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INTERACTIONS AMONG MECHANISMS OF SEXUAL SELECTION ON MALE BODY SIZE AND HEAD SHAPE IN A SEXUALLY DIMORPHIC FLY

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Abstract.—Darwin envisaged male-male and male-female interactions as mutually supporting mechanisms of sexual selection, in which the best armed males were also the most attractive to females. Although this belief continues to predominate today, it has been challenged by sexual conflict theory, which suggests that divergence in the interests of males and females may result in conflicting sexual selection. This raises the empirical question of how multiple mechanisms of sexual selection interact to shape targeted traits. We investigated sexual selection on male morphology in the sexually dimorphic fly *Prochyliza xanthostoma*, using indices of male performance in male-male and male-female interactions in laboratory arenas to calculate gradients of direct, linear selection on male body size and an index of head elongation. In male-male combat, the first interaction with a new opponent selected for large body size but reduced head elongation, whereas multiple interactions with the same opponent favored large body size only. In male-female interactions, females preferred males with relatively elongated heads, but male performance of the precopulatory leap favored large body size and, possibly, reduced head elongation. In addition, the amount of sperm transferred (much of which is ingested by females) was an increasing function of both body size and head elongation. Thus, whereas both male-male and male-female interactions favored large male body size, male head shape appeared to be subject to conflicting sexual selection. We argue that conflicting sexual selection may be a common result of divergence in the interests of the sexes.

Key words.—Competition, Piophilidae, *Prochyliza xanthostoma*, sexual conflict, sexual dimorphism, sexual selection, shape.

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Darwin believed that male-male (intrasexual) interactions such as combat or scramble competition and male-female (intersexual) interactions such as courtship and mate choice would generate mutually supporting (reinforcing) sexual selection on male phenotypes, arguing that ‘‘[females] will select those [males] which are vigorous and well armed, and in other respects the most attractive. . . ’’ (Darwin 1874, p. 229–230). The idea that intrasexually competitive mates may confer direct or indirect benefits underlies much evolutionary thinking to this day (e.g., Berglund et al. 1996; Wiley and Poston 1996). This reasoning assumes that all vectors of selection will favor the same features, and that individuals in high condition will exaggerate those features (see Rowe and Houle 1996).

However, this is clearly not the case for life-history traits, which often experience conflicting selection (Roff 1992; Stearns 1992), and need not be the case for metric traits, such as morphological characters (Schluter et al. 1991). Thus, it is not obvious that sexual selection will necessarily be reinforcing (Moore 1990). Moreover, sexual conflict theory (Parker 1979) suggests that mate quality (i.e., net effect on a mate's fitness) need not covary positively with intrasexual competitiveness (Bussière 2002). For example, intrasexually competitive males may injure females (see Chapman 2001; Pitnick and García-González 2002), or sire low-quality daughters (Chippindale et al. 2001). Indeed, several recent studies have reported conflicting sexual selection through male-male and male-female interactions (e.g., Warner et al. 1995; Moore and Moore 1999; Andersson et al. 2002; Sih et al. 2002). The relative paucity of evidence for conflicting sexual selection may reflect the tendency to focus on a single selective mechanism, even though multiple mechanisms may operate in many (most?) systems (see Andersson 1994; Berglund et al. 1996; Bonduriansky 2003).

The sexually dimorphic carrion fly *Prochyliza xanthostoma* (Diptera: Piophilidae) offers an ideal opportunity to address this problem because males possess exaggerated head traits (elongated, narrow head capsule and antennae) that appear to function as a unit in both combat and courtship. Male head shape also covaries with condition: males reared on high-quality food have longer, narrower heads than males reared on low-quality food (R. Bonduriansky and L. Rowe, unpubl. ms.). In the wild, males typically defend territories and search for females in sunspots on vegetation near carcasses, where oviposition occurs (Bonduriansky and Brooks 1999a; Bonduriansky 2003). In combat, males grasp each other's forelegs and repeatedly strike down at each other with their heads and antennae (Fig. 1a,b). Courting males perform repeated side-to-side steps while holding the anterior end of the body elevated with the antennae erect and apart in a ‘‘V,’’ and periodically vibrating their forelegs (Fig. 1c). Receptive females respond by orienting and reaching out to touch the male's forelegs (acceptance response; Fig. 1d), after which the male attempts to somersault onto the female's back (precopulatory leap) and establish copulation. In the laboratory, males often miss or fall off the female at this stage, and must resume courtship to re-elicit acceptance (see Results). Following copulation, females expel and ingest ejaculate fluids and sperm, and this ejaculate meal appears to increase female fecundity without reducing survivorship (R. Bonduriansky, J. Wheeler, and L. Rowe, unpubl. ms.).

