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Interaction between natural and sexual selection during the evolution of mate recognition

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The interaction between natural and sexual selection is central to many theories of how mate choice and reproductive isolation evolve, but their joint effect on the evolution of mate recognition has not, to my knowledge, been investigated in an evolutionary experiment. Natural and sexual selection were manipulated in interspecific hybrid populations of *Drosophila* to determine their effects on the evolution of a mate recognition system comprised of cuticular hydrocarbons (CHCs). The effect of natural selection in isolation indicated that CHCs were costly for males and females to produce. The effect of sexual selection in isolation indicated that females preferred males with a particular CHC composition. However, the interaction between natural and sexual selection had a greater effect on the evolution of the mate recognition system than either process in isolation. When natural and sexual selection were permitted to operate in combination, male CHCs became exaggerated to a greater extent than in the presence of sexual selection alone, and female CHCs evolved against the direction of natural selection. This experiment demonstrated that the interaction between natural and sexual selection is critical in determining the direction and magnitude of the evolutionary response of the mate recognition system.

Keywords: natural selection; sexual selection; mate recognition; experimental evolution

1. INTRODUCTION

Many of the most influential hypotheses concerning the evolution of mate choice within populations and reproductive isolation between populations involve the interaction between the processes of natural and sexual selection (Kirkpatrick & Ryan 1991; Schluter 2001; Turelli *et al.* 2001). There are three main ways by which natural and sexual selection may interact during the evolution of mate recognition. First, when divergence in mate recognition occurs in allopatry as a consequence of divergent or uniform natural selection, sexual selection may amplify the divergence in mate recognition initiated by natural selection (Schluter 2001). Second, after secondary contact of diverging populations before reproductive isolation is complete, sexual and natural selection may interact during the reinforcement of mate recognition by natural selection (Dobzhansky 1951; Kirkpatrick & Servedio 1999). Third, even in the absence of divergent or reinforcing natural selection, natural and sexual selection may interact within populations to affect the evolution of mate recognition. When females discriminate between potential mates within populations (sexual selection), natural selection may act directly on that choice, or indirectly through an association between preference genes and other genes that are under natural selection. Direct natural selection on female choice may occur if females gain benefits from males, such as nuptial gifts, or when there is a cost to exercising the preference, such as deleterious pleiotropic effects of preference alleles on female life-history traits (Kirkpatrick 1987; Pomiankowski 1987). Indirect natural selection on female choice may occur if the expression of the preferred male trait indicates that a male carries alleles for high fitness (Trivers 1972; Zahavi 1975), or solely through the generation of a genetic correlation between male trait and female preference (Fisher 1958; Lande 1981).

Although the interaction between natural and sexual selection is central to how mate recognition may evolve, there is little direct experimental evidence from evolutionary experiments for the joint effect of these two evolutionary processes on the evolution of mate recognition. Here, I directly manipulate the opportunity for natural and sexual selection in replicate populations of *Drosophila* to determine how the interaction between natural and sexual selection affects the evolution of a mate recognition system. I concentrate on the simplest situation in which there is no additional selective force, such as a difference in environmental conditions between populations (divergent natural selection) or the presence of a second species (reinforcement).

Mate recognition in the *Drosophila serrata* complex is closely associated with cuticular hydrocarbons (CHCs). Where the two sibling species, *D. serrata* and *D. birchii*, are sympatric in nature, reproductive character displacement in male and female CHCs has evolved, demonstrating that CHCs are an important component of mate recognition in field populations (Higgie *et al.* 2000). In experimental hybrid populations between the two species, there is a high genetic correlation between CHC composition and hybrid mate recognition in both sexes (Blows & Allan 1998), indicating that CHCs are likely to respond when mate recognition is under selection. This has been confirmed in populations of *D. serrata* under laboratory conditions, where CHCs evolve rapidly when mate recognition is under selection (Higgie *et al.* 2000). Therefore, CHCs provide an accurate and readily quantifiable measure of how mate recognition evolves in this complex.

