The evolution of female choice when the preference and the preferred trait are linked to the same inversion system

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This study reports results of computer simulations of the evolution of female mating preferences when both the preference and the preferred character are associated with the same chromosomal inversion system. When there is strong heterosis associated with the inversion system and no direct selection acting on mating preferences, a pattern of disassortative mating with respect to the inversion is predicted to evolve. Females mating disassortatively produce highly fit heterokaryotypic offspring. However, when heterosis is weak, Fisherian sexual selection can maintain strong assortative preferences, but the inversion polymorphism is lost. Assortative preferences are only likely to be maintained in conjunction with a polymorphic inversion system if direct sexual selection is operating. The results of this study are discussed with respect to the seaweed fly, *Coelopa frigida*, in which the preference and preferred trait are associated with the $\alpha\beta$ inversion system.

Keywords: chromosomal inversions, *Coelopa frigida*, female choice, sexual selection.

Introduction

Models of sexual selection by female choice in species with non-resource-based mating systems have focused on the evolution of female mating preferences through indirect selection acting on their offspring (reviewed by Kirkpatrick & Ryan, 1991; Andersson, 1994). These models are of two types: the Fisherian process (Fisher, 1930; Lande, 1981; Kirkpatrick, 1982; Pomiankowski *et al.*, 1991) and the 'good genes' or viability indicator mechanisms (Zahavi, 1975; Bell, 1978; Andersson, 1982, 1986; Hamilton & Zuk, 1982; Kirkpatrick, 1986; Pomiankowski, 1987a; Charlesworth, 1988; Iwasa *et al.*, 1991). In the Fisherian process, females choosing to mate with attractive males produce attractive male offspring. Because sons carrying the preferred trait gain a mating advantage, the preference also has an advantage through its genetic correlation with the trait. In the viability indicator mechanism the preferred trait acts as an indicator of the genetic quality of some character affecting viability. In this case the preference becomes genetically correlated with the viability trait.

An alternative mechanism by which female preferences could arise involves direct selection. By diverse means (see Andersson, 1994) the female herself could gain an advantage as a result of exercising choice; for example, she may obtain an advantage by gaining protection or by avoiding or reducing costs.

Female seaweed flies (*Coelopa frigida*) express a mating preference for large males in several populations in northern Europe (Gilburn *et al.*, 1992, 1993; Gilburn & Day, 1994a). There is considerable variation in adult size and natural populations exhibit high coefficients of variation in both sexes (8.6–19.4 in males; 5.2–13.4 in females), although in every population males are more variable than females (Gilburn & Day, 1994b). Under controlled laboratory conditions, adult size has been shown to have a heritability between father and son of about 70 per cent (Wilcockson *et al.*, 1995), and much of the genetic variation can be attributed to the $\alpha\beta$ inversion system on chromosome I (Butlin *et al.*, 1982; Gilburn & Day, 1994b; Wilcockson *et al.*, 1995). $\alpha\alpha$ homokaryotypes are the largest, $\beta\beta$ s the smallest, and $\alpha\beta$ s are intermediate. A similar pattern exists in females, although the differences between the karyotypes are considerably smaller. As in many chromosomal inversion systems (Dubinin & Tiniakov, 1946;

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Dobzhansky, 1947; Birch, 1955; da Cunha, 1955; Lewontin & White, 1960; Budnik *et al.*, 1971; Anderson *et al.*, 1975), there is strong heterosis associated with the $\alpha\beta$ inversion system (Day *et al.*, 1983; Butlin *et al.*, 1984; Butlin & Day, 1985, 1989).

