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Contrasting Mutual Sexual Selection on Homologous Signal Traits in *Drosophila serrata*

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ABSTRACT: The nature of male mating preferences, and how they differ from female mating preferences in species with conventional sex roles, has received little attention in sexual selection studies. We estimated the form and strength of sexual selection as a consequence of male and female mating preferences in a laboratory-based population of *Drosophila serrata*. The differences between sexual selection on male and female signal traits (cuticular hydrocarbons [CHCs]) were evaluated within a formal framework of linear and nonlinear selection gradients. Females tended to exert linear sexual selection on male CHCs, whereas males preferred intermediate female CHC phenotypes leading to convex (stabilizing) selection gradients. Possible mechanisms determining the nonlinear nature of sexual selection on female CHCs are proposed.

Keywords: male choice, mutual mate choice, selection gradients, sexual selection.

The evolution of female mating preferences has received considerable attention in sexual selection theory (Andersson 1994), but the importance of male mating preferences and how they differ from female mating preferences remain unclear. In some species both males and females are choosy, indicating potential for each sex to gain direct and/or indirect benefits from their choice of mating partner. There are now many species in which mutual mate choice has been demonstrated (Hill 1993; Jones and Hunter 1993; Monaghan et al. 1996; Hunt et al. 1999; Sandvik et al. 2000; Velando et al. 2001; Chenoweth and Blows 2003).

When mutual mate choice occurs on homologous signal traits, any intersexual differences in the strength or form of sexual selection generated by mate choice will have consequences for the expected level of sexual dimorphism.

A net selection differential among the sexes is a prerequisite for the evolution of sexual dimorphism (Lande 1980). This net selection differential is often thought to be a result of directional sexual selection acting on males. However, in species in which male choice also occurs on the same trait, the opportunity for sexual selection on female as well as male traits means that the net selection differential among the sexes cannot be fully understood without an analysis of sexual selection on each of the sexes. Importantly, the link between choosiness per se and the type of sexual selection that it generates (directional, stabilizing, or disruptive) needs to be quantified.

The presence of male mating preferences for female signal traits in species with conventional sex roles provides a challenge for sexual selection theory (Amundsen 2000) because of the limited conditions under which such behavior might evolve (Kokko and Johnstone 2002). Theoretically, male choice may be adaptive when male parental investment is high and/or the cost of searching for a mate is low and/or the variance in female quality is high (Burley 1977; Parker 1983; Owens and Thompson 1994; Johnstone et al. 1996; Kokko and Monaghan 2001). In insects, male choice has been found to be strongly associated with female traits that are indicators of fecundity such as body mass or body size (Bonduriansky 2001), although there is less evidence for sexual selection on female signal traits.

The impact of mating preferences on trait values in the opposite sex can be investigated in two ways (Wagner 1998). First, the distribution of individual preference functions in one sex can be measured and compared to the distribution of trait values in the other sex (Ritchie 1996). This approach provides information on whether different types of mating preferences exist within a population (Wagner 1998). Second, a "population-based" approach can be used in which individuals are allowed to choose (once only) among potential mates that are randomly drawn from the population (Wagner 1998). Although this method does not supply information on within-population variation in individual mating preferences, by accounting for the natural variation in display traits within a population, this method is analogous to statistical selection analyses (Lande and Arnold 1983). Lande and Ar-

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nold's (1983) approach allows the direct quantification of sexual selection in the form required to determine whether the population will respond to selection when information is available on the quantitative genetic basis of the traits involved (Lande 1979) and facilitates comparisons between groups such as populations (Kraushaar and Blanckenhorn 2002) or species (Kingsolver et al. 2001). As yet, there has been no formal analysis of sexual selection in a system with mutual mate choice that compares sexual selection gradients between the sexes.

Female *Drosophila serrata* discriminate among males on the basis of cuticular hydrocarbons (CHCs; Hine et al. 2002; Blows et al. 2004). Male *D. serrata* also choose among females on the basis of CHCs (Chenoweth and Blows 2003), but it is currently not known what benefits males may receive by exercising this choice. The presence of mutual mate choice for the same signal traits in *D. serrata* provides the opportunity to directly contrast the form of sexual selection on male and female signal traits within the formal statistical framework provided by selection gradients (Lande and Arnold 1983).

