Genet. Res., Camb. (1994), **64**, *pp.* 19–25

The inheritance of female mating behaviour in the seaweed fly, *Coelopa frigida*

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(*Received 20 April 1994 and in revised form 17 May 1994*)

Summary

In order to understand the evolution of female mate preferences it is important to determine whether the genes for the preference and those for the preferred character are linked. It has previously been shown that female preference in the seaweed fly, *Coelopa frigida*, varies with the $\alpha\beta$ inversion system on chromosome I. This inversion system is known to genetically determine, at least in part, the male preferred character, large size. This study was undertaken to determine whether the genes determining mate preferences, as well as those determining female receptivity, co-inherit with the inversion. In the full sibs of animals recently collected from a natural population in Sweden it is shown that high acceptance rate and strong preference for large male size both co-segregate with the α form of the inversion, and that low acceptance rate and a weak preference for large size co-segregate with the β form of the inversion. Both sets of genes appear to be located in or near the $\alpha\beta$ inversion. The heterogeneity between crosses suggests the natural population from which the animals were collected was polymorphic for behavioural genes on the β haplotype. Crosses involving animals that had been in laboratory culture for seven generations indicated that variation in female mating behaviour had been lost. Possible reasons for the apparent instability of such behaviour are discussed.

1. Introduction

Many models have attempted to describe the evolution of female mating preferences in species with non-resource based mating systems (see review by Kirkpatrick & Ryan, 1991). The two most studied models, the 'good genes' mechanism (Zahavi, 1975; Bell, 1978; Hamilton & Zuk, 1982; Andersson, 1982, 1986; Kirkpatrick, 1986; Pomiankowski, 1987; Iwasa, Pomiankowski & Nee, 1991) and the Fisherian process (Fisher, 1930; Lande, 1981; Kirkpatrick, 1982; Pomiankowski, Iwasa & Nee, 1991) both require the development of a genetic correlation between the female preference and an advantageous character. In the good genes mechanism the other character is assumed to be a viability trait, whereas in the Fisherian process it is assumed to be the male preferred trait, which gains its advantage from the expression of the preference itself.

Empirical tests of the good genes mechanism have concentrated on correlations between the preferred trait and male viability. Milinski & Bakker (1990) found a positive correlation in the three-spined stickleback, *Gasterosteus aculeatus*, between the preferred character, the intensity of redness in males, and male health, as routinely estimated in fisheries research by the weight/length ratio. They also showed that infection with parasites reduces male colour intensity. The implication is that the more intensely red males are indicating that they carry genes for parasite resistance. In a similar study, Møller (1990) not only found a correlation between male tail length and the level of mite infestation in the barn swallow, *Hirundo rustica*, but also demonstrated a genetic basis to mite resistance. However, none of these studies directly demonstrated that a genetic correlation exists between the female mating preference and parasite resistance.

The Fisherian process is extremely difficult to test empirically since the crucial characters are sex limited – the preference is expressed in females, and the preferred trait in males. Bakker (1993) obtained indirect evidence for a genetic correlation by showing that the most discriminating female sticklebacks tend to produce intensely red sons. In laboratory selection experiments using stalk-eyed flies (*Cyrtiodiopsis dalmanni*), Wilkinson & Reillo (1994) observed a

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correlated response in the female preference to selection on the preferred trait.

A much more detailed and direct study of correlations between the preference and other characters would be possible if the genes determining female mating preference could be identified. However, these genes have so far proved elusive (see Ritchie, 1992). Particular chromosomes appear to be important in determining both male and female mate choice between species in *Drosophila arizonensis* and *D. mojavensis* (Zouros, 1981), but the relevant loci have not been studied. In laboratory strains of *D. melanogaster*, the frequency of mating with males carrying the *yellow* mutation is consistent with the presence of recessive, X-linked alleles increasing female receptivity to *yellow* (Heisler, 1984).

