

OPPOSING SELECTION ON A SEXUALLY DIMORPHIC TRAIT THROUGH FEMALE CHOICE AND MALE COMPETITION IN A WATER BOATMAN

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Abstract.—Female choice and male-male competition are traditionally considered to act in concert, with male competition facilitating female choice. This situation would enforce the strength of directional selection, which could reduce genetic variation and thus the benefits of choice. Here I show that in a water boatman, *Sigara falleni*, the direction of selection through female choice and male competition vary among traits under laboratory conditions. The two forces were mutually enforceive in acting on body size but exerted opposing selection on a sexually selected trait, male foreleg palae size. Female choice favored large palae, whereas male competition favored smaller palae, suggesting that large palae are costly in competition. This conflicting selection through female choice and male competition could be one of the forces that contribute to the maintenance of genetic variation in sexually selected traits.

Key words.—Corixidae, disruptive selection, mating behavior, sexual conflict, sexual dimorphism, sexual selection, *Sigara falleni*.

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An intriguing question of sexual selection theory is whether female choice and male competition are mutual or counteractive in selecting for specific traits. Traditionally, the two forces have been thought to work in unison, with male competition facilitating female choice (Andersson 1994; Berglund et al. 1996). However, an increasing number of studies have found the two forces counteracting, with male competition hampering female choice (Howard et al. 1997; Lantot et al. 1998; Moore and Moore 1999; Wollerman 1999; Kangas and Lindström 2001; Lopez et al. 2002; Sih et al. 2002; Bonduriansky and Rowe 2003; Wong 2004). For example, in the sand goby, *Pomatoschistus minutus*, females prefer subordinate males because competitive dominant males are poor fathers and direct material benefits, such as parental care, are of higher importance than indirect genetic benefits associated with dominance (Forsgren 1997).

While much attention has been given to the questions of the occurrence and commonness of opposing female choice and male competition (Qvarnström and Forsgren 1998), little attention has been paid to the phenotypic traits that are the focus of opposing selection, to attempt to quantify the strength of the two selective forces and investigate possible correlations with other traits that could enforce or counteract selection. Female choice and male competitive ability often involve several traits with selective forces that can act in unison or conflict (Andersson 1994; Andersson et al. 2002; Candolin 2003). Although female choice and male competition could be in conflict for selection on dominance, the two forces could still act mutually for selection on other traits, depending on the strength of indirect selection through correlated traits, which constrains direct selection (Brodie et al. 1995; Roff 1997; Brooks and Endler 2001).

Conflict or congruency of female choice and male competition could influence the genetic variation of traits (Roff 1997). An unresolved question of sexual selection theory is how genetic variation is maintained so that female choice for indirect benefits remains beneficial (i.e., the lek paradox; Borgia 1979; Kirkpatrick and Ryan 1991; Rowe and Houle 1996; Kotiaho et al. 2001; Houle and Kondrashov 2002; Kokko et

al. 2003). Strong directional selection is expected to drive beneficial alleles to fixation and reduce genetic benefits of choice. Opposing selection through female choice and male competition could be one force that prevents the fixation of alleles, especially if the strength of the two forces varies in time or space (Roff 1997).

Here I investigated under laboratory conditions selection through female choice and male competition on body size and foreleg palae size in a water boatman, *Sigara falleni*. This semiaquatic insect inhabits rivers and lakes of Europe and aggregates in patches along shores of rivers and lakes in early spring (Jansson 1996). The mating attempts of males take place under male competition when males try to disrupt each others mounting attempts. Females resist most copulation attempts, and both female choice (or resistance) and male competition therefore determine mating success. In contrast to many other water boatmen, *S. falleni* do not stridulate. Instead males have enlarged foreleg palae, sexually dimorphic clawlike tarsal segments (Jansson 1996). Males court females by shaking their bodies and enlarged foreleg palae in front of the females. Thus, the palae could be sexually selected and used both as visual signals to the female and as structures for clasping the female during mating. The size of the palae is determined during the juvenile stage, whereas bodyweight is determined by conditions experienced both as juvenile and adult (U. Candolin, unpubl. ms.).

