Behaviour and Random Mating

In the last few years there has been a rapidly awakening interest in the field of behaviour genetics[1-3]. A consequence is an increased number of experiments where the direct observation of mating involving choice between different genotypes is carried out, although some such experiments have been reported for many years[1,4] especially in *Drosophila*. Enough data have now been accumulated to enquire whether mating generally occurs at random or not. This is an important question since much work in population genetics is based on this assumption.

Clearly some loci are not involved directly in mating behaviour. However, it is likely that many loci have pleiotropic effects involving mating behaviour. The assessment of whether mating occurs at random or not is often made indirectly by fitting progenies to expectations based on the Hardy-Weinberg Law. This is not a particularly sensitive test, and many factors may play a part between mating and the scoring of progenies.

Sturtevant[4] in 1915 carried out male and female choice experiments for 4 mutant strains and a wild type strain in *D. melanogaster*. For example, considering experiments involving white-eyed and wild-type flies, it was found that white-eyed females mate more frequently in the male choice situation, and wild-type males in the female choice situation. Thus there is non-random mating due to differences in the vigour of sexual behaviour, i.e. there is sexual selection. A number of experimenters working with mutant genes have demonstrated sexual selection determined by differences in the vigour of one or both sexes. Sturtevant[4] used direct observation in his experiments, but often mating is assessed from female dissection tests[5]. Recently, various mating chambers have been developed for direct observation so permitting the study of multiple choice matings involving 2 or more genotypes per sex[5-7]. One of these chambers[7] consists of a glass jar where mating pairs are removed with an aspirator for scoring. In 5 experiments with this chamber, where yellow and wild type (Canton-S) flies were mixed in equal proportions (20 per genotype per sex), it was found that there were 26 +♀ × +♂, 26 *y*♀ × +♂, 5 +♀ × *y*♂, and 18 *y*♀ × *y*♂ matings at the stage when $^3/_4$ of the total possible matings had occurred, thus showing extreme non-random mating due to the lack of success of *y* males with + females. Other such experiments, for example with wild type and white-eyed flies, showed non-random mating due to overall differences in the activities of the males of the 2 genotypes, and with yellow and white flies few matings occurred except between yellow flies.

Petit[8] studied multiple choice matings using Bar-eyes with wild-type and white-eyes with wild-type, and demonstrated sexual selection mainly under the control of the genotype of the male. She assessed her results by classifying the progeny of inseminated females. Bar males were always disadvantageous compared with wild-type males, but the level of disadvantage was greatest when Bar was most frequent. For white and wild-type males, the white males were disadvantageous when 40–80% of males in the population were white, but outside these limits when white males were rare or abundant, they were advantageous. Thus in both cases, mating success depends on the proportion as well as the nature of the competing genotypes. Using Elens-Wattiaux chambers[6] in which matings are observed directly and pairs are not removed, it was found for homokaryotypic strains of Arrowhead and Chiricahua in *D. pseudoobscura*, that the minority genotypes were often more successful in mating than when they were in a majority[9,10]. Perhaps there is intense competition between like common genotypes, and any rare genotype would not compete quite so intensely, having a slightly different behaviour pattern from the common genotypes. The rare genotype would then perhaps mate more frequently than expected on the basis of its frequency. There is certainly strong competition between males in determining mating speed in *D. pseudoobscura* for ST/ST, ST/CH and CH/CH (ST = Standard, CH = Chiricahua) karyotypes, since the mating speed is substantially greater when 3 males are placed with one female, compared with 3 females with one male[11].

When there is a general tendency for like phenotypes to mate more frequently than expected at random, then the population shows positive assortative mating as has been found in some *Drosophila* species for strains from different localities[5,12]. In *D. melanogaster* positive assortative mating has been found recently for sternopleural bristle number, which is a metrical trait, by placing virgin females and males in a mating chamber where mating pairs are removed with an aspirator[7]. Correlation coefficients between mated pairs fell between 0.1 and 0.2 and were significantly greater than zero. Similar results were obtained for abdominal bristle number. Thus there is a tendency for flies with similar bristle numbers to mate. This could be a direct effect of fly size, since sternopleural bristle number and fly size are directly correlated when fly size is altered by environmental means[13], or perhaps there may be slight courtship behaviour differences between flies of different sizes[14]. There is a need to ascertain the degree of assortative mating in natural populations, to find out its importance in modifying the genetic constitution of populations[5].