Methods

We used an experimental strategy that allowed the form of sexual selection to be contrasted between the sexes. Details of the laboratory experiment have been described in our earlier work (Chenoweth and Blows 2003), where the genetic basis of sexual dimorphism was analyzed and the presence of mutual mate choice was first reported. In brief, mate choice tests were used to quantify the strength and form of sexual selection on CHCs exerted by male and female mating preferences. In each test, a 5-day-old virgin female (male for male choice) was given a choice of two virgin males of the same age (females for male choice) that were randomly selected from the population stock (Forster population; Hine et al. 2002; Blows et al. 2004). After a successful mating was observed, the chosen and rejected flies from each mate choice test had their CHCs assayed using gas chromatography (Blows and Allan 1998). A total of 216 female choice tests and 209 male choice tests were conducted. These mate choice tests are a variation of the "simultaneous two-stimulus" choice test outlined by Wagner (1998), in that potential mating partners are drawn at random from the population instead of two fixed stimuli being presented to each individual. By using stimuli that reflected the naturally occurring variation within the Forster population, we were able to calculate standardized linear and nonlinear selection gradients (Lande and Arnold 1983), which we detail below.

The CHC profile of each chosen and rejected individual was analyzed using established techniques (Blows and Allan 1998; Higgie et al. 2000). Briefly, the area under each

individual CHC peak was integrated, and relative amounts of each CHC were expressed as a proportion of the total amount of all CHCs measured on an individual. Individual proportions were transformed into logcontrasts (Blows and Allan 1998), removing the unit-sum constraint associated with compositional data (Atchison 1986). A total of eight logcontrasts, representing eight individual CHCs were individually standardized ($\sim N(0, 1)$) prior to the selection and genetic analyses below.

Male and female preferences for individual CHCs were first visualized using univariate cubic splines to determine the form of selection without constraining the relationships between CHCs and mating success to be linear or quadratic in form (Schluter 1988). Splines were conducted using the TPSPLINE procedure in SAS (ver. 8.02; SAS Institute, Cary, NC). The TPSPLINE procedure assumes normality, and our binomial mating success score approximated this distribution well, given the large sample size and equal probabilities of chosen and rejected individuals. The smoothness of cubic splines is determined by a smoothing parameter that is usually chosen by finding the value of λ that minimizes the generalized cross-validation (GCV) score. In our case, we chose the same λ value ($\log_{10}(n\lambda) = 2$) for each spline on the eight CHCs to facilitate direct comparison (Green and Silverman 1994). In no case did splines using this GCV minimum λ value suggest that relationships between mating success and CHCs were more complex than second-order polynomials. To statistically model the linear and quadratic components of the spline visualizations, univariate linear regressions were then used to estimate standardized linear selection gradients, and separate second-order polynomial regressions were used to estimate standardized nonlinear selection gradients for individual CHCs (Brodie et al. 1995).

Multivariate second-order polynomial regression was used to estimate the nonlinear (quadratic and correlational) partial regression coefficients of the γ matrix (Lande and Arnold 1983) for each of the sexes. To interpret the form of selection operating on a set of traits when correlational selection is present, a canonical analysis is used to rotate the original trait axes to find the canonical axes of the response surface (Phillips and Arnold 1989; Blows and Brooks 2003). The canonical rotation eliminates correlational selection, allowing selection along the canonical axes of the response surface to be simply interpreted as concave or convex along each canonical axis. Significance of concave or convex selection along the canonical axes was determined by placing the new synthetic variables representing the canonical axes back into a second-order polynomial regression (Bisgaard and Ankenman 1996; Blows and Brooks 2003). Convex selection may be interpreted as stabilizing selection only if a sta-

tionary point is present (Mitchell-Olds and Shaw 1987); therefore, we refer to convex rather than stabilizing selection in this study.

To test whether linear and nonlinear sexual selection on male and female CHCs differed, we employed a sequential model-building approach for response surface designs containing both quantitative (CHCs) and qualitative (sex) variables as outlined by Draper and John (1988). The full details of this approach are outlined in appendix A.