MATERIALS AND METHODS

Water boatmen were collected with dip nets from the shores of Wohlensee, near Bern, Switzerland, before the breeding season in January 2002. *Sigara falleni* overwinter as adults, and reproductive activities start as soon as the temperature of the water starts to rise (Hungerford 1977; Jansson 1996). The insects were brought to the laboratory and species and sex identified. Male and female *S. falleni* were kept in separate tanks at 22°C under a light-dark cycle of 16:8 h to stimulate reproduction. They were fed daily with frozen chironomid larvae. Prior research showed that both

males and females reach reproductive condition when held for a week under the described maintenance conditions.

After two weeks of maintenance, when the insects were in reproductive condition, they were submitted to the experimental procedures described below. Each individual was used only once.

Female Choice

A male and a female were placed in a 0.5-L jar with sand as substrate. The chosen volume of water forced the insects to quickly detect each other while allowing normal movements, thus mimicking encounters under natural conditions. The insects were observed every 10 min, for a maximum of 1 h, to determine whether the males succeeded in mating within 1 h. Males that did not mate within 1 h had usually made numerous mounting attempts and were therefore regarded as rejected by the females. Mating success depends on female agreement, as males are not able to force copulation and most copulation attempts fail (pers. obs.). Copulation generally lasts for 20–40 min (pers. obs.).

Inclusion of Male Competition

Two randomly selected males marked with different colors of acrylic paint on the pronotum were placed in a 0.5-L jar. One of the males was randomly chosen as the focal male to determine his mating success under male competition. Thirty minutes after the introduction of the males, a female was added and the insects were observed every 10 min, for a maximum of 1 h, to determine whether the focal male succeeded in mating within 1 h. Males frequently attempted to disrupt each other's courtship and mounting attempts, until one male managed to monopolize the female.

Body Measurements

After the trials, the insects were dried on blotting paper for 1 min and weighed to the nearest 0.001 g. Body size was measured by photographing the males with a video camera mounted on a microscope and connected to a computer. Male body length and the area of the two foreleg palae were measured with ImageJ version 1.28u (<http://rsb.info.nih.gov/ij/>). Body length was measured from the front of the pronotum to the end of the left forewing, corium. Each character was measured twice and the average value was used in the analyses.

Analyses

To assess the intensity and direction of selection on the measured traits under the two selection regimes, female choice and male competition, standardized linear selection differentials (s') and gradients (β') were calculated using simple and multivariate regression methods (Lande and Arnold 1983; Endler 1986). Selection differentials describe the total selection on a trait (both direct and indirect), whereas selection gradients describe only the direct selection, by holding effects of other traits constant. Mating success, that is, mated (1) or not mated (0), was converted to relative fitness with a mean of one by dividing the individual fitness estimates by the mean fitness of the individuals under each se-

TABLE 1. Standardized linear selection differentials (s') and gradients (β') for morphological traits under female choice and when male competition was included ($N = 100$).

	Selection differentials		Selection gradients	
	s' (SE)	P	β' (SE)	P
A. Female choice				
Body length	0.48 (0.26)	0.001	-0.12 (0.48)	0.597
Body weight	0.45 (0.26)	0.003	0.06 (0.40)	0.672
Pala size	0.65 (0.26)	0.001	0.71 (0.50)	0.003
B. Male competition				
Body length	0.74 (0.33)	0.002	1.34 (0.72)	0.013
Body weight	0.77 (0.39)	0.001	0.79 (0.53)	0.027
Pala size	0.29 (0.26)	0.181	-1.39 (0.59)	0.005

lection regime. Each measured body trait was standardized to a mean of zero and a standard deviation of one. Linear selection differentials, s' , and gradients, β' , were calculated from linear models, $w = a + sz$ and $w = a + \sum \beta_i z_i$, where w is relative fitness, a is constant, z is the standardized morphological traits, and i is the individual traits. Least-square regression was used to derive the selection estimates, whereas logistic regression was used to test for significance because the response variable was binary (Mitchell-Olds and Shaw 1987).

To test for differences in selection under the two selection regimes, logistic regression was carried out with the standardized morphological traits as covariates, selection regime as fixed factor, and mating success as a binary response variable. Interaction terms between selection regime and morphological traits test for differences in slopes of linear selection under the two selection regimes.