We staged male-male and male-female pairings in laboratory arenas to quantify male performance in several distinct tasks that are likely to affect male reproductive success

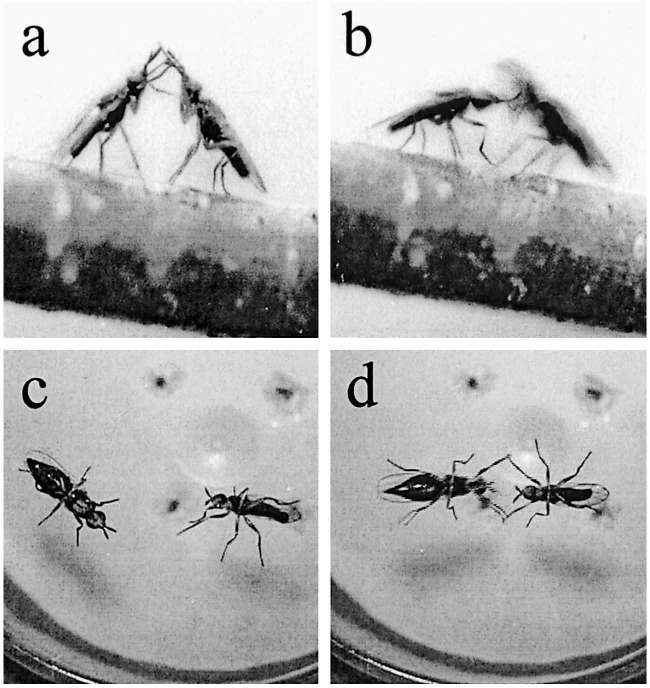

FIG. 1. Sexual behavior of *Prochyliza xanthostoma*: (a) wild males on a branch, holding each other's foretarsae (side view); (b) the male on the left striking his opponent with his head and antennae; (c) a male (on the right) courting a female inside the pairing arena under a dissecting microscope (ventral view); (d) the female (on the left) exhibiting the acceptance response.

(henceforth called ''mechanisms of sexual selection''). We then calculated coefficients of direct, linear selection on male head shape and body size to determine whether these multiple mechanisms of sexual selection exerted reinforcing or conflicting selection.

MATERIALS AND METHODS

Rearing of Flies

Gravid females of *Prochyliza xanthostoma* (Walker) ($N = 70$) were collected from carcasses of moose (*Alces alces*) at the Wildlife Research Station in Algonquin Park, Ontario, and transferred to 1.5-l cages with mesh windows. Cages contained sources of water, sugar cubes, and petri dishes with extra-lean ''organic'' (i.e., non-hormone treated) ground beef for oviposition. The offspring (sired in the wild) were transferred as final-instar larvae to individual pupation jars. Emerging adults were maintained in same-sex groups of about 10 in 1.5-l cages.

Male-Male Pairings

Males were matched with opponents of similar body size (post-hoc correlation of opponents' thorax lengths: $N = 180$, $r = 0.82$, $P < 0.0001$; Fig. 2) because field observations suggest that mating aggregations are stratified by male body size, so that males tend to interact with similar-sized opponents. Laboratory reared males were also matched by age. In each of the 180 pairs (88 pairs wild-caught, 92 pairs lab-reared), opponents were marked with distinguishing codes on the thoracic notum (see Bonduriansky and Brooks 1997), and maintained individually for 24–48 h prior to pairings. Pairings were performed in a 200-ml transparent-plastic arena containing a branched twig, sugar cube, and source of water, at an ambient temperature of 18–22°C. The arena was illuminated by a 100-watt incandescent spotlight about 50 cm away (producing long wavelengths and moderate heat) and a four-watt broad-spectrum fluorescent light with electronic (high flicker-frequency) ballast about 3 cm away (producing short and UV wavelengths, but very little heat). Opponents were released simultaneously into the arena, and several bouts of combat (mean = 46, SD = 16) between them were observed and timed with a hand-held stopwatch over 20–30 min. For each bout of combat, the winner was determined as the individual that remained in its original place or chased its opponent. If both males retreated or fell, the outcome was considered a tie. Males were frozen after the pairing.

