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Evolution of the genetic covariance between male and female components of mate recognition: an experimental test

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The evolution of a positive genetic correlation between male and female components of mate recognition systems will result as a consequence of assortative mating and, in particular, is central to a number of theories of sexual selection. Although the existence of such genetic correlations has been investigated in a number of taxa, it has yet to be shown that such correlations evolve and whether they may evolve as rapidly as suggested by sexual selection models. In this study, I used a hybridization experiment to disrupt natural mate recognition systems and then observed the subsequent evolutionary dynamics of the genetic correlation between male and female components for 56 generations in hybrids between *Drosophila serrata* and *Drosophila birchii*. The genetic correlation between male and female components evolved from 0.388 at generation 5 to 1.017 at generation 37 and then declined to −0.040 after a further 19 generations. These results indicated that the genetic basis of the mate recognition system in the hybrid populations evolved rapidly. The initial rapid increase in the genetic correlation was consistent with the classic assumption that male and female components will coevolve under sexual selection. The subsequent decline in genetic correlation may be attributable to the fixation of major genes or, alternatively, may be a result of a cyclic evolutionary change in mate recognition.

Keywords: genetic correlation; mate recognition; hybridization

1. INTRODUCTION

When mate recognition systems diverge during speciation (Dieckmann & Doebeli 1999; Kondrashov & Kondrashov 1999) or when mate choice within species results in sexual selection (Lande 1981; Bakker & Pomiankowski 1995; Kirkpatrick & Barton 1997), the traits that determine how males and females choose mates coevolve as a result of assortative mating. One consequence of assortative mating at the genetic level is the generation of linkage disequilibrium (Crow & Kimura 1970; Lynch & Walsh 1998) between the genes underlying these male and female traits. The genetic correlation that arises from such a process has been central to the development of formal quantitative genetic models of sexual selection, begining with Lande's (1981) demonstration of Fisher's (1930) 'runaway' process. Although the presence of this genetic correlation cannot distinguish between Fisher's (1930) process and alternative models of sexual selection (Bakker & Pomiankowski 1995), determining whether such genetic correlations are present in experimental and natural populations has been a critical first step in the empirical evaluation of these models (Pomiankowski & Sheridan 1994; Bakker & Pomiankowski 1995).

A number of studies have reported evidence of positive genetic correlations between female preferences and male traits in a variety of taxa (reviewed in Bakker & Pomiankowski 1995). Unfortunately, positive genetic correlations do not only arise from linkage disequilibrium, but may be caused by pleiotropy or physical linkage between genes. Pleiotropy has been considered an unlikely cause of genetic correlation since morphological (male traits) and neurological (female preferences) characteristics are phenotypically very different (Boake 1991; Lande 1981). This assumption may be unrealistic for two reasons: first, pleiotropy is considered the major cause of genetic correlation in general (Falconer 1981) and, second, other rationalizations may be developed to suggest that pleiotropy may be important, such as a condition-dependent expression of traits and preferences (Bakker & Pomiankowski 1995). That a genetic correlation between male and female components of a mate recognition system is a consequence of linkage disequilibrium has yet to be demonstrated in an experiment that excludes pleiotropy as an alternative explanation. In addition, assortative mating has not been shown to be able to generate genetic covariance under any experimental conditions (Heisler 1994).

To study the genetic basis of the relationship between male and female components of mate recognition and how this relationship evolves, the mate recognition system of a population needs to be disrupted. There are two ways in which this can be achieved. First, disruption can be achieved by artificial selection for a trait which contributes to recognition (reviewed in Bakker & Pomiankowski 1995). However, artificial selection experiments cannot distinguish pleiotropy from linkage disequilibrium as the genetic basis of correlated responses, nor is it clear whether the selection procedure applied is closely associated with how mate choice would operate under

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unmanipulated conditions. A second way of perturbing mate recognition systems is through interspecific hybridization (Wallace *et al.* 1983; Carson *et al.* 1994; Blows 1998). Hybridization between closely related species enables the genetic relationship between male and female components to be established in the reduced presence of linkage disequilibrium as a consequence of recombination, and enables the subsequent evolution of mate recognition systems to be investigated under unmanipulated conditions.