A consequence of the large amount of genetic variation in the male character is that there is great potential for the Fisherian process to operate. Furthermore, the fact that most, if not all of this genetic variation is determined by a single inversion system means that extremely strong correlations between the preference and the trait could develop. Trickett & Butlin (1994) added an inversion system to the Kirkpatrick (1982) model of the Fisher process and found that stronger genetic correlations between the preference and the preferred trait were generated. This resulted in a steeper gradient in the lines of selection moving the population towards the line of equilibria. Trickett and Butlin's model was a population simulation of a haploid organism. However, the association of the male preferred character with an inversion polymorphism exhibiting strong heterosis may have other effects on sexual selection that would only be apparent in a diploid model. Otto (1991) found that overdominance in the male trait coupled with linkage of the preference and trait loci could lead to the origin of a new mating preference. Strong heterosis generates substantial fitness differences upon which a viability indicator system could operate. In *C. frigida* male size, rather than signalling directly that the male is of high quality, could be acting as an indicator of inversion karyotype. Females are predicted to prefer males of a complementary karyotype thereby increasing the proportion of heterokaryotypes in their offspring. In other words, homokaryotypes are predicted to mate with opposite homokaryotypes.

There is evidence that genetic differences in female mating behaviour also coinhere with the $\alpha\beta$ inversion (Gilburn & Day, 1994c). Because there is no recombination in the region of the inversion (Day *et al.*, 1982), loci determining mating behaviour could evolve independently on the two forms of the inversion; $\alpha\alpha$ and $\beta\beta$ females could possess distinctly different mating preferences. For $\beta\beta$ s both good genes and Fisherian sexual selection would lead to a mating preference for large size, and in all populations studied $\beta\beta$ females do indeed exhibit such a preference (Gilburn *et al.*, 1992, 1993; Gilburn & Day, 1994a). The overall preference in every population was for large males, and thus any preference for large size will gain a Fisherian benefit. For $\alpha\alpha$ females the situation is more complex, and it is the evolution of the preference on the α form of the

inversion that we investigate in the current models. If they exercise a preference for large male size they gain a Fisherian advantage, but at a cost in terms of progeny viability. However, if they mate with small males they gain a good genes advantage, but incur a Fisherian cost. A pattern of disassortative mating with respect to inversion karyotype was found in a Channel Island population (Gilburn & Day, 1994a), but $\alpha\alpha$ females in three other populations (Gilburn *et al.*, 1993; Gilburn & Day, 1994a) preferred large males, and in two further populations they showed no preference (Gilburn *et al.*, 1992; Gilburn & Day, 1994a). Estimates of the change in offspring fitness attributable to the preference expressed by $\alpha\alpha$ females, showed that offspring fitness was reduced in all but one of nine populations (Gilburn *et al.*, submitted); only in the Channel Island population was fitness increased. Because the measures of offspring fitness included both Fisherian and good genes effects, the Fisherian advantage appears to be insufficient to counteract the viability disadvantage.

Here we report computer simulations that clarify under what conditions $\alpha\alpha$ females are predicted to exhibit a Fisherian type of preference for large ($\alpha\alpha$) males, or a good genes preference for small ($\beta\beta$) males.

Methods

The model

The model simulated an infinitely large population of diploid individuals in which a single locus is segregating. This locus determines female mating preference, the preferred character in males, as well as egg-to-adult viability, in a similar fashion to the α and β inversions in *C. frigida*. There are four 'alleles': α^A , α^R , α^D and β . The three α alleles can be viewed as alternatives on one form of the inversion, and β as an allele at fixation on the other inversion sequence. The mating behaviours of the genotypes are summarized in Table 1. Females homozygous for the α^A allele are a times more likely to accept an $\alpha\alpha$ male than other males. Likewise, $\alpha^D\alpha^D$ females are a times more likely to mate with a $\beta\beta$ male than other males. This mating preference is identical to that used in several previous models (Kirkpatrick, 1982; Pomiankowski, 1987b; Trickett & Butlin, 1994). The β allele confers the same mating preference as the α^A allele: they are a times more likely to accept an $\alpha\alpha$ male than other males. The α^R allele codes for random mating and is recessive to all the preference alleles. $\alpha^A\alpha^D$ and $\alpha^D\beta$ heterozygotes are assumed to mate randomly. In summary, the population

Table 1 The relative likelihood of females of each genotype accepting males of different karyotypes

Female genotype	Male karyotype		
	$\alpha\alpha$	$\alpha\beta$	$\beta\beta$
$\alpha^A\alpha^A$	a	1	1
$\alpha^A\alpha^R$	a	1	1
$\alpha^A\alpha^D$	1	1	1
$\alpha^A\beta$	a	1	1
$\alpha^R\alpha^R$	1	1	1
$\alpha^R\alpha^D$	1	1	a
$\alpha^R\beta$	a	1	1
$\alpha^D\alpha^D$	1	1	a
$\alpha^D\beta$	1	1	1
$\beta\beta$	a	1	1

contains a polymorphic inversion system with two alternative forms; all females homozygous for one form ($\beta\beta$) express a disassortative mating preference for $\alpha\alpha$ males. On the second form of the inversion (α) there are three alternative alleles coding for disassortative, assortative, or random mating. The simulations attempted to determine which of these alleles are advantaged under various conditions.

