Kinship, pheromones and reproduction

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1. INTRODUCTION

Mating with close relatives can have deleterious effects on offspring fitness (Partridge, 1983). By recognising close relatives an animal may avoid such matings. Kin recognition may promote outbreeding either by behavioural mechanisms (Bateson, 1983) or by direct effects on an animal's reproductive physiology (Lendrem, 1985). But is there a pathway by which kinship can exert its effects on reproductive physiology ? One potential route is the olfactory system, and urinary pheromones may be the vehicles for such kinship effects. In this chapter, I want do discuss the effect of kinship on reproductive physiology and consider its implications for the individual in society.

2. KINSHIP EFFECTS ON FEMALE MICE

Previous studies have shown that female mice exposed to unfamiliar males, their urine or soiled bedding show an acceleration of first oestrus relative to controls (Vanderbergh 1967, 1969; Colby and Vandenbergh 1972). This effect is mediated by small, non volatile urinary peptides (Vandenbergh et al. 1976). These peptides stimulate gonadotrophin release via the secondary olfactory pathway (for a review see Keverne, 1983). Lendrem (1985) used soiled bedding to investigate the effect of kinship on puberty acceleration in mice.

This study compared the acceleration of first oestrus within litters of the CFLP strain. A matched sujects design was employed with litter-mates being randomly allocated to one of five treatments. Controls were transferred to individual cages where they received a daily allocation of fresh bedding. Females in the four experimental groups were transferred to individual cages where they received a daily allocation of 40 cc of soiled bedding from individually housed males differing in their degree of relatedness to the female. Each female received bedding from either a) her father, b) an uncle, c) a male cousin, or d) an unrelated male.

Table 1 shows the ages at first oestrus in control and experimental groups. Females exposed to unrelated males show a significant acceleration (relative to controls) of about four days. Females exposed to fathers and uncles showed no such acceleration.

3. KINSHIP EFFECTS ON MALES

Juvenile female mice exposed to the soiled bedding of first cousins and unrelated males show an acceleration of puberty compared with controls. In contrast, females exposed to soiled bedding from close relatives (fathers and uncles) show no such acceleration (above). Kinship delays puberty in

The individual and society, Ed. by Luc Passera & Jean-Paul Lachaud, Privat, I.E.C., Toulouse, 1986, pp. 67-71.

females. There are good, sound functional reasons for such a delay. By delaying puberty a female can avoid mating with a close relative. Thus kin recognition allows a female to avoid inbreeding (Bateson, 1983; Partridge, 1983). But does the same hold true for males ?

	Soiled bedding from				
	Control	Father	Uncle	First cousin	Unrelated male
Days to first oestrous	35(+0.67)	33(+0.80)	33(+0.27)	31(+0.40)	30(+1.07)

Table 1. Age at first oestrus (mean and SEM) for females exposed to soiled bedding from close kin (n = 12 in each treatment). Those exposed to close kin show delayed puberty.

Male rats housed with females have heavier testes an accessory reproductive gland weights and higher testosterone levels than males living in isolation or with other males (Drori & Folman, 1964; Pranzarone, 1969; Purvis & Haynes, 1972). Although it has not been established that olfactory stimuli alone produce this effect (Brown, 1979), Vendenbergh (1977) has shown that male hamsters exposed to the soiled bedding of an oestrous female show accelerated testicular growth. Lendrem (in review) tested for such kinship effects on puberty acceleration in male mice.

As in the first experiment (above), a matched subjects design was employed with litter-mates being randomly allocated to one of four treatments. Males in the control group received fresh bedding. Males in the experimental groups received soiled bedding from individually housed females differing in their degree of genetic relatedness. Each male received bedding from either (a) his mother, (b) an aunt, or (c) an unrelated female.

At 39 days of age males were killed, weighed ant the testes, epididymes, seminal vesicles, preputial glands and kidneys were removed, stripped of fat, and weighed. There was significant variation in testes weights and a marginally significant difference in seminal vesicles ($p < 0.10$). Males exposed to mothers and aunts had smaller testes and seminal vesicles than those exposed to unrelated females ($p < 0.02$; see table 2). There was no significant variation in bodyweight, kidney size or any of the other organs.

	Soiled bedding from			
	Control	Mother	Aunt	Unrelated female
Testes weights : (mg)				
mean	210.3	196.3	196.9	216.5
SEM	13.5	11.4	14.0	13.7

Table 2. Testes weights at 39 days of males exposed to soiled bedding from close kin.

4. DISCUSSION

Kinship clearly exerts a significant effect on puberty acceleration. Males and females exposed to the soiled bedding of close relatives show inhibited development.

By delaying puberty in the presence of closely related males females may avoid inbreeding with close genetic relatives. Bronson (1979) suggests that the population dynamics of Mus should allow puberty delay to be a singificant factor in promoting outbreeding. Studies of other small mammals such as Peromyscus maniculatus (Hill 1974) report long delays between pairing and conception when a female is paired with a close genetic relation. Unfortunately it is not clear from these studies whether such reproductive delays are attributable to pheromonal effects on the reproductive system or to behavioural mechanisms. Drickamer (1976) reports that in Mus the sex composition of a litter can influence the age of first oestrus. Specifically litters with two or more males show a delay in oestrus compared to litters with none or only one male. One interpretation is that females reared with male siblings delay puberty in order to avoid inbreeding.

Kinship also has an important effect on male development. Males exposed to the soiled bedding of close relatives (mothers and aunts) show inhibited testicular development. Either males delay their sexual maturation (which seems unlikely) or females inhibit the sexual maturation of their sons. By delaying the development of their male offspring, females may avoid inbreeding with their sons.

One question which is still unanswered is how mice recognise the pheromones of close kin. Behavioural studies of the CFLP strain suggest that they can use familiarity as a rule-of-thumb index of kinship. In the wild, closely related individuals are likely to be familiar with each other. However, CFLP can even recognise relatives they have never before encountered (Kareem 1983; Kareem and Barnard 1982; Lendrem 1985). Since the present study employed unfamiliar genetic relations the differences reported here must be due to genetic differences.

One possibility is that urinary pheromones act as "recognition alleles" (see Hepper, this volume). Urinary peptides could provide a simple mechanism for kin recognition. Closely related individuals may share a "cocktail" of urinary peptides. During development, individuals may learn the peptide profile of close relatives (from the mother, other siblings and self). Then, when a stranger is encountered for the first time, its peptide profile can be matched to this learned template. Such a mechanism would allow an individual to identify kinship groups even in a shifting society. This opens the door to strong kin selection in unstable populations.

Acknowledgements :
The Science & Engineering Research Council, U.K. gave financial support. Sue McHugh and Yvonne Cardwell provided technical instruction and assistance.

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