The experiments presented here are a continuation of a longitudinal study of the genetic basis of mate recognition in 30 isofemale lines established from a reciprocal cross between *Drosophila serrata* and *Drosophila birchii* (Blows 1998). Here, I investigate the long-term changes in the genetic correlation between male and female components of mate recognition under unmanipulated conditions. After four generations of recombination (five generations after the hybridization event) between the genomes of the two species, the genetic correlation between male and female components as a consequence of pleiotropy (or tight physical linkage) was estimated as $r = 0.388$ (Blows 1998). I now demonstrate that the male and female components of mate recognition rapidly coevolved during the next 50 generations, resulting in the generation and subsequent loss of substantial genetic covariance.

2. METHODS

(a) *Generation of hybrid isofemale lines*

In this study, I compared the genetic correlation between male and female components at generations 5, 37 and 56 (denoted G5, G37 and G56, respectively) after hybridization. The data for G5 have previously been presented in Blows (1998) and details of the generation of the hybrid lines can be found therein. Briefly, one successful mating between a *D. serrata* female and a *D. birchii* male ($S♀ \times B♂$) and one from the reciprocal cross ($B♀ \times S♂$) were generated. From each female, 15 F_1 female progeny were collected as virgins and each sib mated to a single male. Each pair founded an isofemale line (30 lines in total), which were maintained in subsequent generations in one culture bottle each at $n \approx 100$.

(b) *Measurement of male and female components of mate recognition*

At G37 and G56, the mating success of the hybrid lines was determined using the same basic method as that used at G5 to estimate the male and female components of mate recognition (Blows 1998). Briefly, this method consisted of determining the proportion of five *D. serrata* females that produced progeny after confinement in a vial for four days with a single hybrid male as the measure of the male component of mate recognition. The proportion of five hybrid females that produced progeny after confinement with a single *D. serrata* male represented the female component of mate recognition. I have therefore relied on the coevolution of male and female components within hybrid lines to be reflected in the standard comparison to the *D. serrata* parent. This methodology does not assume that the hybrid lines were selected towards the *D. serrata* mate recognition system, but does assume that male and female components of the hybrids respond in the same way to the *D. serrata* phenotype.

The advantages and disadvantages of this measure have been discussed in Blows (1998) in relation to the association between mating success and mate recognition. Most importantly, however, the male and female mating success measures were found to be highly genetically correlated with the cuticular hydrocarbon profile (Blows & Allan 1998), a common mechanism of mate choice (Jallon 1984) and sexual isolation (Coyne *et al.* 1994; Buckley *et al.* 1997; Coyne & Charlesworth 1997) within the *melanogaster* species group. The genetic correlation between mating success and the cuticular hydrocarbon profile (mean ± s.d.) was 0.78 ± 0.24 for females and 0.90 ± 0.08 for males, indicating that mating success was predominately determined by chemical communication. This demonstrated that the measure of mating success was an accurate indicator of mate recognition. Since both males and females appear to make mating decisions on the basis of the cuticular hydrocarbon profile and males as well as females discriminate between potential mates, at least at the species level (A. Hoikkala, S. Crossley and C. Castillo-Melendez, unpublished manuscript), this system does not appear to match the simple male trait–female preference model which is the basis of many of the models investigating the genetic basis of sexual selection. Nevertheless, these measures are relevant to the general question of the coevolution of the genes underlying male and female mating decisions.

(c) *Estimation of genetic correlations*

At G5, the genetic correlation was estimated as a between-line, product-moment correlation. This method assumes that the relationship between male and female components within each isofemale line had yet to be affected by selection, but was rather a consequence of recombination and segregation between the genomes of the two species. As the number of generations after hybridization increased, this assumption did not hold as selection began to determine the relationship between the components within each line. This situation is similar to that between natural populations, where male and female components may become correlated between populations, as has been found in guppies (Endler & Houde 1995) and *Drosophila melanogaster* (Hollocher *et al.* 1997). As a consequence, the variation between lines no longer reflected the genetic relationship between the two traits (Houde 1993).