Studies on the two-spot ladybird, *Adalia bipunctata*, involving a selection experiment on preference for melanic males, showed an increase in frequency of the preference and suggested a genetic basis for this character (Majerus, O'Donald & Weir, 1982; Majerus *et al.* 1986). Isofemale lines derived from the selected line were then tested for preference: the lines fell into four distinct categories, which was consistent with the presence of a single dominant gene for the preference. However, a second set of isofemale lines subsequently derived from the same (Keele) population, exhibited no female preference, and the original isofemale lines now appeared to mate at random (Kearns *et al.* 1992). O'Donald & Majerus (1992) suggested that the different behaviour resulted from a reduction in the frequency of the preference gene in the Keele population. A drop in frequency of melanic males from 0·35 to 0·10 was observed in the three years between the two studies, and it is possible the female mating preference may also have declined in frequency. A third set of isofemale lines was extracted from a population at Glasgow known to have a relatively high frequency of melanics; O'Donald & Majerus once more found evidence that female preference was inherited, and could be explained by a single dominant gene.

Female seaweed flies, *Coelopa frigida*, from a number of populations exhibit a mating preference for large males (Gilburn, Foster & Day, 1992, 1993; Gilburn & Day, 1994*a*). This species has a particular advantage in the study of the evolution of female mating preferences. The male preferred character is known to be determined, at least in part, by the $\alpha\beta$ inversion system on chromosome I which can be typed in both males and females (Butlin, Read & Day, 1982; Gilburn & Day, 1994*b*). This allows the genes being carried by females for the male preferred character to be directly identified. A positive correlation between the preference and the preferred character was shown to exist in a Swedish population, suggesting that the Fisherian process may well be operating in this population (Gilburn *et al.* 1993). There are at least two interpretations of these results. If the genes for the preference and the preferred trait are unlinked, a genetic correlation could develop in the classical fashion due to non-random mating between the choosiest females and the most preferred males. If, on the other hand, the preference was determined by loci within the inversion then very strong genetic correlations could be established between the preference and the trait due to physical linkage. In this case, however, the preference would evolve independently on the two forms of the inversion. Individuals carrying either form of the inversion would gain a Fisherian advantage from preferring large males, and there would be no predictable pattern to the genetic correlation between female preference and female karyotype.

A second polymorphism involving female mating behaviour exists in seaweed flies. This involves a general willingness to mate, or receptivity. Irrespective of male size, the two forms of the inversion appear to exhibit different acceptance rates. In the Swedish population where the genetic correlation between the preference and the trait was seen, the inversion sequence associated with large male size and strong female mating preference, was also associated with the highest acceptance rate.

It is clearly of considerable consequence in understanding the evolution of female mating behaviour in this species, to establish whether or not the genes determining preference and those determining acceptance rate are located in the same chromosomal inversion system as the genes for the preferred character, male size. This study was undertaken to determine whether these genes co-inherit with the inversion in a Swedish population in which strong positive genetic correlations have been found.

2. Methods

The animals were collected as larvae from a population at Träslövsläge on the west coast of Sweden during March and October 1990. Virgin adults eclosing from the March sample were paired, and the offspring from a cross between an *Adh-BB* female and an *Adh-BC* male used to establish the so-called $B+C$ line. Alleles at the alcohol dehydrogenase (*Adh*) locus are in complete linkage disequilibrium with the $\alpha\beta$ inversion system; the *Adh-B* allele is inherited exclusively with the α form of the inversion, and is associated with large male size. The *Adh-D* allele is inherited with the β form of the inversion, and is associated with small male size (Day *et al.* 1982). The *C* allele (as defined by starch gel electrophoresis) does not exhibit linkage disequilibrium of this type, but the *C* allele present in the $B+C$ line is almost certainly associated with the β sequence, since *CC* homozygotes are of the small size characteristic of $\beta\beta$ homokaryotypes (Butlin *et al.* 1982; Gilburn & Day, 1994*b*).