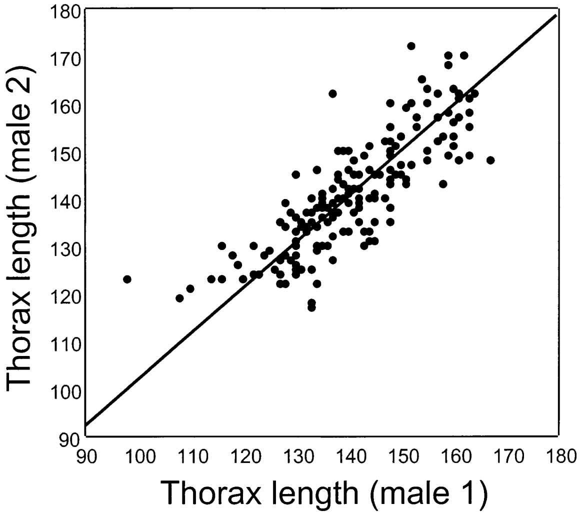

FIG. 2. Thorax lengths (mm × 100) of paired males, showing the correlation of opponents' body sizes achieved by size matching, with fitted reduced major axis (slope = 0.96, intercept = 5.70).

Male-Female Pairings

Laboratory-reared males and females aged 2–10 d were paired randomly ($N = 235$ pairs) in a transparent-plastic arena (3.2 cm diameter, 1.1 cm depth) under a dissecting microscope (see Fig. 1c,d) at an ambient temperature of 18–22°C. An opaque cylinder was placed over the arena to reduce visual disturbance. The arena was illuminated with a small incandescent light source about 10 cm away and two four-watt fluorescent lamps about 1 cm away (see above). The number of side-to-side courtship steps (determined using a manual counter) delivered by the male prior to acceptance, and the sequence of male and female behaviors (e.g., acceptance responses, precopulatory leaps, copulation) were recorded manually by the same observer for all pairings. These ''no-choice'' trials simulated typical male-female interactions in the wild (see Bonduriansky 2003). Flies were frozen at −20°C after genital separation or, if no copulation occurred, after 30 min. Between pairings, the arena was wiped with ethanol on lint-free tissue to remove chemical residues.

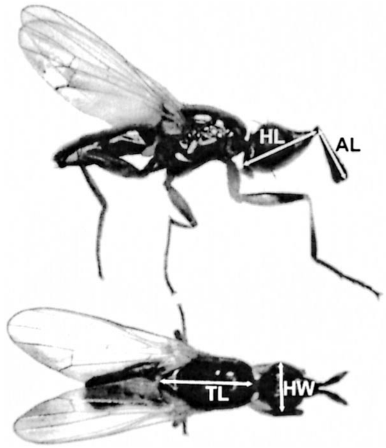

FIG. 3. Morphological measurements of male traits: head length (HL) and antenna length (AL), shown on a male viewed from the side, and head width (HW) and thorax length (TL), shown on a male viewed from above.

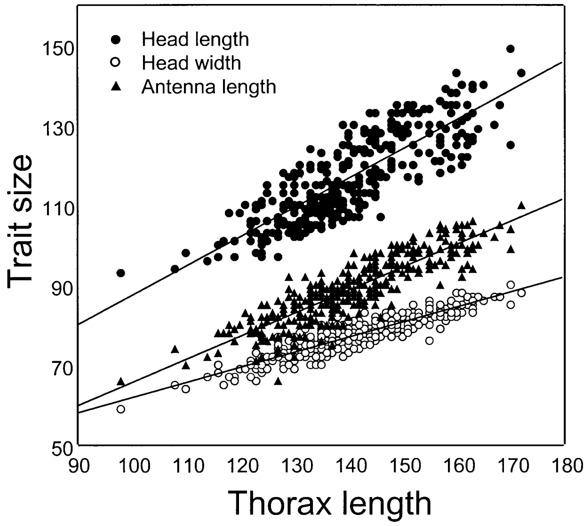

FIG. 4. The scaling of head length, head width, and antenna length with thorax length (mm × 100) in the *Prochyliza xanthostoma* males used in male-male pairings ($N = 360$), showing least-squares regression lines on which residual trait sizes are based.