In mice, some experiments[15,16] are of interest in relation to the imprinting of environmental effects. Young mice were reared by parents perfumed with an absolutely foreign odour, an extract of *Violetta odorata*, and the sexual behaviour of offspring which were allowed to choose between 2 individuals of the opposite sex, one perfumed and one normal, was studied. The 2 individuals were placed in separate compartments to avoid fighting between them. It was found that females reared by perfumed parents tended to choose perfumed males, and control females tended to choose control males. Hence the sexual preferences of female mice are strongly influenced by the precocious learning of the parents' traits

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i.e. by imprinting. Similarly, preferences between strains vary according to whether females are reared by both mother and father, or by the mother alone. It thus seems important to attempt to find out the importance of early learning in determining mating preferences, although it is known to be important in certain other species[17].

All the mechanisms discussed represent deviations from random mating, and it is difficult to know their evolutionary significance. However, an extreme form of sexual selection is polygyny, which occurs in nearly all anthropoid apes and is likely in primitive hominids[18]. A leader of a group with several wives will contribute a far greater than average share to the genetic composition of the next generation. Thus reproductive success would be closely correlated with genetic superiority, so allowing a more rapid rate of evolution than under random mating.

The density-dependent system where rare genotypes are more successful in mating than common ones, ensures the maintenance of rare genotypes in the population, and so enhances genetic heterogeneity. This is also true for positive assortative mating[19] and may be true for many of the mechanisms discussed. Under certain circumstances, these mating systems may lead to balanced polymorphisms without heterozygote advantage. Another example of this is the preferential mating recently found in the mimetic butterfly, *Papilio glaucus*[20].

For the density-dependent mating system where rare genotypes are favoured, a consequence in a polymorphic situation may be that the component of the genetic load[18,21] due to rare unfit homozygotes is reduced due to their advantage in mating. This may be important in outbreeding species where a great number of polymorphic systems seem likely[22], although it can also be argued that only a proportion of polymorphisms are under selection in a given environment, so that most polymorphisms are relics of previous selection[22]. In a general sense, mating behaviour variations probably enhance genetic heterogeneity without contributing greatly to the genetic load, but this needs further theoretical investigation.

Studies in the field of behaviour genetics have therefore brought to light numerous variations of the breeding system leading to deviations from random mating and so affecting rates of evolution. In any organism exhibiting variable courtship rituals, deviations from random mating may be more common than not for loci involved directly or indirectly with mating behaviour[23].

Résumé. Des expériences portant sur le comportement sexuel chez plusieurs espèces, telles que la drosophile et la souris nous montrent que l'hypothèse qu'elles s'accouplent par hasard, hypothèse dont on fait état assez fréquemment dans la génétique des populations, n'est valable dans cadre des populations naturelles qu'avec de sérieuses restrictions.

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Quantitative Changes in the Phosphorus Fractions of Transplanted Brain Tumors During Complete Ischemic Incubation

A previous investigation has demonstrated that a variety of human and experimentally induced brain tumors, when incubated under conditions of complete ischemia, generated lactate in significant excess to that expected from glucose and glycogen disappearance[1]. Furthermore, P_i (inorganic phosphate) was found to accumulate in excess of that expected from changes in measured phosphorylated metabolites. The fact that the increments of P_i were of about the same magnitude as those of the unexplained lactate seemed a possible clue to the source of this extra lactate. Consequently in the present study measurements have been made of the changes which occur during anaerobic incubation in the levels of various phosphorus containing fractions. In most cases significant decreases in the levels of acid-soluble organic phosphorus and nucleic acid phosphorus were observed, with a concomitant increase in P_i. Lipid phosphorus and residual phosphorus fractions exhibited no significant change during the incubation.

Experimental. 3 different types of experimentally induced malignant mouse brain tumors were studied. Ependymoblastomas and glioblastomas were transplanted in C_3H mice, and medulloblastomas in C-57 mice. The 2 medulloblastomas studied (designated M-1, M-2) were composed of uniform small cells with hyperchromatic nuclei and indistinct cytoplasm. The 2 glioblastomas (G-1, G-2) were extremely cellular tumors with areas of focal necrosis, cellular palisading and vascular proliferation. Ependymoblastomas (E-1, E-2) were cellular tumors containing closely packed epithelial cells. Electron micrographs of the ependymoblastomas demonstrated prominent terminal bars, characteristic of tumors of ependymal origin.

Tumors were selected for study 3 weeks after transplantation, at which time they were about 1 cm in diameter. Half of the tumor was removed and frozen within 2–3 sec of extirpation in Freon-12 (CH_2F_2) chilled to near its freezing point (– 156 °C) by liquid nitrogen. The remaining portion of the tumor was resected and incubated under mineral oil at 37 °C for 4 h, and then frozen. Dissected frozen samples, about 20 mg in weight, were weighed at – 20 °C and homogenized in 70 μl of $3M$ $HClO_4$ at – 8 °C. 330 μl of a 4 mM EDTA solution was added and homogenization continued at 4 °C.

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