate); (2) total number of male mountings before copulation was achieved (indicating male persistence and female reluctance to mate); (3) cumulative (i.e. total) amount of pre-copulatory female shaking (indicating female resistance, which is infrequent and brief in *Scath. stercoraria* but common and long in *S. cynipsea*); (4) first appearance and cumulative amount of (post-copulatory) female shaking as copulation proceeds (indicating female willingness to terminate copulation; not present in *S. cynipsea*); and (5) total copula duration. For *S. cynipsea*, we additionally recorded: (6) the total number of male genital strokes; (7) the total number and duration of temporary genital contacts (both indicating male attempts to force copulation); and (8) whether copulation occurred or not. Shaking time and the number of mountings were additionally divided by the total time the mates were together (which varied), yielding relative measures. Moreover, several covariates were recorded: temperature, age of males and females, state of males and females (virgin or not), time between two copulation trials, date and time of the day. Trials were conducted in a climate chamber at 19°C in the case of *Scath. stercoraria* and at (variable) room temperature (22–26°C) in the case of *S. cynipsea*.

For each trial, three outcomes were possible: (a) copulation occurred, and the experiment was terminated 2 min after genital separation (almost certain in *Scath. stercoraria*, but infrequent in *S. cynipsea*); (b) the male(s) did not mount the female, in which case the trial was stopped 10 min after the introduction of the female (rare in both species); and (c) the male mounted the female but there was no copulation, in which case the experiment was stopped after an arbitrary period of 30 min (cf. Blanckenhorn *et al.*, 2000; almost non-existent in *Scath. stercoraria*, but frequent in *S. cynipsea*). Copulation was defined by genital contact lasting more than 5 min, meaning that sperm was transferred; temporary genital contacts (see above) were much shorter. Females that copulated were assigned to another male of the other size class about 1 week later, whereas males were used only once. The two additional *S. cynipsea* males were removed as soon as one male copulated.

Statistical analysis

Female *Scath. stercoraria* typically copulated twice, whereas female *S. cynipsea* did not (see Results). We therefore performed two-way repeated-measures analyses of variance for *Scath. stercoraria*, with male (crossed) and female (repeated) body size class as factors. For *S. cynipsea*, we used factorial analysis of variance (ANOVA) with male and female size class as crossed factors; whether copulation occurred or not was treated as an additional blocking factor. To normalize distributions, all data were $\log(x + 1)$-transformed. Analogous logistic regression models were used for 0/1 variables. All covariates were first introduced in the models, but retained only when significant ($P < 0.05$), except for temperature effects on copula duration, which are known to exist in both species (Parker, 1970b, 1972a). One planned paired comparison was performed between the exaggerated normal sexual size dimorphism and the reversed sexual size dimorphism [i.e. large male/small female pairing (LS) *vs* small male/large female pairing (SL)]. All *P*-values were Bonferroni corrected (Rice, 1989).

RESULTS

In 135 trials with *Scath. stercoraria*, only one female did not copulate, 21 copulated only once (i.e. died or escaped between the two trials), 9 refused to copulate the second time and 52 copulated twice. We only analysed the 104 trials of these latter 52 females, using repeated-measures ANOVA. Of 144 trials with *S. cynipsea*, 60 virgin females did not copulate and 48 copulated once, none of which copulated again. We analysed only the 108 trials with virgin females, using factorial ANOVA. Data from the three *S. cynipsea* males (per trial) were always summed – that is, we took the female perspective. In general, we expected qualitative or at least quantitative shifts in behaviour due to sexual size dimorphism reversal to result in significant interactions between male and female size class in the analyses of variance, independent of any main effects.

Time to first mounting turned out not to be meaningful in our small bottles, as it largely depended on how females entered the bottle and where males were located at that instant. Interpretation of post-copulatory guarding in *Scath. stercoraria* (cf. Parker, 1970b) is equally problematic in the laboratory. Both variables were therefore not considered in the final analysis. Results were qualitatively similar whether we used the absolute or relative shaking durations and number of mountings (see Methods), so we report only the former.

For both species, experimental manipulation of phenotypic body size had the desired effect, producing size classes that differed significantly from each other ($P < 0.001$ for all comparisons; Table 2). Furthermore, reversal of the sexual size dimorphism was successful, although the average sexual size dimorphism of the small male/small female combination for *S. cynipsea* was also slightly reversed (Table 2).

