*Genet. Res., Camb.* (1970), **16**, *pp.* 355–357
*Printed in Great Britain*



# Disturbed segregation at the transferrin locus of the deer mouse

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(*Received* 3 *August* 1970)

SUMMARY

Anomalous frequencies of transferrin phenotypes were found among the offspring of matings between deer mice heterozygous for the two forms of transferrin most common in natural populations. Matings involving other phenotypes produced offspring in the expected phenotypic frequencies. Selective penetration by facility, occurring only in the reproductive tract of the heterozygous females, appears to provide the most satisfactory explanation for the observations.

In a recent investigation of serum protein polymorphisms in natural populations of the deer mouse, *Peromyscus maniculatus borealis*, in western Canada (Canham, 1969), six forms of transferrin were distinguished by their rate of migration during starch gel electrophoresis. The serum of each deer mouse examined contained either one or two transferrins, and when two forms were present they were in equal quantities. In litters born in captivity to parents of known transferrin phenotype, no offspring was of a phenotype inconsistent with the hypothesis that the transferrins were under the control of a series of codominant alleles at a single autosomal locus. This mode of inheritance is indicated for the transferrins of all species for which breeding data are available (Manwell & Baker, 1970), including *P. maniculatus* in northern Arizona (Rasmussen & Koehn, 1966).

Of 383 successful matings in captivity, 361 involved only deer mice which possessed one or both of the two forms of transferrin (named J and M) most common in each of the natural populations. The results of these matings are shown in Table 1. Among the offspring from matings between deer mice both having the TfJM phenotype (i.e. heterozygotes possessing J and M forms of transferrin), the phenotypic frequencies of the transferrins differed significantly ($P < 0{\cdot}0003$) from those expected on the basis of control by codominant alleles which are randomly paired at fertilization. In addition, the ratio of $Tf^J$ to $Tf^M$ alleles in these offspring differed significantly ($P < 0{\cdot}003$) from 1:1. Deviations from expected frequencies were not restricted to a small proportion of highly aberrant litters; an excess of TfM young occurred in a majority of litters from TfJM parents captured at each of several locations in Alberta and the Northwest Territories during a 3-year period and from TfJM parents themselves born in captivity.

The possibility that selection against zygotes, embryos or foetuses with phenotypes TfJ and TfJM caused the anomalous phenotypic frequencies is remote. Litters from matings between TfJM deer mice had a similar mean size to those from each of the other types of mating, and the latter showed no evidence of prenatal selection at the transferrin locus. Furthermore, a count of the corpora lutea from 112 pregnancies in deer mice indicated that a mean of 6·70 ova were released at oestrus—too few, in TfJM females mated with

TfJM males, to account for live births (4·70 per pregnancy), the necessary number of selective prenatal deaths (1·90 per pregnancy), prenatal deaths from other causes, and ova lost without being fertilized.

The alternative explanation for the observations is that selection took place against $Tf^J$ alleles during gametogenesis, sperm transport or conjugation. Bateman (1960) has defined four possible categories of selective conjugation, a phenomenon which 'reflects special associations among gametic nuclei carrying particular alleles'. Either of the two varieties of selective retention may apply when the locus in question is on the crossover

Table 1. *Results of matings between deer mice of known transferrin phenotype*

| Tf phenotype of parents ♀ × ♂ | Number and mean size of litters | | Total young of each phenotype | | | Expected total for each phenotype* | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | J | JM | M | J | JM | M | $P$† |
| J × J | 78 | 5·14 | 402 | — | — | 402 | — | — | — |
| J × M | 31 | 4·65 | — | 144 | — | — | 144 | — | — |
| M × J | 8 | 5·38 | — | 43 | — | — | 43 | — | — |
| M × M | 23 | 4·83 | — | — | 111 | — | — | 111 | — |
| J × JM | 50 | 5·02 | 131 | 120 | — | 125·5 | 125·5 | — | > 0·5 |
| JM × J | 50 | 4·58 | 116 | 113 | — | 114·5 | 114·5 | — | > 0·8 |
| M × JM | 37 | 4·78 | — | 91 | 86 | — | 88·5 | 88·5 | > 0·7 |
| JM × M | 21 | 5·19 | — | 58 | 51 | — | 54·5 | 54·5 | > 0·5 |
| JM × JM | 63 | 4·70 | 67 | 125 | 104 | 74·0 | 148·0 | 74·0 | < 0·0003 |

* Based on hypothesis of control by codominant alleles at an autosomal locus.

† Probability in chi-square test of argument between observed and expected phenotypic frequencies. Yates's correction applied where appropriate.

segment of a chromosome. In the passive variety of selective retention each allelic type of sperm from a heterozygous male would be able to retain preferentially one allelic type of chromatid in the ova of a heterozygous female at the second meiotic division, whereas in the active variety only one type of sperm would have this property. Selective penetration, either by distribution or by facility, may apply when the locus is not on a crossover segment. In selective penetration by distribution one allelic type of ovum would be able to attract an excess of one allelic type of sperm, depleting the numbers of that type of sperm at the remaining ova and causing either an excess or a deficiency in both classes of homozygotes at fertilization. In selective penetration by facility the two types of sperm would remain evenly distributed, but one type would have a greater ability than the other to fertilize one type of ovum, with the result that the frequency of only one of the classes of homozygotes would deviate from the expected value.

Selective sperm transport can be ruled out as a possible cause of the observed deviations in phenotypic frequency, because the number of TfJM young differed significantly ($P < 0·01$) from half of the total offspring in matings between TfJM deer mice. Selective gametogenesis, the active and passive varieties of selective retention and selective penetration by distribution can also be eliminated, because each would also have affected the phenotypic frequencies in litters from at least one other type of mating. However, selective penetration by facility, with $Tf^M$ sperm able to fertilize a majority of $Tf^M$ ova in matings between TfJM deer mice, is compatible with the observed deficiency of TfJM and excess of TfM young. Although a deficiency of TfJM offspring from matings between T*f*M females and TfJM males might also have been expected, this would not have occurred if $Tf^M$ sperm had an advantage only in the conditions prevailing in the reproductive tract of TfJM females. Selective penetration by facility is therefore able to

provide a simple and satisfactory explanation for the observations, in contrast to the other mechanisms described.

Intrauterine selection at the transferrin locus is known to occur in cattle (Ashton & Fallon, 1962), but there has been no previous indication of selective fertilization at this locus in any species. Well-substantiated examples of disturbed segregation are very few in mammals (Beatty, 1970), perhaps because an insufficient amount of breeding data is generally obtained in studies of their polymorphisms. If segregation disturbances are in fact widespread, it may be hazardous to draw conclusions from an investigation in the field of population genetics unless it is complemented by an adequate programme of controlled breeding.

This work was supported by National Research Council of Canada awards to D. G. Cameron and W. A. Fuller, and was performed while R. P. Canham held a Canadian Commonwealth Scholarship. Mrs R. Smiley provided technical assistance.

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