Kin recognition in the rat

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KIN RECOGNITION IN THE RAT

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CHAPTER 7

NEPOTISM IN THE RAT

The major proposal of kin selection theory is that related individuals, because they share genes in common, would be expected to respond differentially to kin and non-kin to maximise their inclusive fitness (see Chp. 1). The theory although originally applied to explain the evolution of altruism (e.g., Hamilton, 1964a,b) can also be applied to co-operative behaviour, where kin can increase their inclusive fitness by preferentially responding to kin over non-kin (Harvey et al., 1980). In the following chapters the behaviour of sibling rats is observed to see if they respond differentially to their sibs and non-sibs in their huddling, play and mating behaviour.

Co-operative behaviour should be especially prominent in siblings because of their close genetic relatedness (Alexander, 1974). By co-operating with siblings individuals have been shown to increase their chances of mating and keeping their mate, for example, lions, *Panthera leo*, Bygott et al., (1979); Tasmanian native hens, *Tribonyx mortierii*, Maynard-Smith and Ridpath, (1972). Preferential responding to siblings has been found in huddling, for example, spiny mice, *Acomys cahirnus*, Porter et al., (1978), and in play, for example, common marmosets, *Callithrix jacchus* ERXL 1777, Voland (1977); baboons, *Papio anubis*, Owens, 1975.

In the rat, suprisingly perhaps considering its extensive use by researchers, there have been few studies considering whether individuals act nepotistically. Early studies attempted to demonstrate the existence of altruism or co-operative behaviour by using a "double-motive" learning task. Tsai (1950) trained pairs of rats to press separate electric keys simultaneously in order to obtain food and found rats were capable of this. In a different task, Daniel (1942,1943) used a situation in which there was food in the middle of an electrified floor, with a platform out of reach of the food on which a rat had to sit in order to turn off the shock. The idea was that whilst one rat sat on the platform, another could obtain food without receiving shock. Daniel found that rats alternated between the platform and food tray, so that both were adequately fed and avoided as much shock as possible. Whether these tasks can be considered as true co-operation or a complicated learning task requiring control by the second rat as a discriminative stimulus is unclear, especially as the degree of relatedness between the subjects is not given. A study of "altruism" in the rat by Rice and Gainer (1962) demonstrated that rats would lower a distressed suspended rat to the floor, but in a criticism of this study Lavery and Foley (1963) suggested this effect is due to arousal rather than altruistic behaviour.

Other examples of altruistic or co-operative behaviour may possibly come from observations of the rats' behaviour. Mothers will defend their young against predators or other individuals of the colony who come too close (Svare, 1981) and this may be an instance of altruistic behaviour. Another possible behaviour which may be termed altruistic is the attacking of unfamiliar males by the dominant males of an established colony (Barnett, 1975; Calhoun, 1962; Lore and Flannelly, 1977). Dominant males of the colony risk injury during the attack, but the benefits gained by keeping away alien males, of increasing their chances of reproduction and protection of young already sired, may outweigh any possible costs.

The following chapters examine the huddling, play and mating partner preferences of rats to see if they respond differentially to sibs and non-sibs. Chapter 3 demonstrates that sibling recognition can be achieved via either a socially or genetically mediated mechanism and the effects of acquiring sibling recognition by these mechanisms on partner preference is also assessed.

CHAPTER 8

HUDDLING PARTNER PREFERENCES IN THE RAT

8.1

INTRODUCTION

One of the most prominent behaviours of the rat is that termed huddling, which laboratory rats and wild rats engage in throughout their life (Barnett, 1975; Calhoun, 1962). Huddling can be defined as a behaviour which leads to the formation and maintenance of clumps of rats, both young and adults. The precociality of rats to engage in this activity has lead to this species to being labelled a "contact" species (Barnett, 1975).

8.2

THE FUNCTION OF HUDDLING BEHAVIOUR

Huddling is important for thermoregulation, especially in young rats who are unable to control their body temperature in response to changing environmental temperatures (Alberts, 1978a). Infant rats produce less heat (Taylor, 1960) and lose it more quickly due to lack of insulative fur and subcutaneous fat and lack of control over their vascular flow (Hull, 1972). Low body temperature depresses the growth rate of young pups (Barnett and Mount, 1971) and it is therefore important for these pups unable to regulate their temperature internally to maintain it behaviourally by huddling. True temperature independence does not occur until day 73

(Adolph, 1957), although by day 15 the pups are able to maintain a relatively constant body temperature over a wide range of temperatures (Lytle and Keil, 1974). Experiments by Alberts (1978a) have demonstrated that huddling serves as a behavioural mechanism to regulate the temperature of pups: it attenuates heat loss, even in neonates 5 days old and provides an efficient means of reducing metabolic rate (as measured by oxygen consumption). These benefits are derived from the fact that by huddling the rats are able to reduce their surface/volume ratio and thus reduce heat loss.

However, even when adult and fully homoiothermic, rats still persist in huddling and it is only in the warmest of temperatures that they may be persuaded to stop huddling (personal observation). This persistence of huddling throughout life has lead writers to suggest that huddling performs other functions. Thus Small in his study on the "Psychic Development of the Rat" (1899), after observing the huddling behaviour of rats was "led to ask whether these huddling movements are not the first expression of the social instinct" (p. 85). Other authors regarding the persistence of this behaviour have also pondered on functions huddling may serve other than thermoregulation (e.g., Barnett, 1975; Telle, 1966). One such function may be to provide "contact comfort". Harlow in a series of studies on the development of the affection system in rhesus monkeys, Macaca mulatta, (1958,1959,1962), examined the importance of certain tactile cues for normal development and found that these cues were preferred over food (Harlow 1958). From this work he formed a concept of "contact comfort" as an innate reinforcer. A similar function may be served by huddling in the rat. The view that huddling serves more than a thermoregulatory function is echoed by Alberts (1978b). Investigating the sensory control of huddling he concludes that "the breadth of the sensory controls of huddling no doubt ensures that this multidimensional behaviour will be expressed reliably by the developing litter and provide a contact for ontogenetic events of immediate and future significance to the developing rat" (p. 229). Thus although not specifically known, it is assumed that huddling behaviour serves some beneficial social function in the rat as well as being important for thermoregulation.

8.3

EXPERIMENT 8.1: HUDDLING PARTNER PREFERENCES IN THE RAT

In this experiment pups were tested for their preferences for either siblings or unrelated individuals as huddling partners. The effects of acquiring sibling recognition through only socially or only genetically mediated mechanisms on huddling partner preference were also assessed.

Pups in this experiment were examined at 16 days of age when some control of thermoregulation has been accomplished (Lytle and Keil, 1974) but the full adult ability has yet to be achieved (Conklin and Heggeness, 1971). Thus pups may derive some benefits from huddling in conserving temperature along with benefits accruing through social contact. At this age olfactory stimuli exert control over the huddling behaviour and pups respond preferentially to odours associated with the maternal nest (Brunjes and Alberts, 1979). Previous experiments (see Chp. 3) have demonstrated that pups at this age can recognise their siblings and that this is achieved by olfactory cues. Thus it was hypothesised that because of the benefits which may be obtained by huddling, individuals would prefer to huddle with their 'siblings' rather than with non-siblings, thereby maximising their inclusive fitness.

8.3.1

Subjects

Fifteen litters of Sprague-Dawley rat pups born to females supplied by B & K (Animal Suppliers) Ltd., were used. Care was taken to ensure that none of the parents were related to each other (r=0.0). The females were time mated and all litters born on the same day (termed day 0). On day 2 all litters were culled to 7 pups and placed in one of 2 rearing conditions.

Rearing Condition 1: 8 litters were placed in this condition and all individuals remained in their original litters for the duration of the experiment.

Rearing Condition 2: 7 litters were placed in this condition. Litters were then rearranged to form 7 new litters each containing only one member of each original litter. These litters were then left for the duration of the experiment.

These two rearing conditions produced 3 experimental conditions. Natural siblings from rearing condition 1 were pups both socially and genetically related (SG). 'Siblings' only socially related ($S\tilde{G}$) were obtained from rearing condition 2 as were siblings only genetically related ($\tilde{S}G$). A control condition was added of pups neither socially nor genetically related ($\tilde{S}\tilde{G}$) obtained from rearing conditions 1 and 2.

All pups were marked daily with a Carioca black felt-tip pen for identification from day 2 to day 12, by writing the appropriate number on the rat's back. From day 13 onwards all rats were marked with alcoholic Picric acid and thereafter when necessary. Rat pups were housed in plastic Bowman's cages (16"x12"x7") with food and water freely available. Pups were kept on a 12 hour light/dark cycle, darkness commencing at 1200 hours.

8.3.2

Procedure

Pups were tested in groups of 4, 'quartets'. Each quartet was composed of 2 test animals; related by one of the three experimental conditions SG, $S\tilde{G}$, $\tilde{S}G$ or the control condition $\tilde{S}\tilde{G}$, and 2 controls, which were unrelated ($\tilde{S}\tilde{G}$) both to each other and to the 2 test animals. Six quartets were used in each condition, each individual being used only once.

All rats were tested on day 16. They were taken to the testing room at least 1 hour before testing, to allow habituation to the room. Tests were carried out under red light and in cages identical to those in which the rat lived, with the exception of the wire top which was replaced by one of clear perspex. Clean shavings were placed in the cage for each test, all tests were performed between 1300 and 1600 hours.

The four animals were introduced simultaneously to the test cage, placed equidistantly apart and left for 15 minutes. The pups behaviour was recorded on video using National Panasonic time lapse V.T.R. (NV 8030) and National Panasonic Camera, for later analysis. All rats were marked with Reeves black indian ink to enable identification on the videotape.

8.3.3

Analysis

A time sampling method was used to analyse the behaviour. The videotape was replayed and stopped every 15 seconds to record for each quartet which rats were in contact (to enable this the 2 test individuals were labelled A and B and the 2 control individuals C and D for each quartet). Two rats were recorded as being in contact if any part of their bodies, excluding the tail or whiskers, was touching. The number of times in contact was used as an indication of huddling behaviour, the more times a particular pair were in contact the greater the huddling preference for each other. For each quartet the number of times each pair (AB,AC,AD,BC,BD,CD) was in contact for the duration of the experiment was obtained.

An analysis of variance (see Winer, 1962) was performed on the number of times the test pair was in contact in the four test conditions (SG, $S\tilde{G}$, $\tilde{S}G$, $\tilde{S}\tilde{G}$). This gave a 2 x 2 contingency table of social relatedness ($S/\tilde{S}$) and genetic relatedness ($G/\tilde{G}$) which was used to assess the effect of 'social' and 'genetic' relatedness on the amount of huddling between 'siblings'.

It was hypothesised that the SG condition would show a greater preference for siblings as huddling partners than $S\tilde{G}$ or $\tilde{S}G$ which would show equal preference and showing the lowest preference the $\tilde{S}\tilde{G}$ or control condition. To examine this a Jonckheere trend test was performed (see

Leach, 1979) on the number of times the test pair (AB) was in contact in each condition.

In any quartet, if no preference was shown then one would expect all pairs (AB,AC,AD,BC,BD,CD) to be in contact equally often, whereas if the related individuals showed a preference for each other, AB would occur more often than the other pairs. To examine this a matched pairs t-test was carried out (see Robson, 1975). The number of times the test pair (AB) was in contact was compared with the mean number of times every other pair in that quartet was in contact (termed E, the expected value, = the number of contacts for AC+AD+BC+BD+CD / 5).

8.3.4

Results

8.3.4.1

Analysis of Variance

There was a significant effect of genetic relatedness (F=4.4579, df=1,20, p=0.0452), rats genetically related showing a greater number of contacts than those not genetically related (mean no. of contacts: G, 38.417; G̃, 31.417). There was no significant effect of social relatedness on huddling partner preferences nor an interaction effect between social and genetic relatedness (see table 8.1). The results from this analysis indicate that a significant huddling preference is shown by siblings for each other.

TABLE 8.1

The effect of social and genetic relatedness on the huddling partner preferences of 16 day old rats.

Summary of Analysis of Variance

SOURCE	DF	SS	MS	F	PROB
SUBJ	23	1853.8333			
S	1	160.1667	160.1667	2.4286	0.1315
G	1	294.0000	294.0000	4.4579	0.0452
S x G	1	80.6667	80.6667	1.2231	0.2817
ERROR	20	1319.0000	65.9500		
WITHIN CELLS	0	0.0			

S = Social relatedness.
G = Genetic relatedness.

8.3.4.2

Jonckheere Trend Test

To examine whether there was a trend in the preference exhibited by the four test conditions a Jonckheere trend test was performed. For this it was hypothesised that the order of greatest preference would be SG>S̃G>SG̃>S̃G̃, the ordering of S̃G then SG̃ because of the significant G effect found in the ANOVA. The results indicated a significant trend in the predicted direction (p=0.0286, 2-tailed, see fig. 8.1). The results of the trend test indicate that factors of social and genetic relatedness combine to produce a greater preference than either factor alone. The results support the ANOVA as pups only genetically related show a greater preference for each other than pups non-genetically related. It should also be noted that the factor of social relatedness, although not producing a significant effect when analysed by the ANOVA, pups only socially related did show a greater preference for each other than pups neither socially nor genetically related (S̃G̃).

8.3.4.3

Matched-pairs t-test

The results of the t-test support the findings of the ANOVA (see table 8.2 for summary). Test pairs in both the SG condition (t=2.6495, df=5, 0.05>p>0.01) and the S̃G condition (t=3.3473, df=5, 0.05>p>0.01) show a significantly greater number of contacts than expected (i.e., the mean of all other pairs). Natural siblings

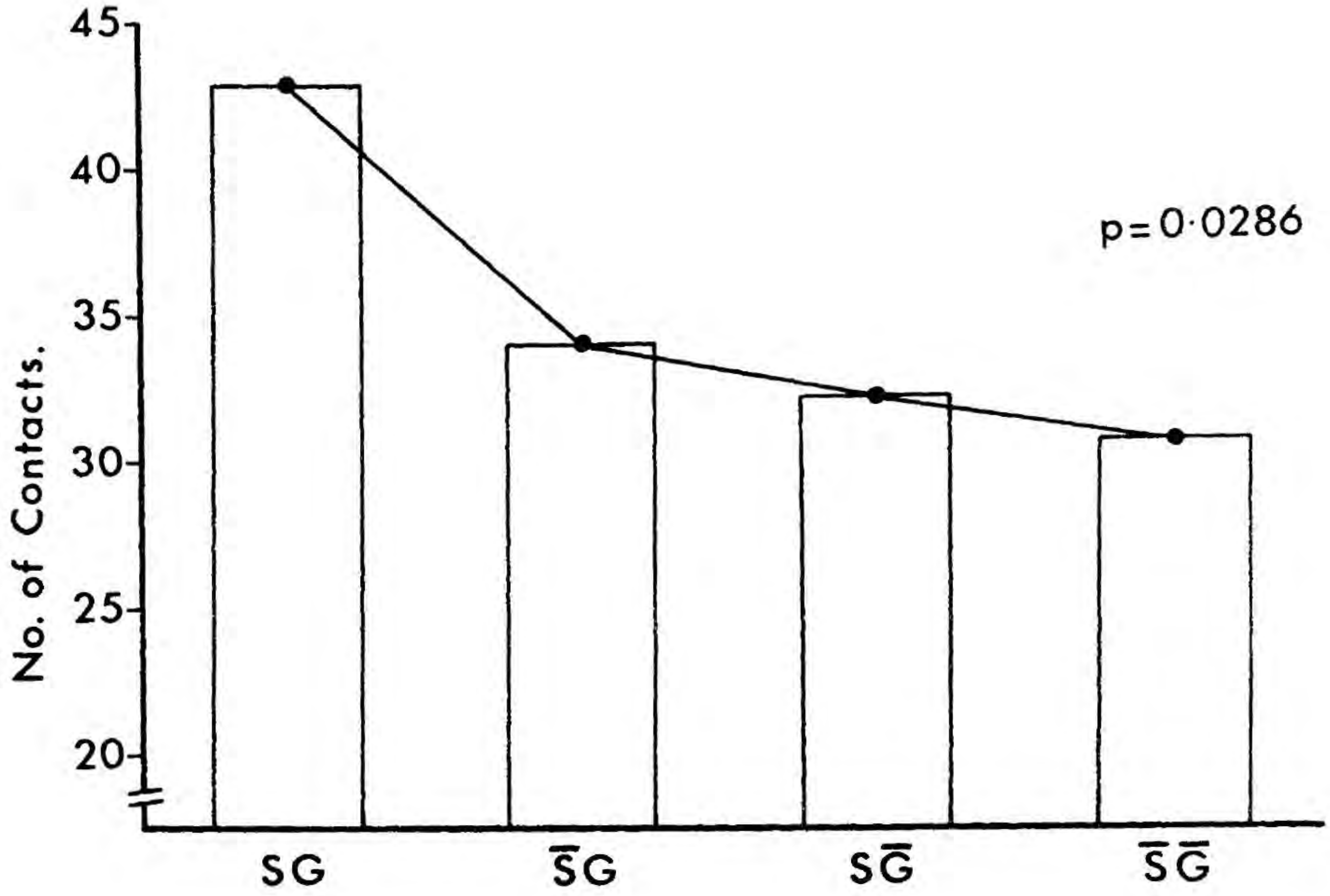

FIGURE 8.1
Mean number of contacts for each test condition with Jonckheere trend probability.

TABLE 8.2

Summary of t-test results for comparison of the number of contacts between the test pair (AB) and the expected value (E) for each test condition.

CONDITION	t	DF	PROB	MEAN NO. OF CONTACTS AB	MEAN NO. OF CONTACTS E
SG	2.6495	5	0.05>P>0.01	42.8333	34.6333
SG̃	1.8340	5	0.2>P>0.1	32.1667	27.4667
S̃G	3.3473	5	0.05>P>0.01	34.0000	26.8000
S̃G̃	0.2557	5	P>0.2	30.6667	31.5000

were in contact more than other pairs (mean number of contacts: SG, 42.833; E, 34.633), and siblings only genetically related with no postnatal experience of their siblings were in contact more than other pairs (mean number of contacts: test pair, 34.000; E, 26.800). There was no significant difference in the $S\tilde{G}$ or $\tilde{S}\tilde{G}$ conditions between the number of contacts for the test pair (AB) and the expected value (E).

The results of these t-tests provide evidence that rats do prefer to huddle with their natural siblings. There was evidence that the G factor is sufficient for this preference to be shown, and that rats only socially related although showing some preference for their 'sibs' do not do so significantly.

In summary, the results of these experiments indicate that rat pups do prefer to huddle with their siblings rather than unrelated individuals. The results indicate that individuals genetically related exhibit a greater preference for sibling huddling partners than individuals socially related and this may reflect the recognition capabilities of these individuals. Only socially related individuals being less able to recognise their 'sibs' than individuals only genetically related. However socially related individuals do show a greater preference than control individuals indicating social relatedness does exert an effect on huddling partner preferences.

8.3.5

Discussion

Although the results demonstrate quite strongly that natural siblings do show a preference for each other, the effects of social and genetic relatedness are less consistent.

The results from the ANOVA and Jonckheere trend test indicate that the factor of genetic relatedness exerts a stronger effect upon huddling preferences than social relatedness. This may be due to the fact that although individuals only socially and only genetically related could both recognise their sibs (see Chp. 3), individuals genetically related have a better idea of who their sibs are than individuals only socially related and are therefore better able to show a preference. This is supported by studies examining sibling recognition (Chp.3). These experiments indicated that at days 10-14, pups only genetically related have a better idea of who their sibs are than pups only socially related whereas on days 18-22 the reverse is true and pups only socially related have a better idea of who their sibs are than individuals only genetically related. Thus at some time there must be a changeover in which factor exerts the strongest effect and it may be that at the time of testing the factor of genetic relatedness exerted a stronger effect and therefore pups G related have a better knowledge of who their sibs are and show a greater preference than individuals only socially related.

Another factor which may have reduced the overall preference shown by the pups is the time of testing. Pups at 16 days of age have been demonstrated to show no preference for either familiar or unfamiliar odours (Carr et al., 1979b) and thus testing at this age may have reduced the preferences shown by the pups such that only those with the best knowlege of who their siblings are show any preference.

In conclusion, the results of this experiment indicate that rat pups use the ability to recognise their siblings to huddle with them preferentially. Genetic relatedness seems to be important for the exhibition of this preference although the results are suggestive of a role for social relatedness and testing at a later date may have shown a stronger effect of this factor.

8.4

CONCLUSION

Siblings do prefer to huddle with each other, and as such they must possess some mechanism for recognising their siblings. Previous experiments (Chp. 3) have demonstrated that rat pups are capable of sibling recognition and olfactory cues are used as the primary source of information concerning kinship. Similar studies on the olfactory control of huddling (Brunjes and Alberts, 1979) have demonstrated that nest odour plays an important role in this recognition; thus in this case pups presumably recognise their siblings by means of olfactory cues.

In conclusion, huddling behaviour one of the most prominent activities of the rat demonstrates that rats do conform to predictions of kin selection theory and preferentially engage in this behaviour with their siblings, thereby gaining additional increases in their inclusive fitness (from thermoregulation and social development).

CHAPTER 9

PLAY PARTNER PREFERENCES IN THE RAT

9.1

INTRODUCTION

Observers watching animal or human behaviour seem readily able to state what is and is not play (Bekoff,1976; Miller, 1973), and most can agree on certain qualities of play (Poole and Fish, 1975) but all find it very difficult to pin down and define. The main problem seems to be because of the wide diversity of behaviours involved in play a definition that encompasses all aspects is difficult (Smith, 1978). Some authors define play operationally in the particular species they are studying (e.g., Humphreys, 1982), whereas others attempt no definition and leave it up to the reader (e.g., Lorenz, 1956). Wilson (1975) states: "Largely from our personal experience, we know intuitively that play is a set of pleasurable activities, frequently but not always social in nature, that imitate the serious activities of life, without consumating serious goals." (p. 164) and I shall use this as a definition of play. For a more comprehensive discussion of the various definitions of play, see Fagen (1981). Play may be divided into two categories, social play in which two or more conspecifics are involved or solitary play, which can be subdivided into locomotor or object play, in which a single individual is involved. In this chapter I shall be concerned only with the social play of rats, and examine the play partner preferences of sibling rats, and the effect of social and genetic relatedness on these preferences.

9.2

THE PLAY OF RATS

The play of laboratory rats is almost entirely social in nature (Humphreys, 1982), it commences around day 18 (Barnett, 1975; Panksepp, 1981; Small 1899) and lasts until the rats are 50-60 days old. Play behaviour peaks at about day 30 (Humphreys, 1982; Panksepp, 1981) which coincides with the time of the rats emergence from the burrow (Calhoun, 1962). The number of play bouts per day decreases between days 21-56, whereas the play bout length increases to a peak around day 25 remains stable until approximately day 45, and then decreases (Humphreys, 1982). Most play occurs in the dark and consequently more play bouts occur in the dark (Humphreys, 1982). As for the behaviours involved in social play, Pocle and Fish (1975), identify 14, Meaney and Stewart (1981), identify 8 and Humphreys (1982) identifies 5. These catagories can all be placed into three basic areas, those of wrestling (play-fighting), chasing and paws-on.

Observation of play behaviour in wild rats, although indicating that they play has not demonstrated the same variation or frequency of play behaviour as observed in laboratory animals (Telle, 1966), and this increase in play in laboratory rats is probably due to the results of captivity.

9.3

THE FUNCTION OF PLAY

Many authors agree that play serves an important function in the socialisation of mammals (Wilson, 1975), but there are different views as to its specific role. Early theories of play regarded the behaviour as serving to rid the individual of excess energy (Spencer, 1878), whilst Groos (1898) argued for play to be important in the practicing of skills. Other authors have proposed different functions for play and these are detailed briefly below (for fuller discussion see Fagen, 1981; Smith, 1982).

Practice: The similarities of play and adult behaviour have lead certain authors (e.g., Symons, 1978) to propose that play serves to practice adult behaviour in a situation without the pressures of adult life.

Physical Training: The active nature of most play enhances the physical capacity of the body. Byers (1980) lists four measurable consequences (benefits) of such training: bones thicken and are remoulded in response to specific stress activity; muscles used in the activity hypertrophy and undergo biochemical and cellular changes so they are able to function better; cardiopulmonary capacity and efficiency increases and metabolic pathways are altered so that the individuals show increased endurance; smoothness and increased efficiency of action that repeated exercise allows.

Social Capability: This encompasses a number of behaviours all of which generally increase the social capability of the individual. Possible functions which may be served are: to enable learning of fighting or predatory/predator avoidance skills (Smith, 1982, see also practice); to develop complex social behaviours and communicatory skills (Poirer and Smith, 1974); the establishment of social rank (Meaney and Stewart, 1981).

Cognitive/Environmental Training: This encompasses a class of behaviours. Individuals may learn about the environment during play (more likely during social play), or may form innovative skills, that is , the composition of novel behaviour patterns which may be adaptive to the individual. Finally individuals during play may become more flexible and adaptive to different environmental demands.

Kin Recognition: An idea advanced by Bekoff (1978,1981). Through playing individuals initiate and maintain bonds of kinship.

Although there have been many studies of social play covering many different species (e.g., Bekoff, 1976; Fagen, 1976; Ficken, 1977; Wiesler and McCall, 1976) the benefits which accrue to individuals who participate in such activities have remained elusive (Bekoff, 1978). Attempts to guage the importance of play have mainly involved deprivation studies, for example, Harlow and Harlow (1962). Although such isolation studies go some way in indicating the importance of play, the animals have been deprived of more than just play experience and care must be taken in the interpretation of these results. Some studies have attempted to deprive individuals of only play (Chepko, 1971; Muller-Schwarze, 1968), but doing this introduces other confounding variables (Vandenberg, 1978), for example, constant human intervention and again the results cannot solely be attributed to play deprivation.

The benefits of play, although widely acknowledged, have yet to be specifically elucidated. A further problem with the benefits of play is that they do not seem to be immediately realised but rather play prepares the individual for adulthood and as such the advantages of playing may not be gained until this time, after the play period has ended.

The costs of play, however, are somewhat more apparent and immediate. First, the energy used during play is large and this constitutes a loss to the individual which must be made up. Too much energy loss may leave the individual unable to respond to other stimuli, for example, predators. During play there is a possibility of physical injury, especially during play fighting. Individuals may become separated from the mother or group during play and therefore may be more at risk to predation and may lose maternal care. Finally, play behaviour involves much activity and movement and this may draw the attention of predators to the playing individuals. Thus there are costs associated with play, which for the most part will be shared equally amongst the participants.

In summary, play behaviour involves costs that are immediately realisable and gains/benefits which are delayed and the individual may not reap these until after the play period. It does seem however that play is a mutually beneficial co-operative social behaviour, with the benefits outweighing the costs, and participants receiving equal benefits and equal costs. Thus as such individuals who participate in this activity with kin can gain increases in their inclusive fitness over those individuals not participating with kin.

9.4

EXPERIMENT 9.1:

PLAY PARTNER PREFERENCES IN THE RAT

This experiment investigates the preferences of individuals for play partners between siblings and non-siblings. In a previous study of play partner preferences (Humphreys and Einon, 1981), rat pups were found to prefer a free cagemate over a confined one, and to prefer a normally behaving agemate over an abnormally behaving individual. In this experiment rats were given a choice between siblings and unrelated individuals as play partners to see if they preferred to play with their siblings. The effect of social relatedness and genetic relatedness on this preference was also examined. It was hypothesised that individuals should prefer their siblings as play partners over unrelated individuals.

The treatment of subjects, procedure and analysis was the same as used to investigate huddling partner preferences (Chp. 8) and shall only be discussed briefly here along with points of difference. Fuller details may be found in chapter 8, section 8.3.

9.4.1

Subjects

The subjects were 29 litters of Sprague-Dawley rats born to females supplied by B &K (Animal Suppliers) Ltd. Fifteen of these litters had been previously used to investigate huddling partner preferences (Chp. 8). All pups were born within 48 hours of each other, the day of birth termed day 0. On day 2 all litters were culled to 7 and placed in one of two rearing conditions.

Rearing Condition 1: 15 litters were placed in this condition and pups remained in their original litters for the duration of the experiment.

Rearing Condition 2: 14 litters were used in this condition and were divided into 2 groups of 7. Each group was treated identically to that of rearing condition 2 in chapter 8 to form new litters each containing 7 unrelated individuals.

These rearing conditions produced 3 experimental conditions: SG, natural siblings from rearing condition 1; $S\tilde{G}$, only socially related 'siblings' from rearing condition 2; $\tilde{S}G$, only genetically related siblings from rearing condition 2. Pups neither socially nor genetically related ($\tilde{S}\tilde{G}$) were used as controls.

Pups were weaned on day 24, all other details concerning the treatment of the pups were identical to those for pups in chapter 8.