Mate recognition in most populations is likely to be at an equilibrium, where natural and sexual selection on male trait(s) are in balance, resulting in no net evolutionary force acting on the female preference (Kirkpatrick 1987). Therefore, to study how the processes of natural

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and sexual selection affect the evolution of mate recognition, the mate recognition system of a population needs to be disrupted from equilibrium. Here, I use a hybridization event between *D. serrata* and *D. birchii* to perturb the mate recognition system (Wallace *et al.* 1983; Carson *et al.* 1994; Blows 1998), allowing an investigation of the evolution of mate recognition under non-equilibrium conditions. Hybrid mate recognition evolves rapidly under unmanipulated non-equilibrium conditions (Blows 1998, 1999). Consequently, to study the evolution of sexually selected traits in hybrid populations, there is no need to impose artificial sexual selection on male traits, an alternative method of perturbation. An important advantage of hybridization over artificial selection is that the sexual selection process is determined by the animals themselves, rather than by the experimenter. In addition, hybridization disrupts the balanced genetic systems of each species, initiating a bout of natural selection in response to this new genetic environment. Hybrid populations therefore supply a system in which levels of sexual and natural selection may be manipulated by simply denying the opportunity for these forces to operate.

2. MATERIAL AND METHODS

(a) *Selection experiment*

A hybrid population was created from a successful cross between a *D. serrata* female and a *D. birchii* male, which was maintained as a mass-bred population at $n > 300$ for nine generations. At the 10th generation, 12 replicate populations were established from this hybrid population. Natural and sexual selection were manipulated in these replicate hybrid populations in a factorial experimental design (figure 1). Three replicate populations experienced both natural and sexual selection (NS), three experienced neither sexual nor natural selection (XX), three experienced just natural selection (NX) and three experienced just sexual selection (XS). On day 0, each population was established using 20 pairs of virgin males and females. In populations that experienced natural selection, all the virgin flies from the 20 vials were pooled, from which 20 males and 20 females were randomly selected to contribute to the next generation, ensuring that more productive females contributed to the next generation to a greater extent, on average. In populations that did not experience natural selection, one male and one female were selected from each of the 20 vials, eliminating natural selection on female productivity. The manipulation of natural selection therefore did not completely remove all forms of natural selection operating through other fitness components such as larval viability, although many such fitness components do contribute to overall productivity. In populations that experienced sexual selection, the 20 males and 20 females were placed together in a bottle in which they were allowed to choose their mates. In populations that did not experience sexual selection, individual males and females were randomly assigned into 20 pairs, eliminating the opportunity for sexual selection. On day 6, females from all lines were transferred into fresh individual vials without males and removed 4 days later. Upon emergence in these vials, virgin flies were collected to contribute to the next generation.

(b) *Response of cuticular hydrocarbons to selection*

After 20 generations of selection, the CHCs of 20 males and 20 females from each of the 12 experimental populations were individually assayed. Individual flies were washed in 50 µl of hexane for 4 min, followed by 1 min of agitation on a vortex mixer. Samples of 0.2 µl were injected into a HP6890 gas chromatograph fitted with a BPX5 column of 50 m × 0.32 mm internal diameter. The temperature programme ran from 50–220 °C at 15 °C min^{-1}, followed by 220–320 °C at 30 °C min^{-1}, then held for 15 min.

Gas chromatography revealed 18 peaks that were used in subsequent analyses. Peak areas, as a proportion of total CHC content for each individual, were transformed to logcontrasts, following established protocols for the analysis of multivariate CHC data (Blows & Allan 1998; Higgie *et al.* 2000). All subsequent statistical analyses were performed on the male and female means of each of the 12 populations, as these represented independent applications of the four treatment combinations (XX, NX, XS, NS). The factorial experimental design then allowed a direct test of the effects of natural and sexual selection in isolation, as well as the effect of the interaction between natural and sexual selection on the evolution of mate recognition after 20 generations.

3. RESULTS

A canonical discriminant analysis was used to display the relationship between male and female means for the 12 populations in CHC composition (figure 2). The first two canonical variates (CV1, CV2) explained 86.2% and 7.8% of the variation between population means, respectively. Three-way fixed effects univariate analyses of variance were used to determine whether the treatments had affected CHC composition. Both CV1 and CV2 displayed strong three-way interactions between sex and the applications of natural and sexual selection (CV1: $F_{1,16} = 129.982$, $p < 0.001$; CV2: $F_{1,16} = 30.007$, $p < 0.001$). To determine how the eight treatment combinations defined by sex, sexual selection and natural selection (figure 2) contributed to these three-way interactions, Tukey's test for pairwise *post hoc* comparisons between treatment combinations was used. *Post hoc* comparisons were conducted within a one-way ANOVA framework to control for type I errors with $q_{0.05,16,2}$ degrees of freedom and probability levels for each of the pairwise comparisons are reported below.