It was therefore necessary to nest a full-sib design within isofemale lines to determine the genetic correlation between the male and female components at G37 and G56. This design allowed the partitioning of the covariance between the isofemale line and full-sib levels within a nested analysis of covariance (Grossman & Gall 1968), where lines were nested within the reciprocal cross and families nested within lines using the SAS NESTED procedure. This analysis was not used for significance testing of the sources of variation because of the unbalanced nature of the data. For each of the isofemale lines included in an experiment, five full-sib families were generated and the progeny of these families were used in three replicates for measurement of the male and female components of mating success for each family, resulting in a total of 15 replicates in each line for both components. The data were log transformed using $x' = \log_{10}(x + 1)$ before analysis.

The components of the genetic covariances from the G5 and G37/56 experiments differed as a consequence of the differences in experimental design. At G5, the genetic covariance was approximately $\mathrm{COV}_{G5} = 6/8V_a + 1/8V_d + 36/64V_{aa} + 6/64V_{ad} + 1/64V_{dd}$ (Blows 1998). At G37 and G56, the genetic covariance was that of full-sibs, $\mathrm{COV}_{G37/56} = 4/8V_a + 2/8V_d + 16/64V_{aa} + 8/64V_{ad} + 4/64V_{dd}$ (Falconer 1981). Therefore, the genetic correlation at G5 had a higher proportion of additive to non-additive genetic

Table 1. *Analysis of covariance for the male and female components of mate recognition at G37 and G56*

source of variation	d.f.	sums of products		
		male	male/female	female
G37				
mating	1	100.2	−17.0	2.9
line	24	4651.3	−60.0	4434.3
family	99	7474.7	1479.9	6869.2
error	215	14 586.0	964.1	11 946.0
total	339	26 813.0	985.9	23 252.0
G56				
mating	1	215.2	207.3	199.7
line	19	4560.9	78.7	2578.1
family	78	8922.6	719.1	6540.2
error	170	9984.5	1752.8	11 951.0
total	268	23 683.0	2758.0	21 269.0

Table 2. *Variance and covariance components for the male and female components of mate recognition at G37 and G56*

source of variation	variance components		covariance component
	female	male	
G37			
mating	−1.09	−0.57	0.27
line	8.80	9.04	−5.78
family	5.13	2.84	3.88
error	55.56	67.84	4.48
total	69.49	79.73	2.85
G56			
mating	0.47	−0.25	1.57
line	4.03	9.73	−0.40
family	5.02	20.62	−0.40
error	70.30	58.73	10.31
total	79.83	89.08	11.08

variance than the traditional broad-sense definition from the full-sib design used at G37 and G56.

3. RESULTS

(a) *Estimation of the genetic correlations at G37 and G56*

The covariance between the male and female components at G37 and G56 was partitioned between the reciprocal cross, isofemale line and full-sib (family) levels by ANCOVA (table 1). The variance and covariance components from these ANCOVAs are presented in table 2, from which component correlations, representing the genetic correlation at the full-sib level, were calculated. At G37 the component correlation at the full-sib level was 1.017, which then declined to −0.040 at G56.

(b) *The change in genetic correlation between generations*

To test for a change in the genetic correlation between G37 and G56, the randomization procedure outlined by Lynch & Walsh (1998, p. 652) was followed. Since it was the difference between the correlations at the full-sib level that was of interest, randomizations were performed by maintaining the covariance structure within families. All families from the two generations were pooled and then