The mating behaviour of *Scath. stercoraria*

Male body size class generally affected mating behaviour, whereas female body size class did not; in particular, there were no significant interactions (Table 3). Of all the covariates, only female age had a significant effect, and only on copula duration: copulations with older females were shorter (Table 3). Even though pre-copulatory female shaking in this species is typically brief, it was longer with small males than with large males, suggesting stronger female resistance (Fig. 1A; Table 3). Small males needed more mating attempts (mountings), indicating greater male persistence and/or female resistance (Fig. 1B; Table 3). Copula duration was longer for small males, a common male effect (e.g. Parker and Simmons, 1994); at the same time, copulations of small females tended to be shorter (Fig. 1C; Table 3). Post-copulatory shaking occurred at the end of only 33 of the 104 copulations observed: in 8 of 24 trials when small males were paired with small females (SS treatment), in 13 of 28 trials in the SL treatment, in 6 of 24 trials in the LS treatment, and in 6 of 28 trials in the LL treatment. Logistic regression indicates that post-copulatory shaking occurred marginally more often with small males (which copulate for longer, $\chi^2_{1,100} = 3.18$, $P = 0.074$; female size class effect and interaction, $P > 0.3$).

The mating behaviour of *S. cynipsea*

In general, whether copulation occurred or not strongly affected mating behaviour, but main and interactive effects of male and female size class were rare (Table 4; Fig. 2).

Table 2. Hind tibia length for *Scath. stercoraria* and *S. cynipsea* males and females for the four size class combinations, with the mean male/female size ratios and sample sizes (the same *Scath. stercoraria* females were used with large and small males) (mean ± standard error)

		Hind tibia length (mm)			
Species	Combination	Male	Female	*n*	M/F size ratio
Scath. stercoraria	SS	2.49 ± 0.04	2.39 ± 0.05	24	1.04
	SL	2.68 ± 0.05	2.94 ± 0.03	28	0.91
	LS	3.56 ± 0.04	2.39 ± 0.05	24	1.49
	LL	3.61 ± 0.02	2.94 ± 0.03	28	1.23
S. cynipsea	SS	1.03 ± 0.01	0.97 ± 0.02	27	1.06
	SL	1.04 ± 0.01	1.30 ± 0.01	26	0.80
	LS	1.26 ± 0.01	0.97 ± 0.01	26	1.29
	LL	1.27 ± 0.01	1.32 ± 0.01	25	0.96

Table 3. Repeated-measures analyses of variance for the main variables for *Scath. stercoraria*

	Pre-copulatory shaking duration			Number of mountings			Copula duration[a]		
	MS	$F_{1,50}$	P	MS	$F_{1,50}$	P	MS	$F_{1,48}$	P
Female size	0.12	0.31	0.580	0.02	2.77	0.102	0.05	3.64	0.062
Error	0.40			0.01			0.01		
Male size	4.06	16.62	< **0.001**	0.04	8.81	**0.005**	0.29	18.28	< **0.001**
Interaction	0.37	1.53	0.222	0.00	0.17	0.683	0.00	0.00	0.981
Error	0.24			0.00			0.02		

[a] Temperature ($r = 0.21$, $P = 0.313$) and female age ($r = -0.44$, $P = 0.03$) were used as covariates.
Note: P-values significant after Bonferroni correction are in **bold**.