(a) *Natural selection*

Natural selection had a direct influence on total CHC content. Total CHC content of males and females decreased in the presence of natural selection (figure 3), indicating a fitness cost to CHC production. Because natural selection was manipulated through female productivity in this experiment, females in NX populations may have been favoured by natural selection if they were able to produce more progeny by allocating smaller amounts of hydrocarbon to the cuticle. A direct trade-off between egg production and CHC production has been observed in *D. melanogaster* using the mutation *ovo* that severely reduces egg production (Wicker & Jallon 1995). Females homozygous for the amorphic (*ovo*^{r}) or partial loss-of-function (*M1*) alleles increased total CHC production by over three times. Similar increases in CHCs were observed in the German cockroach, in which vitellogenesis and oocyte development were arrested by allatechomy, indicating that the cuticle and ovaries are targets

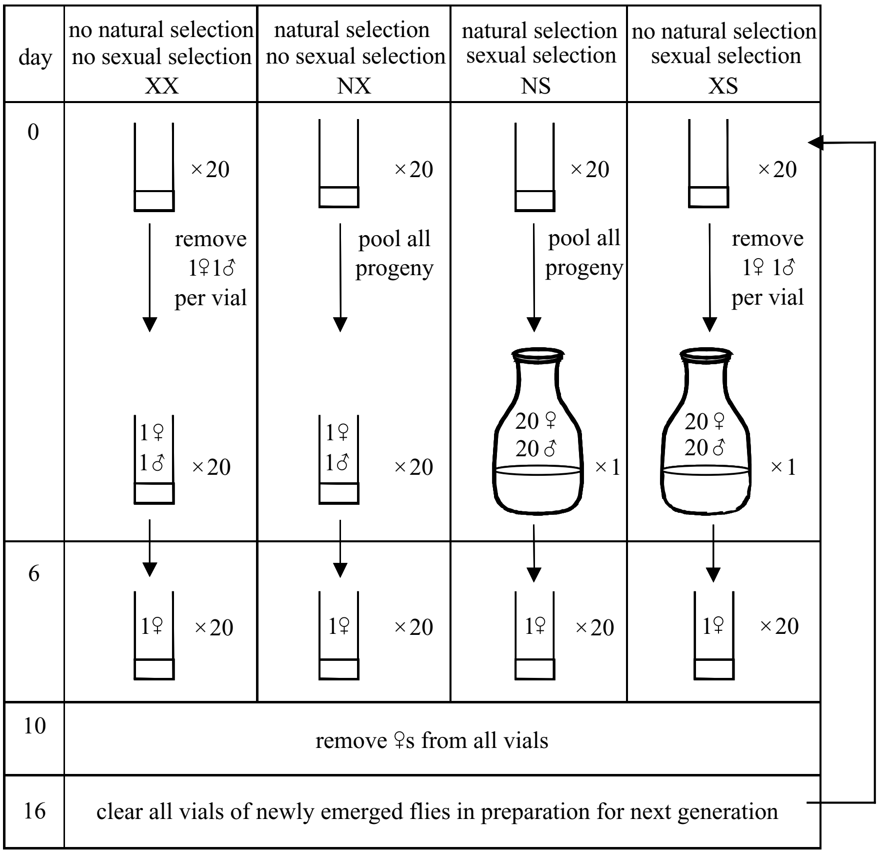

Figure 1. The application of natural and sexual selection in a two-way factorial experimental design in replicate hybrid populations.

for deposition of internal hydrocarbons from the same pool (Schal *et al.* 1994). It is difficult to determine if the reduction in male CHC production in NX populations is a consequence of an as yet unknown hydrocarbon allocation trade-off in males, or is a consequence of a pleiotropic correlated response to the reduction of CHC deposition on the cuticle in females.

Female CHC composition also responded to natural selection on both canonical variates (XX–NX, CV1: $p < 0.001$; CV2: $p = 0.021$). Females in NX populations may have been able to increase fecundity by evolving CHCs that were less costly to produce than others, as well as by allocating lower amounts of hydrocarbon to the cuticle. In contrast to females, males did not respond to natural selection in CHC composition (XX–NX, CV1: $p = 0.999$; CV2: $p = 1.000$).