Mate preferences are the only force of sexual selection, but the model does incorporate three types of reproductive cost. The first is a cost to choice whereby a proportion, c , of all choosing females fail to produce any offspring. This cost arises because discriminating females run the risk of encountering no acceptable mate during their life — an idea proposed by Kaneshiro (1987), and for which there is experimental evidence in *Coelopa* (Day *et al.*, 1992). The second cost is a cost of mating, which refers to a reduction in longevity incurred by females with high acceptance rates. Again it is a differential cost, so that those females which accept all males incur a higher cost than do discriminating females. It is therefore paid only by $\alpha^R\alpha^R$ females and results in a proportion, m , of females failing to produce progeny. As in other insect species (Partridge *et al.*, 1987; Fowler & Partridge, 1989; Rowe *et al.*, 1994), mating in seaweed flies carries a cost; Pita (1991) found that females allowed unlimited matings died younger than did virgin females. Furthermore, a positive correlation exists between the frequency of rejection and female longevity (Gilburn & Day, in preparation). It is therefore possible that rejection confers a direct benefit to the female in terms of increased survival. The third cost refers to the additional time and energy required to reject some males rather

than others. In *Coelopa* there are large differences in male size, and it seems plausible that it is more costly to reject large males compared to small ones. This 'cost of rejection' is treated as a differential cost and so in the model is paid only by females expressing a preference for $\beta\beta$ males (the $\alpha^D\alpha^D$ and $\alpha^R\alpha^D$ females), and results in a proportion, r , failing to produce offspring.

Viability selection was also included in the model. All $\alpha\beta$ heterokaryotypes were assumed to have a fitness of one. The $\alpha\alpha$ homokaryotypes had a fitness of $1 - s$, and $\beta\beta$ s a fitness of $1 - t$. Generations were discrete and runs were started with all alleles at equal frequencies unless otherwise stated. In each generation reproductive costs were applied first, followed by sexual selection and the production of zygotes. Viability selection was then applied to generate the adults for the next round of mating. The simulations were run until an equilibrium was reached.

Results

Indirect sexual selection

Initially the simulations included no costs of reproduction, and the only two forms of selection operating were indirect sexual selection and heterosis. The first set of simulations included three alleles, α^A , α^R and β . The strength of the preference, a , and the strength of heterosis, s and t , were varied (Fig. 1a). When heterosis was strong the α^A allele was generally lost from the population; the α^R and β alleles remained at equilibrium. This suggests that Fisherian sexual selection is not strong enough to maintain an assortative mating allele in the presence of strong heterosis — the penalty of producing unfit offspring is too great. When the strength of viability selection was reduced, indirect sexual selection could maintain an assortatively mating allele. However, although the α^A allele was maintained, the β allele was lost; Fisherian sexual selection was stronger than the heterosis maintaining the inversion polymorphism. The assortative mating preference and the inversion polymorphism could not be maintained together.

The invasion conditions required for the initial spread of the α^A allele were then investigated. The starting frequency of the α^A allele was 0.01, with the α^R allele set at 0.49 and β at 0.5. Even with extremely favourable conditions ($a = 1000$, $s = t = 0.01$), the α^A allele could not reach a frequency higher than 0.025 without the loss of the inversion polymorphism. Once the β inversion is

lost, no further evolution can occur, and the population remains dominated by random maters. The invasion conditions required for the initial spread of the α^R allele were also studied. The starting frequency of the α^R allele was 0.01, with the α^A allele