Morphometric Data and Dissections

All measurements were made using a dissecting microscope with an ocular micrometer. Flies were thawed and glued to pins by the right side of the thorax using Super Tacky glue (Lewiscraft, Toronto, Canada). We measured male thorax length, head capsule length and width, and left antenna length (Fig. 3). Females were dissected to determine ovule size and ejaculate volume. The abdomen was severed using microscissors, placed in a drop of biological saline solution on a glass slide, and torn open with microprobes. Because there is little variation in ovule size within females (Bonduriansky and Brooks 1999a), we measured the length and width of one randomly selected ovule. Ejaculate volume was estimated by squeezing the sperm mass out of the bursa copulatrix and measuring its length and width. Ovule size and sperm mass size were estimated as the volume of an ellipsoid $(1/6 \times \text{length} \times \pi \times \text{width}^2)$.

We used thorax length as an index of body size because it exhibited the highest loading (0.97) on the first principal component of 17 measurements of legs, head, antenna, wings, and thorax (mean loading = 0.91) made on each of 36 males. ‘‘Head elongation’’ was calculated as the sum of residual head and antenna length minus residual head width from least-squares regressions of trait sizes on thorax length (Fig. 4). The head elongation index thus represents a gradient from relatively wide, short heads and short antennae to relatively narrow, long heads and long antennae. This reflects a natural gradient of variation, since male head length and antenna length are positively genetically correlated, but both are negatively genetically correlated with head width (R. Bonduriansky and L. Rowe, unpubl. data). Because analyses combine data from two years and from wild and laboratory-reared flies, residuals were standardized by fly origin and year. Thorax length and head elongation were uncorrelated ($N = 360$, $r = 0.00$, $P = 1.0$).

Selection Analysis

For each of the five indices of male performance (see Results), the two male traits (in male-female pairings), or differences between opponents in these traits (in male-male pairings), were included as factors in separate multiple regression models to estimate direct, linear selection gradients (Lande and Arnold 1983; Arnold and Wade 1984). For male-male pairings, success in the first bout of combat (win = 1, tie = 0.5, loss = 0), and the overall proportion of combat bouts won, were analyzed separately because these indices corresponded to single-bout and multiple-bout interactions in the wild. Of 138 male-male interactions (comprising >400 bouts of combat) observed in the wild, 73 interactions (53%) involved a single bout of combat that ended with one male running or flying away, and 65 interactions (47%) involved multiple bouts of combat between the two opponents (although note that these are rough estimates, since most individuals could not be distinguished). Female receptivity increases as the reproductive system develops in some insects (Manning 1967; Cook 1973; Trabalon and Campan 1984; Moore and Moore 2001), potentially confounding data on female preference. Hence, we tested for an effect of female physiological age, quantified as ovule size (Adams and Hintz 1969), on female receptivity. Male-male pairings in which one or both males failed to engage in combat ($n = 20$) were excluded from analyses. Females with developmental abnormalities ($n = 9$) and those that copulated without exhibiting an acceptance response ($n = 2$) were excluded from analyses of male courtship and leaping, and data on ovule size, leaping or sperm quantity are not available for some pairs (see Tables 1 and 2 for actual sample sizes).

RESULTS

Male-Male Interactions

Success in the first bout of combat increased with body size, but decreased with head elongation (Table 1; Fig. 5). However, when multiple bouts of combat were considered, the overall proportion of bouts won depended only on body size (Table 1; Fig. 5). These two indices of male combat

TABLE 1. Multiple regression results for two indices of male performance in male-male interactions: success in the first bout of combat with a new opponent, and the proportion of combat bouts won. Significant factors are highlighted in bold.

Performance index		N	r	F	β	SE_β	P
First bout of combat	Model	160	0.24	4.87			0.0089
	Body size				+0.16	0.0781	0.0489
	Head elongation				−0.17	0.0781	0.0350
All bouts (% won)	Model	160	0.39	13.89			<0.0001
	Body size				+0.38	0.0742	<0.0001
	Head elongation				−0.04	0.0742	0.62

success were weakly correlated ($N = 160$, $r = 0.29$, $P = 0.0002$).

Male-Female Interactions

Females that did not copulate had smaller (i.e., less developed) ovules than females that did (Mann-Whitney U-test: $N_{cop} = 153$, $N_{no\ cop} = 87$, $U = 1338$, $z = -10.29$, $P < 0.0001$; Fig. 6). Moreover, there was no significant difference between males that copulated and those that did not in either body size (t-test: $N_{cop} = 155$, $N_{no\ cop} = 89$, $t = -1.518$, $P = 0.1305$) or head elongation (t-test: $N_{cop} = 155$, $N_{no\ cop} = 89$, $t = -1.428$, $P = 0.1549$). These results suggest that female physiological age, rather than male phenotype, largely determined whether copulation ultimately occurred.