Results

Cubic splines relating CHCs of males and females to mating success (fig. 1) indicated that second-order polynomial regression was adequate to model the association between CHCs and mating success. In general, sexual selection on male CHCs appeared linear in shape on most CHCs, whereas sexual selection on female CHCs had a convex shape in most cases. Univariate linear regressions revealed significant linear sexual selection on male Z,Z-5,9-C_{25:2}, 2-Me-C₂₈, Z,Z-5,9-C_{29:2}, and 2-Me-C₃₀, but no quadratic selection was detected on individual male CHCs (table 1). In contrast, no significant linear sexual selection was found on individual female CHCs, but significant convex selection was identified on Z-9-C_{26:1} and 2-Me-C₂₆ (table 1).

Multivariate second-order polynomial regression gave an overall test for the presence of linear and nonlinear sexual selection on male and female CHCs that did not rely on multiple univariate tests that increase the probability of Type I error. This analysis supported highly significant linear sexual selection on male CHCs but no nonlinear selection (neither quadratic nor correlational selection; table 2). In addition, no single nonlinear selection gradient was significant in the male CHC γ matrix (table B1). For female CHCs, a significant level of linear sexual selection was indicated (table 2), as was a highly significant level of correlational sexual selection. Correlational selection on female CHCs was largely a consequence of correlational selection between Z-9-C_{25:1} and the three methylalkanes 2-Me-C₂₆, 2-Me-C₂₈, and 2-Me-C₃₀ (table B1).

Linear sexual selection on male and female CHCs differed significantly (partial *F*-test, models [A1] vs. [A2]: $F = 17.67$, $df = 8, 832$, $P < .001$). To investigate which individual CHCs were under differential linear sexual selection between the sexes, the interactions between sex and the terms measuring linear and nonlinear selection from model (A7) (the complete multivariate second-order polynomial model with the categorical variable of sex) are displayed in table B2. Linear sexual selection significantly differed between male and female 2-Me-C₂₆, 2-Me-C₂₈, Z,Z-5,9-C_{29:2}, and 2-Me-C₃₀. In all these cases, it was male CHCs that were under significant linear sexual selection

(or nearly so in the case of 2-Me-C₂₆) but not female CHCs.

Quadratic sexual selection did not differ between the sexes (partial *F*-test, models [A4] vs. [A5]: $F = 0.71$, $df = 8, 816$, $P = .683$). However, nonlinear sexual selection along axes not parallel to the individual traits (i.e., correlational selection) was significantly different between the sexes (partial *F*-test, models [A6] vs. [A7]: $F = 1.89$, $df = 28, 760$, $P = .004$). Correlational selection between Z-9-C_{25:1} and the three methylalkanes, 2-Me-C₂₆, 2-Me-C₂₈, and 2-Me-C₃₀, was significantly different between the sexes, as was correlational selection between Z,Z-5,9-C_{29:2} and 2-Me-C₃₀ and between Z,Z-5,9-C_{29:2} and Z,Z-5,9-C_{25:2}.

To interpret the form of correlational selection on CHCs, we conducted a canonical analysis of the γ matrices in table B1 (Phillips and Arnold 1989; Blows and Brooks 2003). We found no significant nonlinear selection on any major axis for female choice. In contrast, four canonical axes of the male preference response surface had significant nonlinear selection ($\lambda_2 = 0.192$, $P = .031$; $\lambda_5 = -0.069$, $P = .009$; $\lambda_6 = -0.091$, $P = .010$; $\lambda_7 = -0.124$, $P = .040$), of which three had negative eigenvalues indicating convex selection along those axes. The eigenvalues (λ_i) of the canonical axes are exactly analogous to standardized quadratic selection gradients (Blows and Brooks 2003). The difference in correlational sexual selection on male and female CHCs was primarily a consequence of convex selection on female CHCs exerted by male mating preferences.

Discussion

The difference in form of male and female sexual selection suggests that male and female *Drosophila serrata* exercise preference in fundamentally different ways. Female preference resulted in primarily linear sexual selection on male CHCs. There was very little indication that female preference for individual male CHCs had any convex component, indicating that female preferences may be open-ended. In other words, based on the male CHC phenotype presented to females in this study, there is no evidence that female preferences asymptote at higher trait values. In direct contrast, male preference resulted in primarily nonlinear sexual selection on female CHCs, which was predominantly convex.