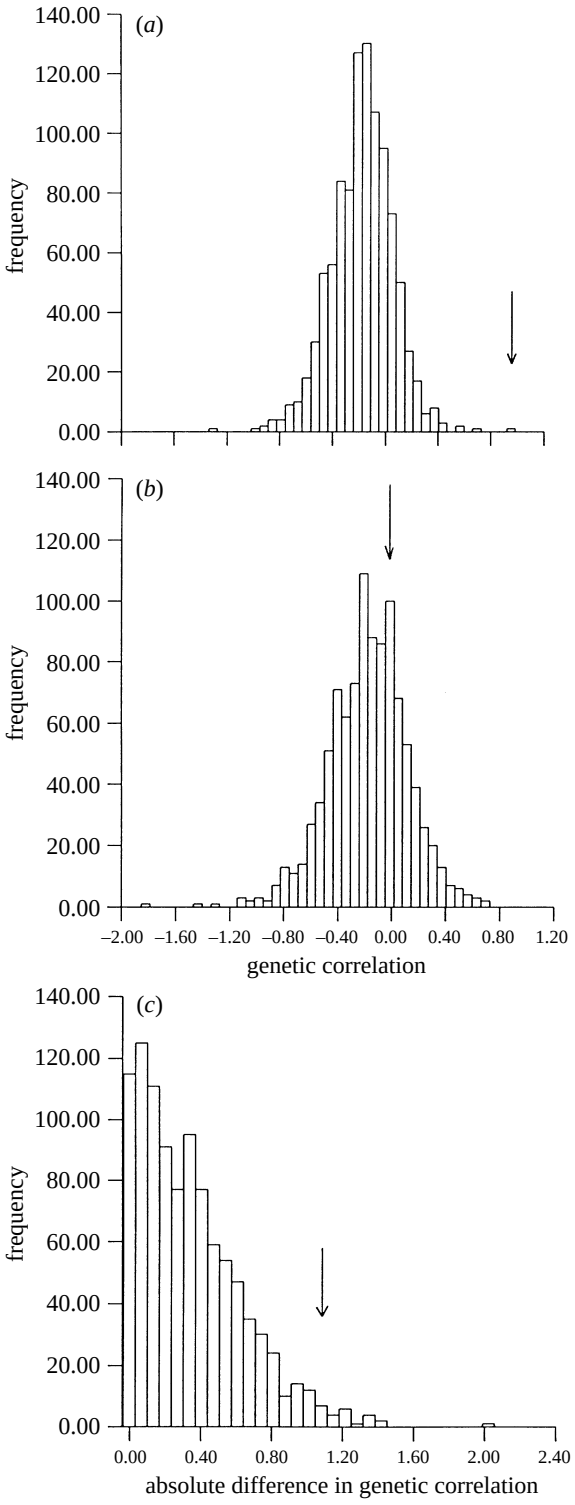

Figure 1. Results of 1000 randomizations testing for a difference between the G37 and G56 genetic correlation. (*a*) Distribution of the genetic correlation in the pseudo-population with sample size equal to G37. (*b*) Distribution of the genetic correlation in the pseudo-population with sample size equal to G56. (*c*) Absolute difference in genetic correlation between the 1000 randomized pairs from the two pseudo-populations. Arrows indicate the size of the observed genetic correlations (*a*,*b*) and their difference (*c*).

randomly assigned to two pseudo-populations with family sizes equal to the original G37 and G56 experiments. The component correlation at the full-sib level within each pseudo-population was then calculated by nested ANCOVA as above. This process was repeated 1000 times. The distributions of the two estimates of genetic correlation for both pseudo-populations are shown in figure 1*a*,*b*, respectively. The observed estimate of the full-sib genetic correlation at G37 was higher than any of the 1000 estimates from the randomization procedure in the pseudo-population with the same number of families, indicating that the addition of any number of families from the G56 population decreased the correlation. The observed estimate of the full-sib genetic correlation at G56 lay close to the centre of the distribution of the genetic corrrelation in the pseudo-population with that sample size. The test for a significant difference between the two generations was conducted by taking the absolute difference between the 1000 randomized pairs of genetic correlations (figure 1*c*). The observed difference of 1.057 was larger then 968 of the differences from this distribution, indicating that the observed estimates of genetic correlation at G37 and G56 were significantly different ($p = 0.032$, two-tailed test).