Fig. 1 The evolutionary outcome of varying the strength of female mating preferences and the strength of heterosis in populations segregating for the α^A , α^R , and β alleles. The α^A and α^R alleles, present on the same form of an inversion, determine assortative and random mating, respectively; the β allele located on the alternative form of the inversion encodes a disassortative mating strategy. Different starting frequencies were used for the alleles: (a) simulations were started with equal frequencies of the alleles, (b) the α^R allele was started at a low frequency ($\alpha^A = 0.49$, $\alpha^R = 0.01$ and $\beta = 0.5$).

set at 0.49 and β at 0.5. The higher starting frequency of the α^A allele enabled it to be maintained in a population with higher levels of heterosis before being displaced by the α^R allele (Fig. 1b).

The second set of simulations included the α^D allele. When heterosis was strong, a stable equilibrium was established with just two alleles, α^D and β , segregating — a pattern of completely disassortative mating evolved (Fig. 2). When heterosis was weak and the strength of the preference was strong, then all four alleles were maintained, although the frequency of the β allele was usually very low (<0.05). Either the α^A or the α^D allele was always the most common at equilibria. There was a gradient in the frequencies of the two across the region of the four-way equilibria. When one increased in frequency it did so at the expense of the other. If very strong preferences were present in conjunction with weak heterosis then the β allele, and therefore also the inversion polymorphism, were lost. The transition zone (the lower line in Fig. 2) between all four alleles being maintained, and the β allele being lost, is clearly complex. The point of inflexion that occurs when log preference increases beyond one, is associated with a sudden increase in the ratio of the α^A allele to the α^D allele at equilibrium. This reduction in frequency of the α^D allele,

Fig. 2 The evolutionary outcome of varying the strength of female mating preferences and the strength of heterosis in populations segregating for the α^A , α^R , α^D and β alleles. The alleles segregating were the same as in Fig. 1 with the addition of α^D , a third allele on the α form of the inversion, which determines disassortative mating. The starting frequencies of the alleles were equal.

which helps to maintain the β allele, results in a sudden increase in the strength of heterosis required to maintain the β allele.

These results suggest that very strong preferences can favour the Fisher process over good genes sexual selection. In other words, the advantage gained through the production of sexy offspring more than outweighs the disadvantage of producing progeny of low viability. However, unlike the first simulations in which the α^A and β alleles could not be maintained at equilibrium together, the addition of the disassortative mating allele allows the maintenance of both, although the β allele was usually present at very low frequencies at equilibrium. The α^A allele is maintained through Fisherian sexual selection, the α^D allele through good genes sexual selection, and the β allele is maintained at a low level by the disassortative preference expressed by the α^D allele. β alleles are retained because they gain a rare-male mating advantage. However, an assortative mating preference on one form of an inversion is unlikely to be maintained by Fisherian sexual selection without reducing the other form of the inversion to very low frequencies.

When heterosis is strong, a pattern of completely disassortative mating evolves because the advantage of producing offspring of high viability is greater than the Fisherian advantage gained by producing sexy offspring. The potential benefit from mating disassortatively and thereby producing offspring of relatively high viability, depends on the level of heterosis; the stronger the heterosis, the larger the benefits of disassortative mating.

The invasion conditions required for the spread of the α^A and α^D alleles were investigated. The α^R allele never became the most frequent allele on the α form of the inversion if there was no cost to choice and the α^A and α^D alleles were both present in the population. Consequently, the α^R allele was not considered any further in this series of simulations. The conditions required for the spread of the α^D allele (Fig. 3) were determined in a population in which most α females mate assortatively ($\alpha^A = 0.49$, $\alpha^D = 0.01$ and $\beta = 0.5$). The α^D allele displaces the α^A allele if heterosis is relatively strong. In other words, the advantage gained from good genes sexual selection is greater than that from the Fisher process. The strength of preference also affects the evolutionary outcome, with stronger preferences favouring Fisherian over good genes sexual selection. As the strength of preference increases, so the level of heterosis required to enable good genes preferences to evolve increases. A similar pattern was seen when the invasion conditions required for

an assortative preference to displace a disassortative preference were investigated (Fig. 3), although the low initial frequency ($\alpha^A = 0.01$, $\alpha^D = 0.49$ and $\beta = 0.5$) means that even stronger preferences and weaker heterosis are required to allow the assortative mating preference to persist at high frequencies at equilibrium.