9.4.2

Procedure

Pups were tested between 29 and 32 days of age. On the day prior to testing pups were isolated from conspecifics and placed in individual cages 12"x5"x5" (North Kent Plastics) with food and water freely available. This procedure was adopted to increase the amount of play behaviour exhibited during the experimental session. Twenty-four hours after isolation the pups were tested, the procedure identical to that used in the huddling test.

Pups were tested in groups of 4, quartets, each group composed of 2 test animals, related by one of the four possible test conditions SG, $S\tilde{G}$, $\tilde{S}G$, $\tilde{S}\tilde{G}$, and 2 controls, $\tilde{S}\tilde{G}$. Twelve quartets were used for each condition. The test session lasted 25 minutes and was recorded on videotape.

9.4.3

Analysis

Time sampling was used to analyse the behaviour, the tape was stopped every 10 seconds to record which pairs of rats were in contact. For this the test pair was labelled A and B and the control pups C and D. The total number of times each pair (AB,AC,AD,BC,BD,CD) was in contact was obtained. The results were analysed by using an ANOVA, a Jonckheere trend test and matched pairs t-test, fuller details of which may be found in the previous chapter.

9.4.4

Results

9.4.4.1

Analysis of Variance

No significant effects of social relatedness, genetic relatedness nor any interaction effect was found, see table 9.1. The results of the ANOVA indicate there was no significant difference in the amount of contact between the test pairs in the four test conditions.

TABLE 9.1

The effect of social and genetic relatedness on the play partner preferences of juvenile rats.

Summary of Analysis of Variance

SOURCE	DF	SS	MS	F	PROB
SUBJ	47	5114.6667			
S	1	208.3333	208.3333	1.9105	0.1706
G	1	96.3333	96.3333	0.8834	0.6452
S x G	1	12.0000	12.0000	0.1100	0.7407
ERROR	44	4798.0000	109.0455		
WITHIN CELLS	0	0.0			

S = Social relatedness.
G = Genetic relatedness.

9.4.4.2

Jonckheere Trend Test

It was hypothesised that the order for the greatest number of contacts would be $SG > S\tilde{G} > \tilde{S}G > \tilde{S}\tilde{G}$. The ordering of $S\tilde{G}$ then $\tilde{S}G$ based upon results from examination of sibling recognition, chapter 3, which indicated that by day 18-22 social relatedness exerted a greater effect on preferences than genetic relatedness. Although observation of the graph (see fig. 9.1) indicates that the number of contacts does show a trend in the predicted direction this does not reach significance ($p=0.1118$).

The results indicate their was no trend in the amount of contact between the test pair in the four test conditions, although there may be some slight increase in the number of contacts for individuals socially related over individuals non-socially related. It thus seems that the test pairs were in contact equally often in all four conditions.

9.4.4.3

Matched-pairs t-test

Individuals socially and genetically related showed a significantly greater number of contacts than expected ($t=2.7498$, $df=11$, $0.02>p>0.01$, mean number of contacts: SG, 70.3333; E, 63.8667). There was no significant difference in the number of contacts between the test pair (AB) and the expected value (E) in the $S\tilde{G}$, $\tilde{S}G$ or $\tilde{S}\tilde{G}$ conditions (see table 9.2).

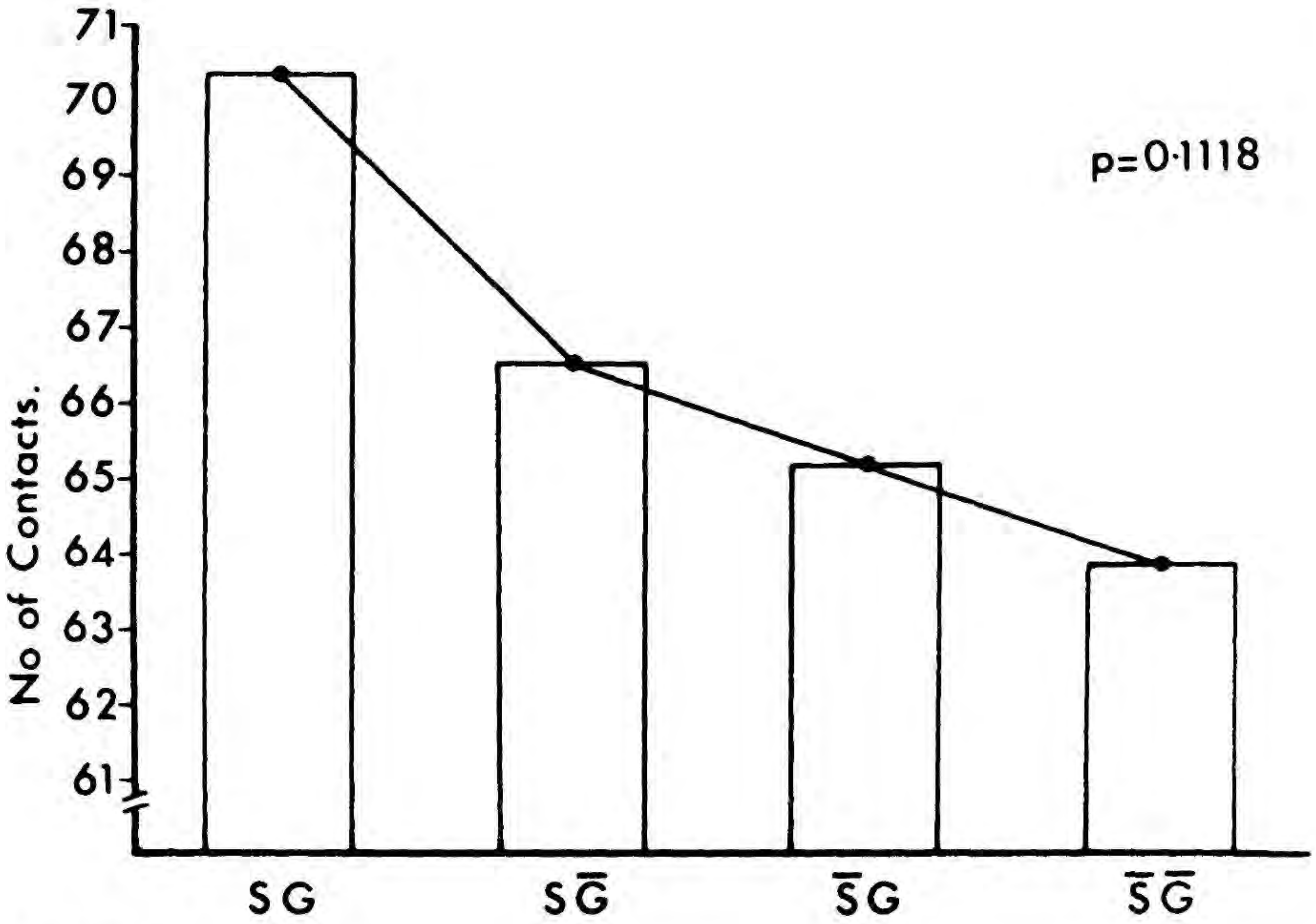

FIGURE 9.1
Mean number of contacts for each test condition with Jonckheere trend probability.

TABLE 9.2

Summary of t-test results for comparison of the number of contacts between the test pair (AB) and the expected value (E) for each condition.

CONDITION	t	DF	PROB.	MEAN NO. OF CONTACTS AB	MEAN NO. OF CONTACTS E
SG	2.7498	11	0.02>P>0.01	70.3333	63.8667
SG̃	1.4557	11	0.2>P>0.1	66.5000	63.1000
S̃G	1.9712	11	0.1>P>0.05	65.1667	57.1000
S̃G̃	0.3660	11	0.8>P>0.7	63.8333	63.0750

In summary, the results of this experiment do suggest that individuals are in contact with their siblings more than with unrelated individuals, and that sibs need to be both socially and genetically related for this preference to occur.

9.4.5

Discussion

This experiment indicates that individuals prefer to play with their natural siblings rather than with unfamiliar agemates. The effects of only social or only genetic relatedness on play partner preference are less clear.

Previous studies investigating sibling recognition (Chp. 3) show that rats socially or genetically related possess the ability to recognise their siblings at 22 days of age, but by day 40 only rats socially related exhibit signs of this ability. It was concluded from these studies that individuals acquiring sib recognition through a genetically mediated mechanism require some social experience of their sibs to maintain their preference/recognition. This may explain the lack of preference exhibited by S̃G rats for sibling play partners, as they were unable to recognise them. This is partially supported by the Jonckheere trend test, where although the trend was not significant it did suggest a stronger preference shown by socially related individuals over non-socially related individuals.

Poor recognition of siblings by SG̃ related individuals may also explain why no preference was exhibited by these rats as compared to natural siblings (SG). When the strength of preference for siblings was compared between SG and SG̃ pups at days 18-22, the results showed the SG pups showed a stronger preference , although this did not reach significance ($0.1 > p > 0.05$, section 3.6.5). It may be that social and genetic experience combines to allow a stronger representation of siblings to be held than just social experience. The possibility also exists that both social and genetic factors may combine in some way unknown, for example, to produce greater behavioural similarity, which again may allow better recognition of siblings.

It may be that the task itself produces indiscriminate play behaviour and only those individuals most strongly attracted to their siblings (SG) show this preference. Individuals were deprived of play for 24 hours prior to the test to increase their play when tested and this may have led to an indiscriminate tendency to play.

A final consideration is whether the measure used, the number of contacts, reflects true play partner preferences. In the huddling task, contact scores were pertinent to the behaviour studied, but the same cannot be said for play. Poole and Fish (1975) identify 14 elements of rat social play, implying that play is obviously more complicated than measures of contact behaviour can suggest. The task itself used a procedure which increased the amount of play exhibited by the individuals and observation of the task indicated between 70-80% of the time some of the animals were engaged in social play. Thus it is likely that when in contact the animals were playing and thus the contact measure does reflect to some extent represent play activity. The initiation of play is usually heralded by a "paws-on" (Humphreys, 1982; Poole and Fish, 1975) type of behaviour and observation of rat play indicates they do not search for a partner but "paws-on" the nearest pup (personal observation). Again contact behaviour would be an appropriate measure for play preferences, as the pup in contact is the one most likely to be played with. In conclusion, to a large extent the measure of contact behaviour probably does reflect the play behaviour of rats and can be used to give an indication of play partner preferences.

In summary, the play behaviour of 29-32 day old rats does suggest that these rats prefer to play with their siblings, and that both social and genetic relatedness is necessary for this preference to be shown.

9.5

CONCLUSION

As individuals prefer to play with their siblings, these individuals may gain greater increases in their inclusive fitness than individuals not playing preferentially with their siblings. One important function of this nepotism in play partner preferences is the development of kin recognition (Bekoff, 1978,1981).

Playing with siblings may increase kin recognition by 2 means. Simple exposure to siblings may allow further learning of the kin identifier, which leads to better kin recognition in the future. Second it may lead to increased social and behavioural compatibility between kin. Social play has been postulated to develop complex social behaviour (Baldwin and Baldwin, 1974) and communicatory skills and social integration (Poirer and Smith, 1974), and as such if these social behaviours develop during play, then individuals playing together may develop similar behaviours and may become more likely to respond together in the future. Thus if kin respond together during play they may develop similar behaviour patterns which will lead to better kin recognition.

In conclusion, it does seem that sibling rats prefer to play with each other rather than unrelated individuals thereby acting in accordance with kin selection theory and maximising their inclusive fitness as well as possibly enhancing their ability to recognise kin.

CHAPTER 10

INBREEDING AVOIDANCE IN THE RAT

10.1

INTRODUCTION

An individual's fitness is ultimately measured in terms of its reproductive success, that is, how well it is able to maintain its genes in the next generation. The previous 2 chapters have investigated factors which have indirectly contributed to this success by affecting the individual's normal development. In this chapter I investigate the mating partner preferences of rats and investigate one factor which may directly affect an individual's fitness, inbreeding, and examine what steps if any rats take to avoid this.

10.2

INBREEDING

Inbreeding is defined as mating between two individuals who are related to each other by having one or more ancestors in common. The degree of inbreeding is dependent on the closeness of the genetic relationship between the mated individuals. The closer the individuals are related, that is, the more genes they have in common, the greater the degree of inbreeding. Generally, closely related individuals that inbreed suffer from inbreeding depression; a decrease in some or all components of biological fitness (Barash, 1977). Some of the most commonly associated signs of inbreeding are increased juvenile mortality (Wright S., 1977), increased susceptibility to diseases (Ralls et al., 1979) and decreased reproductive capacity (Falconer, 1960).

10.2.1
The Genetic Consequences Of Inbreeding

The loss in fitness associated with inbreeding may be due to one or a combination of three genetic consequences. As the individual becomes more inbred it comes to be homozygous for more genes (Cavalli-Sforza and Bodmer, 1971). This reduces the genotypic potential of the individual and consequently the ability of the individual to respond successfully to different environmental consequences is lessened due to the loss of heterozygosity, this factor is especially important in resistance to diseases.

As individuals become more inbred they become increasingly more homozygous and recessive alleles which have been masked by dominant alleles in the heterozygous form come to the fore and can now exert an effect in the homozygous individual. Many of these recessive genes have deleterious consequences and when they are able to exert an effect they act to reduce the fitness of the individual (Bodmer and Cavalli-Sforza, 1976).

Finally individuals contain a large number of polygenes, these are groups of genes each of which on its own exerts little or no effect, but in sum act together to influence the development of the individual. In heterozygous individuals the genes making up the the polygenes are in balance and add to the fitness of the individual, however inbreeding leading to homozygosity tends to upset the balance of the polygenic system of the individual leading to poor developmental stability and a reduction in fitness (Mather, 1955).

10.2.2 The Phenotypic Consequences Of Inbreeding

One does not directly observe the genetic consequences of inbreeding, but observes the expression of these effects in the individual's behaviour, that is, its phenotype. The effects of inbreeding have been observed in a number of different species. Inbreeding has been shown to retard development in mice, *Mus* sp., (Wainwright, 1980); decrease the probability of surviving to maturity and reproducing in the Japanese quail, *Coturnix coturnix japonica*, (Sittman et al., 1966); reduce the reproductive capability of drosophila, *Drosophila obscura*, (Hollingsworth and Maynard-Smith, 1955; Maynard-Smith; 1956), reduce the hatchability and number of surviving fry in the rainbow trout, *Salmo gairdneri*, (Kincaid, 1976); result in poor reproductive performance in prairie deer mice, *Peromyscus maniculatus bairdii*, (Hill, 1974); increase nestling mortality in the great tit, *Parus major*, (Greenwood et al., 1978). Similar defecits resulting from inbreeding have been reported in a wide range of ungulates (see Ralls et al., 1979) and domestic animals (e.g., see

Falconer, 1960; Wright S., 1977).

10.2.3

Inbreeding Avoidance

As there are clear disadvantages of inbreeding it may be expected that social groups will display behavioural mechanisms which preclude inbreeding. Mechanisms which may have evolved to avoid inbreeding can be divided into 2 broad catagories.

First, 'out of site, out of mind'. In this catagory the possibility of inbreeding is reduced by the removal of individuals of one sex from the site of related individuals of the opposite sex. Male chimps, *Pan troglodytes*, remain in their natal community whilst the females transfer to other communities during adolescence (Pusey, 1980). In the olive baboon, *Papio anubis*, however, it is the males who transfer between groups and the females who remain (Packer, 1975, 1979). In the mountain gorilla, *Gorilla gorilla*, both sexes tend to leave the natal group, the males to wander alone and try to attract other females, and the females to another already established group (Harcourt et al., 1976). Female African wild dogs, *Lycaon pictus* TEMMYNCK, emigrate from one group to another (Frame and Frame, 1976) and in lions, *Panthera leo*, subadult males are driven away from the pride by the dominant males (Bertram, 1973). In this way relatives of opposite sex may be separated and inbreeding avoided.

In the second mechanism, 'in sight, but out of mind', individuals do not leave the natal group but are inhibited from sexual behaviour by the presence of other related individuals. In the Acorn woodpecker, *Melanerpes formicivonus*, offspring are inhibited from reproducing by the presence of the parent of the opposite sex (Koenig and Pitelka, 1979). A similar explanation has been offered to explain the incest taboo in humans (Bixler, 1982; Wolf, 1966,1970) and studies of an Israeli kibbutz in which children were brought up communally, found individuals never married anyone with whom they associated in childhood, even if they were not close relations (Shepher, 1971).

Prairie dogs, *Cynomys ludovicianus*, use both mechanisms to avoid inbreeding (Hoogland, 1982): young males leave the natal group and young females are less likely to come into oestrus if the father is present.

10.2.4

Possible Advantageous Consequences Of Inbreeding

Although inbreeding generally acts to reduce fitness, in certain circumstances individuals may gain in fitness through inbreeding. Bengtsson (1978) argues that if the costs incurred by the individual in leaving its natal group to find another are greater than those incurred by inbreeding then the individual may be expected to engage in inbreeding. Seger (1976) provides evidence that inbreeding may benefit individuals by reducing competition in the intra-uterine environment. Likewise inbreeding may favour social evolution by allying "group members by kinship and making altruism profitable through the promotion of autozygous genes (hence ones own genes) among the recipients of altruism" (Wilson, 1975, p. 80).

Individuals are therefore placed in a certain amount of conflict: by inbreeding they may reduce the costs incurred by leaving the group to find other mates, reduce competition amongst kin and gain advantages in their social evolution, but in doing so they will tend to lower their biological fitness and suffer depression of performance and loss of genetic adaptability such that gene survival may be threatened. To overcome this individuals may be expected to strike a balance between inbreeding and outbreeding (Bateson 1978b). In experiments on the Japanese quail, Coturnix coturnix japonica, Bateson (1978a,1980,1982) has found that the birds do strike such an optimal balance, preferring to mate with their first cousins over siblings, third cousins and unrelated individuals.

10.3

INBREEDING IN THE RAT

The effects of inbreeding in the rat are somewhat contradictory. Most of the strains used by experimenters today have been derived from stock originally inbred to promote qualities of docility and large litter size, for example, Sprague-Dawley rats were originally inbred for 20 generations prior to outbreeding (McClintock, 1974). These strains do not seem to have suffered the consequences of increased mortality, decreased litter size, poor reproductive performance, usually associated with inbreeding.

Some investigators however have found that inbreeding reduces fertility and vitality in the rat (Ritzema-Bos, 1894) and may also cause the appearance of physical abnormalities (Crampe, 1883). King (1918a-c,1919) found little evidence for inbreeding depression in rats, however the homozygosity usually resulting from inbreeding may to a certain extent have been avoided by selecting rats for mating vigour, indeed later analysis of the rats used indictated that heterozygosity remained at some loci (see Wright S., 1977).

10.3.1

Inbreeding Avoidance In The Rat

Little is known about the mechanisms, if any, used by the rat to avoid inbreeding. Studies of rats in natural or semi-natural enviroments (Barnett, 1975; Calhoun, 1962; Telle, 1966) throw little light on the subject giving no indication of one or other sex leaving the group or any prevention of mating with related individuals.

One experiment which may indicate a means of inbreeding avoidance was performed by Kagan and Beach (1953). In this experiment male rats were reared in isolation from infancy to adulthood. Experimental groups were given weekly exposure to either a sexually receptive female or a male of the same age, control groups remaining isolated. At 99 days of age individuals were exposed to a receptive female and, although there was no difference in the occurence of copulation, those individuals given exposure to either a male or female rat ejaculated less frequently. Kagan and Beach argued that play habits formed during prepuberal exposure interfered with the competing tendency to copulate. Although this study indicates that events in the prepuberal period can interfere with the copulatory response these effects may not be due to play as Kagan and Beach suggest. If play did compete with copulatory behaviour one would expect an effect to be exerted on copulatory behaviour and not just on ejaculation frequency. Also males receiving exposure were compared to isolated individuals. There have been a number of studies indicating that isolation produces behavioural deficiences in rats (e.g., see Einon and Morgan, 1977; Einon, Morgan and Kibbler, 1978; Morgan, 1973) and the effects may be due to an increased ejaculation frequency in isolated rats rather than a decrease in the ejaculation frequency of those rats exposed to conspecifics. A study by Chambers et al. (1982) indicates that sexual behaviour in adult rats is disrupted by a period of isolation. Thus although Kagan and Beach (1953) demonstrate that prepuberal experience does affect certain aspects of mating behaviour, whether this is due to competing play behaviour or the effects of isolation rearing is unclear.

10.4

EXPERIMENT 10.1

INBREEDING AVOIDANCE IN THE RAT: THE EFFECT OF DIFFERENT PREPUBERAL RELATIONSHIPS ON THE TIME OF LITTER BIRTH AND THE NUMBER OF PUPS BORN

This experiment investigates the mating behaviour of sibling rats and considers the consequences of 2 different prepuberal relationships on the outcome of this behaviour. The types of relationship afforded siblings were, first, 'social' relatedness, where individuals remained together during puberty, and second, 'genetic' relatedness, where individuals were full siblings, r=0.5. The effects of social and/or genetic relatedness on the time of mating, as indicated by time of litter birth, and on the number of pups born were investigated. Both these measures have been shown to be affected by inbreeding, related individuals being inhibited from mating, for example, Hoogland (1982) and producing fewer offspring when mating does take place, for example, Kincaid (1976). It was hypothesised that if social and/or genetic relatedness was important for inbreeding avoidance in the rat, then siblings so related would show a delay in reproduction and/or fewer pups being born.

10.4.1

Subjects

Eleven litters of Sprague-Dawley albino rats born to unrelated parents were used in this experiment. The day the pups were born was termed day 0 and on day 2 all litters were culled to 8, 4 males and 4 females and placed into one of two rearing conditions.

Rearing Condition 1: Three litters were placed in this condition and were left in their original birth litters for the duration of the experiment.

Rearing Condition 2: Eight litters of rats were placed in this condition. Each litter was numbered 1-8 and pups in each litter marked accordingly (marking took the form of writing the appropriate number on the back of the rat). The litters were then rearranged to form 8 new litters each containing one member from the 8 original litters. Rats were then left in these litters for the duration of the experiment.

Rats were marked daily with a black Carioca felt tip pen until day 12 and then marked with alcoholic Picric acid when necessary. Food and water were freely available and the rats were kept on a 12 hour light/dark cycle, darkness commencing at 1200 hours. Rats were kept in plastic Bowman's cages (16"x12"x7") and were weaned at 25 days of age.

10.4.2

Procedure

On day 40 all rats were housed individually for 24 hours in N.K.P. cages (12"x5"x5") with food and water freely available. After 24 hours of isolation rats were replaced in Bowman's cages in groups of 4, 2 males and 2 females, according to one of 4 test conditions.

Condition 1: SG. Rats in this condition were placed with individuals with whom they had been reared until day 40, socially related, and who were their siblings, genetically related.

Condition 2: $S\tilde{G}$. Rats in this condition were placed with rats with whom they had been reared until day 40 but who were genetically unrelated.

Condition 3: $\tilde{S}G$. Rats in this condition were placed with rats who were their siblings but from whom they had been separated since birth, genetically related but socially unrelated.

Condition 4: $\tilde{S}\tilde{G}$. This group was used as a control and contained rats neither socially nor genetically related.

Five groups of 4 rats were used in each condition.

The rats were left in these groups and checked daily for birth of litters. After the first litter was born cages were checked twice daily. When a litter was born the mother and litter were removed from the cage and rehoused separately. The date the litter was born was recorded, and the number of pups born also noted. The experiment continued until all females had given birth.

10.4.3

Analysis

Two scores were obtained for each female. First the age of the female at the time of litter birth, and second, the number of pups born alive in each litter. Both scores were kept separate and analysed using an analysis of variance (ANOVA) for factors of social and genetic relatedness (see Winer, 1962).

10.4.4

Results

10.4.4.1

The age of the female at parturition

The ANOVA (see table 10.1 for summary) indicated a significant effect of social relatedness (F= 6.9781, df 1,36, p=0.0117), individuals who were socially related producing their litter at a later age (mean 88.8 days of age) than those individuals not socially related (mean 83.7 days of age). There was no effect of genetic relatedness (F=0.1112, df 1,36, p=0.7398) nor an interaction effect (F=0.3480, df 1,36, p=0.5657).

TABLE 10.1

Effect of social and genetic relatedness on the age of female at parturition.

Summary of Analysis of Variance

SOURCE	DF	SS	MS	F	PROB
SUBJ	39	1650.9750			
S	1	265.2250	265.2250	6.9781	0.0117
G	1	4.2250	4.2250	0.1112	0.7398
S x G	1	13.2250	13.2250	0.3480	0.5672
ERROR	36	1368.3000	38.0083		
WITHIN CELLS	0	0.0			

S = Social relatedness.
G = Genetic relatedness.

10.4.4.2
The number of pups born

The ANOVA (see table 10.2 for summary) indicated there to be no significant effect of social relatedness (F=0.8694, df 1,36, p=0.6400), genetic relatedness (F=0.1852, df 1,36, p=0.6730) or an interaction effect (F=0.4167, df=1,36, p=0.5295). The number of pups born alive in a litter is unaffected by either genetic or social relatedness.

In summary, the results of this experiment indicate that rats who have been in contact with each other from days 2 - 40 tend to produce litters at a later age than those separated during this time period. There seems to be no effect of genetic relatedness, nor once fertilization has taken place does there seem to be an effect of social or genetic relatedness.

10.4.5
Discussion

This study demonstrates that social exposure of individuals prepuberally leads to a delay in the litter production by these individuals compared to those individuals not socially exposed prepuberally. There appears to be no affect of genetic relatedness on litter production and this may be due to the fact that at this age individuals only genetically related no longer prefer their siblings (see Chp. 3, section 3.7). There was no effect of relatedness on number of pups born.

TABLE 10.2

The effect of social and genetic relatedness on the number of pups born in each litter.

Summary of Analysis of Variance

SOURCE	DF	SS	MS	F	PROB
SUBJ	39	728.4000			
S	1	16.9000	16.9000	0.8694	0.6400
G	1	3.6000	3.6000	0.1852	0.6730
S x G	1	8.1000	8.1000	0.4167	0.5295
ERROR	36	699.8000	19.4389		
WITHIN CELLS	0	0.0			

S = Social relatedness.
G = Genetic relatedness.

The main effect of this experiment was that individuals delayed litter production if reared together. This has also been observed by Hill (1974) in the prairie deer mouse, Peromyscus maniculatus bairdii, where individuals paired prepuberally showed delayed reproduction when adult compared to individuals not previously exposed to each other. Both this study and Hill (1974) argue for a behavioural mechanism to be involved in this delay, and there may be a number of possible mechanisms to explain this.

Individuals reared together may be less sexually attracted to each other (a hypothesis first advanced by Westermarck (1921) to explain the incest taboo in man). Westermarck (1921) argues for this reduced attractivenss to be instinctive, however later workers argue for experiential determination and Bateson (1980) proposes 4 mechanisms which could lead to a reduction in attractiveness: a) Punishment. Individuals constantly exposed to one another compete for various resoures and because they sometimes loose the other individuals become mildly aversive and therefore decrease in attractiveness. b) Frustration. Individuals early sexual advances are thwarted and this leads to frustration and these individuals are avoided in later life. A similar idea was proposed by Freud (1913) to explain the human incest taboo, similarly by Fox (1962). c) Sexual Boredom. Individuals achieve copulation with littermates during adolescence and become habituated to them and when adult are more strongly attracted to novel conspecifics. d) Aesthetic hypothesis. Individuals become familiar with fellow adolescents and when adult it is individuals who are slightly different from these that are preferred. All the above mechanisms result in the socially related individuals becoming less attractive.

Mating behaviour may have been interfered with by other activities. It has previously been argued that play behaviour habits established prior to puberty interfere with adult copulatory behaviour in rats (Kagan and Beach 1953). It may be that individuals who are together for the play period come to arrive at particular kinds of behaviour which are preferred, behavioural matching. Thus when re-introduced on day 41, the socially related rats, as they have behaviours in common can carry on playing. The unrelated rats who may not have as many behaviours in common, have to develop other behaviours, mating being one of these, and these individuals mate earlier.

A final possibility which may explain the deficit is physiological inhibition, that is, the animals may equally well copulate but in socially related animals physiological mechanisms prevent production of young. Sexual maturation may be delayed by the presence of familiar members of the opposite sex (cf., Hoogland, 1982; Koenig and Pitelka, 1979). There may be a prevention of fertilization or implantation, or a resorption of embryos.

Thus there are a number of possible mechanisms which could delay sibling mating in the rat and allow inbreeding to be avoided, and I shall consider how this delay in reproduction may serve the rat in inbreeding avoidance later. First I shall consider the mating situation more closely and analyse the behaviours occuring during this to see if the behaviours exhibited are affected by the relatedness of the individuals.