Unfortunately, a similar direct test of the difference between the genetic correlations at G5 and G37 was not possible as different experimental designs were used. Bootstraping of the component correlations at both generations would have been the most appropriate method of calculating confidence intervals (the product-moment, between-line correlation at G5 of 0.388 used to approximate the genetic correlation was very similar in this instance to the component correlation of 0.351). The correct bootstrapping procedure in this case would have been to resample between the lines within each of the reciprocal crosses for G5 and between the five families within each line for G37. This is because the line was the level containing the genetic information at G5, but the family was the level containing the genetic information at G37 (Goodnight & Schwartz 1997). However, it is unlikely that resampling between such a small number of data points would give a reliable approximation of the distribution in each case, a fundamental assumption behind the bootstrapping procedure (Manly 1997). For example, if one was to ignore the higher levels in the bootstrapping procedure and resample across all 125 families in the G37 experiment then the covariance due to the families would be redistributed between all levels in the analysis, not just at the family level, resulting in an incorrect estimate of the covariance for this level. A satisfactory test of the difference between these two estimates of genetic correlation does not then appear to be possible using this approach. However, some confidence in the size of the genetic correlation at G37 can be gained from figure 1*a*, which indicates that the addition of any number of families from the G56 data set reduces the correlation (the next highest value was 0.732), suggesting that there is a very large genetic correlation between the male and female components at this time. For the G5 genetic correlation, 95% confidence intervals can be placed on the product-moment correlation using standard methods, resulting in $r = 0.025 < 0.388 < 0.660$.

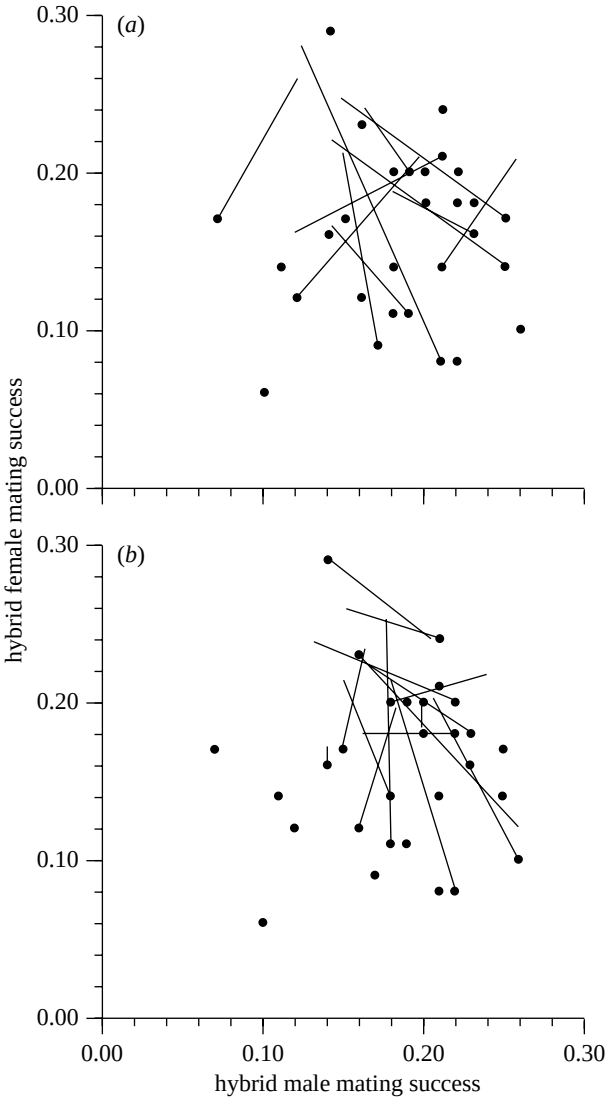

Figure 2. Evolutionary trajectories for isofemale lines from G24 to G37. Closed circles represent the position of a line at G24 and the end of the trajectory represents its position at G37. (*a*) Trajectories for those lines which were initially above the G5 genetic regression and (*b*) trajectories for those lines initially below this line.