What may have led to the evolution of female mating signals in *D. serrata*? It has been argued that if males can assess female fecundity directly, then display traits that trade off with fecundity could become redundant (Fitzpatrick et al. 1995). However, male preference for female signal traits could arise initially as a correlated response to the evolution of female mating preferences for the same signal trait in males (Amundsen 2000). In addition, it has

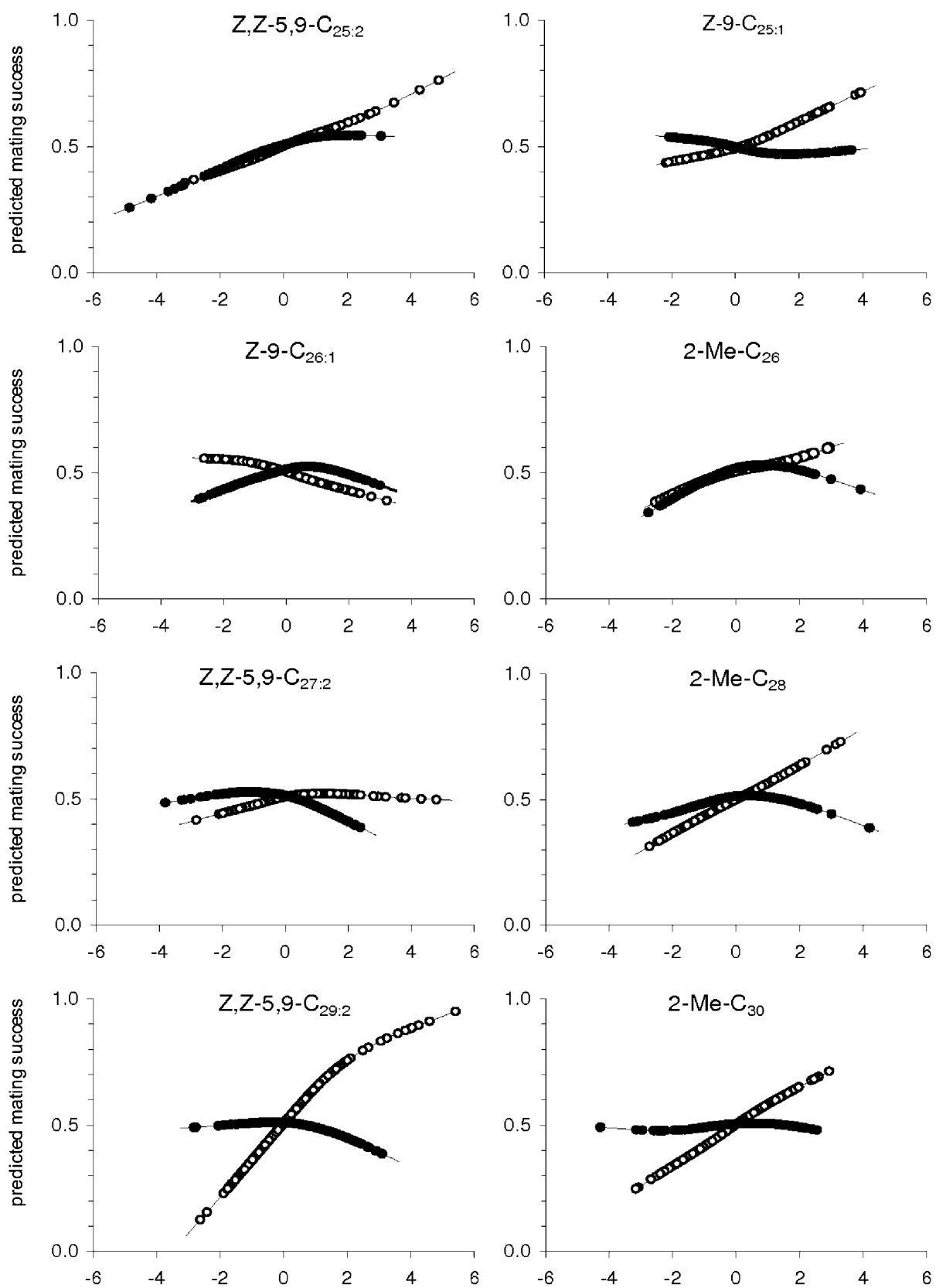


Table 1: Standardized univariate sexual selection gradients for male and female CHCs