10.5

THE ROLE OF THE MALE AND FEMALE IN MATING

Traditional views of the mating situation argue that the female should be more discriminating in her sexual behaviour than the male (Barash, 1977). This view arises from a comparison of the investments made by the male and female in mating. Females invest more starting off from gamete production. In mammalian species where anisogamy is present, the female gamete is much larger than the male gamete. Once pregnant, it is the females who carry the developing embryo and are unable to remate, whereas the male can continue mating. From this dichotomy it has been proposed that the female should be more selective than the male (Trivers, 1972), and this leads to two different strategies being proposed for the mating behaviour of males and females. The male, because he can produce an unlimited supply of gametes and has the potential to mate with many different females, should be expected to do just that and mate indiscriminately with as many females as possible. Females on the other hand, because of their greater investment and limited opportunity to mate, should be expected to choose and mate with the best possible male.

Although the female invests more and should therefore be more selective, the view that the male incurs trivial costs has been questioned. Dewsbury (1982) points out that although one for one the male gamete (sperm) is considerably 'less expensive' than the female gamete (egg), male gametes are not produced singly but in vast quantities (the ejaculate) and it is this which should be compared to the egg. The view that repeated ejaculations have an insignificant effect on male reproductive success is also questioned. For insemination to occur, the sperm count must be high and repeated ejaculation decreases the sperm count (e.g., see Halliday, 1976) and thus decreases the likelihood of insemination. Thus although the female's investment in mating is greater than that of the male the male's investment is not trivial and the male does incur costs by engaging in mating. Inbreeding reduces fitness and as such should be avoided by both sexes, with the possibilty of the female showing more signs of this than the male as her investment is greater.

This view of the female being more selective has coloured the view taken by investigators studying mating behaviour in the rat. With the male's motives considered to be to copulate and ejaculate as fast as possible to achieve sperm transmission (Dewsbury, 1982) investigators have viewed the male as being the controlling influence on the mating situation (McClintock, 1974) and accordingly most studies of rat mating behaviour have concentrated on male determined measures and behaviour. The majority of studies of rat mating behaviour have been performed in the laboratory and can be challenged on two grounds. First and obviously, the behaviour has taken place in an artificial physical setting with unusual social conditions, for example, Dewsbury (1967), studied rat mating in pairs, a situation rarely occuring naturally. Second, the female is often described as passive when there is evidence that the female plays an active role (McClintock, 1974).

The induction of the progestational state necessary to allow implantation of the ova and the maintenance of pregnancy requires multiple intromissions (Adler, 1969), these intromissions being necessary to ensure sperm transport from the vagina to through the cervix into the uterus (Chester and Zucker, 1970). However the female requires these intromissions to be appropriately spaced or the progestational state may not be induced (McClintock, 1974) and intromissions too soon after an ejaculation may inhibit sperm transport (Adler and Zoloth, 1970). The female adopts an active role by the use of soliciting behaviour which can induce the male to mate. Using such behaviour the female can control the amount and spacing of intromissions and can therefore regulate the induction of the progestational state required for successful fertilization (McClintock, 1974). The females also remain quiescent after an ejaculation and prevent the inhibition of sperm transport through premature intromission (McClintock et al., 1982). It does therefore seem that the female as well as the male exerts an effect over the mating situation and one may expect both sexes to act to avoid inbreeding.

10.6

THE MATING BEHAVIOUR OF RATS

Whilst there have been many studies of the mating behaviour of rats in the laboratory there have been few studies of the mating behaviour of rats in the wild. Telle (1966) reports that females do not mate with a single mate but when receptive are followed by a number of males which may mate with her.

In contrast to the scarcity of the naturalistic observations, the mating behaviour of rats has been well documented in the laboratory. For a more thorough and comprehensive study of rat mating behaviour readers are referred to Barnett (1975), Beach (1956), Dewsbury (1967), Diakow (1975), Grant and McIntosh (1963), McClintock (1974), Munn (1950), Sachs and Barfield (1976) and references therein.

Typically the mating behaviour of rats commences with a period of investigatory behaviour, in which both sexes sniff each other, concentrating on the anogenital region.

The male then chases the female, who may respond with a dart hop, the male then mounts the female gripping her sides and the female adopts the lordosis position. The male then may then produce a series of rapid pelvic thrusts, an intromission, terminated by rapid dismounting. After a number of intromissions, often separated by sniffing or licking of the anogenital region by the male, and sometimes the female, the male ejaculates. After ejaculation the male undergoes a period of quiesence where he is unable to mate, the absolute refractory period. After a time the male is able to commence mating and the sequence is repeated, however there is no investigatory behaviour.

10.7

EXPERIMENT 10.2:

INBREEDING AVOIDANCE IN THE RAT: THE EFFECT OF DIFFERENT PREPUBERAL RELATIONSHIPS ON THE BEHAVIOUR OF THE MALE AND FEMALE DURING MATING

In this experiment it was decided to investigate more closely the mating behaviour of 'sibling' rats to see if they showed signs of inbreeding avoidance. The effect of social and/or genetic relatedness on the 'siblings' behaviour was examined. Social relatedness refers to pups which had been in contact prior to the time of testing and genetic relatedness refers to whether the pups were siblings (r=0.5). Four test conditions were used, individuals that were socially and genetically related (SG), individuals only socially related ($S\tilde{G}$), individuals only genetically related ($\tilde{S}G$), and a control condition in which individuals were neither socially or genetically related ($\tilde{S}\tilde{G}$).

The behaviour of the individuals was divided into three catagories, investigatory behaviour, male determined behaviour and female determined behaviour. It was hypothesised that as the female invests more than the male one may expect more signs of inbreeding avoidance to be noticed in female determined behaviour, however as the male also invests in mating there may also be some effects in male determined behaviour.

Rats were observed in trios, two females and a single male. The male and one female (the related female, R) were related by one of the four test conditions. The other female (the unrelated female, $\tilde{R}$) was unrelated both socially and genetically to the other rats. Trios were used because although not mimicing the natural situation it may allow signs of inbreeding avoidance to be observed. It allows the male to direct his behaviour to one or other female, and comparison of the behaviour of each female may indicate a difference in their behaviour to the male.

The effects of inbreeding avoidance may be observed in two ways. First, there may be overall differences in the behaviour of each trio dependent on the relatedness of the pair within each trio. Second, there may be a difference within trios between the behaviour of the male to the R and $\tilde{R}$ female or in the behaviour of the R and $\tilde{R}$ females to the male. The effects of repeated ejaculations on behaviour was also examined, for this each trio was observed for four ejaculations to see if this exerted any effect on behaviour.

10.7.1

Subjects

Twenty litters of Sprague-Dawley rats were used in this experiment. All litters were born in the Department of Psychology, University of Durham, to parents originally supplied by B & K (Animal Suppliers) Ltd. All parents were unrelated to each other. The day each litter was born was termed day 0, each litter was culled to 8 members on day 2, 4 males and 4 females, and placed into one of 2 rearing conditions.

Rearing Condition 1: 12 litters were placed in this condition, each litter was left as born and the pups remained in these litters for the duration of the experiment.

Rearing Condition 2: 8 litters were placed in this condition. Litters were then rearranged to form 8 new litters such that each new litter contained one member from each of the original litters. These litters were then left for the duration of the experiment.

All pups in the experiment were marked with a black

Carioca felt tip pen for identification from day 2-12 and thereafter when necessary with alcoholic Picric acid, until approximately 30 days when all rats were ear punched for individual identification. All litters were housed in plastic Bowman's cages (16"x12"x7"), with food and water freely available. The rats were kept on a 12 hour light/dark cycle with darkness commencing at 1200 hours. Pups were left with their mother until day 25 and then the mother was removed and the pups weaned.

To ensure that the females were equally receptive, it was decided to ovariectomize the females and use hormone replacement treatment. Females were ovariectomized under ether anesthesia between days 45-55 (see Waynforth, 1980, for surgical technique). All females were left for three days after the operation before commencing hormone replacement treatment. Females were given 0.1cc oestradiol (10 micrograms oestradiol benzoate per 0.1cc) injected subcutaneously daily for three days and thereafter given 0.2cc every other day until the time of testing.

After ovariectomy, the males and females in each litter were separated from each other to prevent mating. Litters were rehoused in 0.5" wire mesh stock cages (Bowman's, 33"x16"x8"), the stock cages were divided into 2 by a half inch wire mesh dividing wall and the males and females placed on either side, this allowed the males and females to experience their littermates but prevented mating.

10.7.2

Procedure

Rats were tested in groups of three consisting of one male and two females. In these trios the male was related to one of the females (R) by one of the 4 possible test conditions, the other female ($\tilde{R}$) was unrelated to both other rats.

Condition 1: SG. In this condition the male and female were both socially related (had been reared together) and genetically related (siblings). These rats were obtained from rearing condition 1.

Condition 2: $S\tilde{G}$. In this condition the male and female were only socially related. These rats were obtained from rearing condition 2.

Condition 3: $\tilde{S}G$. In this condition the male and female had been separated since day 2 and were thus socially unrelated but were genetically related. These rats were obtained from rearing condition 2.

Condition 4: $\tilde{S}\tilde{G}$. In this condition the male and female were neither socially nor genetically related and this was used as the control condition.

Ten trios were used for each condition, and no rat was used more than once. Testing took place in a circular open field, 90 cm in diameter, 30 cm high with blackened walls. Clean shavings were placed on the floor. Prior to testing all animals were habituated to the arena by placing them individually in the arena for 30 minutes. All tests took place in the dark part of the lighting cycle under dim red light commencing approximately two hours after darkness (1400 hrs.) and no test was started 5 hours after the onset of darkness (1700 hrs.). No rats had any prior copulatory experience and were tested between 80-90 days of age. Each female up until the time of testing had received hormone replacement treatment for 30-32 days, and observations at this laboratory indicated this to be adequate to make the female receptive.

For each test the male was placed into the open field first and left for 5-10 minutes. Both females were then introduced simultaneously into the arena, females were marked for identification with an odourless felt tip pen. Each test was recorded on video for later analysis. A video timer was started with the introduction of the females to allow the time course of the behaviour to be recorded. Testing continued until the male achieved four ejaculations and was stopped after the first intromission after the fourth ejaculation.

10.7.3

Behavioural Analysis

For analysis the mating situation was divided into three periods.

The Introductory Period (I.P.): The period from the introduction of the female into the arena until the first mount/intromission by the male.

The Ejaculation Latency Period (E.L.P.): The period from the first mount/intromission in a mating series to the ejaculation.

The Post-Ejaculatory Interval (P.E.I.): The period following ejaculation until the next mount/intromission.

A mating series comprised of an E.L.P. followed by the P.E.I., as rats were mated for four series there were 4 E.L.P.'s and 4 P.E.I.'s. The following behaviours were recorded.

10.7.3.1

The Introductory Period

The number of times the male sniffed each female: This behaviour was defined after Dewsbury (1967) as occuring when the male approached the female and sniffed part of her body and remained orientated with his head to the female's body but not attempting to mount. This behaviour classified as an investigatory behaviour.

The number of times each female sniffed the male: This behaviour was defined as for male sniffing except that it is the female who approaches the male and sniffs part of his body. This was likewise classified as an investigatory behaviour.

10.7.3.2
The Ejaculation Latency Period

The time of the first mount/intromission in each series: A mount/intromission was defined as the male approaching the female from behind, mounting her by placing its front feet on her flanks and the female adopting the lordosis position, back arched downwards, head and anal region raised and tail deflected to one side. The male then produces a series of rapid pelvic thrusts which are terminated by a rapid step backwards.

The time of ejaculation in each series: An ejaculatory response was very similar to that of mount/intromission except that the pelvic thrusting continues for longer period of time (2-3 times longer, personal observation) and is terminated by the male 'falling' off rather than a rapid step backwards.

The time of ejaculation latency: This was the time taken from the first mount/intromission to the ejaculation in each series. The above three measures have been traditionally regarded as male determined measures of sexual behaviour and have been considered as such here.

The female of first mount/intromission in each series: The female which the male first mounted/intromitted in each series was recorded.

The female of ejaculation in each series: The female of ejaculation in each series was recorded.

Number of mount/intromissions to each female: The number of mounts/intromissions each female received was recorded. This behaviour was considered as mainly male determined behaviour.

The number of times the male sniffed each female: see Introductory Period.

The number of times each female sniffed the male: see Introductory Period.

The number of solicitations used by each female: A solicitation was defined behaviourally as the female running towards the male, usually to its head, then turning (if necessary) and stopping in front of the male facing away and then possibly hopping forward. The episode from running to dart hop was considered as one solicitation. This behaviour was regarded as a female determined behaviour.

The number of times each female was nearer: The video was halted every ten seconds and which female was nearest the male recorded. If the two females were in contact then it was decided to call the females equally near.

10.7.3.3
The Post-ejaculatory Interval

The number of times the male sniffed the female: see Introductory Period.

The number of times each female sniffed the male: see

Introductory Period.

The number of solicitations used by each female: see Ejaculation Latency Period.

The number of times each female was nearer: see Ejaculation Latency Period.

Time of post-ejaculatory interval: The time from ejaculation to next mount/intromission was recorded for each series.

10.7.4

Analysis

For the purposes of analysis each trio was considered as a single unit. The results were analysed by using an analysis of variance (ANOVA). This experiment investigates the effects of four factors on the various behaviours involved in mating. Two between-trio factors: social relatedness, ($S/\tilde{S}$), and genetic relatedness, ($G/\tilde{G}$), and 2 within-trio factors: female relatedness, ($R/\tilde{R}$), and mating series, (1-4).

The time of first mount/intromission in each series and the time of ejaculation in each series were analysed using a 2x2 ANOVA of between-trio factors of social relatedness and genetic relatedness (see Winer, 1962).

The effect of series, social and genetic relatedness on the time of ejaculation latency and the time of the post-ejaculatory interval was examined by a 2x2x4 ANOVA (see Winer, 1962) with 2 between-trio factors of social and genetic relatedness and a within-trio factor of series.

In the I.P. the number of times the male sniffed each female and the number of times each female sniffed the male was analysed by a 2x2x2 ANOVA (see Winer, 1962) with between-trio factors of social and genetic relatedness and a within-trio factor of female relatedness.

The remaining behaviours, the number of times the male sniffed each female, and the number of times each female sniffed the male, the number of times each female solicited the male, the number of times each female was nearer in both the E.L.P. and the P.E.I., and the number of mount/intromissions in the E.L.P. were analysed by a 2x2x2x4 ANOVA (see Winer, 1962) with between-trio factors of social and genetic relatedness and within-trio factors of series and female relatedness.

The female of first mount/intromission and the female of ejaculation were analysed separately for each of the four test conditions. The number of times the male choose the related female (R) in each series and overall was analysed by means of a binomial test (see Siegel, 1956).

10.7.5
Results

Only details of significant results will be discussed below, full summary tables of the ANOVA's can be found in the appendix, see appendix 10.

10.7.5.1
Introductory Period

The number of times the male sniffed the female: There was a significant interaction between female relatedness and genetic relatedness (F=4.8649, df 1,36, p=0.0319). The male sniffed the related female less than the unrelated female when she was genetically related, but sniffing the related female more when not genetically related (see fig. 10.1).

The number of times each female sniffed the male: There was a significant effect of female relatedness (F=4.1436, df 1,36, p=0.0466), the related female sniffing the male less (mean no. of sniffs 1.225) than the unrelated female (mean no. of sniffs 1.800).

10.7.5.2
Ejaculation Latency Period

The female of first mount/intromission: No significant effects.

The female of ejaculation: No significant effects.

Time of first mount/intromission in each series: No significant effects.

Time of ejaculation in each series: No significant

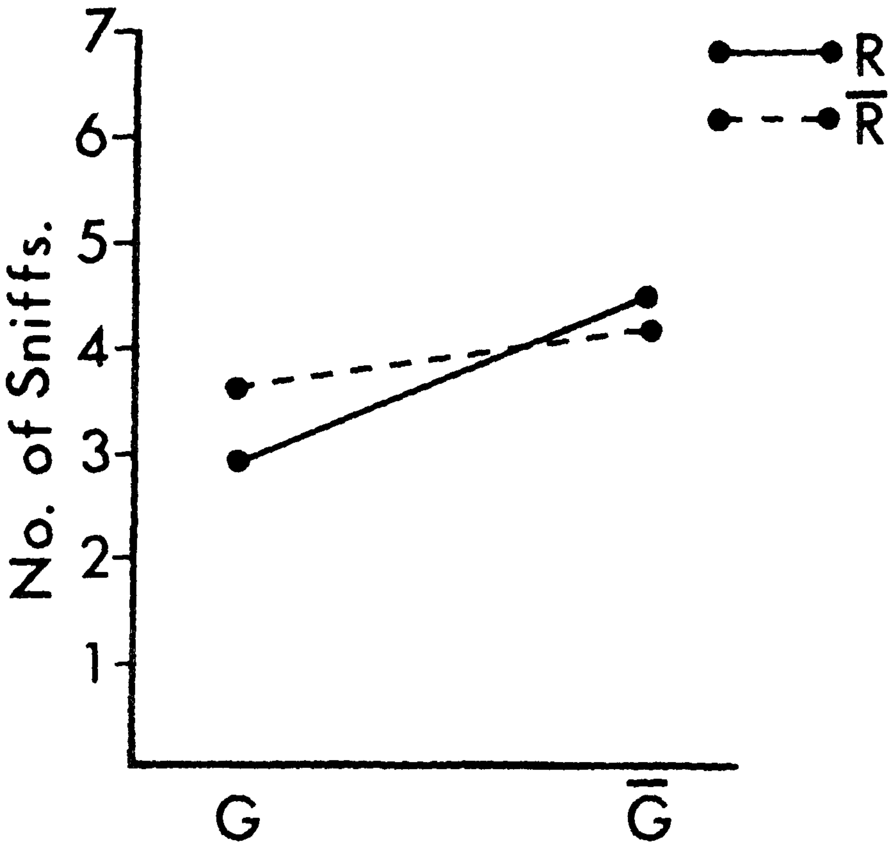

FIGURE 10.1
Mean number of times the male sniffed the related (R) and unrelated ($\tilde{R}$) female in trios where the related female is either genetically (G) or non-genetically ($\tilde{G}$) related to the male during the I.P.

effects.

Length of Ejaculation latency period: There was a significant effect of series (F=51.2758, df 3,108, p<0.0001). The time to achieve ejaculation decreased with successive ejaculations (see fig. 10.2). The effect seems mainly due to a large decrease in the time to ejaculate after the first ejaculation.

Number of mount/intromissions to each female: There was a significant effect of series (F=39.5954, df 3,108, p<0.0001), there being fewer mount/intromissions with successive ejaculations (see fig. 10.3). This decrease reflects the decreasing time taken to ejaculate in successive series (cf. fig. 10.2). There was also a significant effect of female relatedness (F=11.8527, df 1,36, p=0.0018), related females receiving fewer mount/intromissions (mean, 6.575) than unrelated females (mean, 8.581).

There were also significant interactions between series, social relatedness and genetic relatedness (F=2.9031, df 3,108, p=0.0374, see fig. 10.4) and between female relatedness, series and genetic relatedness (F=2.8534, df 3,108, p=0.0398, see fig. 10.5). Observation of the graphs of these interactions (fig. 10.4,10.5) indicates that the results of series 1 are very different from those of series 2-4 in numerical size, and it may be this large difference which causes the interaction effects. The ANOVA was thus repeated using log+1 transformed scores. The main effects of familiarity

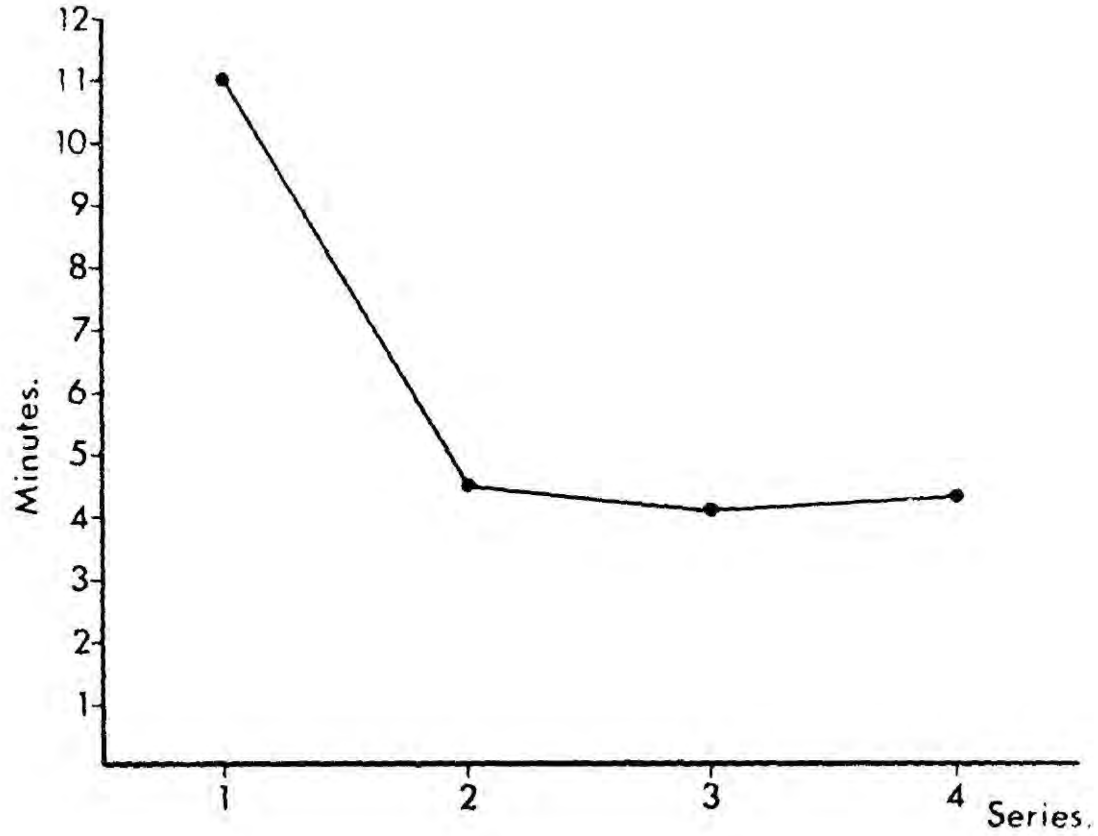

FIGURE 10.2
Mean length of ejaculation latency period in each mating series.

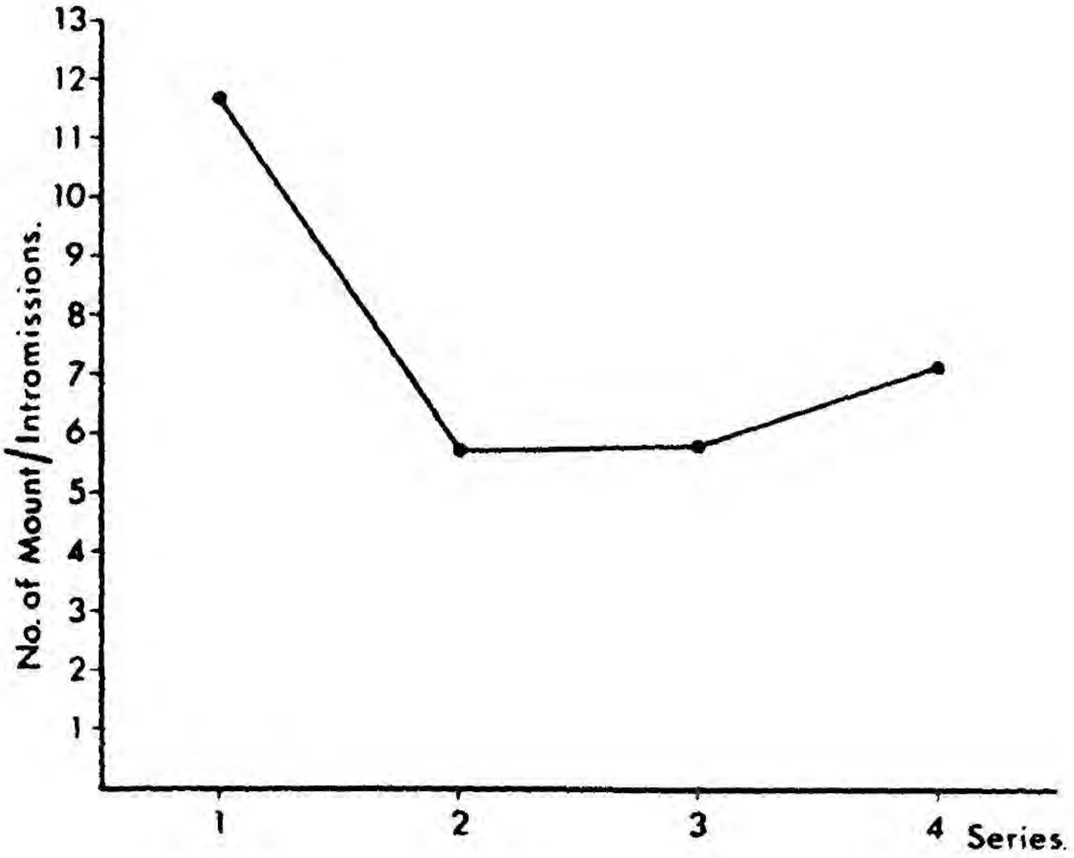

FIGURE 10.3
Mean number of mount/intromissions in each mating series during the E.L.P.

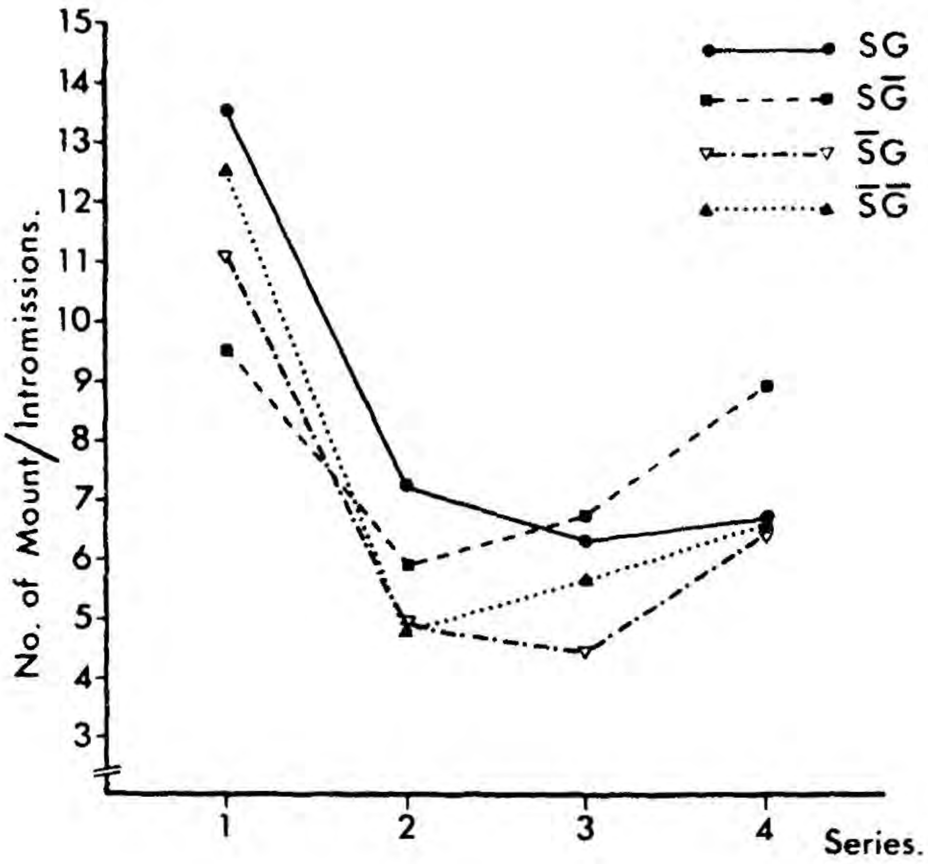

FIGURE 10.4
Mean number of mount/intromissions given by the male in trios containing an SG, SG̃, S̃G, and S̃G̃ related pair in each series during the E.L.P.