Large numbers of flies from the October sample were used to create a broad-based, laboratory popu-

https://doi.org/10.1017/S001667230003250X Published online by Cambridge University Press

lation in which a substantial fraction of the natural genetic variation was retained. Virgin females from the first generation of offspring from this laboratory stock were paired with males from the $B+C$ line. When progeny eggs were seen, the *Adh* genotypes of all parents were determined. If the male parent was *BC* and the female *BD*, the larvae were allowed to develop; larvae from all other crosses were discarded. The intention was to generate progeny among which there were no recombinants within the area of the inversion. Since there is no recombination in males, nor between the α and β sequences in heterokaryotypes (Day *et al.* 1982), the parental haplotypes – including any associated genes for female preference – should be inherited intact.

The progeny were collected as virgin adults and stored at 4 °C until required. Before use in behavioural trials, they were transferred to 26 °C for 2 d of sex-deprivation. The males were kept separately during this period, whereas females were kept in groups of up to 25. Individual pairs were then placed in mating chambers (without the use of anaesthesia) and the reaction of the female to the male's initial mount determined (Gilburn *et al.* 1992). If she prevented the male from making genital contact, she was scored as rejecting the male; if the male was allowed to copulate, she was recorded as accepting the male. The mating behaviour of *C. frigida* has been described in detail by Day, Foster & Engelhard (1990). Females were used in only one trial. The *Adh* genotype of each female was subsequently determined using starch gel electrophoresis (Butlin *et al.* 1982). All the female progeny from eight pairs of parents from the first generation were typed.

Eight further crosses were carried out using females from the Träslövsläge line that had been maintained in laboratory culture for six generations. The males were taken from the $B+C$ line as before. All other procedures were the same as in the first experiment.

The acceptance rates and preferences of groups of females were compared by logistic regression analysis using the Generalized Linear Interactive Modelling program (GLIM, Numerical Algorithms Group). The methods have been fully described by Gilburn *et al.* (1992). Briefly, acceptance rate – a measure of general willingness to mate – was calculated as the proportion of trials in which the female accepted the male. Preference (or discrimination) refers to the ability of a female to distinguish between males of different phenotype, and was estimated by the regression coefficient of acceptance on male size. Following this initial regression, groups of females were added to the model as a categorical variable in order to compare the acceptance rates of females of different karyotype and different genotype. Finally, an interaction term was fitted to compare preferences.

3. Results

The results and analyses of the first generation females will be described in detail; those from the seventh generation are given at the end of this section.

(i) *Is there variation in female acceptance rate between the different female genotypes?*

The acceptance rates of the four daughter genotypes from the $BC \times BD$ cross are given in Table 1, with no regard to the sizes of males with which they were paired. It is apparent that the presence of the *Adh-B* allele (which is being used simply as a marker for the α inversion) is associated with high acceptance rate. Direct comparisons of acceptance rates were made after the variation in male size had been removed (Table 2). Highly significant differences were revealed between *BB* females and all other genotypes, and also between *BC* and *CD* females. Several points are worthy of comment.

The difference between *BB* and *BC* females suggests that the inversion haplotype inherited from the father affects female receptivity. In other words, the paternal α haplotypes contained alleles associated with higher receptivity than the paternal β haplotypes. However, because there is no recombination in males, these differences could also be due to genetic variation on chromosome I as a whole, rather than just the $\alpha\beta$ inversion system.

Table 1. *The acceptance rates of first generation females carrying different* Adh *genotypes with no regard to the sizes of males with which they were paired*

Adh genotype	Inversion karyotype	No. of observations	Acceptance rate
BB	$\alpha\alpha$	75	0·76
BC	$\alpha\beta$	62	0·48
BD	$\alpha\beta$	65	0·42
CD	$\beta\beta$	69	0·28

Table 2. *Comparison of the acceptance rates of different pairs of female* Adh *genotypes calculated from the regression of female acceptance rate on female genotype, after acceptance rate was regressed on male size. Data are from the first generation*

Adh genotypes	*F*	D.F.	*P*
BB BC	10·00	1, 134	0·002
BB BD	17·38	1, 157	$\ll$ 0·001
BB CD	41·13	1, 141	$\ll$ 0·001
BC BD	0·51	1, 144	0·51
BC CD	5·69	1, 128	0·019
BD CD	2·86	1, 151	0·093

https://doi.org/10.1017/S001667230003250X Published online by Cambridge University Press