(b) *Sexual selection*

Sexual selection resulted in the evolution of male CHC composition. Males responded significantly to sexual selection on CV1 (XX–XS, CV1: $p < 0.001$; CV2: $p = 0.190$), indicating that females preferred males with a particular CHC composition. Although the experimental application of sexual selection did not distinguish between female choice and male competition, male–male competition may be largely ruled out as females of both species exercise a degree of cryptic female choice during courtship and have evolved a number of mechanisms to control the success of copulations (Hoikkala & Crossley 2000). In addition, females of *D. serrata* show a consistent preference for a particular male CHC composition (M. W. Blows, unpublished data). Sexual selection in the *D. serrata* complex appears therefore to be driven by female choice rather than male–male competition.

Female CHC composition did not respond to sexual selection (XX–XS, CV1: $p = 0.996$; CV2: $p = 0.263$). The independence of male and female responses to sexual selection was consistent with the low pleiotropic genetic correlation between male and female CHC composition (Blows & Allan 1998) and male and female behavioural mate recognition (Blows 1998) in hybrid populations. Sexual selection in XS populations resulted in male CHCs evolving in the opposite direction to female CHCs in NX populations exposed to natural selection, indicating that females preferred CHCs of males that would result in lower fecundity when expressed in female offspring.

(c) *Interaction between natural and sexual selection*

The interaction between natural and sexual selection had a dramatic influence on the evolution of male and female CHCs. Although male CHC composition did not respond to natural selection, the evolution of male CHCs was enhanced by the interaction between natural and sexual selection. Males in NS populations evolved more rapidly than in XS populations (XS–NS, CV1: $p < 0.001$; CV2: $p = 0.278$). Furthermore, the direction of evolution of male CHCs in the presence of natural and sexual selection was the same as that in the presence of sexual selection alone.

Female CHCs evolved against the direction of natural selection in the presence of sexual selection (XX–NS,

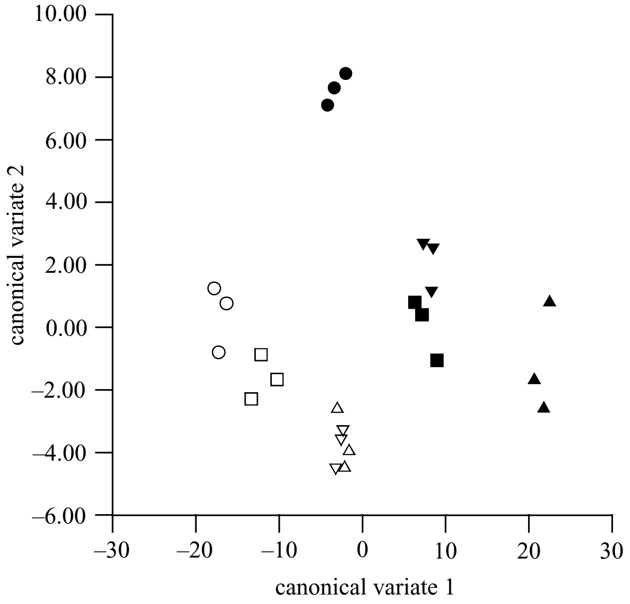

Figure 2. The response of CHC composition to natural and sexual selection in hybrid populations (filled circles, NS females; open circles, NS males; filled upright triangles, NX females; open upright triangles, NX males; filled squares, XS females; open squares, XS males; filled down-pointing triangles, XX females; open down-pointing triangles, XX males).

CV1: $p < 0.001$; CV2: $p < 0.001$), even though sexual selection had no direct effect on female CHCs when applied in isolation in XS populations. In both sexes, the magnitude of response to selection was greatest when natural and sexual selection operated in combination in NS populations. In addition, NS populations were the only populations in which males and females responded to selection in the same direction.

4. DISCUSSION

The manipulation of natural and sexual selection had large and highly repeatable effects on the mate recognition systems of the experimental populations. Both male and female CHCs responded to natural selection in isolation and only male CHCs responded to sexual selection in isolation, but the overriding response to selection was seen in both sexes in response to the interaction between natural and sexual selection. In males, the interaction between the two processes resulted in male CHCs evolving to a greater extent than under sexual selection in isolation. In females, CHCs displayed a dramatic reversal in the direction in which they evolved, compared with the direction of evolution under natural selection in isolation. This experiment has demonstrated that the interaction between natural and sexual selection was critical in determining the direction and magnitude of the evolutionary response of the mate recognition system. It will be a major challenge for future experimental studies of mate recognition evolution to determine if natural and sexual selection display similarly strong interactions when forms of diversifing natural selection are used in place of natural selection on female productivity, as proposed in ecological speciation models (Schluter 2001).