We tested for female preference using variation in the number of courtship steps until the female's first acceptance response (Fig. 1d): a male that performed fewer courtship steps before acceptance was assumed to be more attractive. Because female receptivity increased with physiological age (log-log transformed data: $N = 148$, $r = -0.44$, $F = 35.01$, $P < 0.0001$; Fig. 6), we controlled for female receptivity by including log ovule size as a factor in the model. The results suggested that male attractiveness was an increasing function of male head elongation, but was not related to male body size (Table 2; Fig. 7).

Following acceptance, a male must successfully perform the precopulatory leap to achieve copulation. The number of leaping attempts required to achieve copulation did not depend on female physiological age, which predicts receptivity ($N = 144$, $r = 0.035$, $F = 0.17$, $P = 0.67$), suggesting that leaping success was a male effect, rather than a result of female discrimination. Leaping success was an increasing function of male body size and, possibly, a decreasing function of male head elongation (Table 2; Fig. 7).

Males varied substantially in the quantity of sperm they transferred to females (Fig. 7). The quantity of sperm transferred was an increasing function of both body size and head elongation (Table 2; Fig. 7).

DISCUSSION

We investigated sexual selection on male body size and head shape through male-male and male-female interactions, subdivided into five mechanisms of sexual selection (Table 3), in the sexually dimorphic fly *Prochyliza xanthostoma*. Results suggested that male body size was subject to reinforcing sexual selection, whereas male head shape was subject to conflicting sexual selection (Table 3). Males with relatively elongated heads appeared to be disadvantaged in combat (Table 1) and, perhaps ($P = 0.08$) in precopulatory leap performance (Table 2). In contrast, males with more elongated heads were more attractive to females, and transferred more sperm (Table 2). Thus, the striking head shape of *P. xanthostoma* males appears to represent a grotesque compromise among competing vectors of sexual selection.

Conflicting Sexual Selection

Conflicting sexual selection may be common in systems subject to multiple mechanisms of sexual selection. Because of divergence in the interests of the sexes, resource allocation trade-offs, and functional constraints on target traits, different selective mechanisms are likely to pull a target trait off its viability optimum to a different degree, or even in a different direction, resulting in a tug-of-war among sexual selection

TABLE 2. Multiple regression results for three indices of male performance in male-female interactions: the log-transformed number of courtship steps before the female's first acceptance response, the standardized number of precopulatory leaps until copulation, and the log volume of sperm transferred. Significant factors are highlighted in bold.

Performance index		N	r	F	β	SE_β	P
Courtship	Model	148	0.47	13.78			<0.0001
	Body size				−0.09	0.0743	0.21
	Head elongation				−0.15	0.0738	0.0392
	Ovule size				−0.43	0.0739	<0.0001
Leaping success	Model	143	0.30	6.87			0.0012
	Body size				−0.25	0.0811	0.0027
	Head elongation				+0.14	0.0811	0.0815
Sperm transferred	Model	128	0.25	4.07			0.0194
	Body size				+0.19	0.0870	0.0292
	Head elongation				+0.17	0.0870	0.0488