Sex and CHC	Linear	Quadratic
Males:		
Z,Z-5,9-C _{25:2}	.050*	.003
Z-9-C _{25:1}	.043	.012
Z-9-C _{26:1}	-.033	-.010
2-Me-C ₂₆	.034	-.009
Z,Z-5,9-C _{27:2}	.017	-.011
2-Me-C ₂₈	.066*	.001
Z,Z-5,9-C _{29:2}	.124*	-.019
2-Me-C ₃₀	.081*	-.004
Females:		
Z,Z-5,9-C _{25:2}	.037	-.012
Z-9-C _{25:1}	-.017	.009
Z-9-C _{26:1}	.018	-.033*
2-Me-C ₂₆	.027	-.042*
Z,Z-5,9-C _{27:2}	-.025	-.028
2-Me-C ₂₈	.010	-.023
Z,Z-5,9-C _{29:2}	-.016	-.026
2-Me-C ₃₀	.005	-.005

* $P \leq .05$.

been shown in a different context (female choice for direct benefits provided by males) that if there is sufficient quality variation in one sex, a costly trait can function as a simultaneous cue for both indirect and direct benefits, despite an intrinsic trade-off between the trait and the direct benefit obtained (Kokko 1998). This suggests that male preferences for female indicator traits can be adaptive.

The detection of convex sexual selection gradients on female CHCs may be due to two underlying patterns. There may be significant variation in individual male mating preferences within the assayed population. Different individual males may exercise directional mating preferences for the same CHCs but in opposing directions (i.e., different preference functions) and largely nonoverlapping ranges of trait values. Thus, over the entire population, the net result is a sexual selection gradient that resembles stabilizing selection. Alternatively, individual male mating preferences may be truly convex in nature, with all males within the population preferring females with intermediate values of some CHCs. In this situation, the sexual selection gradients approximate male mating preferences within the population. Distinguishing between these alternative patterns underlying convex sexual selection gradients will re-

Table 2: ANOVAs for the full second-order polynomial regression of mating success on male and female CHCs

Source	df	SS	F	P
Male CHCs:				
Linear	8	10.887	5.96	<.001
Quadratic	8	2.388	1.31	.239
Cross-product	28	6.324	.99	.484
Residual	387	88.401		
Female CHCs:				
Linear	8	4.698	2.69	.007
Quadratic	8	2.561	1.47	.167
Cross-product	28	15.909	2.61	<.001
Residual	373	81.330		

quire the measurement of within-population variation in individual male mating preferences.

Assuming that there is limited variation in mating preferences among males, convex male mating preferences could have come about in at least two ways. First, they may be a consequence of genetic constraints on the allocation of resources by females to both signaling and fecundity. For example, in *Drosophila melanogaster*, female CHCs display an allocation trade-off with egg production (Wicker and Jallon 1995) because the cuticle and ovaries appear to be competing targets for the deposition of internal hydrocarbon from the same pool in some insects (Schal et al. 1994). Therefore, a female who becomes very attractive by allocating too many hydrocarbon resources to the cuticle may produce fewer offspring or offspring of lesser quality. If such a trade-off exists in *D. serrata*, convex male preferences may have evolved to provide a way for males to optimize the trade-off between signal and fecundity in females.

Alternatively, rather than preferences themselves being optimized by selection, male preferences for intermediate female CHC values may be due to physiological constraints on male CHC receptors. For example, in species that have acoustic mating signals where receivers must be tuned to particular signal frequencies, females may discriminate against males who signal at frequencies that are either too high or too low, preferring to mate with those that signal at intermediate frequencies (Ryan and Wilczynski 1988). This pattern leads to stabilizing individual preference functions (Ritchie 1996) without the mating preferences themselves being adaptive. However, the pattern displayed in

Figure 1: Univariate cubic spline visualizations of sexual selection on male (white) and female (black) CHCs in *Drosophila serrata* exerted by female and male mating preferences, respectively. Individual points are predicted mating success scores (vertical axis) for males and females with observed CHC values (horizontal axis). Lines passing through each group of points represent predicted spline curves for each sex. Significance testing of linear and nonlinear terms modeling the relationship between individual CHCs and male and female mating success is provided in the text.

D. serrata may preclude this explanation because female preferences for the same CHCs in males are linear. Thus it is difficult to reconcile how male CHC receptors for the same compounds would be under different physiological constraints in females.