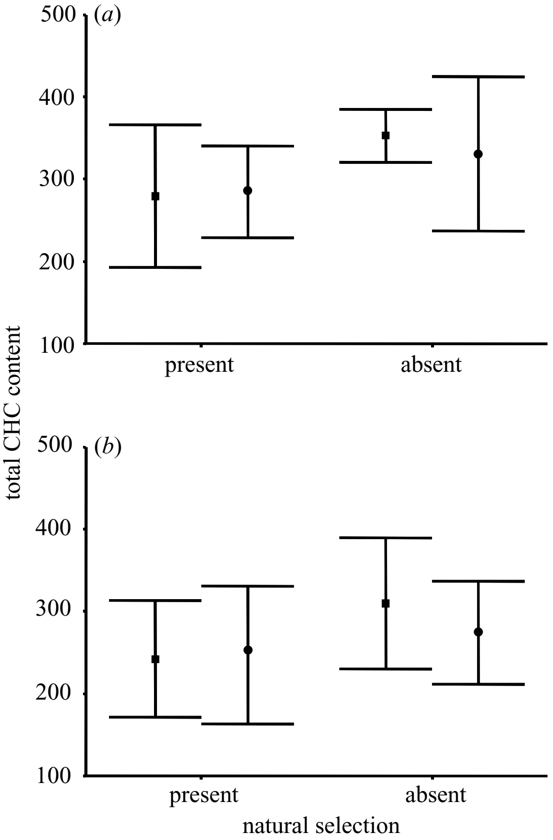

Figure 3. The response of total CHC content to natural and sexual selection in hybrid populations of (*a*) females and (*b*) males. Means and 95% confidence intervals are based on the three replicate populations for each treatment combination. Sexual selection absent (circles); sexual selection present (squares). Two-way fixed-effects ANOVAs (natural and sexual selection as factors) were used to determine if total CHC content had changed between treatments in females and males. In the presence of natural selection, total CHC content of individuals decreased in females (main effect of natural selection: $F_{1,8} = 12.965$, $p = 0.007$) and males ($F_{1,8} = 7.494$, $p = 0.026$). The main effect of sexual selection and the interaction between natural and sexual selection were not significant in these analyses.

The pattern of selection response to these two evolutionary processes and the direction in which populations evolved in were consistent with the action of indirect selection on female preference for male CHCs. The effect of natural selection in isolation in NX populations indicates that CHCs were costly to produce for males and females. The effect of sexual selection in isolation indicates that females preferred males with a particular CHC composition and that this composition was more costly to produce, at least when expressed in female offspring, as females experiencing natural selection in isolation evolved in the opposite direction. Costly male traits may be preferred by females if they indicate males that carry alleles for high fitness (Trivers 1972; Zahavi 1975). However, it should be noted that this experiment provides no direct evidence that the preferred male CHC composition is costly when expressed in males. This is because natural selection was manipulated through female productivity, leaving little opportunity for natural selection to have a strong effect on male phenotypes.

In XS populations, the opportunity for females to gain indirect benefits from their choice of males has been reduced, as natural selection on female productivity has been removed from these populations. When sexual and natural selection were allowed to operate together in NS populations, an indirect benefit to females may have been gained through their choice of males. When females were permitted to contribute to the next generation in proportion to offspring production in NS populations, more male offspring may have exhibited the chosen CHCs than in XS populations without natural selection. Thus, the interaction between natural and sexual selection may have driven the further exaggeration of the sexually selected male trait as a consequence of the indirect genetic benefits gained by females from their choice of mates. Such indirect genetic benefits to female choice have been suggested in other *Drosophila* species (Partridge 1980; Taylor *et al.* 1987; Promislow *et al.* 1998). Although sexually antagonistic sexual selection may also explain the exaggeration of male traits (Holland & Rice 1998; Gravrilets *et al.* 2001), it is unlikely to explain its evolution here as female CHCs in NS populations evolved further away from their natural selection optimum (NX populations), indicating that female preference for male CHCs, rather than resistance to them, underlies male and female responses in NS populations.