Cost to choice

The expression of female mating preferences may incur a cost. For example, a female may die before she encounters a male of the preferred type. When a cost to choice was added to Fisherian models of sexual selection, Parker (1983), Kirkpatrick (1985) and Pomiankowski (1987b) showed that both the preference and the preferred trait are lost from the population (but see Pomiankowski *et al.*, 1991).

Consider first the effects of introducing a cost to choice when conditions favour the spread of the α^A allele — in other words, preferences are very strong and heterosis is weak ($\alpha^A = 0.25$, $\alpha^R = 0.25$, $\alpha^D = 0.25$, $\beta = 0.25$, $a = 1000$, $s = t = 0.05$ and $c = 0.001$). The Fisherian sexual selection imparted by the preference allele results in rapid loss of the β form of the inversion, leaving only the three α alleles. The two preference alleles are then also lost. This is because indirect sexual selection no longer

Fig. 3 The evolutionary outcome of varying the strength of female mating preferences and the strength of heterosis in populations segregating for the α^A , α^D and β alleles. Two sets of starting frequencies of the alleles were used: the first (circles) with the α^D at low frequency ($\alpha^A = 0.49$, $\alpha^D = 0.01$ and $\beta = 0.5$), and the second (squares) with the α^A at low frequency ($\alpha^A = 0.01$, $\alpha^D = 0.49$ and $\beta = 0.5$).

operates — there is no genetic variation in the male trait — yet there is still a cost to choice. In contrast, when a cost to choice is added to a model in which completely disassortative mating is favoured (in other words, heterosis is strong and preference relatively weak: $\alpha^A = 0.25$, $\alpha^R = 0.25$, $\alpha^D = 0.25$, $\beta = 0.25$, $a = 2$ and $s = t = 0.5$), then quite large costs ($c = 0.05$) could be withstood before random mating became fixed on the α form. As heterosis increased so disassortative maters could withstand greater costs to choice. This is expected because the strength of heterosis determines the potential benefit from mating disassortatively.

Costs to mating

A cost to mating drastically reduced the ability of the α^R allele to compete with the α^A allele. For example, with a weak preference ($a = 1.1$) only a very small cost to mating ($m = 0.001$) was enough to fix the α^A allele even from low starting frequencies.

A cost to mating had little effect on simulations that included all four alleles, other than to promote the total loss of the α^R allele, but in any case random mating was never the predominant mating strategy under these conditions. A cost to mating did not alter the relative strength of selection acting on the α^A and α^D alleles.

Costs to rejection

The addition of a cost to rejection to a model lacking the α^D allele has no effect on the evolutionary outcome, because it imparts no new selection pressures on the other three alleles. When a cost to rejection ($r = 0.05$) is added to a model in which completely disassortative mating is strongly favoured (initial frequencies: $\alpha^A = 0.25$, $\alpha^R = 0.25$, $\alpha^D = 0.25$, $\beta = 0.25$ and $a = 2$, $s = t = 0.4$), random mating predominates (at equilibrium: $\alpha^A = 0$, $\alpha^R = 0.60$, $\alpha^D = 0$ and $\beta = 0.40$). However, the addition of a cost to mating ($c = 0.05$) to this model started with low frequencies of assortative and disassortative maters ($\alpha^A = 0.01$, $\alpha^R = 0.58$, $\alpha^D = 0.01$, $\beta = 0.40$, $a = 2$ and $s = t = 0.4$), results in the rapid replacement of the α^R allele by the α^A allele (equilibrium frequencies: $\alpha^A = 0.67$, $\alpha^R = 0$, $\alpha^D = 0$ and $\beta = 0.33$).

Application of models to seaweed flies

The simulations described have used the whole range of values for parameters determining preference and heterosis. However, the strength of prefer-

ence and heterosis has been measured in samples from natural populations of *C. frigida* (Gilburn *et al.*, submitted). The mean value of a based on data from nine populations was 1.11, the mean strength of viability selection (s) against $\alpha\alpha$ homokaryotypes was 0.46, and the equivalent (t) against $\beta\beta$ s was 0.26. A final series of simulations was performed using these measured values of preference and heterosis.