Regardless of the mechanism behind convex sexual selection gradients on female CHCs in *D. serrata*, significant convex sexual selection gradients imply that the expected response to sexual selection by females will be qualitatively different from that of males. Although it is necessary to statistically detect a stationary point on the fitness surface to demonstrate stabilizing selection (Mitchell-Olds and Shaw 1987), the combination of significant linear and non-linear (convex) selection (sensu Phillips and Arnold 1989, fig. 1C) suggests that CHC evolution may be less extreme in females compared with males. This is consistent with the idea that male interest in female reproduction limits the resources expended by females on display traits, while female mating preferences continue to search for extreme values of male traits.

It should be noted that the strength of sexual selection on female CHCs under field conditions would most likely vary from the values reported in the present study. This is because the frequency with which male *D. serrata* encounter females may vary. If, for example, in a natural population males were rarely able to simultaneously assess multiple females, the strength of sexual selection may be considerably reduced. Actual male mate encounter rates

under field conditions are yet to be quantified in this species.

The differences in the form of sexual selection on male and female CHCs described here might represent one of the forces behind the evolution of sexual dimorphism in this species. Two prerequisites for the evolution of sexual dimorphism are less-than-perfect intersex genetic correlations (Lande 1980) and a net selection differential between the sexes. In *D. serrata*, intersex genetic correlations are low for many CHCs due in part to sex-limited expression of X-linked genetic factors (Chenoweth and Blows 2003). It is possible that the difference in form (rather than direction and strength) of sexual selection between the sexes may have provided part of the necessary net selection differential between the sexes for the evolution of sexual dimorphism in this species.

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APPENDIX A

Sequential Model Building Procedure

To start, the dummy variable, sex (coded as 0 or 1), was included in a reduced model with only linear terms (eq. [4.1] in Draper and John 1988):

$$M = \beta_0 + \alpha_0 \text{Sex} + \sum_{i=1}^n \beta_i C_i + \varepsilon, \quad (\text{A1})$$

where M was the binomial mating success measure, C_i refers to the log-contrast concentration of the i th CHC, n represented the number of CHCs in the model, and ε is unexplained error. From equation (A1), the unexplained sums of squares (SS_r) was compared to the same quantity (SS_c) from a second (complete) model (eq. [4.3] in Draper and John 1988) that included all of the terms in equation (A1) with the addition of the terms $\alpha_i C_i \text{Sex}$, which represents the linear interaction of the dummy variable, sex, and the i th CHC:

$$M = \beta_0 + \alpha_0 \text{Sex} + \sum_{i=1}^n \beta_i C_i + \sum_{i=1}^n \alpha_i C_i \text{Sex} + \varepsilon. \quad (\text{A2})$$

A partial F -test (Bowerman and O'Connell 1990) was used to compare the unexplained sums of squares from equations (A1) and (A2) to test whether linear sexual selection on CHCs differed between the sexes:

$$F_{a,b} = \frac{(SS_r - SS_c)/a}{SS_c/b}, \quad (\text{A3})$$

where a is the number of terms that differ between the reduced and complete model, and b is the degrees of freedom for SS_c , resulting in an F ratio with $df = 8, 832$.

To test whether quadratic sexual selection on CHCs differed between males and females, the SS_r from the reduced model,

$$M = \beta_0 + \alpha_0 \text{Sex} + \sum_{i=1}^n \beta_i C_i + \sum_{i=1}^n \alpha_i C_i \text{Sex} + \sum_{i=1}^n \beta_i C_i^2 + \varepsilon, \quad (\text{A4})$$

was compared to the SS_c of the complete model,

$$M = \beta_0 + \alpha_0 \text{Sex} + \sum_{i=1}^n \beta_i C_i + \sum_{i=1}^n \alpha_i C_i \text{Sex} + \sum_{i=1}^n \beta_i C_i^2 + \sum_{i=1}^n \alpha_i C_i^2 \text{Sex} + \varepsilon, \quad (\text{A5})$$

using (A3), resulting in an F ratio with $df = 8, 816$.