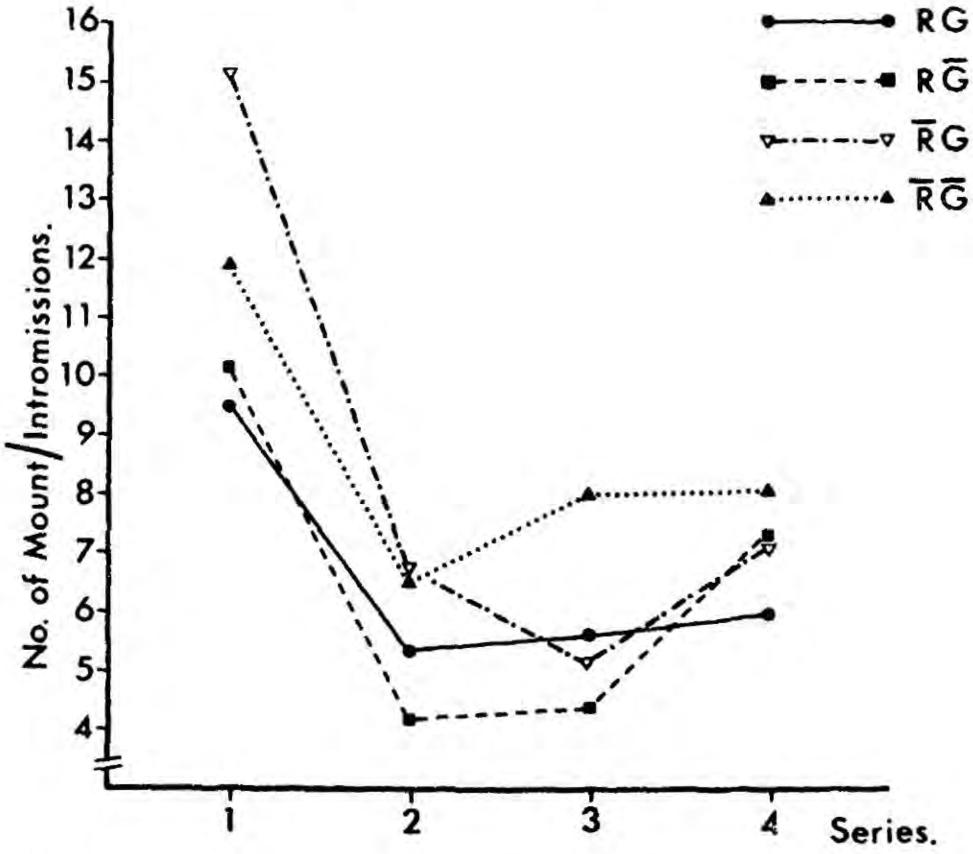

FIGURE 10.5
Mean number of mount/intromissions given by the male to the related (R) and unrelated (R̃) females when either genetically (G) or non-genetically (G̃) related to the male in each series during the E.L.P.

(F=7.3349, df 1,36, p=0.0100) and series (F=52.5922, df 3,108, p<0.0001) remained. The 3-way interactions were eliminated as expected, but there was an interaction between series and social relatedness (F=3.5607, df 3,108, p=0.0165).

Number of solicitations by each female: There was a significant interaction between social and genetic relatedness (F=13.9714, df 1,36, p=0.0009), mainly due to the low number of solicitations given by trios containing a ~SG pair (see fig. 10.6). There was a significant effect of series (F=29.3380, df 3,108, p<0.0001), there being fewer solicitations with successive ejaculations (see fig. 10.7) although this seems to be mainly due to a large decrease in solicitations after the first ejaculation. This decrease may reflect the decrease in ejaculation latency with successive ejaculations (cf. figs. 10.7,10.2). There is a main effect of female relatedness (F=17.2330, df 1,36, p=0.0004), the unrelated female soliciting the male more than the related female (mean no. of solicitations 4.925 and 2.531 respectively). This is further qualified by a significant interaction between female relatedness and social relatedness (F=19.2696, df 1,36, p=0.0002), where in socially related trios the 'related ' female solicits much less than the unrelated female, whereas in non-socially related trios, there is no such difference (see fig. 10.8).

There were also significant interactions between female relatedness and series (F=6.3185, df 3,108,

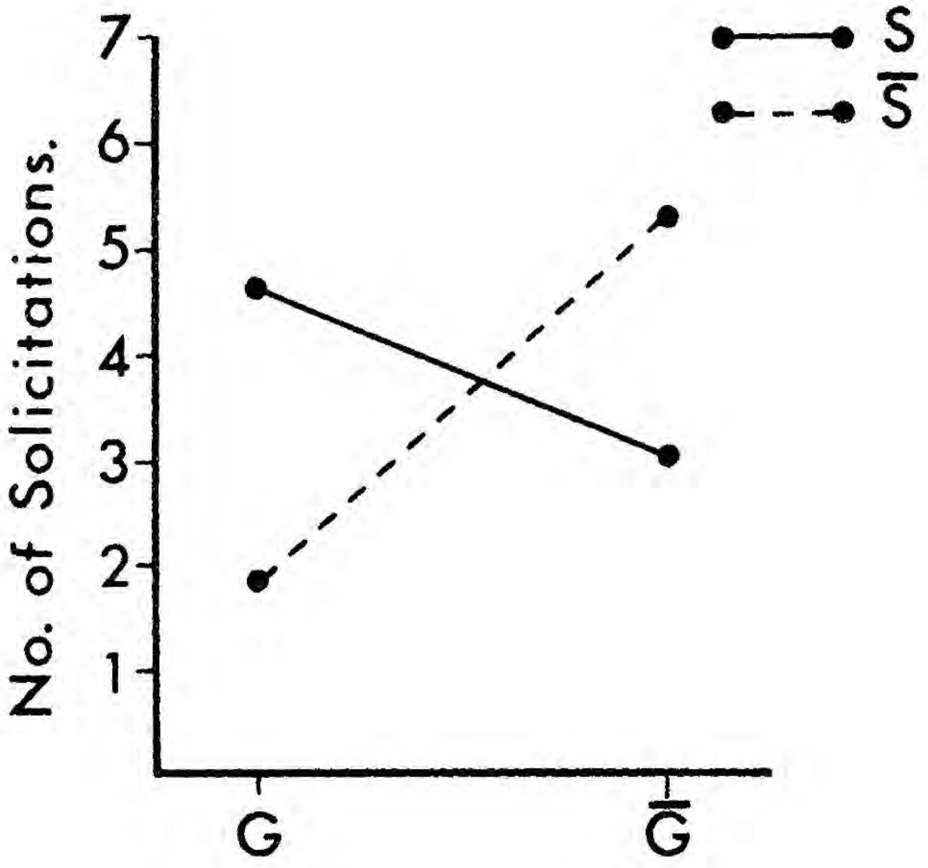

FIGURE 10.6
Mean number of solicitations given by trios containing females SG, SG̃, S̃G and S̃G̃ related to the male during the E.L.P.

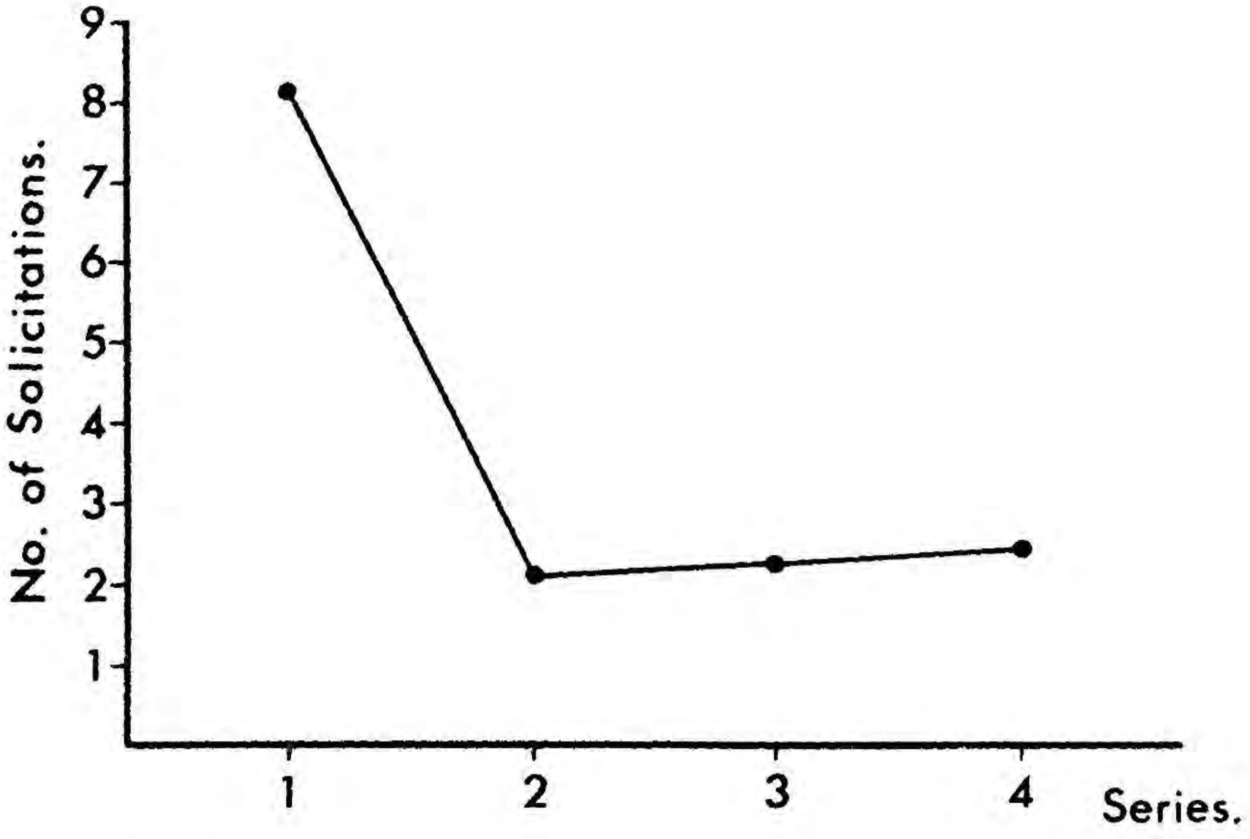

FIGURE 10.7
Mean number of solicitations given by females during the E.L.P. in each series.

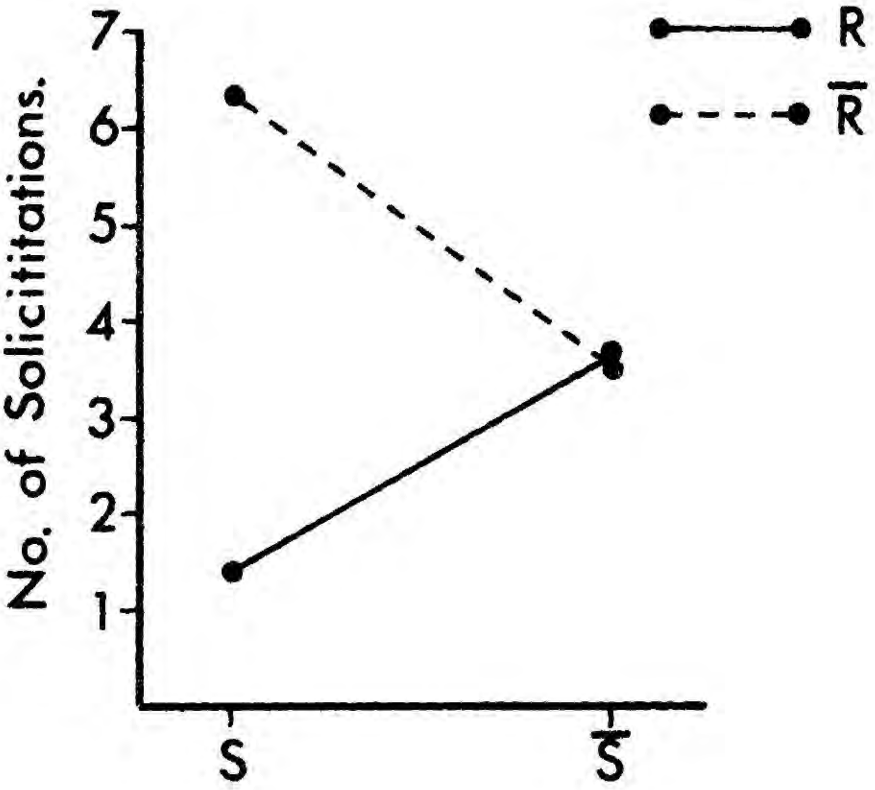

FIGURE 10.8
Mean number of solicitations given by the related (R) and unrelated (R̃) females in trios where where the related female was either was socially (S) or non-socially (S̃) related to the male during the E.L.P.

p=0.0008), social relatedness, series and genetic relatedness (F=4.8597, df 3,108, p=0.0036) and series, female relatedness and social relatedness (F=6.9332, df 3,108, p=0.0005). Observation of these graphs, figures 10.9, 10.10, 10.11 respectively, indicates a large numerical difference between the scores obtained in series 1 and those in series 2-4 which may account for the significance obtained from these results. To overcome this, the scores were transformed (log+1) and the ANOVA repeated. The interaction effects of social and genetic relatedness (F=26.3415, df 1,36, p<0.0001), and the main effect of series (F=28.4028, df 3,108, p<0.0001) and female relatedness (F=24.8622, df 1,36, p=0.0001) and the interaction between female relatedness and social relatedness (F=18.2735, df 1,36, p=0.0003) were still present. The interactions containing a series factor have now disappeared upholding the view these results were due to the large numerical discrepancy between the results in series 1 and series 2-4. The new analysis also produced a significant effect of genetic relatedness (F=6.8776, df 1,36, p=0.0122), genetically related trios giving fewer solicitations than non-genetically related trios.

<u>The number of times the male sniffed each female</u>: There was a significant effect of series (F=64.9491, df 3,108, p<0.0001), there being a decrease in sniffing with successive ejaculations (see fig. 10.12). This decrease is largest between series 1 and series 2-4 and reflects the decrease in ejaculation latency with successive ejaculations (cf. fig. 10.2, 10.12).

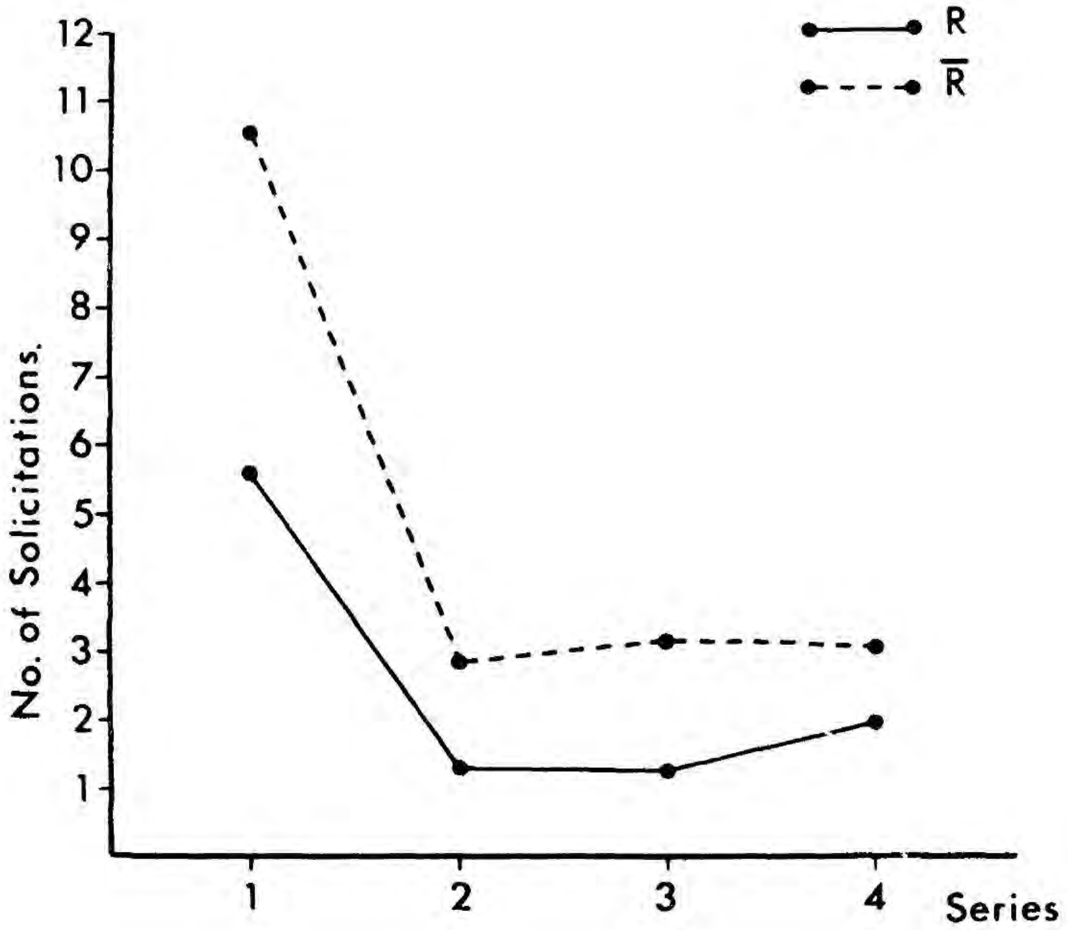

FIGURE 10.9
Mean number of solicitations given by the related (R) and unrelated (R̃) females during the E.L.P. in each series.

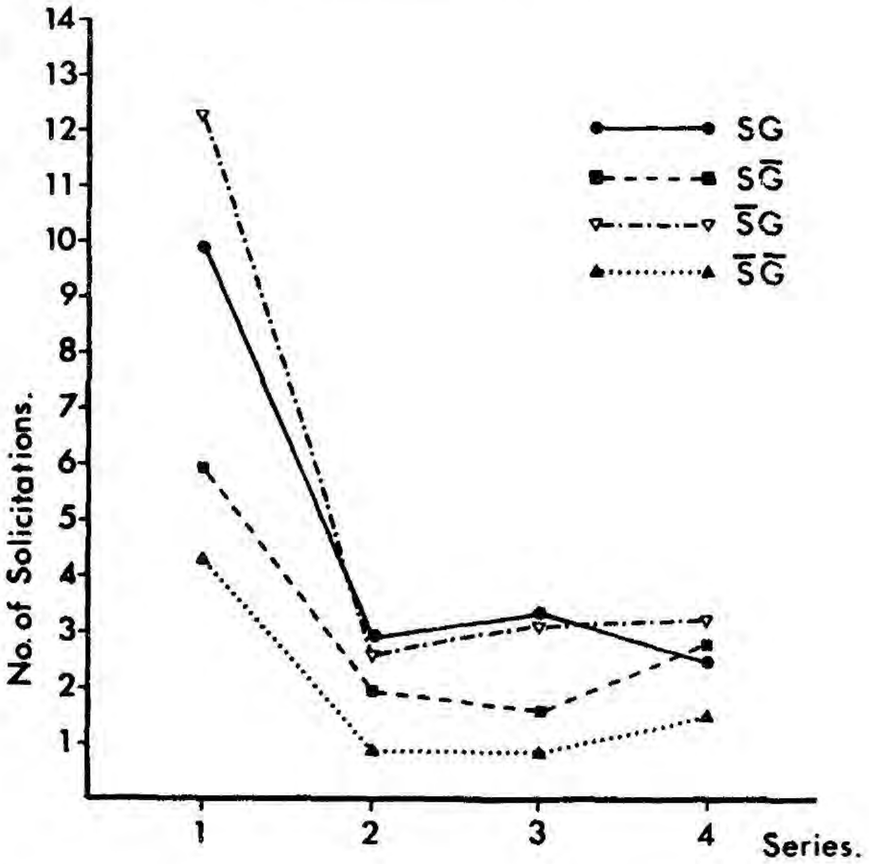

FIGURE 10.10
Mean number of solicitations given by the females in trios containing a SG, SG̃, S̃G, and S̃G̃ related pair during the E.L.P. in each series.

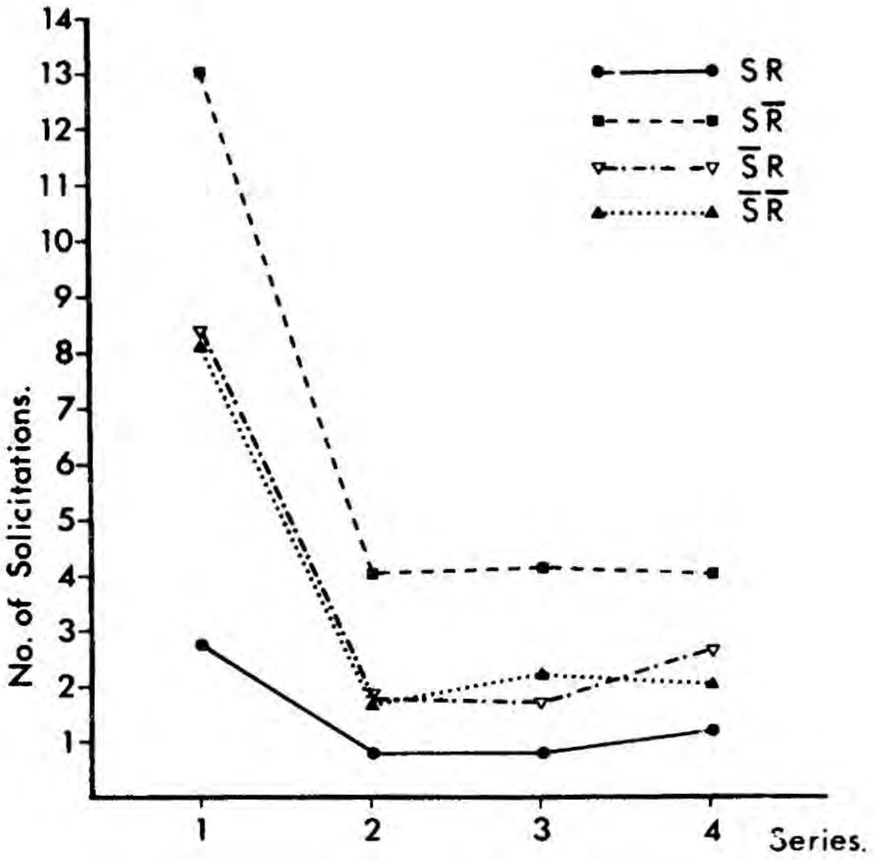

FIGURE 10.11
Mean number of solicitations by related (R) and unrelated ($\tilde{R}$) females in trios where the related female was either socially (S) or non-socially ($\tilde{S}$) related to the male in each series during the E.L.P.

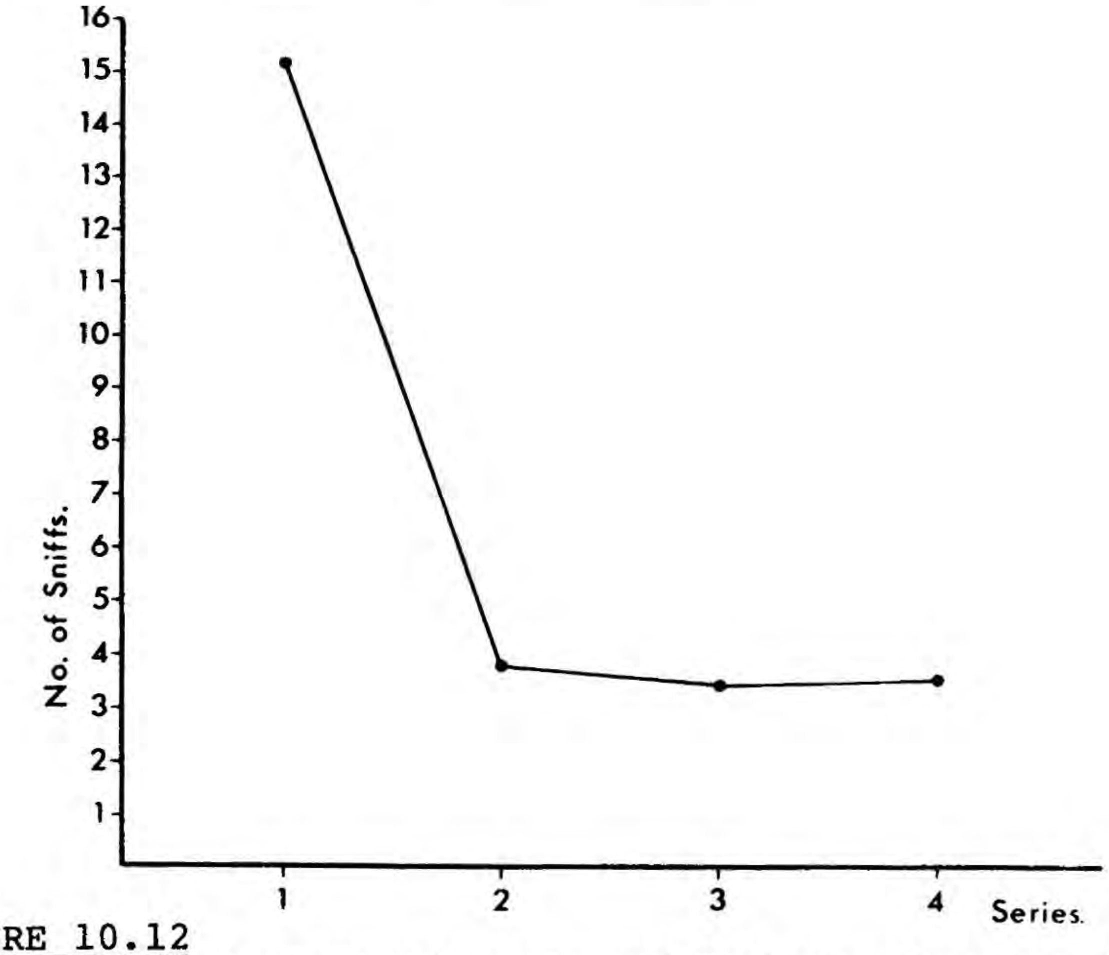

FIGURE 10.12
Mean number of times the male sniffed the females in each series during the E.L.P.

The number of times each female sniffed the male: There was a significant effect of social relatedness (F=6.6210, df 1,36, p=0.0137), socially related trios sniffing less than non-socially related trios (mean no. of sniffs, 4.156, 6.081,respectively. There was a significant effect of series (F=93.0305, df 3,108, p<0.0001), there being a decrease in the amount of sniffing with successive ejaculations (see fig. 10.13), the largest decrease occuring after series 1 and probably reflecting the decrease in ejaculation latency with successive ejaculations (cf. figs. 10.13, 10.2).

There were also significant interactions between series and social relatedness (F=6.9982, df 3,108, p=0.0004) and between female relatedness, series and genetic relatedness (F=4.2589, df 3,108, p=0.0072). Observation of the graphs of these interactions (figs. 10.14, 10.15) indicates that there are large numerical discrepancies between the scores on series 1 and the scores on series 2-4 and as in previous instances this may be causing the effect. The ANOVA was repeated using (log+1) transformed scores. Again there were significant main effects of social relatedness (F=8.6573, df 1,36, p=0.0058) and series (F=111.9328, df 3,108, p<0.0001), however there were no interaction effects, indicating the large numerical discrepancy may have accounted for these results.

The number of times each female was nearer: There was a significant effect of series (F=43.0691, df 3,108,

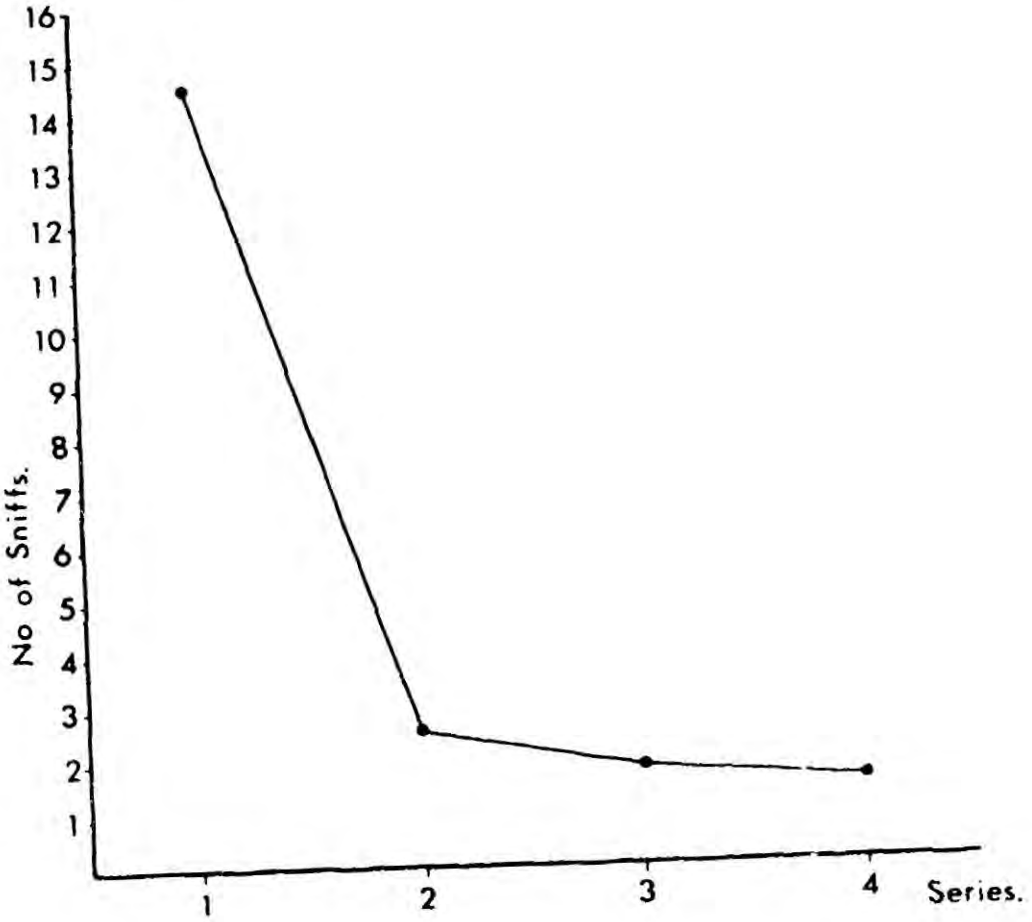

FIGURE 10.13
Mean number of times the females sniffed the male during the E.L.P. in each series.