In contrast to XS and NX populations, male and female CHCs evolved in parallel in NS populations. Parallel evolution between the sexes may have been a result of a correlated response through pleiotropy (Lande 1980) or coevolution, which are not distinguishable in this experiment. The weak pleiotropic genetic correlation between male and female CHCs (Blows & Allan 1998) and the lack of correlated responses in XS and NX populations indicate that coevolution between the sexes may be involved to a greater extent. The lack of correlated response in females in XS populations indicates that no coevolution between male and female CHCs had occurred by sexual selection in the absence of natural selection.

Indirect benefits gained by females by choosing males with a particular CHC composition appeared to be a stronger force than the costs that females suffered by evolving costly CHCs (NS–NX comparison). Evidence for the interaction between natural and sexual selection mediated through indirect selection on female preferences and male traits has come mainly from single-generation experiments testing for positive genetic correlations between sexually selected male traits and offspring performance (Norris 1993; Petrie 1994; Hasselquist *et al.* 1996: Brooks 2000), or female preferences (Bakker & Pomiankowski 1995) under presumably equilibrium conditions in each species. The presence of such genetic associations is necessary for the operation of indirect selection under good genes (Trivers 1972; Zahavi 1975) or Fisherian (Fisher 1958; Lande 1981) sexual selection, but do not demonstrate that the strength of indirect selection acting through these genetic associations was sufficient to result in the evolution of male traits and females' preferences. The strength of indirect selection on female choice, relative to other forces such as costs associated with the preference, will determine if mate choice may evolve through any of the commonly propounded mechanisms of indirect selection. Recent theory indicates that the potential for indirect selection to influence the evolution of mate choice may be small (Kirkpatrick & Barton 1997), but it has yet to be empirically evaluated in any system in an evolutionary experiment. The strength of indirect selection will in part depend on the genetic correlation between the male trait and female preference (eqn 9 in Kirkpatrick & Barton (1997)). A large genetic correlation between male and female behavioural components of mate recognition was generated in hybrid populations under unmanipulated (effectively NS-like) conditions within 37 generations (Blows 1999), indicating that favourable genetic conditions were present for the operation of indirect selection on female preference in populations such as these. Hybridization between species will undoubtedly result in a population with abnormally high levels of genetic variation. The response to indirect genetic benefits gained by females through sexual selection may therefore have been magnified in these hybrid populations, as heritable variation in fitness may be high (Kirkpatrick & Barton 1997). Nevertheless, this experiment indicates that indirect genetic benefits to female preference may substantially exceed costs in the initial stages of sexual selection under non-equilibrium conditions.

Finally, the three replicate populations within each combination of natural and sexual selection responded in a remarkably deterministic manner. Although genetic drift in small populations alone is unlikely to result in the generation of substantial divergence in mate recognition (Rice & Hostert 1993), the interaction between genetic drift and directional processes such as sexual selection has remained an important component of models of the process of speciation (Lande 1981; Turelli *et al.* 2001). The amount of variation generated among replicate XX populations was no less than that among populations that experienced natural and/or sexual selection (figure 2), indicating that genetic drift had little effect on the evolution of CHC composition. The potential for genetic drift to influence evolutionary trajectories in sexual selection models is reduced when there is a cost to female preference, as replicate populations tend to converge to a single equilibrium point (Turelli *et al.* 2001). Unmanipulated hybrid populations between these two species have been observed to converge in male and female mate recognition towards a single equilibrium point rather than evolving along trajectories equal to the genetic regression (Blows 1998). The cost of female preference for male CHCs in this system appears to have the deterministic effect on the evolution of mate recognition predicted by models of sexual selection (Lande 1981; Pomiankowski *et al.* 1991).

In conclusion, the interaction between natural and sexual selection was of critical importance in the evolution of the mate recognition system in these populations of *Drosophila* under non-equilibrium conditions. The selection responses of the experimental populations were consistent with females gaining indirect genetic benefits from their choice of males. The process of indirect selection on female choice for high-quality males should result in the generation of genetic covariance between female preference and male fitness at equilibrium (Kirkpatrick & Barton 1997). I am currently determining if this signature of past female choice for males of high genetic quality exists in populations of *D. serrata*.

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