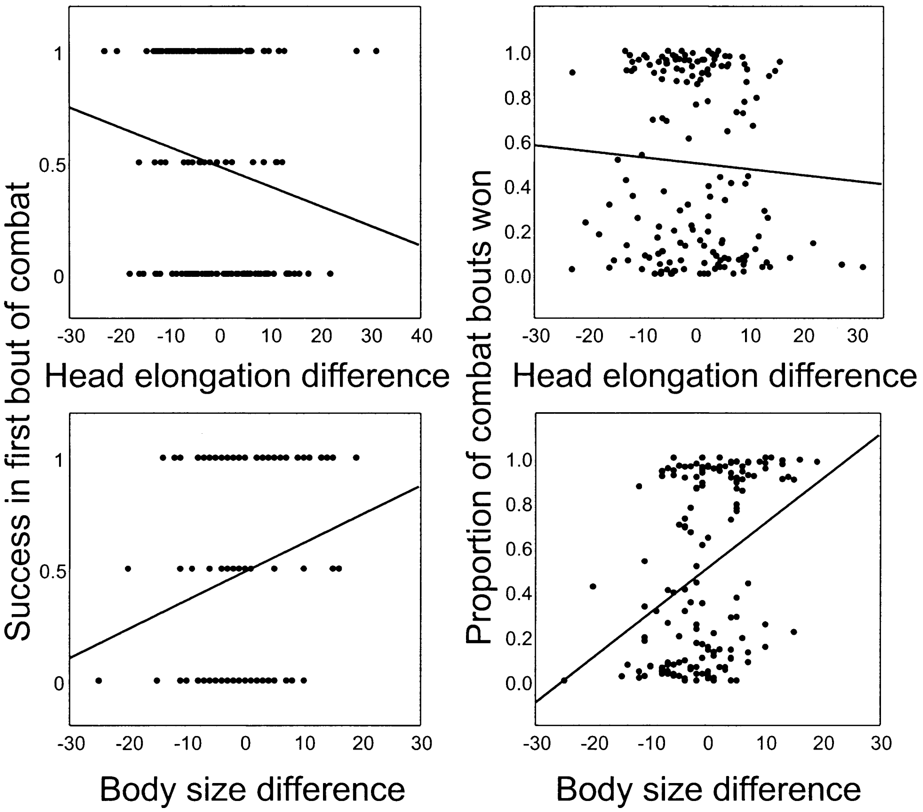

FIG. 5. Male-male interactions: the effect of male body size (thorax length) and head elongation on male success in the first bout of combat with a new opponent (left panels), and the overall proportion of combat bouts won (right panels). Each point represents the difference in body size or head elongation between two opponents (male 1 − male 2) plotted against the success of male 1. Lines are fitted least-squares regressions.

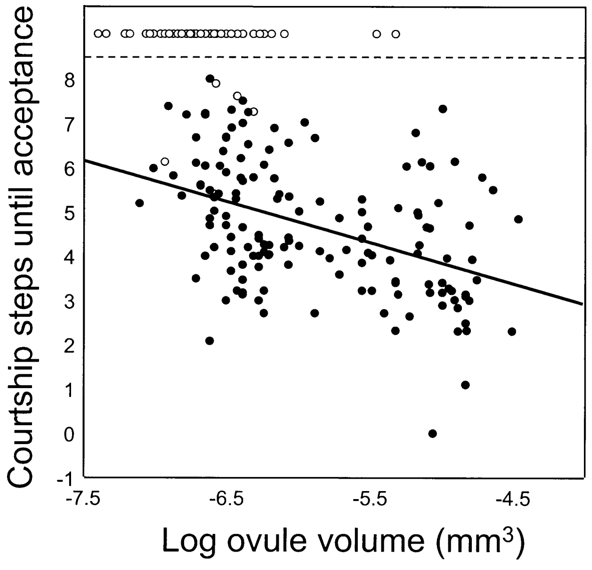

FIG. 6. Female receptivity and physiological age: points below the dashed horizontal line show the relationship between the log number of courtship steps performed by males before the female's first acceptance response and log ovule volume, with fitted least-squares regression (see Results). Points above the dashed horizontal line show the distribution of log ovule volumes for females that never gave the acceptance response. Closed circles represent pairings that resulted in copulation; open circles represent pairings that did not.

vectors. In *P. xanthostoma*, conflicting sexual selection on male head shape is suggested by the interaction of four selection vectors, two positive (both significant) and two negative (one significant, one marginally nonsignificant) (Table 3). We assume that selection was not reversed by artificial conditions, and that the five mechanisms of sexual selection (Table 3) actually affect male reproductive success in the wild. Although male-female pairings did not reveal any significant phenotypic differences between males that mated and those that did not, this was probably an artifact of females' inability to escape from the male.

In this species, conflicting sexual selection may result from a combination of condition dependence and mechanical constraint. The association between head elongation and ejaculate size may result from condition dependence of both traits, since male head shape covaries with condition (see above), and sperm production is condition dependent in some insects (Simmons and Kotiaho 2002). Since male head shape predicts ejaculate size, it may represent an honest signal of male mate quality (although this possibility has not been tested directly). Large ejaculates appear to be beneficial for females in many insect species (e.g., Warner et al. 1995; Baker et al. 2001). Ejaculate size may be particularly important for *P. xanthostoma* females because of their very low mating rate (of 34 females paired repeatedly until age 26 d, only one remated; R. Bonduriansky, unpubl. data). Thus, females may require enough sperm from one mating to fertilize