RESULTS

Female choice favored larger males with larger palae, both when it came to absolute pala size and pala size related to body size (Table 1A, Figs. 1, 2). However, only pala size was under direct selection, whereas body size was indirectly selected for through selection on larger palae, as revealed by the selection gradients (Table 1A). When male competition was included, selection directly favored larger males with smaller palae (Table 1B, Fig. 1B). In particular, large males with large palae in relation to their body size failed to mate when competition was included, as depicted in Figure 2. However, no net selection on pala size occurred under male competition, as revealed by the nonsignificant selection differential (Table 1B).

Analysis for differences in the slopes of selection under the two selection regimes shows that selection on body length and pala size statistically differed between the two selection regimes, female choice and male competition (Table 2). Thus, although female choice could have continued to operate under male competition, the inclusion of male competition did influence the mating outcome. As expected, the inclusion of male competition, and a consequent change in the operational sex ratio, reduced the probability that a particular male would mate with a female (Table 2).

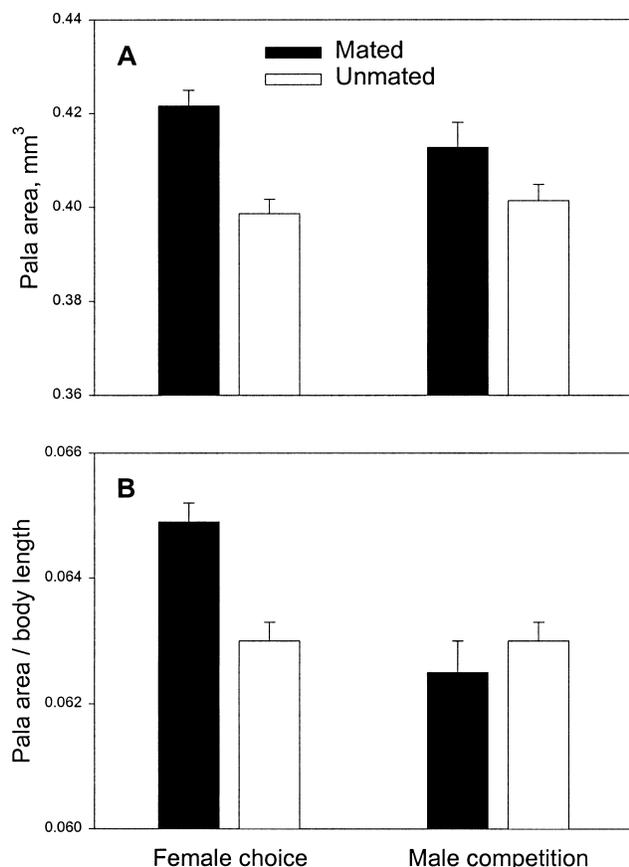


FIG. 1. (A) Absolute and (B) relative pala area (mean \pm SE) of mated and unmated males under female choice and male competition.

DISCUSSION

Selection on the investigated morphological traits differed between the two selection regimes under laboratory conditions. Female choice and male competition acted mutually in selecting for increased male body weight, but differed in their strength for selection on male body length, and were opposed to each other for selection on the size of the males' foreleg palae. Thus, conflicting sexual selection pressures were operating on a sexually dimorphic trait, male pala size.

Why would the sexual selection pressures on a dimorphic trait conflict? The size of the foreleg palae is determined during the juvenile stage and depends on juvenile growth conditions (U. Candolin, unpubl. ms.). The palae of males could therefore indicate direct benefits, such as ejaculate quality, or indirect benefits in the form of heritable viability, which could explain the palae's importance in mate choice. However, the disadvantage of large palae in male competition suggests that increased pala size incurs a fitness cost. This could arise from reduced food intake or increased energy expenditure that reduces the pool of energy available for other fitness components that influence mating success, or by the palae interfering with movement and reducing the males' success in the acquisition of mates. To conclusively demonstrate that fitness costs of large foreleg palae cause the conflicting selection pressures on pala size, experimental ma-