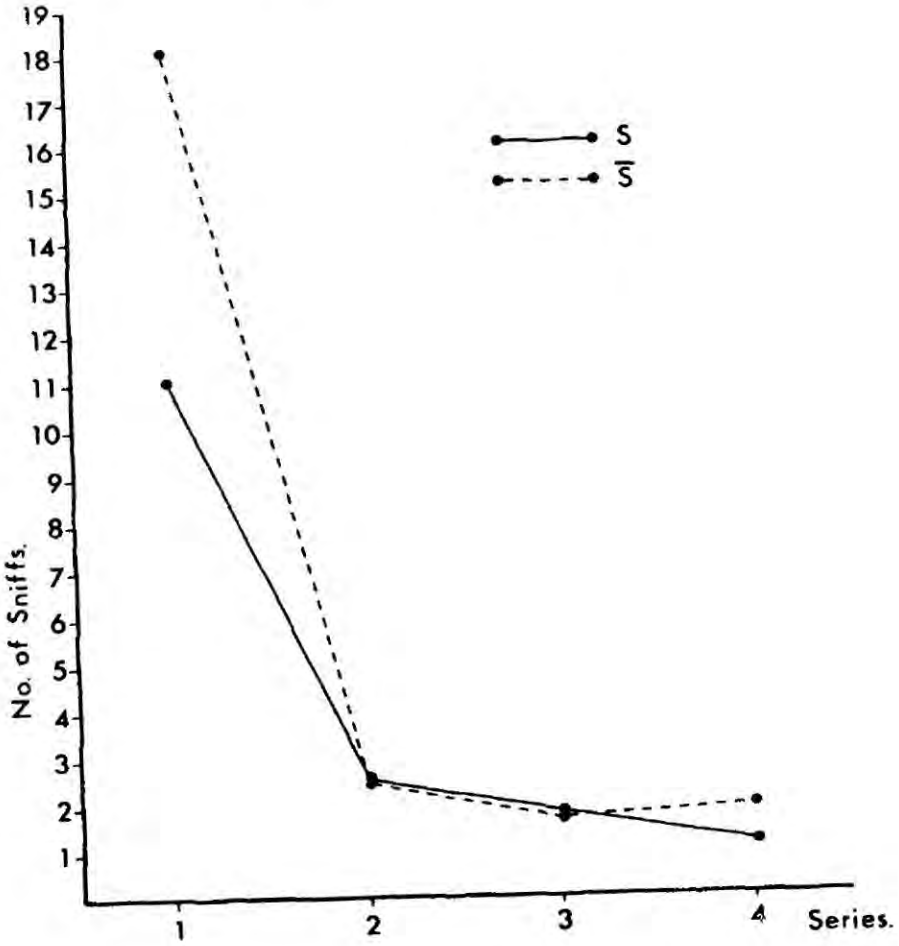

FIGURE 10.14
Mean number of times females in socially (S) and non-socially (S̃) related trios sniffed the male during the E.L.P. in each series.

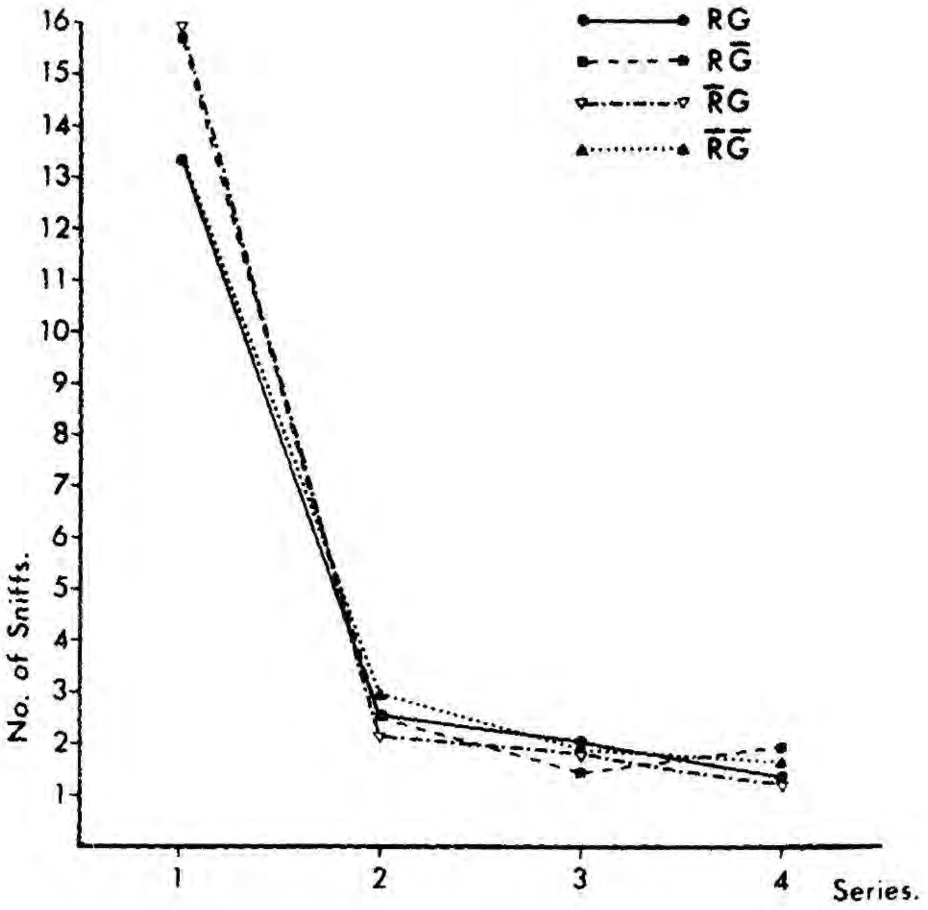

FIGURE 10.15
Mean number of times the related (R) and unrelated ($\tilde{R}$) female sniffed the male when the related female was either genetically (G) or non-genetically ($\tilde{G}$) related to the male in each series during the E.L.P.

p<0.0001), the number of times the females were nearer decreasing with successive ejaculations (see fig. 10.16). This reflects the decreasing time taken to ejaculate with successive ejaculations (cf. figs. 10.16, 10.2).

10.7.5.3
Post-ejaculatory Interval

Length of post-ejaculatory interval: There was a significant effect of series (F=55.7325, df 3,108, p<0.0001), the time taken to recover from successive ejaculations increasing (see fig. 10.17).

The number of times each female sniffed the male: There was a significant effect of series (F=19.2921, df 3,108, p<0.0001), the amount of sniffing decreasing with successive ejaculations (see fig. 10.18).

The number of times the male sniffed each female: There was a significant effect of social relatedness (F=7.2058, df 1,36, p=0.0106). Males in trios containing a socially related female sniffing more (mean no. of sniffs, 3.475) than males in trios without a socially related female (mean no. of sniffs, 1.656).

Number of solicitations used by each female: There was a significant interaction between social and genetic relatedness (F=11.5991, df 1,36, p=0.0020), probably due to the small amount of solicitations used by females in the S̃G trios (see fig. 10.19). There was a significant effect of female relatedness (F=15.3941, df 1,36, p=0.0006), the related female giving fewer solicitations (mean no. of solicitations, 1.594) than the unrelated

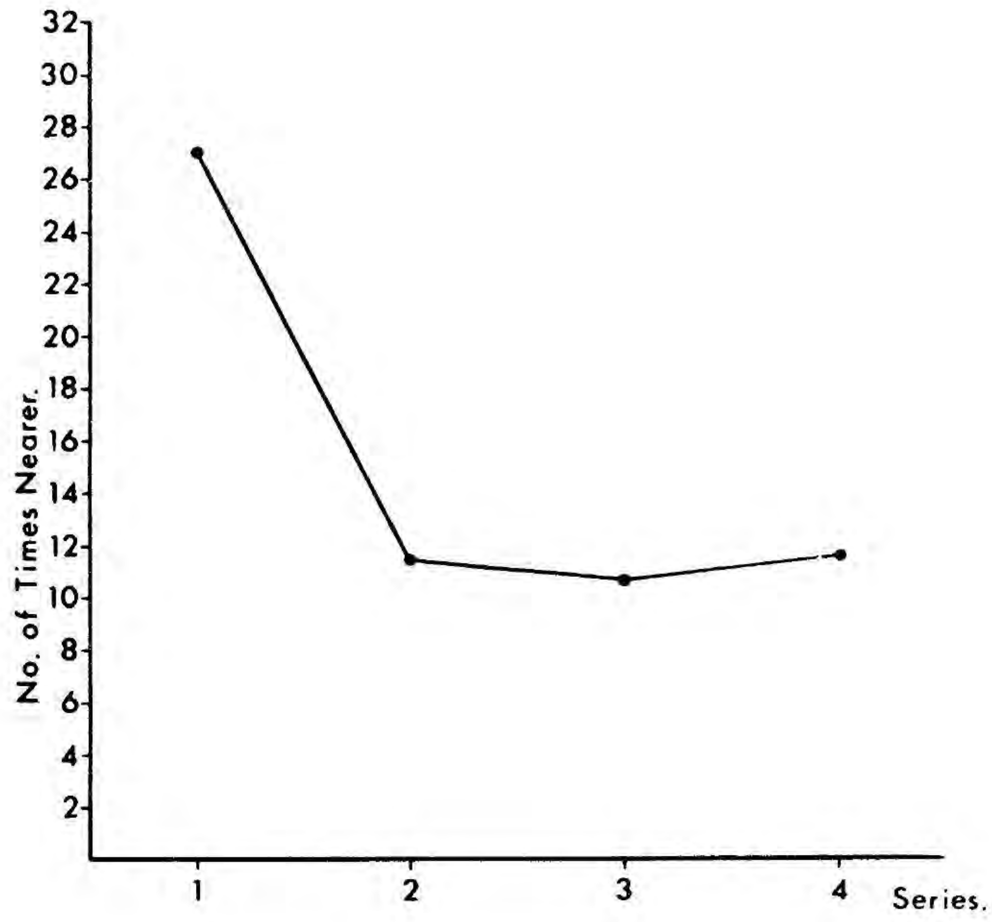

FIGURE 10.16
Mean number of times females were nearer in each series during the E.L.P.

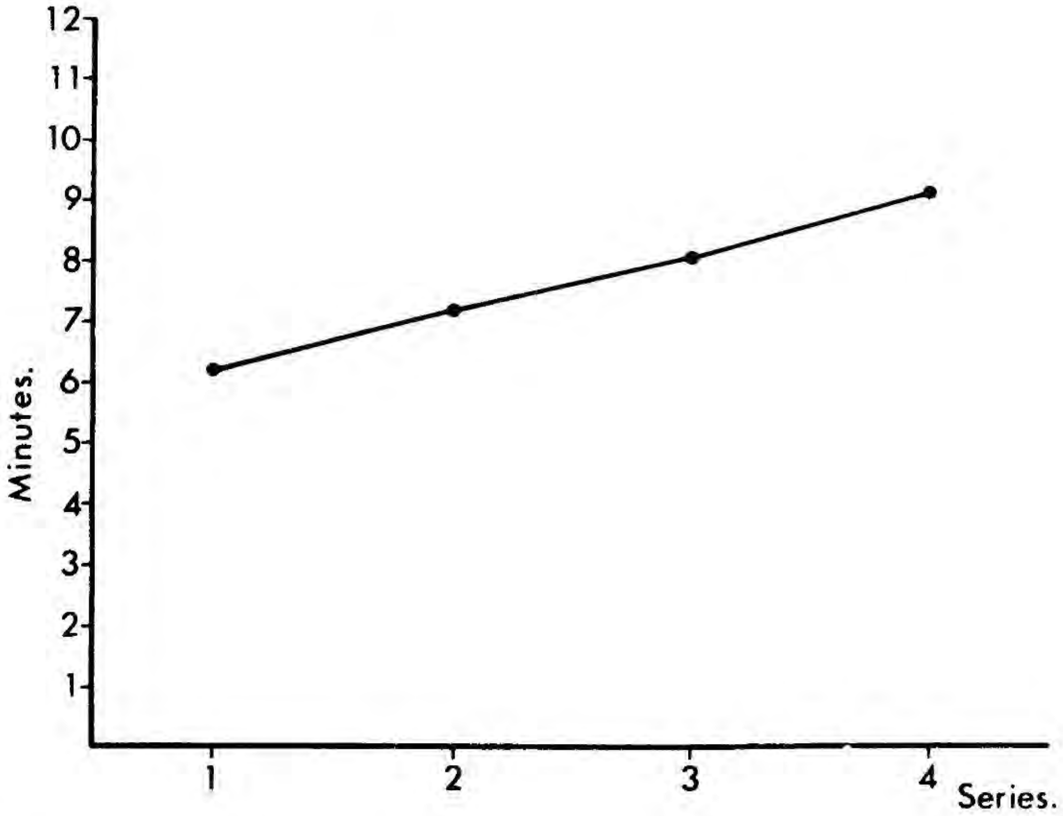

FIGURE 10.17
Mean length of the P.E.I. in each series in minutes.

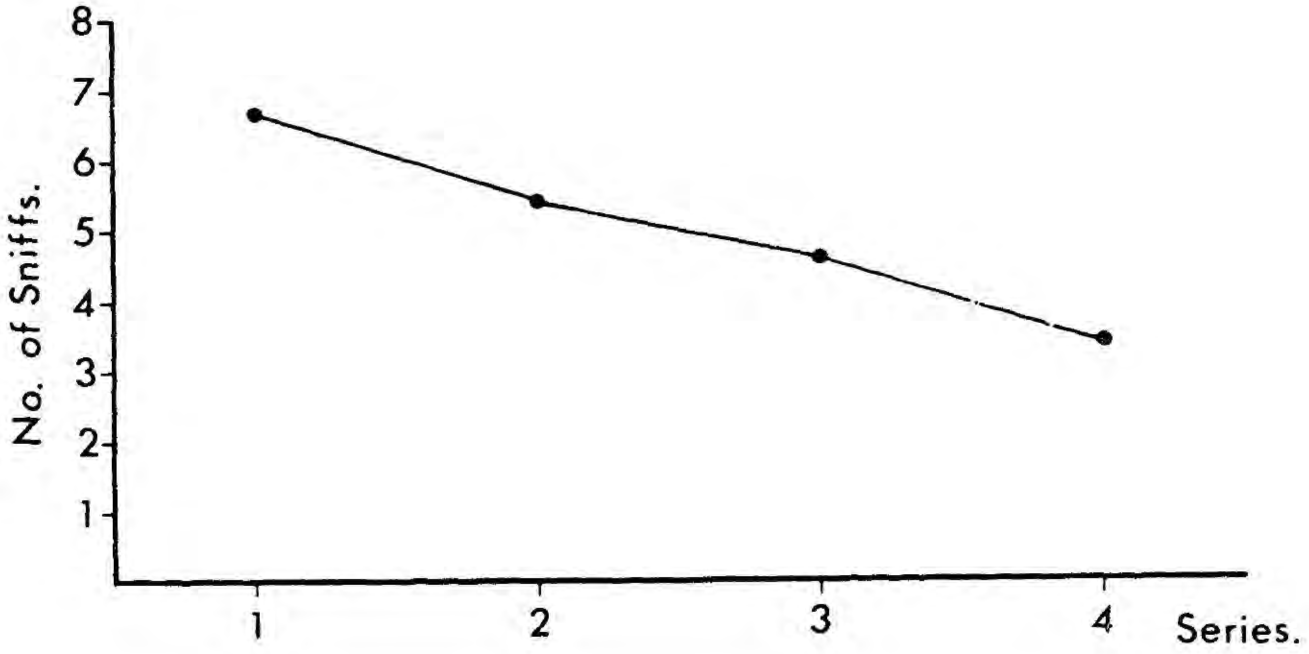

FIGURE 10.18
Mean number of times the females sniffed the male during the P.E.I. in each series.

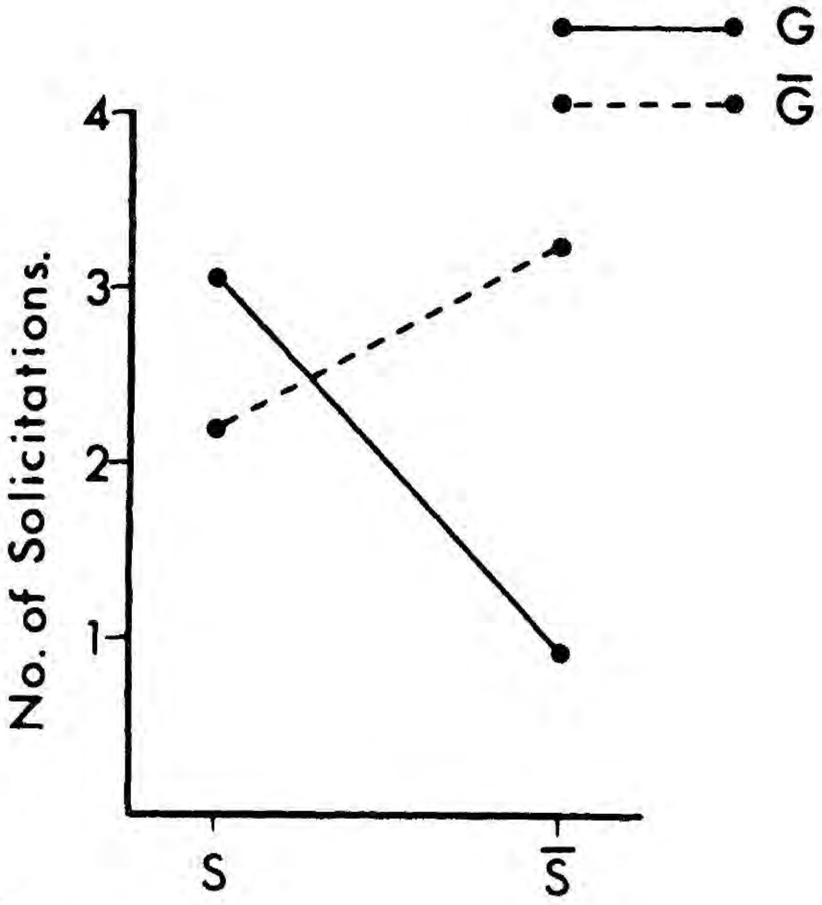

FIGURE 10.19
Mean number of solicitations by females in trios containing an SG, SG̃, S̃G, and S̃G̃ related pair during the P.E.I.

female (mean no. of solicitations, 3.125). This effect is further qualified by a significant interaction between female relatedness and social relatedness (F=22.9279, df 1,36, p=0.0001), in socially related trios the related female gave fewer solicitations than the unrelated female which is not the case in the non-socially related trios (see fig. 10.20).

The number of times each female was nearer: There was a significant effect of series (F=33.8710, df 3,108, p<0.0001), the females being nearer more often with successive ejaculations (see fig. 10.21), this reflects the increasing length of the P.E.I. with successive ejaculations.

10.7.6

Discussion

The results obtained in this study provide some evidence that rats make attempts to avoid inbreeding. In this discussion I shall first consider the various behaviours showing an indication of inbreeding avoidance and then consider the effects of social and genetic relatedness on these.

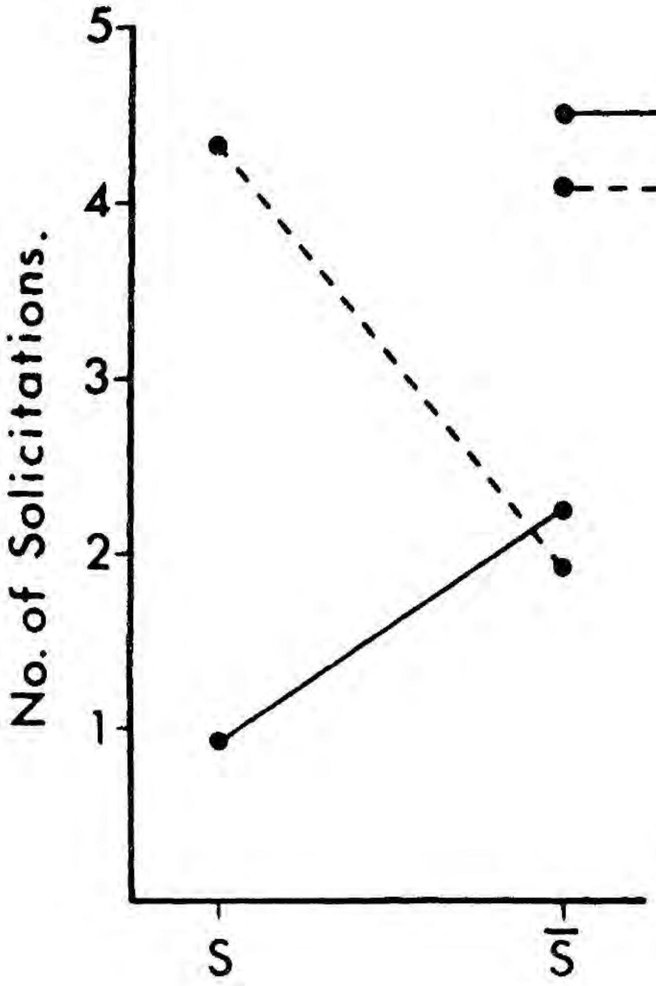

FIGURE 10.20
Mean number of solicitations by the related (R) and unrelated ($\tilde{R}$) females where the related female is either socially (S) or non-socially ($\tilde{S}$) related to the male during the P.E.I.

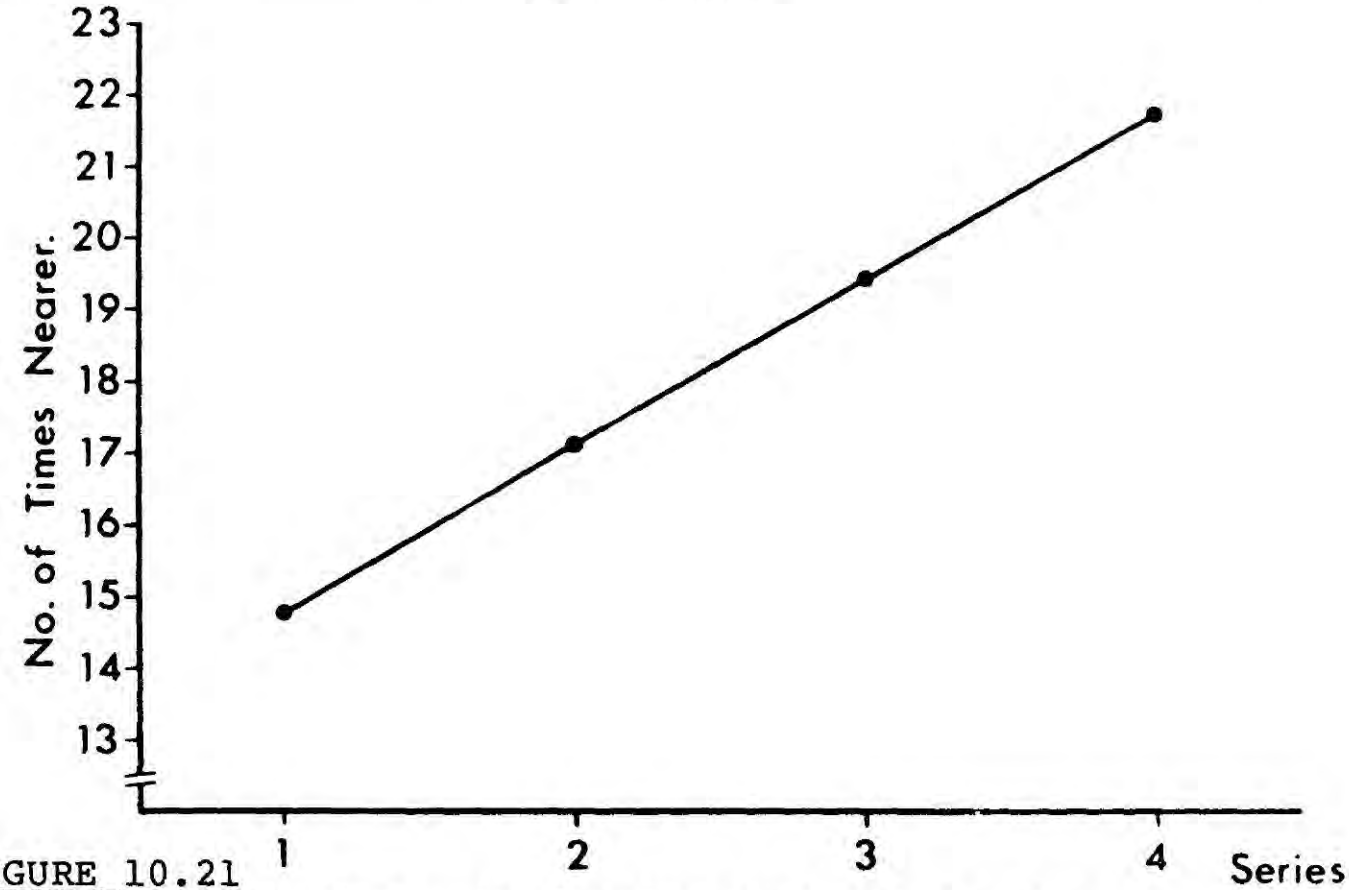

FIGURE 10.21
Mean number of times the females were nearer the male in each series during the P.E.I.

10.7.6.1

Investigatory Behaviour

The investigatory behaviour of of these rats did show signs that they were able to recognise their partners. In the introductory period, male rats were able to discriminate between a sibling (r=0.5) female and an unrelated female, and investigated the unrelated female more. Similarly in this period the females show signs of being able to recognise the male, the related female sniffing the male less than the unrelated female.

In the E.L.P. the male shows no signs of discriminatory behaviour, although overall the males show less sniffing with successive ejaculations. This decrease in sniffing is probably due to the decrease in time of the E.L.P. over successive ejaculations. The mean number of sniffs per series in the E.L.P. can be divided by the time of their respective E.L.P.'s to obtain sniffing rate (see fig. 10.22). Observation of this graph indicates a drop after the first ejaculatory series, then a levelling off. This drop may indicate habituation to the females, after the first ejaculation the male has become familiar with the both females and therefore investigates them less. A similar explanation may explain an almost indentical drop in the female sniffing rate after the first ejaculation (see fig. 10.22). The females in contrast to the males do show some discriminatory investigatory behaviour, and trios containing a socially related pair show less investigatory behaviour than trios

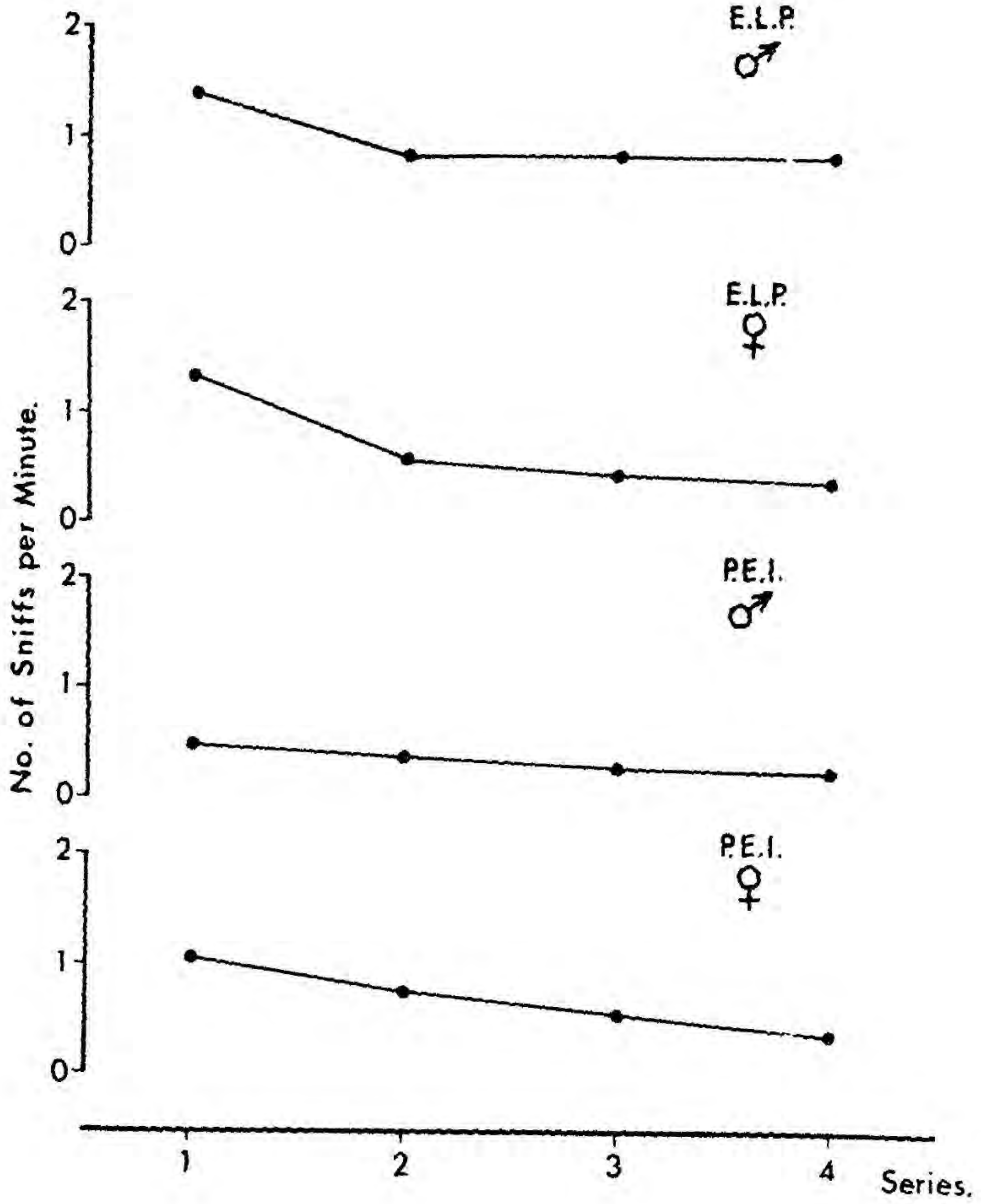

FIGURE 10.22
Sniffing rate of male and females in each series during the E.L.P. and P.E.I.

not containing a socially related pair. This may be due to the fact that the related female need not spend much time investigating the male as she is familiar with him and needs only to investigate the unrelated female and the unrelated female is confronted by two similar smelling individuals through possession of a group odour (Barnett, 1975; Thor, 1979), which may ease recognition. Thus for each female in a socially related trio she may only have to investigate one odour whereas females in non-socially related trios may have to investigate two.