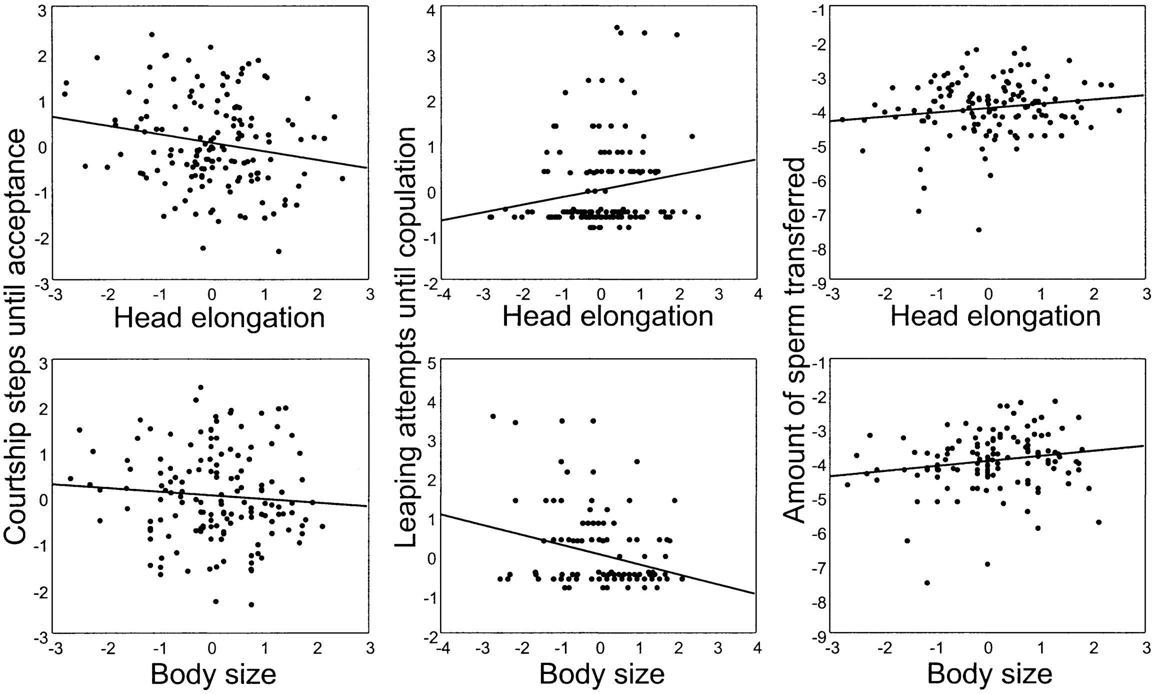

FIG. 7. Male-female interactions: effects of male body size (thorax length) and head elongation on the number of courtship steps until the female's first acceptance response (left panels), the standardized number of precopulatory leaping attempts until copulation (middle panels), and the log volume of sperm transferred to the female (right panels). To remove female receptivity effects (see Results), courtship performance plots show residuals from the regression of log number of courtship steps until the female's first acceptance response on log ovule volume (Fig. 6). Lines are fitted least-squares regressions.

many eggs. Moreover, part of the ejaculate serves as a nuptial gift, increasing female fecundity without reducing survivorship (R. Bonduriansky, J. Wheeler, and L. Rowe, unpubl. ms.), and these fitness benefits may increase with ejaculate size. However, head elongation appears to be disadvantageous in the performance of complex tasks such as combat and possibly leaping (see Tables 1, 2). A negative effect on combat success is not surprising. Given that *P. xanthostoma* males fight in the same manner as many other acalyptrate flies (e.g., see Bonduriansky and Brooks 1999b; Marshall 2000), their ''distorted'' head shape, in comparison with related species (see McAlpine 1977), may represent a mechanical constraint causing reduced coordination, visual acuity, or efficiency of movement.

Notably, in male-male interactions, males with relatively elongated heads were disadvantaged only in the first bout of combat with a new opponent, corresponding to single-bout interactions in the wild. This may have occurred because the outcome of single-bout interactions is determined partly by agility or quality of armament, which depend on head shape, whereas the outcome of multiple-bout interactions is determined mainly by endurance, which depends on body size. Because both single-bout and multiple-bout interactions are commonplace in the wild, we assume that both types of interaction affect male mating success, although we do not know their relative importance. Thus, our results suggest that both head shape and body size are under sexual selection through male-male interactions.