By similar reasoning, the difference between the *BB* and *BD* females is likely to result from the maternal α haplotypes containing alleles associated with higher receptivity than the maternal β haplotypes. In this case, because recombination can occur between homologous chromosomes (though not in the region of the $\alpha\beta$ inversion), we can be more confident that the differences observed are determined by genes located in or near the inversion. That a difference does exist between the two haplotypes inherited from mothers is also suggested by the difference between the *BC* and *CD* females. The smaller differences seen between the two heterokaryotypes (*BC* and *BD*) and the β homokaryotypes (*CD*), suggest that the alleles determining low acceptance associated with the β sequence may show incomplete dominance over those for high acceptance associated with the α.

(ii) *Are there two homogeneous categories of haplotypes?*

In the first experiment females recently collected from a wild population were mated with males from the $B+C$ line. The fathers' contributions to the progeny were therefore relative homogeneous – either a single *C* allele, or one of at most three *B* alleles. The maternal contribution, on the other hand, will have depended on the heterogeneity of the α and β haplotypes in the population at Träslövsläge at the time of sampling. The variation between crosses gives an indication of the homogeneity of the α and of the β haplotypes in the wild population.

The acceptance rates of the eight sets of progeny are given in Table 3. Tests for heterogeneity between crosses for each of the four daughter genotypes, when variation due to male size had been removed, yielded probabilities of 0·79 (*BB*), 0·48 (*BC*), 0·09 (*BD*) and 0·009 (*CD*). The values for *BB* and *BC* daughters suggest, admittedly on the basis of a sample of only eight $\alpha(B)$ haplotypes, that there is no heterogeneity at the loci determining acceptance rate. (It is also consistent with the original three $\alpha(B)$ haplotypes in the $B+C$ line being similar.) In contrast, significant differences between crosses were observed in the *CD* progeny. This is consistent with the $\beta(D)$ haplotypes being heterogeneous in the original population. Inspection of Table 3 allows tentative identification of the variants: the $\beta(D)$ haplotypes inherited in crosses 2 and 4 appear to determine distinctly higher acceptance rates than were seen in the other six crosses. Cross 4 also produced *BD* offspring with the highest acceptance rate, and the females from cross 2 exhibited the second highest acceptance rate. Clearly we cannot be certain on the basis of such a small sample that the relevant loci are genuinely polymorphic, but this result is consistent with others indicating greater homogeneity of the α than of the β sequence (Gilburn – unpublished results).

Table 3. *The acceptance rates of the different progeny female genotypes of each pair separately. Sample sizes are given in brackets. The data are from the progeny of first generation females*

	Progeny genotype			
Pair no.	*BB*	*BC*	*BD*	*CD*
1	0·80 (10)	0·67 (6)	0·40 (5)	0·00 (6)
2	0·71 (7)	0·50 (10)	0·56 (16)	0·56 (16)
3	0·86 (14)	0·63 (11)	0·50 (12)	0·13 (8)
4	0·71 (7)	0·80 (5)	1·00 (4)	0·80 (5)
5	0·73 (11)	0·27 (11)	0·40 (15)	0·00 (8)
6	0·67 (9)	0·33 (6)	0·18 (11)	0·29 (14)
7	0·80 (10)	0·43 (7)	0·27 (11)	0·17 (6)
8	0·71 (7)	0·27 (11)	0·36 (11)	0·11 (9)

Table 4. *The regression coefficients of female acceptance rate on male size for each female genotype from the first generation females*

Adh genotype	Regression coeff.	S.E.	*P*
BB	+3·46	1·08	< 0·01
BC	+0·82	0·63	= 0·19
BD	+0·71	0·48	= 0·14
CD	+1·93	0·66	< 0·01

(iii) *Are the females, regardless of their genotype, expressing a preference for large males?*

Preference was estimated from the logistic regression coefficient of acceptance rate on male size. From such an analysis it was clear that females (with no regard to their genotype) were expressing a strong mating preference for large male size ($F = 16{\cdot}24$; D.F. = 1, 289; $P \ll 0{\cdot}001$). This has been the consistent finding of previous studies on the Träslövsläge population (Gilburn *et al.* 1993).