In the P.E.I. the situation is reversed. The female shows no discriminatory behaviour, but shows a decrease in her sniffing across series (see fig. 10.22). The male also shows signs of a slight decrease in sniffing across series (see fig. 10.22). The male shows signs of discriminatory behaviour, males in trios with a socially related partner sniff more than males in trios not containing a socially related female, the reverse of the situation shown by females in the E.L.P.

There are two issues raised from these results. First, why do females sniff less in socially related trios than in non-socially related trios, whereas the males sniff more. This may be because a female in a trio is presented with a choice of 2 individuals differing in sex as well as on relatedness: this sex difference may make investigation and recognition of trio mates easier. The males on the other hand have to discriminate between individuals of the same sex differing on relatedness and the identical sex of the two trio mates may make recognition more difficult to achieve than in the case of individuals of different sexes and require more investigation.

The second issue raised is why the females show evidence of discriminatory behaviour in the E.L.P. whereas the males exhibit it during the P.E.I. Such behaviour may reflect the different strategies of the male and female in mating. The male's strategy is to mate as rapidly as possible. Thus it would be expected that when able to mate, during the E.L.P., the male would concentrate on mating without losing time on investigatory behaviour. The female on the other hand can be impregnated during the E.L.P. and therefore may be expected to show signs of investigatory behaviour to identify her mate and take avoiding action if necessary. In the P.E.I. the situation is different. The male is incapable of mating and signals this to the female by means of ultrasound (Anisko et al., 1978). The female is therefore 'safe' from being impregnated and need not investigate the male. Also after ejaculation the female requires a period of quiesence to ensure successful impregnation (McClintock et al., 1982) and this too may restrict her investigatory behaviour ensuring she does not arouse the male to begin mating too early. The male cannot mate during this period and may use the time to investigate the females whilst not losing any time which could be devoted to reproduction.

The results suggest that the males and females do show signs of disciminative investigatory behaviour and this is linked to the type of reproductive strategy used by both the male and female.

10.7.6.2
Male Determined Behaviour

There seemed to be little evidence of male determined behaviour showing signs of inbreeding avoidance. The female of first mount/intromission and ejaculation in each series, the time of first mount/intromission and ejaculation in each series showed no difference between differently related trios. There seemed to be little effect of the relatedness of the female on the behaviour of the male.

The length of the ejaculation latency decreased with successive ejaculations and supports previous work indicating shorter ejaculation latencies with increasing numbers of ejaculations (e.g., see Beach and Jordan, 1956), the mount/intromission rate however increased with successive ejaculations. The length of the P.E.I. increased with successive ejaculations and again this supports previous work (e.g., Karen and Barfield, 1975).

Although the male showed no evidence of inbreeding avoidance on measures relating to the time course of mating there was evidence of inbreeding avoidance in the number of mount/intromissions given to each female. The male giving fewer mount/intromissions to the related female than to the unrelated female. This effect seems strongest for trios containing a socially related pair. However it should be noted that although the unrelated female received more mount/intromissions, there was little difference in the distribution of ejaculations, the unrelated female receiving 51.875%, (83/160), ejaculations and the related female 48.125%, (77/160), ejaculations.

10.7.6.3

Female Determined Behaviour

The only female determined behaviour considered in this experiment was that of soliciting and it is this behaviour which shows most signs of inbreeding avoidance. In both the E.L.P. and the P.E.I. the related female gave fewer solicitations than the unrelated female. This effect is strongest in socially related trios, where if the trio contained a socially related pair there was a large difference in the number of solicitations given by the related and unrelated female (the unrelated female giving more) and very little difference in trios not containing a socially related pair. Thus it appears females do practice inbreeding avoidance and do not solicit related males especially those socially related.

In both the E.L.P. and the P.E.I. there was an interaction effect between social and genetic relatedness on the number of solicitations given. This seems to be due in both cases to the low number of solicitations given by the females in the S̃G condition. This may also account for the significant main effect of genetic relatedness in the E.L.P. using (log+1) transformed scores. Why then should there be fewer solicitations given in the S̃G condition ?. A comparison of the difference in the number of solicitations given to the male by the related and unrelated female reveals that although more solicitations are given by the unrelated female in SG, SG̃, and S̃G conditions, the difference is much smaller in the S̃G condition than in the SG and SG̃ conditions (1.625, 5.450, 4.400 respectively in the E.L.P. and 0.425, 3.65, 3.15 respectively in the P.E.I.), which is suggestive of a lack of discrimination by the females in this condition in their soliciting behaviour. It may be that as the females were undiscriminating they do not discourage the males mating attempts from which the male gained encouragement and fewer solicitations were necessary. However comparison with the control condition, where there was no reduction in the number of solicitaions makes this unlikely.

In summary, the soliciting behaviour of the females does show signs of inbreeding avoidance, as females solicit related males less, especially when socially related.

10.7.6.4

The Effect of Social and Genetic Relatedness

Certain behaviours exhibited by the male and female rat in the mating situation exhibit differences attributable to inbreeding avoidance (see previous discussion). Here I shall consider briefly the effects of relatedness on the behaviour of the male and female rat.

Two types of relatedness were examined in this experiment, that of social relatedness and that of genetic relatedness. The results of the previous experiment indicate social relatedness to be the important factor in the delay of reproduction. In both the soliciting behaviour of the female and the mount/intromission behaviour of the male, greater signs of inbreeding avoidance are noticed when rats are socially related than when genetically related. Likewise in the investigatory behaviour of both males and females, although their may be some evidence for discriminative behaviour based upon genetic relatedness in the I.P., there is much stronger evidence for discriminative behaviour based upon social relatedness in both the E.L.P. and the P.E.I. Thus, as with delay of reproduction, the behaviour exhibited by male and female rats in mating is affected by social relatedness foremost. This is probably due to the fact that individuals with only genetic experience of their siblings may be no longer able to recognise them as siblings and are therefore unable to show discriminatory behaviour (see Chp. 3).

10.7.6.5
Summary

From this experiment it appears that in the mating situation a period of social relatedness prior to mating is important in the exhibition of inbreeding avoidance. The female, in this experiment, shows stronger signs of inbreeding avoidance than the male and this may reflect the differential investment by the two sexes in mating.

It is worth noting however that all females used in this experiment received approximately two ejaculations each, and thus even though the related females did show signs of inbreeding avoidance, both females would probably have been impregnated. This may reflect the experimental situation, where although enabling the female to show signs of inbreeding avoidance did not allow her to escape from the male.

10.8
INBREEDING AVOIDANCE IN THE RAT

In two experiments on laboratory rats, two possible mechanisms of inbreeding avoidance have been found: delay of reproduction when kin are present and behavioural avoidance of kin in the mating situation. Both mechanisms depend on a period of social relatedness. I shall now consider how these mechanisms may function in the natural environment.

Rats are born in litters and remain in these at least until weaning. After weaning rats engage in a period of play and it is likely they play with their kin, who are most easily accessible, available and willing to play. Thus the period of social relatedness necessary for the functioning of these mechanisms is present.

Delayed reproduction may function in two ways. First and obviously it may delay mating of kin, and allow mating by unrelated indiviuals. Second it may facilitate the removal of one of the sexes from the group. Although there have been studies of rat colonies (e.g., Barnett, 1975; Calhoun, 1962; Telle, 1966), there has been little mention of individual transference between groups. It is known that adult rats introduced into an alien colony are attacked by the males of the colony (Barnett, 1975) and as such if transference does occur, it must take place prior to adulthood and the achievement of puberty. Thor (1979) reports that juvenile rats are immune to attack from adults by means of an odour, such an odour may prevent attack after dispersal and reaching another group. Thus delay of reproduction may benefit a removal mechanism by a) elongating the period in which transference can take place and b) delaying physical maturity to allow acceptance into new groups.

If dispersal does not occur, then mating between kin may occur in the natal group. Even if dispersal does occur inbreeding may still occur through father-daughter or mother-son matings. Now behavioural avoidance in the mating situation may play a role. Telle (1966) reports that receptive females are followed by a number of males and it may be by soliciting those males with whom she wishes to mate (i.e., non-kin), the female can avoid mating with kin.

CHAPTER 11

KIN RECOGNITION IN THE RAT: CONCLUSIONS

11.1 THE ULTIMATE CAUSATION OF KIN RECOGNITION

Hamilton's (1964a,b) theory of kin selection proposes that individuals will act to maximise their inclusive fitness and, accordingly, that social behaviour between individuals would be expected to be shaped by the degree of relatedness between participants and the costs and benefits to the actors genotype. It was hypothesised from this that individuals would show differential responsiveness in their social behaviour to kin and non-kin.

Chapters 8, 9 and 10 examined this hypothesis. If individuals did act according to kin selection theory then, if given a choice of sibs and non-kin, individuals should prefer to huddle and play with their siblings but prefer to mate with non-kin. Experimental results indicated that the rats did act according to the hypothesis, preferring to huddle and play with sibs but to mate with non-kin. Further support for differential responding to kin and non-kin comes from chapter 4, where mothers were observed to retrieve their own young more quickly than young from other litters.

It does therefore seem that the rats' social behaviour has been shaped according to kin selection theory, and, this supports a growing number of reports in other species indicating differential responsiveness to kin and non-kin.

11.2

THE PROXIMATE CAUSATION OF KIN RECOGNITION

Three questions were asked concerning the proximate causation of kin recognition. What is the perceptual sense used ? What is the nature of the kin identifier ? How is kin recognition achieved ?

Olfaction was found to be the most important sense used in kin recognition reflecting, the importance of olfaction for rats and rodents in general (Cheal, 1975). The nature of the kin identifier was then considered. It was proposed that to be of use to the individual the identifier must possess qualities of consistency and commonality which were best achieved by genetic factors rather than environmental factors.

Three mechanisms were found which may enable the acquisition of kin recognition. Chapter 2 demonstrated that rats could recognise conspecifics individually and thus kin recognition may be achieved through the acquisition of individuality associated with an index of familiarity (Bekoff, 1981). Such a mechanism most likely being used to recognise closely related individuals, for example, sibs, parents.

Rats were also found to be capable of sibling, mother-offspring and offspring-mother recognition and evidence suggests that both socially and genetically mediated mechanisms were involved in the acquisition of this ability. It appears that genetic mechanisms prime the individual to respond to kin at birth and therefore make it more likely that any socially determined mechanism will acquire the characteristics of kin rather than non-kin.

11.3

TWO MECHANISMS DETERMINE KIN RECOGNITION IN THE RAT

The results of this research suggest that two mechanisms are involved in the rats' differential responsiveness to kin and non-kin. First a mechanism which determines how the individual responds to kin and second a mechanism which allows the individual to identify its kin.

Studies of the ultimate causation of kin recognition throw some light on the first mechanism. Each behaviour will have evolved with its own modifier which instructs the individual how to respond to kin. The commands of the modifier will have been shaped by natural selection such that the behaviour emitted maximises the individual's fitness. Both play and huddling are advantageous between kin whereas mating is disadvantageous. If there were only a central command to 'prefer kin' one would expect a similar response to kin for all behaviours. Clearly this does not happen. The precise nature of the modifier for each behaviour could be elucidated by testing the individual's response to a variety of kin, here individuals were tested with sibs and non-kin and therefore one would expect a preferable response to sibs in huddling and play but a non-preferable one in mating. The modifier is probably more specific than this. Bateson (1982) finds that individuals of the Japanese quail, *Coturnix coturnix japonica* prefer their first cousins over siblings, 3rd cousins and non-kin (see also Gilder and Slater, 1978).

This mechanism is genetically determined and tells the individual how to respond to kin. However this mechanism does *not* identify kin and this ability has to be determined separately. If the characteristics of kin did not have to be acquired then one would expect individuals only genetically related, (ŠG), to be able to recognise each other. This is not the case for rats as by 40 days individuals only genetically related no longer prefer each other (Expt. 3.9, section 3.7). Similarly in chapters 9 and 10, no effects were found for individuals only genetically related. Likewise if the characteristics of kin did not have to be acquired then the preferential responsiveness of only socially related individuals in chapters 3, 4, 8, 9 and 10 is difficult to explain.

Thus kin recognition comprises two mechanisms, one to determine the response of the individual to kin and second to identify kin.

11.4

FUTURE RESEARCH ON KIN RECOGNITION

There are a number of questions arising directly from this research which have yet to be answered. For example, how is the knowledge acquired about kin obtained by the modifier to elicit its response ? What does the modifier respond to most preferably, sibs, cousins, etc.?

A logical point has emerged from this research concerning studies of kin recognition. It is clearly not enough to show that an individual can recognise its kin by use of a discrimination or preference task. Although this approach may allow the mechanisms of kin recognition to be elucidated it does not say anything about the way in which individuals normally respond to kin. For this individuals should be observed naturally interacting with kin to see if they do use their ability to recognise kin to respond differentially to them.

APPENDIX

CONTENTS

APPENDIX 2.1

RUNNING ORDERS OF RATS FOR EXPERIMENTS 2.1 AND 2.2

Order in which rats were run for each trial.

	SUBJECT No.					
TRIAL 1	1	2	3	4	5	6
TRIAL 2	2	6	3	5	1	4
TRIAL 3	3	2	1	6	5	4
TRIAL 4	4	6	5	2	1	3
TRIAL 5	5	6	1	2	4	3
TRIAL 6	6	3	2	4	5	1
TRIAL 7	1	5	2	4	3	6
TRIAL 8	3	2	1	6	4	5
TRIAL 9	5	1	2	4	6	3
TRIAL 10	2	5	6	3	4	1

APPENDIX 2.2

POSITION OF S+ RAT USED IN EXPERIMENTS 2.1 AND 2.2

Gellerman series of left and right positions of the S+.

						TRIAL					
		1	2	3	4	5	6	7	8	9	10
	1	L	L	R	L	R	R	L	R	R	L
	2	R	R	L	R	L	L	L	R	R	L
D	3	L	R	L	R	R	L	L	R	L	R
	4	R	R	R	L	L	L	R	L	L	R
A	5	R	R	L	L	R	L	L	L	R	R
	6	L	R	R	R	L	L	R	L	L	R
Y	7	R	L	L	R	L	R	L	R	R	L
	8	R	L	L	R	L	R	R	L	R	L
	9	L	R	L	R	L	R	R	R	L	L
	10	R	R	L	L	R	R	L	R	L	L

APPENDIX 10.1

The effect of social, genetic and female relatedness on the number of times the male sniffed each female during the Introductory Period.

Summary of Analysis of Variance

SOURCE	DF	SS	MS	F	PROB
SUBJ	39	2852.9500			
S	1	0.4500	0.4500	0.0058	0.9380
G	1	22.0500	22.0500	0.2827	0.6044
S x G	1	22.0500	22.0500	0.2827	0.6044
ERROR	36	2808.4000	78.0111		
F	1	0.8000	0.8000	0.7784	0.6127
F x S	1	0.0000	0.0000	0.0000	1.0000
F x G	1	5.0000	5.0000	4.8649	0.0319
F x S x G	1	0.2000	0.2000	0.1946	0.6657
ERROR	36	37.0000	1.0278		
WITHIN CELLS	40	43.0000			

S = Social relatedness.
G = Genetic relatedness.
F = Female relatedness.

APPENDIX 10.2

The effect of social, genetic and female relatedness on the number of times the females sniffed the male during the Introductory Period.

Summary of Analysis of Variance

SOURCE	DF	SS	MS	F	PROB
SUBJ	39	272.4875			
S	1	21.0125	21.0125	3.1804	0.0795
G	1	13.6125	13.6125	2.0603	0.1564
S x G	1	0.0125	0.0125	0.0019	0.9645
ERROR	36	237.8500	6.6069		
F	1	6.6125	6.6125	4.1436	0.0466
F x S	1	0.6125	0.6125	0.3838	0.5463
F x G	1	4.5125	4.5125	2.8277	0.0976
F x S x G	1	0.3125	0.3125	0.1958	0.6647
ERROR	36	57.4500	1.5958		
WITHIN CELLS	40	69.5000			

S = Social relatedness.
G = Genetic relatedness.
F = Female relatedness.

APPENDIX 10.3

The distribution of first mount/intromissions between the related (R) and unrelated (R̃) females by the male in each series and overall for each condition and the accompanying binomial probability (2-tailed).

		SERIES				
CONDITION	FEMALE	1	2	3	4	SUM
SG	R	4	6	6	4	20
	R̃	6	4	4	6	20
BINOMIAL PROB.		0.377	0.377	0.377	0.377	1
SG̃	R	6	5	5	4	20
	R̃	4	5	5	6	20
BINOMIAL PROB.		0.377	0.623	0.623	0.377	1
S̃G	R	2	4	5	3	14
	R̃	8	6	5	7	26
BINOMIAL PROB.		0.055	0.377	0.623	0.172	0.092
S̃G̃	R	5	5	4	6	20
	R̃	5	5	6	4	20
BINOMIAL PROB.		0.623	0.623	0.377	0.377	1

APPENDIX 10.4

The distribution of ejaculations between related (R) and unrelated ($\tilde{R}$) females by the male in each series and overall for each condition and the accompanying Binomial probability (2-tailed).

			SERIES			
CONDITION	FEMALE	1	2	3	4	SUM
SG	R	3	5	6	5	19
	$\tilde{R}$	7	5	4	5	21
BINOMIAL PROB.		0.172	0.623	0.377	0.623	0.881
$S\tilde{G}$	R	5	4	2	4	15
	$\tilde{R}$	5	6	8	6	25
BINOMIAL PROB.		0.623	0.377	0.055	0.377	0.156
$\tilde{S}G$	R	5	7	6	5	23
	$\tilde{R}$	5	3	4	5	17
BINOMIAL PROB.		0.623	0.172	0.377	0.623	0.530
$\tilde{S}\tilde{G}$	R	3	4	5	8	20
	$\tilde{R}$	7	6	5	2	20
BINOMIAL PROB.		0.172	0.377	0.623	0.055	1

APPENDIX 10.5

The effect of social and genetic relatedness on the time of the first intromission in each series.

Summary of Analysis of Variance

SOURCE	DF	SS	MS	F	PROB
SERIES 1					
SUBJ	39	79.2478			
S	1	0.0016	0.0016	0.0007	0.9771
G	1	0.6292	0.6292	0.2898	0.5999
S x G	1	0.4731	0.4731	0.2180	0.6482
ERROR	36	78.1440	2.1707		
WITHIN	0	0.0			
SERIES 2					
SUBJ	39	2332.5142			
S	1	12.4283	12.4283	0.1939	0.6662
G	1	0.1651	0.1651	0.0026	0.9587
S x G	1	12.1331	12.1331	0.1893	0.6698
ERROR	36	2307.7886	64.1052		
WITHIN	0	0.0			
SERIES 3					
SUBJ	39	4577.7791			
S	1	4.5633	4.5633	0.0362	0.8443
G	1	7.5892	7.5892	0.0603	0.8027
S x G	1	31.2289	31.2289	0.2479	0.6271
ERROR	36	4534.3977	125.9555		
WITHIN	0	0.0			
SERIES 4					
SUBJ	39	7060.4186			
S	1	68.6880	68.6880	0.3600	0.5591
G	1	78.5406	78.5406	0.4117	0.5321
S x G	1	44.6963	44.6963	0.2343	0.6365
ERROR	36	6868.4937	190.7915		
WITHIN	0	0.0			

S = Social relatedness.
G = Genetic relatedness.

APPENDIX 10.6

The effect of social and genetic relatedness on the time to complete four mating series.

Summary of Analysis of Variance

SOURCE	DF	SS	MS	F	PROB
SUBJ	39	11292.2995			
S	1	131.8293	131.8293	0.4365	0.5199
G	1	184.9722	184.9722	0.6125	0.5551
S x G	1	103.7381	103.7381	0.3435	0.5682
ERROR	36	10871.7599	301.9933		
WITHIN	0	0.0			

S = Social relatedness.
G = Genetic relatedness.

APPENDIX 10.7

The effect of social and genetic relatedness on the time of ejaculation in each series.

Summary of Analysis of Variance

SOURCE	DF	SS	MS	F	PROB
SERIES 1					
SUBJ	39	1881.1336			
S	1	23.7416	23.7416	0.4614	0.5081
G	1	0.4516	0.4516	0.0088	0.9230
S x G	1	4.7266	4.7266	0.0919	0.7612
ERROR	36	1852.2139	51.4504		
WITHIN	0	0.0			
SERIES 2					
SUBJ	39	3719.1300			
S	1	0.0095	0.0095	0.0001	0.9887
G	1	1.3261	1.3261	0.0129	0.9062
S x G	1	21.7809	21.7809	0.2122	0.6524
ERROR	36	3696.0135	102.6670		
WITHIN	0	0.0			
SERIES 3					
SUBJ	39	6141.1066			
S	1	23.6981	23.6981	0.1414	0.7103
G	1	42.6183	42.6183	0.2543	0.6229
S x G	1	40.9152	40.9152	0.2441	0.6297
ERROR	36	6033.8750	167.6076		
WITHIN	0	0.0			
SERIES 4					
SUBJ	39	9224.9565			
S	1	88.1395	88.1395	0.3571	0.5607
G	1	155.3298	155.3298	0.6293	0.5614
S x G	1	95.1001	95.1001	0.3853	0.5456
ERROR	36	8886.3871	246.8441		
WITHIN	0	0.0			

S = Social relatedness.
G = Genetic relatedness.

APPENDIX 10.8

The effect of social and genetic relatedness and series on the length of the E.L.P.

Summary of Analysis of Variance

SOURCE	DF	SS	MS	F	PROB
SUBJ	39	1445.5365			
S	1	0.4640	0.4640	0.0118	0.9106
G	1	10.5490	10.5490	0.2673	0.6143
S x G	1	13.7575	13.7575	0.3486	0.5654
ERROR	36	1420.7659	39.4657		
SER	3	1342.3353	447.4451	51.2758	0.0001
SER x S	3	57.7254	19.2418	2.2051	0.0903
SER x G	3	24.7073	8.2358	0.9438	0.5760
SER x S x G	3	2.5395	0.8465	0.0970	0.9607
ERROR	108	942.4336	8.7262		
WITHIN CELLS	120	2369.7409			

S = Social relatedness.
G = Genetic relatedness.
SER = Series.

APPENDIX 10.9

The effect of social, genetic and female relatedness and series on the number of intromissions given to each female by the male in the E.L.P.

Summary of Analysis of Variance

SOURCE	DF	SS	MS	F	PROB
SUBJ	39	1854.6719			
S	1	89.2531	89.2531	1.8563	0.1785
G	1	0.0031	0.0031	0.0001	0.9897
S x G	1	34.4531	34.4531	0.7165	0.5925
ERROR	36	1730.9625	48.0823		
SER	3	1905.1844	635.0615	39.5954	0.0001
SER x S	3	48.6844	16.2281	1.0118	0.3916
SER x G	3	86.1344	28.7115	1.7901	0.1519
SER x S x G	3	139.6844	46.5615	2.9031	0.0374
ERROR	108	1732.1875	16.0388		
F	1	322.0031	322.0031	11.8527	0.0018
F x S	1	39.9031	39.9031	1.4688	0.2316
F x G	1	0.7031	0.7031	0.0259	0.8675
F x S x G	1	20.5031	20.5031	0.7547	0.6051
ERROR	36	978.0125	27.1670		
SER x F	3	83.2844	27.7615	1.4845	0.2216
SER x F x S	3	47.8844	15.9615	0.8535	0.5297
SER x F x G	3	160.0844	53.3615	2.8534	0.0398
SERxFxSxG	3	15.3844	5.1281	0.2742	0.8452
ERROR	108	2019.7375	18.7013		
WITHIN CELLS	280	7599.3750			

S = Social relatedness.
G = Genetic relatedness.
F = Female relatedness.
SER = Series.

APPENDIX 10.10

The effect of social, genetic and female relatedness and series on the number of intromissions given to the females during the E.L.P.

Summary of Analysis of Variance (using log+1 transformed scores).

SOURCE	DF	SS	MS	F	PROB
SUBJ	39	4.9272			
S	1	0.1952	0.1952	1.4957	0.2273
G	1	0.0077	0.0077	0.0593	0.8041
S x G	1	0.0258	0.0258	0.1977	0.6633
ERROR	36	4.6984	0.1305		
SER	3	4.4352	1.4784	52.5922	0.0001
SER x S	3	0.3003	0.1001	3.5607	0.0165
SER x G	3	0.1493	0.0498	1.7705	0.1557
SER x S x G	3	0.0707	0.0236	0.8386	0.5218
ERROR	108	3.0360	0.0281		
F	1	0.7003	0.7003	7.3349	0.0100
F x S	1	0.1055	0.1055	1.1051	0.3006
F x G	1	0.0057	0.0057	0.0599	0.8032
F x S x G	1	0.0393	0.0393	0.4115	0.5321
ERROR	36	3.4369	0.0955		
SER x F	3	0.0431	0.0144	0.2435	0.8666
SER x F x S	3	0.0520	0.0173	0.2939	0.8315
SER x F x G	3	0.4629	0.1543	2.6163	0.0537
SERxFxSxG	3	0.0695	0.0232	0.3930	0.7617
ERROR	108	6.3694	0.0590		
WITHIN CELLS	280	19.2761			

S = Social relatedness.
G = Genetic relatedness.
F = Female relatedness.
SER = Series.

APPENDIX 10.11

The effect of social, genetic and female relatedness and series on the number of solicitations given by the females in the Ejaculation Latency Period.

Summary of Analysis of Variance

SOURCE	DF	SS	MS	F	PROB
SUBJ	39	1852.7219			
S	1	5.7781	5.7781	0.1623	0.6918
G	1	67.5281	67.5281	1.8964	0.1739
S x G	1	497.5031	497.5031	13.9714	0.0009
ERROR	36	1281.9125	35.6087		
SER	3	2057.0334	685.6781	29.3380	0.0001
SER x S	3	12.6594	4.2198	0.1806	0.9091
SER x G	3	39.5594	13.1865	0.5642	0.6440
SER x S x G	3	340.7344	113.5781	4.8597	0.0036
ERROR	108	2524.1375	23.3716		
F	1	458.4031	458.4031	17.2330	0.0004
F x S	1	512.5781	512.5781	19.2696	0.0002
F x G	1	104.6531	104.6531	3.9343	0.0521
F x S x G	1	30.6281	30.6281	1.1514	0.2905
ERROR	36	957.6125	26.6003		
SER x F	3	183.7344	61.2448	6.3185	0.0008
SER x F x S	3	201.6094	67.2031	6.9332	0.0005
SER x F x G	3	66.1844	22.0615	2.2760	0.0826
SERxFxSxG	3	28.2594	9.4198	0.9718	0.5896
ERROR	108	1046.8375	9.6929		
WITHIN	280	8564.6250			

S = Social relatedness.
G = Genetic relatedness.
F = Female relatedness.
SER = Series.