Finally, to test whether correlational sexual selection on CHCs differed between males and females, the SS_r from the reduced model,

$$M = \beta_0 + \alpha_0 \text{Sex} + \sum_{i=1}^n \beta_i C_i + \sum_{i=1}^n \alpha_i C_i \text{Sex} + \sum_{i=1}^n \beta_i C_i^2 + \sum_{i=1}^n \alpha_i C_i^2 \text{Sex} + \sum_{i=1}^n \sum_{j \geq 1}^n \beta_{ij} C_i C_j + \varepsilon, \quad (\text{A6})$$

was compared to the SS_c of the complete model,

$$M = \beta_0 + \alpha_0 \text{Sex} + \sum_{i=1}^n \beta_i C_i + \sum_{i=1}^n \alpha_i C_i \text{Sex} + \sum_{i=1}^n \beta_i C_i^2 + \sum_{i=1}^n \alpha_i C_i^2 \text{Sex} + \sum_{i=1}^n \sum_{j \geq 1}^n \beta_{ij} C_i C_j + \sum_{i=1}^n \sum_{j \geq 1}^n \alpha_{ij} C_i C_j \text{Sex} + \varepsilon, \quad (\text{A7})$$

using (A3), resulting in an F ratio with $df = 28, 760$.

After the model comparisons, (A1) versus (A2), (A4) versus (A5), and (A6) versus (A7) were used to test for overall significance of the interaction between sex and linear, quadratic, and correlational selection, respectively, the interaction of individual CHCs with sex terms were inspected from the full model (A7) to investigate which CHCs were responsible for the significance of the partial F -tests.

APPENDIX B

Table B1: Partial regression coefficients (γ matrix) indicating the strength of nonlinear (quadratic and correlational) sexual selection on male and female CHCs of *Drosophila serrata*

	Z,Z-5,9-C _{25:2}	Z-9-C _{25:1}	Z-9-C _{26:1}	2-Me-C ₂₆	Z,Z-5,9-C _{27:2}	2-Me-C ₂₈	Z,Z-5,9-C _{29:2}	2-Me-C ₃₀
Male CHCs:								
Z,Z-5,9-C _{25:2}	-.039							
Z-9-C _{25:1}	.014	.016						
Z-9-C _{26:1}	-.003	.047	.003					
2-Me-C ₂₆	-.170	.101	-.060	-.172				
Z,Z-5,9-C _{27:2}	.110	-.028	.007	.191	-.072			
2-Me-C ₂₈	.214	-.192	.121	.445	-.196	-.295		
Z,Z-5,9-C _{29:2}	-.048	-.007	.061	.005	-.071	.000	.040	
2-Me-C ₃₀	-.078	.079	-.100	-.180	.148	.265	.025	-.095
Female CHCs:								
Z,Z-5,9-C _{25:2}	.004							
Z-9-C _{25:1}	-.024	-.014						
Z-9-C _{26:1}	.040	.050	-.062**					
2-Me-C ₂₆	.121	-.373***	.016	-.001				
Z,Z-5,9-C _{27:2}	-.059	.011	.074	.153	-.058			
2-Me-C ₂₈	-.176	.564***	-.097	-.317	-.273	.347		
Z,Z-5,9-C _{29:2}	.179***	.007	-.008	-.160	-.118	.222	.083	
2-Me-C ₃₀	.069	-.368***	.067	.298	.362*	-.524	-.358**	.223

* $P < .05$.** $P < .01$.*** $P < .001$.**Table B2:** Partial regression coefficients indicating the interactions between the vector of linear selection gradients and sex (β ,Sex) and interactions between the standardized quadratic and correlational selection gradients and sex from model (A7)

	β ,Sex	Z,Z-5,9-C _{25:2}	Z-9-C _{25:1}	Z-9-C _{26:1}	2-Me-C ₂₆	Z,Z-5,9-C _{27:2}	2-Me-C ₂₈	Z,Z-5,9-C _{29:2}	2-Me-C ₃₀
Z,Z-5,9-C _{25:2}	.068	.042							
Z-9-C _{25:1}	-.026	-.038	-.030						
Z-9-C _{26:1}	.047	.043	.003	-.066					
2-Me-C ₂₆	.330*	.291	-.475***	.076	.170				
Z,Z-5,9-C _{27:2}	-.013	-.169	.039	.067	-.037	.014			
2-Me-C ₂₈	-.504*	-.391	.756***	-.218	-.761	-.077	.642		
Z,Z-5,9-C _{29:2}	-.159**	.227**	.015	-.069	-.165	-.047	.222	.043	
2-Me-C ₃₀	.284*	.147	-.447***	.168	.478	.214	-.789	-.383*	.319

* $P < .05$.** $P < .01$.*** $P < .001$.

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