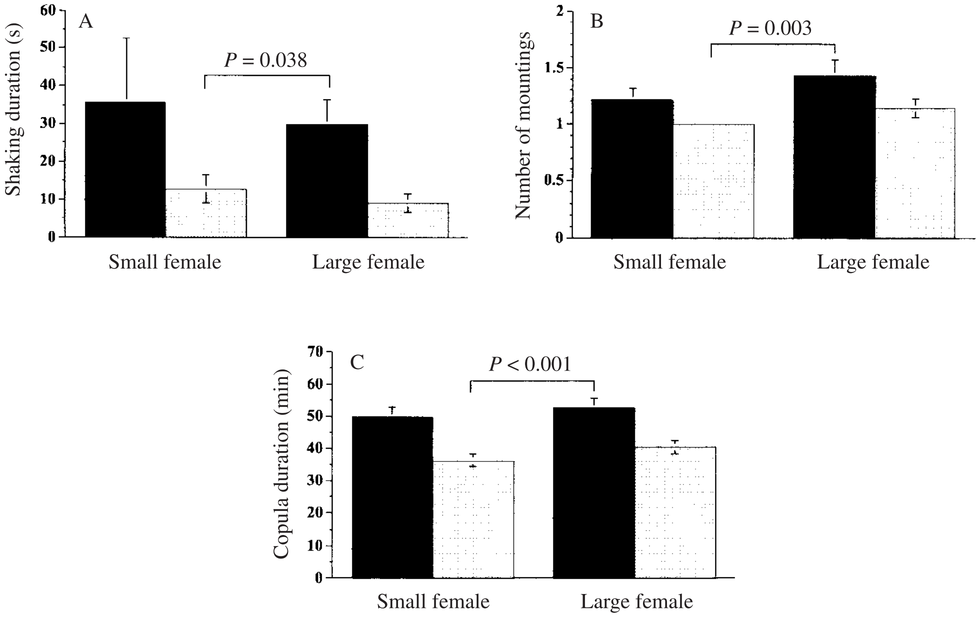

Fig. 1. (A) Pre-copulatory shaking duration, (B) number of male mountings and (C) copula duration for all size class combinations of *Scath. stercoraria*, with *P*-values for the planned paired comparison indicated (mean ± standard error). ■, small male; □, large male.

Furthermore, none of the covariates showed any effect. Shaking duration and number of mountings were naturally lower, and temporary genital contacts and male genital strokes higher, when the females were willing to copulate (Fig. 2A–D). Female pre-copulatory shaking was longer with large males (Fig. 2A; Table 4), indicating greater male persistence and/or female reluctance to mate (cf. Blanckenhorn *et al.*, 2000). For duration of temporary genital contact, we obtained a significant interaction (Table 4): its duration increased when small males were paired with larger females and decreased when large males were paired with larger females (Fig. 2C), contrary to expectation (we had expected the opposite; cf. Table 1). For copula duration, we also obtained a marginally significant interaction (Fig. 3; Table 4); for large males copula duration tended to increase with female body size class, whereas it remained the same for small males. Lastly, males from the large body size class had a marginally better chance to obtain copulations, a common result (Blanckenhorn *et al.*, 1998, 1999, 2000). Large males copulated with 16 of 28 small females and 12 of 25 large females, whereas small males copulated with 11 of 28 and 9 of 27, respectively (logistic regression: $\chi^2_{1,100} = 2.87$, $P = 0.09$; female size class effect and interaction, $P > 0.4$). However, all these main and interactive effects of size class were no longer significant after sequential Bonferroni correction.

DISCUSSION

The aim of this experiment was to determine whether a phenotypic reversal of the sexual size dimorphism of the two dung flies *Scathophaga stercoraria* and *Sepsis cynipsea* would result in qualitative or quantitative changes in various components of their mating

Table 4. Factorial two-way analyses of variance for the main variables for *S. cynipsea*

	Pre-copulatory shaking duration			Number of mountings			Copula duration[a]			Temporary genital contact duration			Number of genital strokes		
	MS	$F_{1,103}$	P	MS	$F_{1,103}$	P	MS	$F_{1,43}$	P	MS	$F_{1,103}$	P	MS	$F_{1,103}$	P
Copulation	5.65	25.03	< **0.001**	5.98	86.36	< **0.001**	—	—	—	6.67	83.04	< **0.001**	1.32	6.25	**0.014**
Female size	0.00	0.01	0.911	0.00	0.07	0.795	16.8	1.57	0.217	0.00	0.02	0.884	0.34	1.59	0.210
Male size	1.01	4.46	**0.037**	0.01	0.17	0.679	22.9	2.14	0.151	0.16	2.04	0.156	0.08	0.36	0.549
Interaction	0.35	1.55	0.217	0.00	0.00	0.975	40.9	3.82	0.057	0.49	6.15	**0.015**	0.45	2.11	0.149
Error	0.23			0.07			10.7			0.08			0.21		

[a] Temperature ($r = -0.14$, $P = 0.339$) was entered as a covariate.
Note: P-values significant after Bonferroni correction are in **bold**.