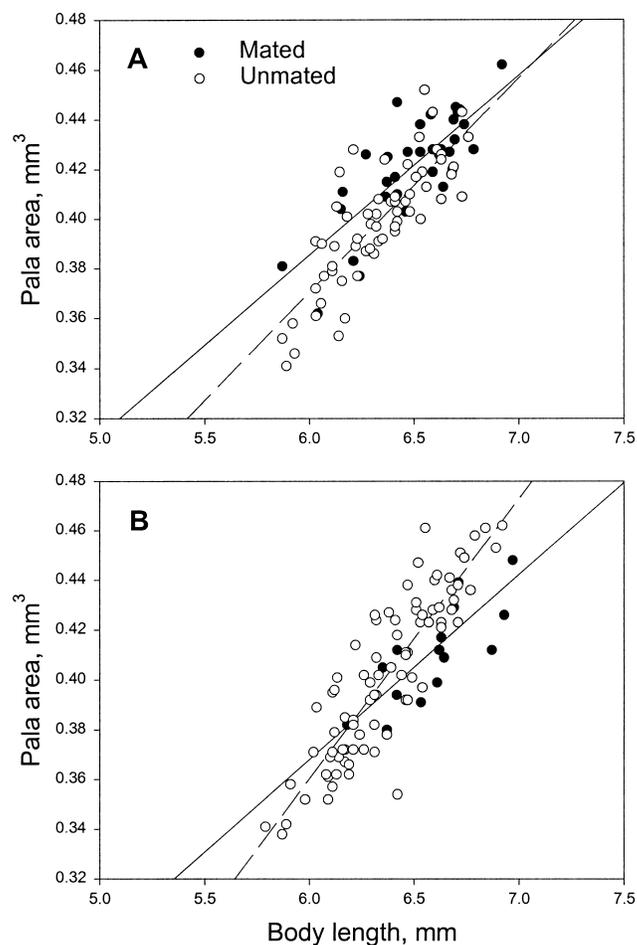


FIG. 2. Relationship between pala area and body length of mated and unmated males under (A) female choice and (B) male competition.

nipulation is needed. Nevertheless, the results show that the two major forces of sexual selection, intra- and intersexual selection, can exert conflicting selection on a dimorphic trait.

Male competition also selected for larger body size, but no direct female preference for body size was detected, although females indirectly favored larger males through their preference for large palae. Selection forces other than female choice probably oppose sexual selection for larger body size, such as viability selection and resource limitation, and pre-

TABLE 2. Dependence of mating probability on male traits and on selection regime, that is, female choice and male competition.

	Probability of mating	
	Wald	<i>P</i>
Body length (BL)	1.17	0.279
Body weight (BW)	3.22	0.073
Pala size	8.27	0.004
Selection regime	9.57	0.002
BL \times regime	10.44	0.001
BW \times regime	2.29*	0.130*
Pala size \times regime	15.26	<0.001
Model	$N = 200$, $df = 6$, $\chi^2 = 59.0$, $P < 0.001$	

* The nonsignificant interaction term was excluded from the analysis.

vent further increases (Blanckenhorn 2000). Male body weight is determined by both juvenile and adult feeding conditions (U. Candolin, unpubl. ms.) and could correlate with genetic quality, since body size often correlates with phenotypic and genetic quality (Maynard Smith 1991; Andersson 1994). Thus, the bias in mating success toward males in the overall best condition under male competition could have facilitated female choice by ensuring the choice of the male of the highest quality (see also U. Candolin, unpubl. ms.).

The intensity of sexual selection as measured in the laboratory, however, may not reflect the intensity of sexual selection in nature. Many additional factors, such as different mate encounter rate and environmental conditions, could influence mating outcome and realized fertilization success. Nevertheless, the results suggest that selection on body traits, especially pala size, could differ depending on whether female choice or male competition dominates, which could depend on mate encounter rate and population density.

Several studies have found female choice and male competition to conflict (see references in introduction). This study shows that female choice and male competition can differ in their effect on different traits. The opposing selection on the sexually dimorphic trait, foreleg pala size, could contribute to the maintenance of genetic variation in the trait by resulting in either no net selection or in disruptive selection on the trait, especially if the strength of selection varies in time or space (Roff 1997; Moore and Moore 1999). An unresolved question of sexual selection theory is how genetic variation in sexual traits is maintained (see references in introduction). This study suggests that selection conflicts arising from opposing female choice and male competition could contribute to the maintenance of genetic variation, especially if the relative importance of female choice and male competition varies with population density, operational sex ratio, or habitat structure, thereby creating temporal and spatial variation of the selection landscape.

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