APPENDIX 10.12

The effect of social, genetic and female relatedness and series on the number of solicitations given by each female during the E.L.P.

Summary of Analysis of Variance (using log+1 transformed scores).

SOURCE	DF	SS	MS	F	PROB
SUBJ	39	11.1652			
S	1	0.0026	0.0026	0.0159	0.8957
G	1	1.1091	1.1091	6.8776	0.0122
S x G	1	4.2480	4.2480	26.3415	0.0001
ERROR	36	5.8055	0.1613		
SER	3	9.0243	3.0081	28.4028	0.0001
SER x S	3	0.3294	0.1098	1.0367	0.3803
SER x G	3	0.0502	0.0167	0.1581	0.9237
SER x S x G	3	0.2710	0.0903	0.8528	0.5293
ERROR	108	11.4381	0.1059		
F	1	4.1630	4.1630	24.8622	0.0001
F x S	1	3.0598	3.0598	18.2735	0.0003
F x G	1	0.4704	0.4704	2.8094	0.0987
F x S x G	1	0.5542	0.5542	3.3095	0.0738
ERROR	36	6.0280	0.1674		
SER x F	3	0.2774	0.0925	2.1219	0.1003
SER x F x S	3	0.2078	0.0693	1.5894	0.1948
SER x F x G	3	0.1515	0.0505	1.1589	0.3288
SERxFxSxG	3	0.0696	0.0232	0.5327	0.6613
ERROR	108	4.7063	0.0436		
WITHIN CELLS	280	40.8010			

S = Social relatedness.
G = Genetic relatedness.
F = Female relatedness.
SER = Series.

APPENDIX 10.13

The effect of social, genetic and female relatedness and series on the number of times the male sniffed each female during the E.L.P.

Summary of Analysis of Variance

SOURCE	DF	SS	MS	F	PROB
SUBJ	39	3166.7000			
S	1	8.4500	8.4500	0.0991	0.7528
G	1	9.8000	9.8000	0.1150	0.7359
S x G	1	80.0000	80.0000	0.9386	0.6592
ERROR	36	3068.4500	85.2347		
SER	3	8054.6750	2684.8917	64.9491	0.0001
SER x S	3	88.5750	29.5250	0.7142	0.5488
SER x G	3	185.5250	61.8417	1.4960	0.2185
SER x G x S	3	49.9250	16.6417	0.4026	0.7550
ERROR	108	4464.5500	41.3384		
F	1	3.6125	3.6125	0.4661	0.5060
F x S	1	12.0125	12.0125	1.5500	0.2190
F x G	1	6.6125	6.6125	0.8532	0.6354
F x S x G	1	12.0125	12.0125	1.5500	0.2190
ERROR	36	279.0000	7.7500		
SER x F	3	2.6125	0.8708	0.1127	0.9517
SER x F x S	3	27.8125	9.2708	1.2000	0.3130
SER x F x G	3	35.6125	11.8708	1.5365	0.2079
SERxFxSxG	3	2.3125	0.7708	0.0998	0.9591
ERROR	108	834.4000	7.7259		
WITHIN CELLS	280	14059.2500			

S = Social relatedness.
G = Genetic relatedness.
F = Female relatedness.
SER = Series.

APPENDIX 10.14

The effect of social, genetic and female relatedness and series on the number of times the female sniffed the male during the E.L.P.

Summary of Analysis of Variance

SOURCE	DF	SS	MS	F	PROB
SUBJ	39	1913.7375			
S	1	296.4500	296.4500	6.6210	0.0137
G	1	1.8000	1.8000	0.0402	0.8364
S x G	1	3.6125	3.6125	0.0807	0.7747
ERROR	36	1611.8750	44.7743		
SER	3	9554.0375	3184.6792	93.0305	0.0001
SER x S	3	718.7000	239.5667	6.9982	0.0004
SER x G	3	7.6500	2.5500	0.0745	0.9728
SER x S x G	3	8.2375	2.7458	0.0802	0.9698
ERROR	108	3697.1250	34.2326		
F	1	0.0000	0.0000	0.0000	1.0000
F x S	1	2.8125	2.8125	0.2003	0.6613
F x G	1	15.3125	15.3125	1.0908	0.3038
F x S x G	1	31.2500	31.2500	2.2261	0.1408
ERROR	36	505.3750	14.0382		
SER x F	3	1.0500	0.3500	0.0414	0.9881
SER x F x S	3	5.3375	1.7792	0.2104	0.8892
SER x F x G	3	108.0375	36.0125	4.2589	0.0072
SERxFxSxG	3	19.6000	6.5333	0.7726	0.5146
ERROR	108	913.2250	8.4558		
WITHIN CELLS	280	15587.7500			

S = Social relatedness.
G = Genetic relatedness.
F = Female relatedness.
SER = Series.

APPENDIX 10.15

The effect of social, genetic and female relatedness and series on the number of times each female sniffed the male during the E.L.P.

Summary of Analysis of Variance (using scores transformed by adding 1 and taking the log).

SOURCE	DF	SS	MS	F	PROB
SUBJ	39	6.0023			
S	1	1.1208	1.1208	8.6573	0.0058
G	1	0.1431	0.1431	1.1051	0.3006
S x G	1	0.0776	0.0776	0.5993	0.5500
ERROR	36	4.6608	0.1295		
SER	3	32.1107	10.7036	111.9328	0.0001
SER x S	3	0.6628	0.2209	2.3103	0.0791
SER x G	3	0.1656	0.0552	0.5772	0.6354
SER x S x G	3	0.2068	0.0689	0.7208	0.5448
ERROR	108	10.3275	0.0956		
F	1	0.0145	0.0145	0.2104	0.6537
F x S	1	0.0352	0.0352	0.5106	0.5138
F x G	1	0.0000	0.0000	0.0002	0.9859
F x S x G	1	0.1250	0.1250	1.8116	0.1838
ERROR	36	2.4837	0.0690		
SER x F	3	0.0149	0.0050	0.1284	0.9423
SER x F x S	3	0.0174	0.0058	0.1493	0.9293
SER x F x G	3	0.1581	0.0527	1.3594	0.2581
SERxFxSxG	3	0.2615	0.0872	2.2485	0.0855
ERROR	108	4.1866	0.0388		
WITHIN CELLS	280	50.7703			

S = Social relatedness.
G = Genetic relatedness.
F = Female relatedness.
SER = Series.

APPENDIX 10.16

The effect of social, genetic and female relatedness and series on the number of the times each female was nearer the male during the E.L.P.

Summary of Analysis of Variance

SOURCE	DF	SS	MS	F	PROB
SUBJ	39	17646.4969			
S	1	10.1531	10.1531	0.0210	0.8803
G	1	175.5281	175.5281	0.3633	0.5573
S x G	1	67.5281	67.5281	0.1398	0.7118
ERROR	36	17393.2875	483.1469		
SER	3	15233.0344	5077.6781	43.0691	0.0001
SER x S	3	673.1064	224.3698	1.9031	0.1320
SER x G	3	228.0844	76.0281	0.6449	0.5916
SER x S x G	3	24.3844	8.1281	0.0689	0.9756
ERROR	108	12732.7625	117.8959		
F	1	118.8281	118.8281	2.0862	0.1539
F x S	1	25.8781	25.8781	0.4543	0.5114
F x G	1	114.0031	114.0031	2.0015	0.1624
F x S x G	1	149.8781	149.8781	2.6313	0.1098
ERROR	36	2050.5375	56.9594		
SER x F	3	266.1844	88.7281	2.0962	0.1036
SER x F x S	3	9.0344	3.0115	0.0711	0.9745
SER x F x G	3	226.6594	75.5531	1.7849	0.1529
SERxFxSxG	3	46.9844	15.6615	0.3700	0.7779
ERROR	108	4571.5125	42.3288		
WITHIN CELLS	280	36470.8750			

S = Social relatedness.
G = Genetic relatedness.
F = Female relatedness.
SER = Series.

APPENDIX 10.17

The effect of social and genetic relatedness and series on the length of the P.E.I.

Summary of Analysis of Variance

SOURCE	DF	SS	MS	F	PROB
SUBJ	39	346.2279			
S	1	19.1230	19.1230	2.1892	0.1441
G	1	10.7916	10.7916	1.2354	0.2732
S x G	1	1.8533	1.8533	0.2122	0.6524
ERROR	36	314.4600	8.7350		
SER	3	189.0242	63.0081	55.7325	0.0001
SER x S	3	2.5571	0.8524	0.7539	0.5254
SER x G	3	1.8532	0.6177	0.5464	0.6559
SER x S x G	3	1.1225	0.3742	0.3309	0.8054
ERROR	108	122.0987	1.1305		
WITHIN CELLS	120	316.6558			

S = Social relatedness.
G = Genetic relatedness.
SER = Series.

APPENDIX 10.18

The effect of social, genetic and female relatedness and series on the number of times each female sniffed the male during the P.E.I.

Summary of Analysis of Variance

SOURCE	DF	SS	MS	F	PROB
SUBJ	39	1114.2219			
S	1	53.6281	53.6281	1.8982	0.1737
G	1	11.6281	11.6281	0.4116	0.5321
S x G	1	31.8781	31.8781	1.1283	0.2955
ERROR	36	1017.0875	28.2524		
SER	3	458.0594	152.6865	19.2921	0.0001
SER x S	3	6.7844	2.2615	0.2857	0.8372
SER x G	3	12.2844	4.0948	0.5174	0.6755
SER x S x G	3	13.2344	4.4115	0.5574	0.6486
ERROR	108	854.7625	7.9145		
F	1	29.4031	29.4031	2.4379	0.1235
F x S	1	14.0281	14.0281	1.1631	0.2880
F x G	1	31.8781	31.8781	2.6431	0.1090
F x S x G	1	0.3781	0.3781	0.0314	0.8546
ERROR	36	434.1875	12.0608		
SER x F	3	19.0594	6.3531	1.0787	0.3618
SER x F x S	3	4.5344	1.5115	0.2566	0.8575
SER x F x G	3	9.7844	3.2615	0.5538	0.6510
SERxFxSxG	3	36.1844	12.0615	2.0480	0.1101
ERROR	108	636.0625	5.8895		
WITHIN CELLS	280	2560.6250			

S = Social relatedness.
G = Genetic relatedness.
F = Female relatedness.
SER = Series.

APPENDIX 10.19

The effect of social, genetic and female relatedness and series on the number of times the male sniffed the female during the P.E.I.

Summary of Analysis of Variance

SOURCE	DF	SS	MS	F	PROB
SUBJ	39	1526.0969			
S	1	250.2781	250.2781	7.2058	0.0106
G	1	18.5281	18.5281	0.5334	0.5235
S x G	1	6.9031	6.9031	0.1987	0.6625
ERROR	36	1250.3875	34.7330		
SER	3	27.3594	9.1198	1.5241	0.2111
SER x S	3	3.5594	1.1865	0.1983	0.8974
SER x G	3	22.5094	7.5031	1.2539	0.2933
SER x S x G	3	11.1844	3.7281	0.6230	0.6055
ERROR	108	646.2625	5.9839		
F	1	9.4531	9.4531	2.6873	0.1062
F x S	1	7.5031	7.5031	2.1330	0.1494
F x G	1	1.1281	1.1281	0.3207	0.5813
F x S x G	1	0.9031	0.9031	0.2567	0.6212
ERROR	36	126.6375	3.5177		
SER x F	3	1.1344	0.3781	0.1480	0.9302
SER x F x S	3	4.0344	1.3448	0.5262	0.6695
SER x F x G	3	1.9094	0.6365	0.2490	0.8627
SERxFxSxG	3	1.7844	0.5948	0.2327	0.8740
ERROR	108	276.0125	2.5557		
WITHIN CELLS	280	1141.3750			

S = Social relatedness.
G = Genetic relatedness.
F = Female relatedness.
SER = Series.

APPENDIX 10.20

The effect of social, genetic and female relatedness and series on the number of solicitations given by the females during the P.E.I.

Summary of Analysis of Variance

SOURCE	DF	SS	MS	F	PROB
SUBJ	39	914.5469			
S	1	24.7531	24.7531	1.3910	0.2445
G	1	42.7781	42.7781	2.4040	0.1261
S x G	1	206.4031	206.4031	11.5991	0.0020
ERROR	36	640.6125	17.7948		
SER	3	12.8344	4.2781	0.6105	0.6136
SER x S	3	17.3594	5.7865	0.8257	0.5148
SER x G	3	6.8344	2.2781	0.3251	0.8095
SER x S x G	3	7.7594	2.5865	0.3691	0.7785
ERROR	108	756.8375	7.0078		
F	1	187.5781	187.5781	15.3941	0.0006
F x S	1	279.3781	279.3781	22.9279	0.0001
F x G	1	20.5031	20.5031	1.6826	0.2002
F x S x G	1	5.2531	5.2531	0.4311	0.5225
ERROR	36	438.6625	12.1851		
SER x F	3	2.3844	0.7948	0.1607	0.9221
SER x F x S	3	0.3344	0.1115	0.0225	0.9949
SER x F x G	3	24.1094	8.0365	1.6248	0.1865
SERxFxSxG	3	3.1094	1.0365	0.2095	0.8898
ERROR	108	534.1875	4.9462		
WITHIN CELLS	280	2297.1250			

S = Social relatedness.
G = Genetic relatedness.
F = Female relatedness.
SER = Series.

APPENDIX 10.21

The effect of social, genetic and female relatedness and series on the number of times each female was nearer the male during the P.E.I.

Summary of Analysis of Variance

SOURCE	DF	SS	MS	F	PROB
SUBJ	39	3765.1219			
S	1	37.1281	37.1281	0.3975	0.5392
G	1	226.1281	226.1281	2.4208	0.1248
S x G	1	139.1281	139.1281	1.4894	0.2283
ERROR	36	3362.7375	93.4094		
SER	3	2141.4094	713.8031	33.8710	0.0001
SER x S	3	0.1344	0.0448	0.0021	0.9997
SER x G	3	35.5344	11.8448	0.5621	0.6455
SER x S x G	3	62.5344	20.8448	0.9891	0.5978
ERROR	108	2276.0125	21.0742		
F	1	376.2781	376.2781	2.0053	0.1620
F x S	1	346.5281	346.5281	1.8467	0.1796
F x G	1	91.3781	91.3781	0.0487	0.5034
F x S x G	1	9.4531	9.4531	0.0504	0.8183
ERROR	36	6755.2375	187.6455		
SER x F	3	81.9844	27.3281	0.3288	0.8069
SER x F x S	3	312.1344	104.0448	1.2518	0.2940
SER x F x G	3	263.2844	87.7615	1.0559	0.3717
SERxFxSxG	3	44.7094	14.9031	0.1793	0.9099
ERROR	108	8976.5125	83.1159		
WITHIN CELLS	280	21773.1250			

S = Social relatedness.
G = Genetic relatedness.
F = Female relatedness.
SER = Series.

REFERENCES

Abugov, R. and Michod, R.E. (1981): "On the relation of family structured models and inclusive fitness models for kin selection." *J. Theoret. Biol.*, *88*, 743-754.

Ackerman, S.H., Hofer, M.A. and Weiner, H. (1975): "Age at maternal separation and gastric erosion susceptibility in the rat." *Psychosom. Med.*, *37*, 180-184.

Ackerman, S.H., Hofer, M.A. and Weiner, H. (1978): "The predisposition to gastric erosions in the rat: Behavioral and nutritional effects of early maternal separation." *Gastroenterology*, *75*, 649-654.

Adams, M.G. (1980): "Odour-producing organs of mammals." *Symp. Zool. Soc. Lond.*, *45*, 57-86.

Adler, N.T. (1969): "Effects of the male's copulatory behavior on successful pregnancy of the female rat." *J. Comp. Physiol. Psychol.*, *69*, 613-622.

Adler, N.T. and Zoloth, S.R. (1970): "Copulatory behavior can inhibit pregnancy in female rats." *Science*, *168*, 1480-1482.

Adolph, E.F. (1957): "Ontogeny of physiological regulations in the rat." *Quart. Rev. Biol.*, *32*, 89-137.

Alberts, J.R. (1978a): "Huddling by rat pups: Group behavioral mechanisms of temperature regulation and energy conservation." *J. Comp. Physiol. Psychol.*, *92*, 231-245.

Alberts, J.R. (1978b): "Huddling by rat pups: Multisensory control of contact behavior." *J. Comp. Physiol. Psychol.*, *92*, 220-230.

Alberts, J.R. and May, B. (1980): "Development of nasal respiration and sniffing in the rat." *Physiol. Behav.*, *24*, 957-963.

Alexander, G. (1978): "Odour, and the recognition of lambs by Merino ewes." *Appl. Anim. Ethol.*, *4*, 153-158.

Alexander, G. and Shillito, E.E. (1978): "Maternal responses in Merino ewes to artificially coloured lambs." *Appl. Anim. Ethol.*, *4*, 153-158.

Alexander, G. and Stevens, D. (1981): "Recognition of washed lambs by Merino ewes." *Appl. Anim. Ethol.*, *7*, 77-86.

Alexander, G. and Walser, E.E.S. (1978): "Visual discrimination between ewes by lambs." *Appl. Anim. Ethol.*, *4*, 81-85.

Alexander, R.D. (1974): "The evolution of social behaviour." *Ann. Rev. Ecol. Systemat.*, *5*, 325- 383.

Alexander, R.D. and Borgia, G. (1978): "Group selection, altruism, and the levels of organisation of life." *Ann. Rev. Ecol. Systemat.*, *9*, 449-474.

Allin, J.T. and Banks, E.M. (1971): "Effects of temperature on ultrasound production by infant albino rats." *Develop. Psychobiol.*, *4*, 149-156.

Allin, J.T. and Banks, E.M. (1972): "Functional aspects of ultrasound production by infant albino rats (*Rattus norvegicus*)." *Anim. Behav.*, *20*, 175-185.

Alpert, S.S. (1978): "The Response of Infant Monkeys to Mothers, Familiars, Strangers and Peers: Development during the First Eight Months of Life." Unpubl. Ph.D. thesis, State University of New York, Downstate Medical Centre.

Altman, J., Brunner, R.L., Bulut, B.G. and Sudarshan, K. (1973): "The development of behaviour in normal and brain damaged infant rats, studied with homing (nest-seeking) as motivation." In: *Drugs and the Developing Brain.* (Eds. A. Vernadakis and N. Weiner.), Plenum Press, N.Y.

Altman, M. (1963): "Naturalistic studies of maternal care in moose and elk." In: *Maternal Behaviour in Mammals*. (Ed. H.L. Rheingold), Wiley, N.Y., pp. 233-253.

Altman, S.A. and Walters, J. (1978): "Review of Kurland. 1977." *Man*, *13*, 324-325.

Amoore, J.E., Johnston, J.W. and Rubin, M. (1964): "The stereochemical theory of odor." *Sci. Amer.*, *210*, 42-49.

Andersson, G., Andersson, K., Brundin, A. and Rappe, C. (1975): "Volatile compounds from the tarsal scent gland of reindeer *(Rangifer tarandus)*." *J. Chem. Ecol.*, *1*, 275-281.

Anisko, J.J., Suer, S.F., McClintock, M.K. and Adler, N.T. (1978): "Relation between 22-KHz ultrasonic signals and sociosexual behavior in rats." *J. Comp. Physiol. Psychol.*, *92*, 821-829.

Astic, L. and Saucier, D. (1982): "Ontogenesis of the functional activity of rat olfactory bulb: Autoradiographic study with 2-deoxyglucose method." *Develop. Brain. Res,*, *2*, 243-256.

Bachus, R.H. and Schevill, W.E. (1966): "Physeter clicks." In: Whales, Dolphins and Porpoises. (Ed., K.S. Norris), University of California Press, Berkeley, pp. 510-528.

Baerends, G.P. and Baerends-Van Roon, J.M. (1950): "An introduction to the study of the ethology of cichlid fishes." Behav. Suppl., 1.

Baker, J.R. (1938): "The evolution of breeding seasons." In: Essays on Aspects of Evolutionary Biology., (Ed., G.R. De Beer.), Oxford Uni. Press, London.

Baldwin, B.A. and Meese, G.B. (1977): "The ability of sheep to distinguish between conspecifics by means of olfaction." Physiol. Behav., 18, 803-808.

Baldwin, B.A. and Shillito, E.E. (1974): "The effects of ablation of the olfactory bulbs on parturition and maternal behaviour in Soay sheep." Anim. Behav., 22, 220-223.

Baldwin, J.D. and Baldwin, J.I. (1974): "Exploration and social play in squirrel monkeys (Saimiri)." Amer. Zool., 14, 303-315.

Balph, D.F., Innis, G.S. and Balph, M.H. (1980): "Kin selection in Rio Grande turkeys: A critical reassessment." Auk, 97, 854-860.

Barash, D.P. (1977): Sociobiology and Behaviour. Elsevier, N.Y.

Barfield, R.J. and Geyer, L.A. (1975): "The ultrasonic postejaculatory vocalisation and the post-ejaculatory refractory period of the male rat." J. Comp. Physiol. Psychol., 88, 723-734.

Barnett, C. (1977): "Chemical recognition of the mother by the young of the cichlid fish, Cichlasoma citrinellum." J. Chem. Ecol., 4, 461-466.

Barnett, S.A. (1975): The Rat: A Study in Behaviour. Uni. of Chicago Press, Chicago.

Barnett, S.A. and Mount, L.E. (1967): "Resistance to cold in mammals." In: Thermobiology. (Ed., A.H. Rose), Academic Press, Lond., pp. 411-477.

Barrows, E.M. (1975): "Individually distinct odors in an invertebrate." Behav. Biol., 15, 57-64.

Barrows, E.M., Bell, W.J. and Michener, C.D. (1975): "Individual odor differences and their social functions in insects." Proc. Nat. Acad. Sci., U.S.A., 72, 2824-2828.

Bartholomew, G.A. (1952): "Behavioural factors affecting social structure in the Alaska fur seal." 18th N. Amer. Wildlf. Conf., 481-502.

Bartholomew, G.A. (1959): "Mother-young relations and the maturation of pup behaviour in the Alaska fur seal." Anim. Behav., 7, 163-171.

Bateson, P.P.G. (1966): "The characteristics and context of imprinting." Biol. Rev., 41, 177-220.

Bateson, P.P.G. (1971): "Imprinting." In: Ontogeny of Vertebrate Behaviour. (Ed., H. Moltz), Academic Press, Lond., pp. 369-387.

Bateson, P. (1978a): "Sexual imprinting and optimal outbreeding." Nature, 273, 659-660.

Bateson, P.P.G. (1978b): "Early sexual experience and sexual preferences." In: Biological Determinants of Sexual Behaviour. (Ed., J.B. Hutchinson), J. Wiley, Chichester, pp. 29-53.

Bateson, P. (1979): "How do sensitive periods arise and what are they for?." Anim. Behav., 27, 470-486.

Bateson, P. (1980): "Optimal outbreeding and the development of sexual preferences in Japanese quail." Z. Tierpsychol., 53, 231-244.

Bateson, P. (1981): "Control of sensitivity to the environment during development." In: Behavioral Development. The Bielefeld Interdisciplinary Project. (Eds. K. Immelman, G.W. Barlow, L. Petrinovich and M. Main), Cambridge University Press, Cambridge, pp. 432-453.

Bateson, P. (1982): "Preferences for cousins in Japanese quail." Nature, 295, 236-237.

Beach, F.A. (1956): "Characteristics of masculine 'sex drive'." Nebr. Symp. Motiv., 4, 1-32.

Beach, F.A. and Jaynes, J. (1956): "Studies of maternal retrieving in rats. 1: Recognition of young." J. Mammol., 37, 177-180.

Beach, F.A. and Jordan, L. (1956): "Sexual exhaustion and recovery in the male rat." Quart. J. Exp. Psychol., 8, 121-133.

Beardsworth, T. and Buchner, T. (1981): "The ability to recognise oneself from a video recording of one's movements without seeing one's body." Bull. Psychon. Soc., 18, 19-22.

Beck, A.J. and Rudd, R.L. (1960): "Nursery colonies in the Pallid bat." J. Mammol., 41, 266-267.

Beer, C.G. (1969): "Laughing gull chicks: Recognition of their parents' voices." Science, 166, 1030-1032.

Beer, C.G. (1970): "Individual recognition of voice in the social behaviour of birds." Adv. St. Behav., 3, 27-74.

Bekoff, M (1976): "Animal play: problems and perspectives." In: Perspectives in Ethology, Vol.2, (Eds., P. Bateson and P.H. Klopfer.), Plenum Press, N.Y, pp. 165-168.

Bekoff, M. (1978): "Social play: Structure, function and the evolution of a cooperative socal behaviour." In: The Development of Behaviour. Comparative and Evolutionary Aspects. (Eds., G.M. Burghardt and M. Bekoff.), Garland Press, N.Y., pp. 367-383.

Bekoff, M. (1981): "Mammalian sibling interactions: Genes, facilitative environments, and the coefficient of familiarity." In: Parental Care in Mammals. (Eds., D.J. Gubernick and P.H. Klopfer.), Plenum Press, Lond., pp. 307-346.

Bengtsson, B.O. (1978): "Avoiding inbreeding: At what cost?." J. Theor. Biol., 73, 439-444.

Berger, L.R. and Lignon, J.D. (1977): "Vocal communication and individual recognition in the pinon jay, Gymnorhinus cyanocephalus." Anim. Behav., 25, 567-584.

Bertram, B.C.R. (1973): "Lion population regulation." E. Afr. Wildlf. J., 11., 215-225.

Bertram, B.C.R. (1977): "Variation in the wing-song of the Flappet lark." Anim. Behav., 25, 165-170.

Bertram, B.C.R. (1979): "Ostriches recognise their eggs and discard others." Nature, 279, 233-234.

Birch, D. and Jacobs, G.H. (1979): "Spatial contrast sensitivity in albino and pigmented rats." Vision Res., 19, 933-937.

Bixler, R.H. (1982): "Sibling incest in the royal families of Egypt, Peru and Hawaii." J. Sex Res., 18, 264-281.

Blass, E.M. and Teicher, M.H. (1980): "Suckling." Science, 210, 15-22.

Blaustein, A.R. (1983): "Kin recognition mechanisms: Phenotype matching or recognition alleles?." Amer. Natural., 121, 749-754.

Blaustein, A.R. and O'Hara, R.K. (1981): "Genetic control for sibling recognition?." Nature, 290, 246-248.

Blaustein, A.R. and O'Hara, R.K. (1982a): "Kin recognition in *Rana cascadae* tadpoles." Behav. Neur. Biol., 36, 77-87.

Blaustein, A.R. and O'Hara, R.K. (1982b): "Kin recognition in *Rana cascadae* tadpoles: Maternal and paternal effects." Anim. Behav., 30, 1151-1157.

Blizard, R.A. and Perry, G.C. (1979): "Responses of captive male red foxes (*Vulpes vulpes*), to some conspecific odors." J. Chem. Ecol., 5, 869-880.

Bodmer, W.F. and Cavalli-Sforza, L.L. (1976): Genetics Evolution and Man. W.H. Freeman, San Francisco.

Bolles, R.C. and Woods, P.J. (1964): "The ontogeny of behaviour in the albino rat." Anim. Behav., 12, 427-441.

Bonnet, P. (1928): "Report on the seals and sea-lions of California." Fish. Bull. Dept. of Fish and Game of California., 14.

Boorman, S.A. and Levitt, P.R. (1972): "Group selection on the boundary of a stable population." Proc. Nat. Acad. Sci., U.S.A., 69, 2711-2713.

Boorman, S.A. and Levitt, P.R. (1973): "Group selection on the boundary of a stable population." Theoret. Pop. Biol., 4, 85-128.

Borror, D.J. and Gunn, W.W.H. (1965): "Variation in white-throated sparrow songs." Auk, 82, 26-47.

Bowers, J.M. and Alexander, B.K. (1967): "Mice: Individual recognition by olfactory cues." Science, 158, 1208-1210.

Bradbury, J.W. (1977): "Lek mating behaviour in the Hammer-headed bat." Z. Tierpsychol., 45, 225-255.

Brake, S.C. (1981): "Suckling infant rats learn a preference for a novel olfactory stimulus paired with milk delivery." Science, 211, 506-508.

Breden, F. and Wade, M.J. (1981): "Inbreeding and evolution by kin selection." Ethol. and Sociobiol., 2, 3-16.

Breder, C.M. (1939): "Variations in the nesting habits of *Ameiurus nebulosus* (Le Sueur)." *Zoologica*, *24*, 367-380.

Breed, M.D. (1981): "Individual recognition and learning of queen odors by worker honeybees." *Proc. Nat. Acad. Sci., U.S.A.*, *78*, 2635-2637.

Breed, M.D. (1983): "Nestmate recognition in honey bees." *Anim. Behav.*, *31*, 86-91.

Brian, M.V. (1980): "Social control over sex and caste in bees, wasps and ants." *Biol. Rev.*, *55*, 379-415.