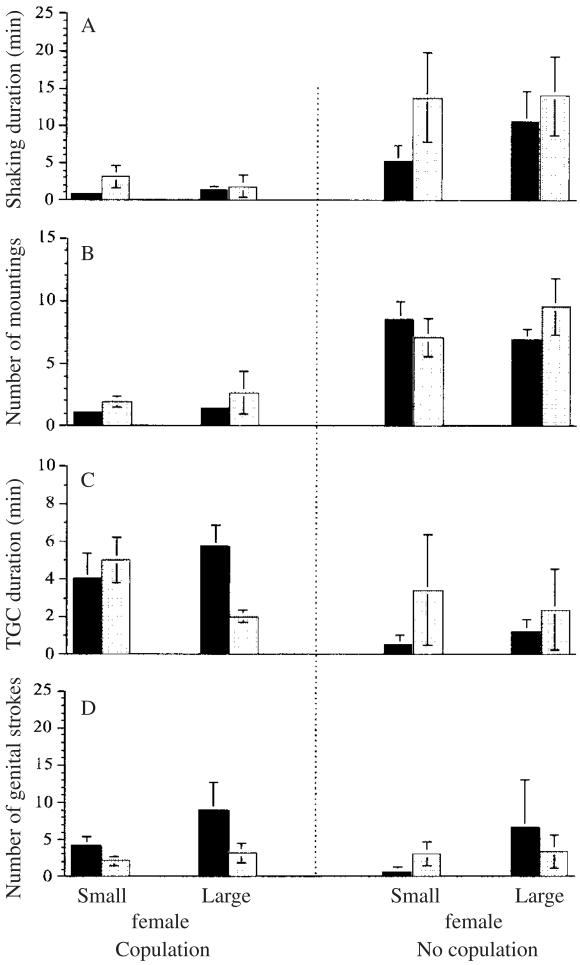

Fig. 2. (A) Pre-copulatory shaking duration, (B) number of male mountings, (C) temporary genital contact (TGC) duration and (D) number of male genital strokes for all size class combinations of *S. cynipsea* when copulation did (left) and did not occur (right) (all planned paired comparisons were non-significant) (mean ± standard error). ■, small male; □, large male.

behaviour. The former species has a mating system dominated by male–male competition for females, as males are larger (Parker, 1970a,b; Borgia, 1981, 1982); the mating system of the latter species is characterized by direct or indirect female choice (Ward, 1983; Blanckenhorn *et al.*, 2000). Our general expectation was that this manipulation would at least partly lead to a shift in the relative control of the mating process from one sex to the other. However, we found little evidence for this in either species and, therefore, conclude that the mating system and the mating conflict are long-term, 'hard-wired' consequences of evolutionary shifts in the sexual size dimorphism.

For *Scath. stercoraria*, male, but not female, size class affected most variables and no interactive effects were detected. These results are in line with those of previous studies describing strong male control (Parker, 1970a,b; Sigurjónsdóttir and Parker, 1981; Borgia,

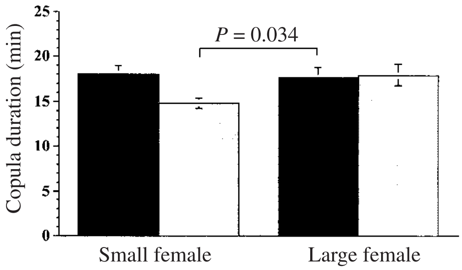

Fig. 3. Copula duration for *S. cynipsea* for all size class combinations, with the *P*-value for the planned paired comparison indicated (mean ± standard error). ■, small male; □, large male.

1982; Otronen, 1993; Parker *et al.*, 1993; Parker and Simmons, 1994) but subtle female control of mating (Ward, 1993, 2000; Hellriegel and Bernasconi, 2000). Copula duration of large males was shorter than that of small males, a common outcome predicted by theory due to greater sperm transfer rates and higher remating probabilities of larger males (Parker and Simmons, 1994, 2000). Contrary to our prediction here (cf. Table 1), copula duration (marginally) increased with female size. This was also found for *Scath. stercoraria* by Meile (1996) and Parker *et al.* (1999); this female effect is generally less marked than the corresponding male effect. If copula duration is largely determined by the male, this can be expected because a greater spermathecal volume has to be filled (Hosken and Ward, 1999; Parker *et al.*, 1999). Even though it is rather subtle, pre-copulatory shaking also occurs in *Scath. stercoraria*, as first described by Meile (1996). We found that small *Scath. stercoraria* males needed more mating attempts and had to endure more shaking before they achieved copulation, both suggesting a greater unwillingness of females to copulate with them. However, although in agreement with our expectations (cf. Table 1), pre-copulatory shaking rarely if ever resulted in successful male rejection and thus is probably pointless. Nevertheless, its subtle presence may be interpreted as a rudimentary trait that has been retained from an evolutionary past, when the sexual size dimorphism was probably less male-biased in this species and female rejection behaviour served a more prominent function. Lastly, *Scath. stercoraria* females also exhibited shaking at the end of about 30% of all pairings, predominantly those with small males, as also first found by Meile (1996). This may be taken as evidence that females prefer shorter copulations than at least small males (whose longer copulations are further away from the female optimum), but probably most males (cf. Parker *et al.*, 1993, 1999; Parker and Simmons, 1994).