Recent evidence has suggested that the female preference for large male size evolved before the inversion (Gilburn & Day, in preparation). Consequently, the starting population for simulations largely comprised females that preferred to mate with $\alpha\alpha$ males ($\alpha^A = 0.38$, $\alpha^R = 0.01$, $\alpha^D = 0.01$, $\beta = 0.60$, $a = 1.11$, $s = 0.46$ and $t = 0.26$). The strengths of the three reproductive costs were varied (Table 2). The equilibrium frequency of the β form of the inversion was independent of any of the costs. However, conditions were found that enabled each of the three α alleles to reach fixation on the α form of the inversion. When no costs were present the α^D allele was favoured, but the addition of a small cost to either choice or rejection resulted in the loss of the α^D allele. The presence of a cost to choice alone

Table 2 Equilibrium frequencies of preference alleles when the cost to choice (c), the cost to mating (m), and the cost to rejecting $\alpha\alpha$ males (r) were varied. The model incorporated preference and heterosis values estimated in samples from wild populations. The preference (a) was 1.11, selection against $\alpha\alpha$ s (s) was 0.46, and selection against $\beta\beta$ s (t) was 0.26. The initial frequencies of preference alleles were: $\alpha^A = 0.38$, $\alpha^R = 0.01$, $\alpha^D = 0.01$ and $\beta = 0.60$

Costs of reproduction			Allele frequencies			
c	m	r	α^A	α^R	α^D	β
0	0	0	0	0	0.37	0.63
0.01	0	0	0	0.37	0	0.63
0	0.01	0	0	0	0.37	0.63
0	0	0.01	0	0.37	0	0.63
0.01	0.01	0	0	0.28	0.09	0.63
0.05	0.01	0	0	0.38	0	0.62
0.01	0.05	0	0	0.07	0.29	0.63
0.01	0.10	0	0	0.04	0.33	0.63
0.01	0.25	0	0	0.02	0.35	0.63
0	0.01	0.01	0.37	0	0	0.63
0.01	0.01	0.01	0	0.37	0	0.63
0.01	0.05	0.01	0.21	0.16	0	0.63
0.01	0.10	0.01	0.29	0.08	0	0.63
0.01	0.25	0.01	0.34	0.03	0	0.63
0.05	0.05	0.01	0	0.37	0	0.63
0.01	0.01	0.001	0	0.34	0.03	0.63

favoured the α^R allele, although when a cost to mating was also present, both α^D and α^R alleles were maintained. The relative frequency of the α^D allele increased as the ratio of mating cost to choice cost increased. In the presence of costs to both mating and rejection, the α^A allele became fixed.

It seems likely that all three costs exist in *Coelopa*, so the simulations with the most relevance to real populations were those that included all three. The α^D allele was always lost unless the cost to rejection was very small, and even then it was maintained at relatively low frequencies. If the α^D allele was lost, the relative strengths of the costs to mating and choice determined the equilibrium frequencies of the other two α alleles. As this ratio increased so did the frequency of α^A . This means that if all three costs do exist in natural populations, we expect $\alpha\alpha$ females to mate assortatively if there is a high cost to mating, but randomly if there is a high cost to choice.

Discussion

Various conclusions can be drawn from the models presented. These will be discussed in general terms before considering to what extent they shed light on the evolution of mating preferences observed in natural populations of seaweed flies.

When a preference and the preferred character are determined by loci associated with an inversion system, there is no recombination between the loci. In addition, heterosis may well be associated with the system resulting in large differences in fitness between karyotypes. Under these conditions a pattern of disassortative mating that generates heterokaryotypes is predicted to evolve, provided there are no substantial costs associated with choice. Even if the cost of choosing is high, strong heterosis can exclude a random mating allele from the population, and if mating itself is expensive, even higher costs to choice do not prevent disassortative mating. The relative strengths of the costs to choice and mating, and the intensity of heterosis, determine whether disassortative or random mating exist.