(iv) *Are there differences in preference between the different daughter genotypes?*

Regression coefficients were calculated for each female genotype separately (Table 4). All four genotypes exhibited a preference for large size, although this was significant only for the *BB* and *CD* females. A difference was found between *BB*s and both *BD*s ($F = 6{\cdot}048$; D.F. = 1,156; $P < 0{\cdot}025$) and *BC*s ($F = 4{\cdot}633$; D.F. = 1, 133; $P < 0{\cdot}05$). The former difference was in the haplotype inherited from their mothers, whereas the latter involved the paternal chromosome I. In other words, both maternal and paternal α haplotypes appear to be associated with a stronger mating preference for large male size than the β haplotypes, although the difference associated with male haplotype could be due to genetic variation from the entire first chromosome.

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Table 5. *The overall acceptance rates of females carrying different* Adh *genotypes. The data are from the seventh generation*

Adh genotype	Inversion karyotype	No. of observations	Acceptance rate
BB	$\alpha\alpha$	43	0·56
BC	$\alpha\beta$	54	0·46
BD	$\alpha\beta$	60	0·45
CD	$\beta\beta$	43	0·37

Table 6. *The acceptance rates of the different progeny female genotypes of each pair separately. Sample sizes are given in brackets. The data are from the seventh generation*

	Progeny genotype			
Pair no.	*BB*	*BC*	*BD*	*CD*
9	0·83 (6)	0·50 (6)	0·33 (3)	0·33 (3)
10	0·83 (6)	0·40 (5)	0·38 (8)	0·75 (4)
11	0·75 (4)	0·67 (6)	0·63 (8)	0.75 (4)
12	0·50 (4)	0·57 (7)	0·36 (11)	0·29 (7)
13	0.60 (5)	0·43 (7)	0·50 (10)	0·14 (7)
14	0·67 (6)	0·20 (5)	0·67 (6)	0·33 (3)
15	0·20 (10)	0·33 (15)	0·14 (7)	0·50 (4)
16	0·00 (2)	0·67 (3)	0·57 (7)	0·27 (11)

Table 7. *The regression coefficients of female acceptance rate on male size for each female genotype from the seventh generation*

Adh genotype	Regression coeff.	S.E.	*P*
BB	+1·09	0·82	0·23
BC	+1·23	0·66	0·09
BD	+1·23	0·61	0·07
CD	+0·80	0·64	0·28

Two further comparisons can be made. The *BC* and *CD* daughters also differed in the haplotype they received from their mothers, but the difference in preference between these two groups was not significant. There was no difference between *BD* and *CD* daughters which differed in their paternally inherited first chromosomes.

(v) *Analysis of the seventh generation females*

Another set of eight crosses was performed using animals from the same two stocks, except that the stocks had been maintained in laboratory culture for an additional six generations. All experimental procedures were exactly the same as for the first experiment. From Tables 5 and 6 it is apparent that clear-cut differences in acceptance rate associated with female inversion genotype found in the first generation were not observed. The *BB* females did exhibit the highest acceptance rate and the *CD* the lowest, but there were no significant differences between the different genotypes. It must also be noted that there was no significant change in the acceptance rates of any female genotype from the first experiment. There was no evidence for heterogeneity in acceptance rates between crosses; the probability values were: 0·29 (*BB*), 0·74 (*BC*), 0·55 (*BD*) and 0·75 (*CD*).

The seventh generation females differed from the first in another respect. No differences in preference were observed between genotypes – indeed, none of the individual genotypes expressed a significant preference, although each did yield a positive regression coefficient (Table 7). Comparing the preferences measured in the first and seventh generations, there were no significant changes for any of the genotypes.