For *S. cynipsea*, mating behaviour was more variable, as is typical in this species (Blanckenhorn *et al.*, 1999, 2000). Consequently, only a few of the variables assessed in this study were found to be related to body size class: pre-copulatory shaking duration tended to be longer with large males, and there were marginal interactive effects of male and female size class on temporary genital contact and copula duration. In particular, female body size class had no effect on mating behaviour. The latter differs somewhat from a recent study of this species, where some effects of female size on aspects of behaviour were found (Blanckenhorn *et al.*, 2000). As could be expected from previous findings (Blanckenhorn *et al.*, 2000), whether copulation occurred or not strongly affected mating behaviour in predictable (and uninteresting) ways: shaking duration and number of mountings were naturally lower, and there were more temporary genital contacts and male genital strokes, when the females were willing to copulate. Copula durations of large (but not small) males with large *S. cynipsea* females were longer, resulting in a marginally significant interaction. As in *Scath. stercoraria* (see above) and other species (e.g. Gage, 1998), this probably relates to more sperm being stored to fertilize the larger number of eggs of larger females, an effect that can largely be interpreted as a male strategy (e.g. Parker and Simmons, 1994). The fact that in *S. cynipsea* only large males increased copula duration may indicate that small males may be more sperm limited, although further evidence is needed to substantiate this. Opposite to *Scath. stercoraria*, large *S. cynipsea* males endured more shaking. Shaking behaviour can generally reflect (1) female assessment of males, (2) female unwillingness to mate or (3) a male's ability to hold on (Ward *et al.*, 1992; Rowe *et al.*, 1994; Weigensberg and Fairbairn, 1994). Blanckenhorn *et al.* (2000) showed that if shaking serves primarily to assess males, thus reflecting direct (active) female choice, it should decrease with male size. Therefore, pre-copulatory shaking duration in *S. cynipsea* primarily reflects female resistance to mate with any male, and relates to mortality costs of mating (Blanckenhorn *et al.*, in press). In combination with the greater persistence of large males, this results in indirect (passive) female choice for larger males, as is typically found in this species (Ward, 1983; Blanckenhorn *et al.*, 1999, 2000), and tended to be the case here. Lastly, although marginally significant, the pattern of temporary genital contact duration did not agree with our expectation that this variable (as well as the number of male genital strokes) should be highest when large males were paired with small females (cf. Fig. 2C). On the contrary, both behaviours were most pronounced when small males were paired with large females. Perhaps our interpretation that this indicates male attempts to force copulation was incorrect. Frequent temporary genital contacts may equally indicate problems with achieving genital intromission, which, according to the lock-and-key hypothesis, may be more likely when the mates differ greatly (and unnaturally) in size (cf. Eberhard, 1985, 1996). This may also explain why more temporary genital contacts and genital strokes were observed when copulation ensued.

In *Scath. stercoraria*, males seem to control copula frequency, whereas females have some opportunity to control paternity by cryptic sperm choice. This probably evolved as a response to forced copulations, as the smaller females cannot fend off males (Ward, 1993, 2000). In *S. cynipsea*, the situation is reversed. Females can behaviourally control copula frequency and with whom they mate (Blackenhorn *et al.*, 2000), whereas males apparently have some means to control paternity indirectly. Blanckenhorn *et al.* (in press) found increased mortality of *S. cynipsea* females that copulated, related to internal injuries inflicted by the male's aedeagus (penis). Johnstone and Keller (2000) showed that, theoretically, such spiteful sexual behaviour can evolve. Under this scenario, females are reluctant to re-mate because of the danger of fatal injuries, and the male which achieved copulation thus faces reduced (sperm) competition and assured paternity.

Rowe *et al.* (1994) suggested that struggle duration and frequency indicate the strength of intersexual conflict. Based on this argument, there appears to be more (overt) conflict in *S. cynipsea* than in *Scath. stercoraria*. But does it? It appears that in *Scath. stercoraria*, and perhaps in other species with male-biased sexual size dimorphism, the conflict is merely shifted to the internal levels of spermathecal morphology and sperm competition (Eberhard, 1985, 1996; Ward, 1993, 2000; Hosken and Ward, 1999). By and large, our results did not yield the expected interactive effects of male and female body size that would have indicated a conserved flexibility in the potential to behaviourally control the outcome of mating when the phenotypic sexual size dimorphism is reversed. This suggests that the mating system, and the mating conflict, are long-term, ‘hard-wired’ consequences of evolutionary shifts in the sexual size dimorphism, which are themselves largely due to sexual selection (Fairbairn and Preziosi, 1994; Fairbairn, 1997). These two rather different mating systems may thus be viewed as being at two different stages of a continuing evolutionary sexual arms race over who controls mating. It would be interesting and important to see whether the results found here hold in other species.

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