(c) *The direction of evolution of the male and female components*

The direction of the evolution of the male and female components in this system has been previously shown to be dependent on the initial position of each population in relation to the G5 genetic regression (Blows 1998). The mean evolutionary trajectory of the male component of mating success between G5 and G24, in populations above and below the G5 regression, was in the direction of greater mating success. However, female mating success was shown to have converged towards the G5 regression. It is therefore possible that the two sets of populations may again have evolved along different trajectories from G24 to G37. To address this possibility, I present analyses on those lines which were initially above and below the G5 regression separately and then on all isofemale lines combined.

The evolutionary trajectories of the isofemale lines from G24 to G37 are displayed in figure 2. The trajectories of

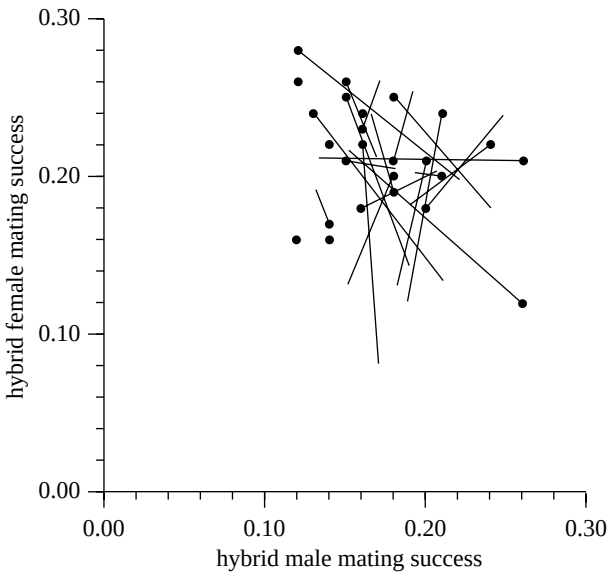

Figure 3. Evolutionary trajectories for isofemale lines from G37 to G56.

those lines which were initially above the G5 genetic regression (figure 2*a*) had a mean angle of 120.7° (taking the *x*-axis to the right as 0°), with a mean vector length of $r = 0.72$ and represented a significant mean direction (Rayleigh *z*-test $n = 12$, $z = 6.169$ and $p < 0.001$). Those lines initially below the G5 regression (figure 2*b*) had a mean angle of 92.5°, with a mean vector length of $r = 0.35$, but did not represent a significant mean direction ($n = 14$, $z = 1.725$ and $0.10 < p < 0.20$). A Watson–Williams test indicated that the mean angles for the two groups did not differ ($F_{1,24} = 0.908$ and $p > 0.50$). Combining all trajectories gives a mean angle of $110.5 \pm 30°$ (95% confidence intervals), with a mean vector length of $r = 0.506$, which represented a significant mean direction ($n = 26$, $z = 6.657$ and $p < 0.001$). No common direction in the evolutionary trajectories was present from G37 to G56 (figure 3).

In summary, earlier work has demonstrated that the isofemale lines evolved in the direction of greater male mating success between G5 and G24, but converged in female mating success towards a single point (Blows 1998). From G24 to G37, the direction of evolution changed in the direction of increasing female mating success and appeared now to be associated with the large genetic covariance at G37. At G56, no significant direction or genetic correlation was found. Caution needs to taken when infering a directional change based upon two points in time; a day effect for instance could be solely responsible for the positions of the isofemale lines in the space described by figures 2 and 3 at any particular generation. However, for each of the intervals G5–G24 and G24–G37, most change was in the direction of only one of the two components of mate recognition; along the axis of increasing male mating success from G5 to G24, then along the axis of increasing female mating success from G24 to G37. These results are unlikely to be attributable to a general day effect on the activity, for example of flies in the experiments, as it would have to affect males and females differentially on each occasion. In addition, the association between directional evolutionary change and the presence of significant genetic covariance are independent of any such day effect.