4. Discussion

The results using females recently collected from the wild showed that full siblings differed in their mating behaviour, and that some of these differences were associated with the chromosome I inversion system. High acceptance rate and strong preference for large male size both co-segregated with the α form of the inversion. On the other hand, low acceptance rate and a weak preference for large size co-segregated with the β form of the inversion. These observations were entirely consistent with the behaviour of females newly collected from a population at Träslövsläge (Gilburn *et al.* 1993). They also suggest that the genetic determinants of two aspects of female mating behaviour – receptivity and discrimination – are located in or near the $\alpha\beta$ inversion.

A second inference to be drawn from these results is that at least the β haplotype is polymorphic in the Träslövsläge population for the loci determining acceptance rate. The α haplotype may also be polymorphic, but in the small sample of chromosomes examined, no heterogeneity was detected.

These results from first generation females offered hope of understanding the inheritance of female mating behaviour. However, the second set of trials suggested the understanding may not be achieved quickly. Although there were no significant differences between the two experiments, it appears that culture of animals in the laboratory for six generations resulted in acceptance rates becoming more homogeneous. Furthermore, there was an apparent homogenization in mate choice. In the first generation clear differences were seen in the mating behaviour of different female karyotypes; after seven generations this variation appears to have been lost. This change is strikingly similar to that observed in *Adalia bipunctata* (Majerus *et al.* 1982, 1986; Kearns *et al.*

https://doi.org/10.1017/S001667230003250X Published online by Cambridge University Press

1992; O'Donald & Majerus, 1992) in which genetic variation in mating preference apparently dissipated during laboratory culture. Why should mating preferences be unstable in this way?

One category of explanation involves changes in haplotype frequencies. Perhaps genetic variation present in the population at Träslövsläge was selected out during laboratory culture. There can be no doubt that cultures maintained in a constant temperature room must experience very unnatural conditions in a number of respects, including temperature, humidity and rainfall. We can be confident there has not been selection for recombinants between the two forms of the inversion since there is no recombination between karyotypes (Day *et al.* 1982). However, if the parental population is polymorphic for one or both forms of the inversion, selection during laboratory culture could have eliminated certain haplotypes. The effect of such selection would be stabilizing if it results in an increase in the acceptance rate and discrimination of $\beta\beta$ homokaryotypes, but a decrease in these characters for $\alpha\alpha$s. Even with quite strong selection, such elimination is likely to take several generations. Changes in gene frequencies were suggested as the explanation for the results obtained with *Adalia bipunctata* by O'Donald & Majerus (1992), although they considered that selection may have occurred in the wild population.

A second possibility is that the loci determining female mating behaviour are closely linked to the inversion system on chromosome I but not actually within the bounds of the inversion. Non-random mating due to the expression of female mating preferences could lead to the generation of a genetic correlation between these loci and the inversion which, in the absence of a natural mating regime, such as may exist in laboratory culture, could breakdown. This would require either that the same gene determines both acceptance rate and preference, or that the relevant loci are very closely linked to each other. These two characters are very likely to be associated as a change in one would almost inevitably result in a change in the other. However, it appears that the genetic variation in the preference had been completely lost in the seventh generation females; while not statistically significant, the associations between acceptance rate and inversion karyotype were in the predicted direction.

A third reason for the apparent instability in mating behaviour seen in laboratory culture may involve non-genetic factors. Although the conditions of culture and of the mating tests were thought to be constant, it is difficult to exclude the possibility that some crucial, environmental factor was uncontrolled.

Thus, the results of this study do not clearly distinguish between these possible reasons for the apparent association seen between female mating behaviour and female inversion karyotype. Genes affecting female mating behaviour could be present in the inversion or alternatively, be genetically correlated with the inversion through the action of sexual selection. However, the results of this study do suggest that genes affecting female mating behaviour, if not actually located within the inversion, are likely to be syntenic with chromosome I, and probably closely linked to the $\alpha\beta$ system. We are currently studying the behaviour of isokaryotypic lines in which all genetic variation associated with the $\alpha\beta$ inversion system has been removed. Any apparent differences in the behaviour of these lines must be either environmental, or due to changes in allele frequencies at loci not associated with the inversion system.

This work was supported by a grant (GR3/7189) from the Natural Environment Research Council and a studentship (to ASG) from the Science and Engineering Research Council.

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