In the absence of costs, assortative mating (through the production of sexy offspring) should only evolve if the preference is sufficiently strong to overcome heterosis, in which case the inversion polymorphism is lost. Assortative mating alleles can only be maintained in a polymorphic inversion system by indirect sexual selection if alleles for disassortative mating are also present on the same karyotype. The disassortative mating preference maintains the inversion polymorphism. Again, the

strength of the preference must be very strong to counteract the cost of producing low viability offspring. It therefore seems unlikely that the Fisherian process operating in isolation could ever maintain a preference for a trait associated with an inversion system. Trickett & Butlin (1994) found that an assortative mating preference could be maintained on a polymorphic inversion without a disassortative mating allele. However, their model allowed the evolution of a line of neutral equilibria as there was a viability cost associated with carrying the male trait. In our model, genes for the preferred trait are fixed on one form of the inversion and absent from the other. The male trait also acts as an indicator of inversion karyotype. In this case all the additive genetic variation in the male trait is a direct result of the inversion karyotype and we do not find any lines of neutral equilibria. This is consistent with recent empirical studies showing that virtually all the additive genetic variation in size in *C. frigida* results from the inversion system (Wilcockson *et al.*, 1995). Introducing additive genetic variation for size within each karyotype is being considered, although a further increase in the number of parameters would make the model exceedingly cumbersome. Diploid models of sexual selection are notoriously complicated and their interpretation extremely difficult (Kirkpatrick, 1982; Gomulkiewicz & Hastings, 1990).

If choosing is costly, assortative maters are at a disadvantage, and are rapidly lost from the population when indirect sexual selection operates alone. This concurs with other models of the Fisherian process (Parker, 1983; Kirkpatrick, 1985; Pomiankowski, 1987b) showing that the Fisherian process cannot tolerate direct costs to the female. However, the addition of a cost to mating can compensate for the cost to choice and allow the evolution of assortative preferences. Disassortative mating can cope with costs to choice without the addition of a cost to mating, although this, of course, will advantage any preference gene in competition with a gene for random mating.

What do these results tell us about the evolution of female mating preferences in *C. frigida*? A preference by $\alpha\alpha$ females for small $\beta\beta$ males (disassortative mating) should evolve when there are no costs to choice or rejection. In other words, the good genes advantage gained through mating with small males is greater than the Fisherian advantage gained through mating with large males. A preference for small male size by $\alpha\alpha$ females has been observed in one natural population (Gilburn & Day, 1994a) and interestingly, male size is a more efficient indicator of karyotype in this population than in any other

(Gilburn & Day, in preparation). However, in all other populations, $\alpha\alpha$ females either express no preference (Gilburn *et al.*, 1992; Gilburn & Day, 1994a), or a preference for large males (Gilburn *et al.*, 1993; Gilburn & Day, 1994a). Perhaps in those populations in which females express no preference, there is a significant cost to choice, but this does not account for the assortative preference present in other populations.

The models suggest that the Fisher process alone is not sufficient to explain the maintenance of an assortative mating allele in *C. frigida*. Nevertheless, we cannot conclude that it has no influence on female mating preferences. In fact, the existence of a positive genetic correlation between the preference and the trait in the population at Träslövsläge (Gilburn *et al.*, 1993) is clear evidence that the Fisher process may contribute to the maintenance of female preferences. However, it is most unlikely to be the only evolutionary force responsible for the evolution of female choice.

If we cannot account for the observed mating preferences in terms of indirect sexual selection we must consider possible forces of direct sexual selection. The preference for large male size may either confer some advantage to discriminating females themselves, or be a consequence of pleiotropy (see Shaw, 1995). No evidence exists of any direct advantage to mating with large males, but this possibility certainly cannot be excluded. There is, however, evidence of a cost to mating in that mating appears to reduce longevity (Pitafi, 1991; Gilburn & Day, in preparation). A similar relationship has been found in *Drosophila melanogaster* (Partridge *et al.*, 1987; Fowler & Partridge, 1989). There may also be an energy cost associated with rejecting males, particularly large ones. In consequence, there may be a bias in the rejection response that could be interpreted as a mating preference for large males. When this situation is modelled by incorporating costs both to mating and to rejecting large males, a preference for large male size can evolve as long as the cost to choice is less than the cost to mating.

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