4. DISCUSSION

This experiment has demonstrated rapid change in the genetic covariance between the male and female components of mate recognition, supporting the basic assumption behind many models of sexual selection that the genes underlying the male and female components of the mate recognition system may coevolve. Nevertheless, these results are not sufficient to demonstrate conclusively the Fisher (1930) process or other models involving indirect selection in action for two reasons. First, in spite of being able to demonstrate the evolution of a large genetic correlation between male and female components of the mate recognition system at G37, I am unable to attribute this to sexual selection directly. A comparison of genetic correlations in an experiment designed to allow sexual selection in some hybrid lines but not in others will be required to accomplish this. In the absence of this manipulation, the change in genetic covariance needs to be interpreted with caution.

Second, the underlying genetic basis of the evolution of the genetic correlation has not been determined by these experiments. After the disruption of the mate recognition system by hybridization, it was expected that the basal correlation at G5 would increase as selection generated a positive genetic correlation between the male and female components as a consequence of linkage disequilibrium. However, it is unlikely that the generation of covariance by linkage disequilibrium alone would result in a correlation of the magnitude found at G37 (Lande 1984). Inbreeding or pleiotropy (including tight physical linkage) may therefore have played a role in the evolution of the genetic correlation. Inbreeding was certainly present in these lines, with an inbreeding coefficient of at least 0.375 at the G3 generation, which probably increased thereafter as a consequence of the small population size of each line. Although inbreeding could explain the high genetic correlation at G37, it is unlikely to explain the reduction in the correlation to zero at G56 without recourse to hypothesizing a differential influence of inbreeding across the generations.

Pleiotropy or tight physical linkage are possible contributing factors to the genetic covariance that are not possible to distinguish between. Pleiotropy or tight physical linkage have similar effects on genetic correlation and would allow the maintenance of a high genetic correlation as seen at G37 (Lande 1984). In addition, the presence of the small but significant genetic correlation at G5 as a consequence of pleiotropy or physical linkage provided the opportunity for either mechanism to have had an effect on the evolution of the genetic correlation. In the only other example of a numeric value for the genetic correlation having been established between male and female components (Bakker & Pomiankowski 1995, table 3), Bakker (1993) found a large broad-sense genetic correlation of 0.75 ± 0.31 between male colour and female preference in sticklebacks. Unfortunately, no information was available on the contribution of linkage or pleiotropy to this estimate. However, the high magnitude of both correlations estimated to date suggests that the factors

influencing the genetic correlation other than linkage disequilibrium need to be accounted for in experimental designs investigating the evolution of mate recognition via sexual selection.

At G56, the genetic correlation had effectively fallen to zero. The fixation of major genes may provide an explanation for the reduction in the genetic correlation at G56. If this was so, it would also be expected that the genetic variances of the male and female components would have been reduced by this process. It can be seen from table 2 that the genetic variance in female mating success did not change between G37 and G56 and that the genetic variance in male mating success actually increased rather than decreased during this period. Alternatively, a cyclic change in mate preference evolution from unstable to stable states (Iwasa & Pomiankowski 1995) may also account for this pattern. After a period of unstable runaway evolution, female preference may decline (Iwasa & Pomiankowski 1995) and with it genetic correlation. Unfortunately, there is little evidence supporting this explanation that can be extracted from this experiment. It is not clear, for instance, whether the association between the presence of a strong genetic correlation and a directional component to the change in trait means (G37) and the lack of genetic correlation and no directional change in trait means (G56) is a reflection of this type of process.

5. CONCLUSION

In conclusion, the genetic correlation between the male and female components evolved rapidly. Evolution during the unstable phase of the Fisher (1930) process is expected to be approximately exponential in nature and the rates of change will be rapid, particularly when the traits involved are measured on a logarithmic scale (Lande 1981), as in the present work. The perturbation of mate recognition systems by hybridization may be one way of allowing us to observe these important bouts of selection, which may otherwise be very uncommon in natural populations relative to the time it takes the Fisher (1930) process to be completed (Lande 1981; Iwasa & Pomiankowski 1995). The longitudinal experimental design used here has established the time-frame over which the evolution of mate recognition will occur in this system and more complex and logistically demanding experiments which manipulate the levels of sexual selection may now be contemplated.

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