Although laboratory assays may reveal the directions of selection vectors, the relative intensities of those vectors and, therefore, the direction of net selection, can be estimated only in the wild. For example, because we have not quantified the opportunity for female mate choice in the wild, we do not know how much it contributes to sexual selection on male head shape. Unfortunately, low female mating rate, short copulation duration (4–6 min), and low site fidelity make mating success extremely difficult to estimate in wild *P. xanthostoma*. Nonetheless, net sexual selection on male head shape

TABLE 3. A summary of sexual selection vectors acting on male body size and head shape in *Prochyliza xanthostoma*: ''up'' indicates selection favoring increased body size or head elongation; ''down'' indicates selection favoring decreased head elongation (the result in parentheses is marginally nonsignificant).

Interactions	Selective mechanism	Body size	Head elongation
Male-male	Success in the first bout of combat	up	down
	Proportion of all combat bouts won	up	
Male-female	Courtship success		up
	Precopulatory leaping success	up	(down)
	Amount of sperm transferred	up	up

may be stabilizing (see Moore 1990; Moore and Moore 1999; Sih et al. 2002). Even if opposing selection vectors do not balance exactly in any single environment, temporal or spatial fluctuations in their relative importance may produce stabilizing sexual selection. Sih et al. (2002) reported temperature-related fluctuations in the relative importance of different mechanisms of sexual selection on male body size in a water strider.

Female Preferences and Male Intrasexual Competitiveness

Should females prefer males that are most successful in intrasexual interactions (see Darwin 1874; Berglund et al. 1996; Wiley and Poston 1996)? We argue that the answer depends on a complex interplay of factors, and that females may actually benefit by choosing less competitive males in some systems.

Berglund et al. (1996) argued that male armaments represent honest signals of phenotypic condition or genetic quality (''good genes'') because they are frequently put to the test of male-male combat. Thus, intrasexually competitive males may provide females with indirect benefits such as high-quality offspring, or direct benefits such as low parasite load. However, several factors may negate this argument in some species. First, unless females can decouple mating from sperm use (see Carlsbeek and Sinervo 2002), direct and indirect benefits may conflict (Bussière 2002). Since direct benefits are probably of greater magnitude (Kirkpatrick 1996; Kirkpatrick and Barton 1997), females should then seek direct benefits at the expense of indirect benefits. Second, recent evidence of sexually antagonistic alleles (Chippindale et al. 2001) challenges the standard concept of ''good genes'' by suggesting that males that sire high-quality sons may sire low-quality daughters. In *P. xanthostoma*, two types of benefits appear to conflict, since males that transfer large ejaculates are relatively poor fighters (see Tables 1, 2). Moreover, the relation between male armament and phenotypic condition is complex, since enhanced nutrition increases both body size (positive effect on combat success) and head elongation (negative effect on combat success; R. Bonduriansky and L. Rowe, unpubl. data). More generally, mounting evidence of conflicting sexual selection (Moore and Moore 1999; Andersson et al. 2002; Sih et al. 2002; this study) and sexually antagonistic alleles (Chippindale et al. 2001) challenges the idea that individuals can be ranked along a one-dimensional gradient of mate quality.

Sexual Selection and Sexual Conflict

Prochyliza xanthostoma may exhibit at least two levels of sexual conflict. First, if males with relatively elongated heads are disadvantaged in combat, they will be less likely to hold mate-searching territories. Thus, male-male interactions may limit females' encounter rate with males of high mate quality (i.e., large ejaculate size). This form of sexual conflict may arise whenever males are territorial (e.g., see Andersson et al. 2002). A second possible form of sexual conflict in this species is intralocus conflict (see Parker and Partridge 1998; Rice and Chippindale 2001). Despite pronounced sexual dimorphism in head shape (Fig. 1), *P. xanthostoma* females possess elongated heads and antennae in comparison with related carrion flies (see McAlpine 1977), perhaps as a result of the positive intersexual genetic correlation for this trait (R. Bonduriansky and L. Rowe, unpubl. data). This suggests that female head shape may deviate from its viability optimum in this species. Yet female mate choice appears to select for increased male head elongation. Thus, female preference for males that confer direct benefits may actually favor male alleles that are detrimental to their daughters, providing a dramatic illustration of the blurred boundaries between ''traditional'' models of sexual selection and sexual conflict (see Chapman et al. 2003).

Conclusions

Our results suggest that multiple mechanisms of sexual selection may exert conflicting selection on a targeted trait. We argue that conflicting sexual selection through male-male and male-female interactions may be a common feature of mating systems, and lead to sexual conflict. Multiple mechanisms of sexual selection may be characteristic of most sexual species, and understanding how they interact to shape phenotypes is a key goal of evolutionary biology.

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