Bronson, F.H. (1971): "Rodent pheromones." *Biol. Reprod.*, *4*, 344-357.

Bronson, F.H. and Eleftheriou, B.E. (1963): "Influence of strange males on implantation in the deermouse." *Gen. Comp. Endocrinol.*, *3*, 515-518.

Brooke, M. de L. (1978): "Sexual differences in the voice and individual vocal recognition in the manx shearwater, *(Puffinus puffinus)*." *Anim. Behav.*, *26*, 622-629.

Brooks, R.J. and Falls, J.B. (1975a): "Individual recognition by song in white-throated sparrows.1. Discrimination of songs of neighbors and strangers." *Can. J. Zool.*, *53*, 879-888.

Brooks, R.J. and Falls, J.B. (1975b): "Individual recognition by song in white-throated sparrows.3. Song features used in individual recognition." *Can. J. Zool.*, *53*, 1749-1761.

Brown, R.E. (1977): "Odor preference and urine-marking scales in male and female rats: Effects of gonadectomy and sexual experience on responses to conspecific odors." *J. Comp. Physiol. Psychol.*, *91*, 1190-1206.

Brown, R.E. (1979): "Mammalian social odors: A critical review." *Ad. St. Behav.*, *10*, 103-162.

Brown, R.E. and Elrick, D. (1983): "Preferences of preweanling Long-Evans rats for anal excreta of adult males and females." *Physiol. Behav.*, *30*, 567-571.

Brownlee, R.G., Silverstein, R.M., Muller-Schwarze, D. and Singer, A.G. (1969): "Isolation, identification and function of the chief component of the male tarsal scent in black-tailed deer." *Nature*, *221*, 284-285.

Bruce, H.M. (1959): "An exteroceptive block to pregnancy in the mouse." Nature, 184, 105.

Bruce, H.M. (1960): "A block to pregnancy in the mouse caused by proximity of strange males." J. Reprod. Fertil., 1, 96-102.

Brunjes, P.C. and Alberts, J.R. (1979): "Olfactory stimulation induces filial preferences for huddling in rat pups." J. Comp. Physiol. Psychol., 93, 548-555.

Buckle, G.R. and Greenberg. L. (1981): "Nestmate recognition in sweat bees (Lassioglossum zephyrum): Does an individual recognise its own odour or only odours of it's nestmates?." Anim. Behav., 29, 802-809.

Buckley, F.G. and Buckley, P.A. (1972): "The breeding ecology of Royal terns Sterna (Thalasseus) maxima maxima." Ibis, 114, 344-359.

Buckley, P.A. and Buckley, F.G. (1970): "Color variation in the soft parts and down of Royal tern chicks." Auk, 87, 1-13.

Burkhardt, D. (1958): "Observations sur la vie sociale du cerf (Cervus elephas) au parc Nationale Suisse." Mammalia, 22, 226-244.

Burns, G.W. (1976): The Science of Genetics. Collier Macmillan, N.Y.

Burton, R.W., Anderson, S.S. and Summers, C.F. (1975): "Perinatal activities in the Grey seal, (Halichoerus grypus)." J. Zool., 177, 197-201.

Buss, I.O., Rasmussen, L.E. and Smuts, G.L. (1976): "The role of stress and individual recognition in the function of the African elephant's temporal gland." Mammalia, 40, 437-451.

Butler, S.R., Suskind, M.R. and Schanberg, S.M. (1978): "Maternal behavior as a regulator of polyamine biosynthesis in the brain and heart of the developing rat pup." Science, 199, 445-447.

Byers, J.A. (1980): "Play partner preferences in Siberian Ibex, Capra ibex sibirica." Z. Tierpsychol., 53, 23-40.

Bygott, J.D., Bertram, B.C.R. and Hanby, J.P. (1979): "Male lions in large coalitions gain reproductive advantages." Nature, 282, 839-841.

Caldwell, M.C. and Caldwell, D.K. (1971): "Statistical evidence for individual signature whistles in Pacific white-sided dolphins." Cetology, 3, 1-9.

Caldwell, M.C., Caldwell, D.K. and Hall, N.R. (1972b): "Ability of an Atlantic bottlenosed dolphin (Tursiops Truncatus) to discriminate between and potentially identify to individual, the whistles of another species, the common dolphin (Delphinus delphus)." Marineland Res. Lab. Tech. Rep., 9, 1-7.

Caldwell, M.C., Caldwell, D.K. and Miller, J.F. (1973): "Statistical evidence for individual signature whistles in the spotted dolphin, Stenella plagiodon." Cetology, 16, 1-21.

Caldwell, M.C., Caldwell, D.K. and Turner, R.H. (1970): "Statistical analysis of the signature whistle of an Atlantic bottlenosed dolphin with correlations between vocal changes and level of arousal." Los Angeles Co. Mus. Nat. Hist. Found. Tech. Rep., 8.

Caldwell, M.C., Hall, N.R. and Caldwell, D.K. (1972a): "Ability of an Atlantic bottlenosed dolphin to discriminate between and respond differentially to, whistles of 8 conspecifics." Marineland Res. Lab. Tech. Rep., 10, 1-5.

Caldwell, R.L. (1979): "Cavity occupation and defensive behaviour in the stomapod, Gonodactylus festai: Evidence for chemically mediated individual recognition." Anim. Behav., 27, 194-201.

Calhoun, J.B. (1962): "The ecology and sociology of the Norway rat." U.S. Pub. Health. Ser. Publ., 1008, U.S. Govt. Print Office, Wash., D.C.

Carr, W.J. and Caul, W.F. (1962): "The effect of castration in the rat upon the discrimination of sex odours." Anim. Behav., 10, 20-27.

Carr, W.J., Demesquita-Wander, M., Sachs, S.R. and Maconi, P. (1979): "Responses of female rats to odors from familiar vs novel males." Bull. Psychon. Soc., 14, 118-120.

Carr. W.J., Hirsch, J.T. and Balazs, J.M. (1980): "Responses of male rats to odors from familiar vs novel females." Behav. Neur. Biol., 29, 331-337.

Carr, W.J., Loeb, L.S. and Dissinger, M.L. (1965): "Responses of rats to sex odors." J. Comp. Physiol. Psychol., 59, 370-377.

Carr, W.J., Loeb, L.S. and Wylie, N.R. (1966): "Responses to feminine odors in normal and castrated rats." J. Comp. Physiol. Psychol., 62, 336-338.

Carr, W.J., Marasco, E. and Landauer, M.R. (1979): "Responses by rat pups to their own nest versus a strange conspecific nest." Physiol. Behav., 23, 1149-1151.

Carr, W.J., Wylie, N.R. and Loeb, L.S. (1970): "Responses of adult and immature rats to sex odours." J. Comp. Physiol. Psychol., 72, 51-59.

Carr, W.J., Yee, L., Gable, D. and Marasco, E. (1976): "Olfactory recognition of conspecifics by domestic Norway rats." J. Comp. Physiol. Psychol., 90, 821-828.

Cattarelli, M (1982a): "Transmission and integration of biologically meaningful olfactory information after bilateral transection of the lateral olfactory tract in the rat." Behav. Brain Res., 6, 313-337.

Cattarelli, M. (1982b): "The role of the medial olfactory pathways in olfaction: Behavioural and electrophysiological data." Behav. Brain Res., 6, 339-364.

Cavalli-Sforza, L.L. and Bodmer, W.F. (1971): The Genetics of Human Populations. W.H. Freeman, San Francisco.

Chalmers, N.R. (1968): "The social behaviour of free living mangabeys in Uganda." Folia Primatol., 8, 263-281.

Chambers, K.C., Sengstake, C.B., Walther, A.M. and Bullis, J.E. (1982): "Disruption of sexual behaviour in socially isolated adult male rats." Behav. Neur. Biol., 34, 215-220.

Charlesworth, B. (1978): "Some models of the evolution of altruistic behaviour between siblings." J. Theor. Biol., 72, 297-319.

Charlesworth, B. and Charnov, E.L. (1981): "Kin selection in age-structured populations." J. Theor. Biol., 88, 103-119.

Charnov, E.L. (1977): "An elementary treatment of the genetical theory of kin selection." J. Theor. Biol., 66, 541-550.

Cheal, M. (1975): "Social olfaction: A review of the ontogeny of olfactory influences on vertebrate behaviour." Behav. Biol., 15, 1-25.

Cheney, D.L. (1978a): "Interactions of immature male and female baboons with adult females." Anim. Behav., 26, 389-408.

Cheney, D.L. (1978b): "The play partners of immature baboons." Anim. Behav., 26, 1038-1050.

Cheney, D.L. and Seyfarth, R.M. (1980): "Vocal recognition in free-ranging Vervet monkeys." Anim. Behav., 28, 362-367.

Chepko, B.D. (1971): "A preliminary study of the effect of play deprivation on young goats." Z. Tierpsychol., 28, 517-526.

Chester, R.F. and Zucker, I. (1970): "Influence of male copulatory behavior on sperm transport, pregnancy and pseudopregnancy in female rats." Physiol. Behav.,5, 35-43.

Chew, L. (1981): "Geographic and individual variation in the morphology and sequential organisation of the song of the Savannah sparrow, (Passerculus sandwichensis)." J. Zool., 59, 702-713.

Chipman, R.K. and Fox, K.A. (1966): "Oestrous synchronisation and pregnancy blocking in wild house mice (Mus musculus)." J. Reprod. Fertil., 12, 233-236.

Clarke, J.R., Clulow, F.V. and Grieg, F. (1970): "Ovulation in the bank vole, Clethrionomys glareolus." J. Reprod. Fertil., 23, 531.

Clulow, F.V. and Clarke, J.R. (1968): "Pregnancy-block in Microtus agrestis and induced ovulator." Nature, 219, 511.

Clulow, F.V. and Langford, P.E. (1971): "Pregnancy block in the meadow vole, Microtus pennsylvanicus." J. Reprod. Fertil., 24, 275-277.

Cole, J.E. and Ward, J.A. (1970): "An analysis of parental recognition by the young of the cichlid fish, Etroplus maculatus (BLOCH)." Z. Tierpsychol., 27, 156-176.

Compton, R.P., Koch, M.D. and Arnold, W.J. (1977): "Effect of maternal odor on the cardiac rate of maternally separated infant rats." Physiol. Behav., 18, 769-773.

Conklin, P. and Heggeness, F.W. (1971): "Maturation of temperature homeostasis in the rac." Amer. J. Physiol., 220, 333-336.

Connor, R.C. and Norris, K.S. (1982): "Are dolphins reciprocal altruists?." Amer. Natural., 119, 358-374.

Cornwell-Jones, C. (1981): "Conspecific odour preferences of male albino rats are reversed by intracerebral 6-hydroxydopamine." Brain Res., 213, 379-385.

Cornwell-Jones, C. and Sobrian, S.K. (1977): "Development of odor-guided behaviour in Wistar and Sprague-Dawley rat pups." Physiol. Behav., 19, 685-688.

Corrigan, J.G. and Flannelly, K.J. (1979): "Ultrasonic vocalisations of defeated male rats." J. Comp. Physiol. Psychol., 93, 105-115.

Craig, R. (1982): "Evolution of eusocialty by kin selection: the effect of inbreeding between siblings." J. Theor. Biol., 94, 119-128.

Crampe, H. (1883): "Zuchtversuche mit zahmen wanderratten." Landwirtsch. Jahrb., 12, 389-458.

Crow, J.F. and Kimura, M (1970): An Introduction to Population Genetics Theory. Harper Row, N.Y.

Crozier, R.H. and Dix, M.W. (1979): "Analysis of two genetic models for the innate components of colony odor in social Hymenoptera." Behav. Ecol. Sociobiol., 4, 217-224.

Dakhlof, L., Hard, E. and Larsson, K. (1978): "Sexual differentiation of offspring of mothers treated with cortisone during pregnancy." Physiol. Behav., 21, 673-674.

Dalland, T. and Doving, K.B. (1981): "Reaction to olfactory stimuli in odor-exposed rats." Behav. Neur. Biol., 32, 79-88.

Daniel, W.J. (1942): "Cooperative problem solving in rats." J. Comp. Psychol., 34, 361-368.

Daniel, W.J. (1943): "Higher order cooperative problem solving in rats." J. Comp. Psychol., 35, 297-305.

Darling, F.F. (1938): A Herd of Red Deer. Oxford Uni. Press, Lond.

Darwin, C. (1859): The Origin of Species by Natural Selection. J. Murray Publ., London. (1979, Penguin Classics Edition, Harmondsworth)

Dausset, J. (1981a): "M.H.C. and general recognition." Devel. Comp. Immunol., 5, 1-4.

Dausset, J. (1981b): "The major histocompatibility complex in man." *Science*, *213*, 1469-1474.

David, J.H.M. (1975): "Observations on mating behaviour, parturition, suckling and the mother-young bond in the bontebok, (*Damaliscus dorcas dorcas*)." *J. Zool.*, *177*, 203-223.

Davis, W.H., Barbour, R.W. and Hassell, M.D. (1968): "Colonial behaviour of *Eptesicus fuscus*." *J. Mammol*, *49*, 44-50.

Dawkins, R. (1976): *The Selfish Gene*. Oxford Uni. Press, Oxford.

Dawkins, R. (1979): "Twelve misunderstandings of kin selection." *Z. Tierpsychol.*, *51*, 184-200.

Dawkins, R. (1982): *The Extended Phenotype*. W.H. Freeman, Oxford.

DeCasper, A.J. and Fifer, W.P. (1980): "Of human bonding: Newborns prefer their mothers' voice." *Science*, *208*, 1174-1176.

Dember, W.N. and Fowler, H. (1958): "Spontaneous alternation behavior." *Psychol. Bull.*, *55*, 412-428.

Dewsbury, D.A. (1967): "A quantitative description of the behaviour of rats during copulation " *Behav.*, *29*, 154-178.

Dewsbury, D.A. (1982): "Ejaculate cost and male choice." *Amer. Natural.*, *119*, 601-610.

Diakow, C. (1975): "Motion picture analysis of rat mating behaviour." *J. Comp. Physiol. Psychol.*, *8*, 704-712.

Dodd, G.H. and Squirrel, D.J. (1980): "Structure and mechanism in the mammalian olfactory system." *Symp. Zool. Soc. Lond.*, *45*, 35-56.

Domjan, M. and Wilson, N.E. (1972): "Specificity of cue to consequence in aversion learning in the rat." *Psychon. Sci.*, *26*, 143-145.

Douglas, R.J. (1966): "Cues for spontaneous alternation." *J. Comp. Physiol. Psychol.*, *62*, 171-183.

Douglas, R.J. (1975): "The development of hippocampal function: Implications for theory and therapy." In: *The Hippocampus. 2. Neurophysiology and Behaviour.* (Eds., R.L. Isaacson and K.H. Pribaum.) Plenum Press, Lond, pp. 327-361.

Douglas-Hamilton, I. (1972): "On the ecology and behaviour of the African elephant." Unpubl. D.Phil. Thesis, Oxford Uni.

Doving, K.B. and Pinching, A.J. (1973): "Selective degeneration of neurones in the olfactory bulb following prolonged odour exposure." *Brain Res.*, *52*, 115-129.

Drewett, R.F. and Spiteri, N.J. (1979): "The sexual attractiveness of male rats. Olfactory and behavioural components." *Physiol. Behav.*, *23*, 207-209.

Eayrs, J.T. and Moulton, D.G. (1960): "Studies in olfactory acuity. 1. Measurement of olfactory thresholds in the rat." *Quart. J. Exp. Psychol.*, *12*, 90-98.

Eberhard, M.J.W. (1969): "The social biology of polistine wasps." *Misc. Publ., Mus. of Zool., Uni. of Michigan, Ann Arbour*. *140*, 1-101.

Eberhard, W.G. (1972): "Altruistic behaviour in a sphecid wasp: Support for kin selection theory." *Science*, *175*, 1390-1391.

Echandia, E.L.R., Foscolo, M. and Broitman, S.T. (1982): "Preferential nesting in lemon-scented environment in rats reared on lemon-scented bedding from birth to weaning." *Physiol. Behav.*, *29*, 47-49.

Edwardson, J.A. and Eayrs, J.T. (1967): "Neural factors in the maintenance of lactation in the rat." *J. Endocrinol.*, *38*, 51-59.

Ehrman, L. and Parsons, P.A. (1976): *The Genetics of Behaviour.* Sinauer Assoc., Mass.

Eibl-Eibesfeldt, I. (1955): "Ethologische studien am Galapagos-Seelowen, *Zalophus wollebacki* SIVERTSON." *Z. Tierpsychol.*, *12*, 286-303.

Einon, D.F. and Morgan, M.J. (1977): "A critical period for social isolation in the rat." *Develop. Psychobiol.*, *10*, 123-132.

Einon, D.F., Morgan, M.J. and Kibbler, C.C. (1978): "Brief periods of socialization and later behavior in the rat." *Develop. Psycholbiol.*, *11*, 213-225.

Ellis, H. (1934): *The Psychology of Sex.* W.Heinmann, London.

Emlen, S.T. (1971): "The role of song in individual recognition in the Indigo bunting." Z. Tierpsychol., 28, 241-246.

Ertman, S.C. and Davenport, D. (1981): "Tentacular nematocyte discharge and "self-recognition" in Anthopleura elegantissima BRANDT." Biol. Bull., 161, 366-370.

Espmark, Y. (1971): "Individual recognition by voice in reindeer mother-young relationship. Field observations and playback experiments." Behav., 40, 295-301.

Espmark, Y. (1975): "Individual characteristics in the calls of reindeer calves." Behav., 54, 50-59.

Estes, R.D. (1963): Antelope Behaviour Study., 3rd. Rep., Aug. 1963 - Jan. 1964. Nat. Geogr. Soc., Cornell Uni., Ithaca, N.Y.

Evans, R.M. (1980): "Development of individual call recognition in young ring-billed gulls, (Larus delawarensis): An effect of feeding." Anim. Behav., 28, 60-67.

Fagen, R.M. (1976): "Exercise, play and physical training in animals." In: Perspectives in Ethology. Vol. 2. (Eds., P. Bateson and P.H. Klopfer) Plenum Press, N.Y., pp. 189-219

Fagen, R.M. (1981): Animal Play Behaviour. Oxford Uni. Press, Oxford.

Falconer, D.S. (1960): Introduction to Quantitative Genetics. Oliver and Boyd, Edinburgh.

Falls, J.B. and Brooks, R.J. (1975): "Individual recognition by song in white-throated sparrows. 2. Effects of location." Can. J. Zool., 53, 1412-1420.

Falls, J.B. and McNicholl, M.K. (1979): "Neighbor-stranger discrimination by song in male blue grouse." Can. J. Zool., 57, 457-462.

Farbman, A.I. (1965): "Electron microscope study of the developing taste bud in the rat fungiform papilla." Develop. Biol., 11, 110-135.

Fass, B., Gutermann, P.E. and Stevens, D.A. (1978): "Evidence that rats discriminate between familiar and unfamiliar putative urinary odorants of adult male conspecifics." Aggr. Behav., 4, 231-236.

Ferns, P.N. (1978): "Individual differences in the head and neck plumage of ruddy turnstones (Arenaria interpres) during the breeding season." Auk, 95, 753-755.

Ficken, R.W. (1963): "Courtship and agonistic behavior of the common grackle, Quiscalus quiscula." Auk, 80, 52-72.

Fleming, A.S. and Tambosso, L. (1980): "Hormonal and sensory control of scent-marking in the desert woodrat (Neotoma lepida lepida)." J. Comp. Physiol. Psychol., 94, 564-578.

Fogden, S.C.L. (1971): "Mother-young behaviour at grey seal breeding beaches." J. Zool., 164, 61-92.

Fox, G.J. (1982): "Potentials for pheromones in chimpanzee vaginal fatty acids." Folia Primatol., 37, 255-266.

Fox, J.R. (1962): "Sibling incest." Brit. J. Sociol., 13, 128-150.

Frame, L.H. and Frame, G.W. (1976): "Female African wild dogs emigrate." Nature, 263, 227-229.

Frank, F. (1952): "Adoptionverscuche bei Feld-mousen (Microtus arvalis PALL.)." Z. Tierpsychol., 9, 415-423.

Freud, S. (1913): Totem and Taboo. (The Standard Edition of the Complete Psychological Works of Sigmund Freud. 1955) Hogarth Press, London.

Fuller, J.L. and Thompson, W.R. (1960): Behavior Genetics. Wiley, N.Y.

Gaioni, S.J. and Platte, P.L. (1982): "Sibling interactions in mallard ducklings (Anas platyrhynchos)." Behav. Anal. Letters, 2, 189-196.

Galef, B.G. (1971): "Social effects in the weaning of domestic rat pups." J. Comp. Physiol. Psychol., 75, 358-362.

Galef, B.G. (1981): "Preference for natural odors in rat pups. Implications of a failure to replicate." Physiol. Behav., 26, 783-786.

Galef, B.G. (1982a): "Studies of social learning in Norway rats: A brief review." Develop. Psychobiol., 15, 249-295.

Galef, B.G. (1982b): "Acquisition and waning of exposure-induced attraction to a nonnatural odor in rat pups." Develop. Psychobiol., 15, 479-490.

Galef, B.G. and Henderson, P.W. (1972): "Mothers milk: A determinant of the feeding preferences of weaning rat pups." J. Comp. Physiol. Psychol., 78, 213-219.

Galef, B.G. and Kaner, H.C. (1980): "Establishment and maintenance of preference for natural and artificial olfactory stimuli in juvenile rats." J. Comp. Physiol. Psychol., 94, 588-595.

Gallup, G.G. (1970): "Chimpanzees: Self-recognition." Science, 167, 86-87.

Gallup, G.G. (1977): "Self-recognition in primates: A comparative approach to the bidirectional proerties of conciousness." Amer. Psychol., 32, 329-338.

Garcia, J. and Ervin, F.R. (1968): "Gustatory-visceral and tele-cutaneous conditioning: Adaptation in internal and external mileus." Comm. in Behav. Biol., 1, 389-415.

Garcia, J. and Koelling, R.A. (1966): "Relation of cue to consequence in avoidance learning." Psychon. Sci., 4, 123-124.

Garcia, J., McGowan, B.K., Ervin, F.R. and Koelling, R.A. (1968): "Cues: Their relative effectiveness as a function of the reinforcer." Science, 160, 794-795.

Gawienowski, A , Orsulak, P.J., Stacewicz-sapuntzakis, M. and Joseph, B.M. (1975): "Presence of sex pheromone in preputial glands of male rats." J. Endocrinol., 67, 283-288.

Gemberling, G.A. and Domjan, M. (1982): "Selective associations in one-day-old rats: Taste-toxicosis and texture-shock aversion learning." J. Comp. Physiol. Psychol., 96, 105-113.

Getz, W.H., Bruckner, D. and Parisan, T.R. (1982): "Kin structure and the swarming behaviour of the honey bee, Apis mellifera." Behav. Ecol. Sociobiol., 10, 265-270.

Getz, W.M. and Smith, K.B. (1983): "Genetic kin recognition: Honey bees discriminate between full and half sisters." Nature, 302, 147-148.

Gilder, P.M. and Slater, P.J.B. (1978): "Interest of mice in conspecific male odours is influenced by degree of kinship." Nature, 274, 364-365.

Gilman, D.P. and Westbrook, W.H. (1978): "Mating preference and sexual reinforcement in female rats." Physiol. Behav., 20, 11-14.

Glanzer, M. (1953): "Stimulus satiation: An explanation of spontaneous alternation and related phenomena." Psychol. Rev., 60, 257-268.

Goethe, F. (1937): "Beobachtungen und Untersuchungen zur Biologie der Silbermowe auf der Vogelinsel Memmerstrand." J. Ornithol., 85, 1-119.

Goldman, P. (1973): "Song recognition by field sparrows." Auk, 90, 106-113.

Goodrich, B.S. and Mykytowycz, R. (1972): "Individual and sex differences in the chemical composition of pheromone-like substances from the skin glands of the rabbit, Oryctolagus cuniculus." J. Mammol., 53, 540-548.

Gorman, M.L. (1976): "A mechanism for individual recognition by odour in Herpestus auropunctatus (Carnivora: Vivveridae)." Anim. Behav., 24, 141-145.

Goz, H. (1941): "Uber den art- und individualgeruch bei fischen." Z. vergl. Physiologie, 29, 1-45

Grant, E.C. and Mackintosh, K.H. (1963): "A comparison of the social postures of some common laboratory rodents." Behav., 21, 246-259.

Grau, H.J. (1982): "Kin recognition in white-footed deermice (Peromyscus leucopus)." Anim. Behav., 30, 497-505.

Greenberg, L. (1979): "Genetic component of bee odor in kin recognition." Science, 206, 1095-1097.

Greenwood, P.J., Harvey, P.H. and Perrins, C.M. (1978): "Inbreeding and dispersal in the great tit." Nature, 271, 52-54.

Gregory, E.H. and Pfaff, D.W. (1971): "Development of olfactory-guided behaviour in infant rats." Physiol. Behav., 6, 573-576.

Groos, K. (1898): The Play of Animals. Appleton, N.Y.

Gubernick, D.J., Jones, K.C. and Klopfer, P.H. (1979): "Maternal 'imprinting, in goats?." Anim. Behav., 27, 314-315.

Guhl, A.M. (1962): "The behaviour of chickens." In: The Behaviour of Domestic Animals. (Ed., E.S.E. Hafez), Balliere Tindall, Lond., pp. 491-530.

Hafez, E.S.E. (1962): *The Behaviour of Domestic Animals*. Balliere Tindall, Lond.

Hafez, E.S.E. and Schein, M.W. (1962): " The behaviour of cattle." In: *The Behaviour of Domestic Animals*. (Ed., E.S.E. Hafez), Balliere Tindall, Lond., pp. 247-296.

Hafez, E.S.E. and Scott, J.P. (1962): "The behaviour of sheep and goats." In: *The Behaviour of Domestic Animals*. (Ed., E.S.E. Hafez) Balliere Tindall, Lond., pp. 297-333.

Hafez, E.S.E., Sumption, L.J. and Jakway, J.S. (1962): "The behaviour of swine." In: *The Behaviour of Domestic Animals*. (Ed., E.S.E. Hafez), Balliere Tindall, Lond., pp. 334-369.

Hafner, M.S. and Hafner, D.S. (1979): "Vocalisations of grasshopper mice (Genus *Onychomys*)." *J. Mammol.*, *60*, 85-94.

Hahn, M.E. and Simmel, E.C. (1968): "Individual recognition by natural concentrations of olfactory cues in mice." *Psychonom. Sci.*, *12*, 183-184.

Hahn, M.E. and Tumulo, P. (1971): "Individual recognition in mice: How is it mediated?." *Bull. Ecol. Soc. Amer.*, *52*, 53-54.

Haldane, J.B.S. (1932): *The Causes of Evolution*. Longmans Green, London.

Halliday, T.R. (1976): "The Libidinous newt. An analysis of variations in the sexual behaviour of the male smooth newt, *Triturus vulgaris*." *Anim. Behav.*, *24*, 398-414.

Halpin, Z.T. (1974): "Individual differences in the biological odors of the Mongolian gerbil (*Meriones unguiculatus*)." *Behav. Biol.*, *11*, 253-259.

Halpin, Z.T. (1976): "The role of individual recognition by odors in the social interactions of the Mongolian gerbil (*Meriones unguiculatus*)." *Behav.*, *58*, 117-130.

Halpin, Z.T. (1980): "Individual odors and individual recognition: Review and commentary." *Biol. Behav.*, *5*, 233-248.

Hamilton, W.D. (1963): "The evolution of altruistic behavior." *Amer. Natural.*, *97*, 354-356.

Hamilton, W.D. (1964a): "The genetical evolution of social behaviour. 1." *J. Theoret. Biol.*, *7*, 1-16.

Hamilton, W.D. (1964b): "The genetical evolution of social behaviour. 2." J. Theoret. Biol., 7, 17-52.

Hamilton, W.D. (1970): "Selfish and spiteful behaviour in an evolutionary model." Nature, 228, 1218-1220.

Hamilton, W.D. (1971): "Selection of selfish and altruistic behaviour in some extreme models." In: Man and Beast: Comparative Social Behaviour. (Eds., J.F. Eisenberg and W.F. Dillon), Smithsonian Institute Press, Washington, pp. 57-91.

Hamilton, W.D. (1972): "Altruism and related phenomena mainly in social insects." Ann. Rev. Ecol. Systemat., 3, 193-232.

Hamilton, W.D. (1975): "Some innate social aptitudes of man: An approach from evolutionary biology." In: Biosocial Anthropology. (Ed., R. Fox), Wiley, Lond., pp. 133-155.

Hansen, E.W. (1976): "Selective responding by recently separated juvenile rhesus monkeys to the calls of their mothers." Develop. Psychobiol., 9, 83-88.

Harcourt, A.H., Stewart, K.S. and Fossey, D. (1976): "Male emigration and female transfer in wild mountain gorilla." Nature, 263, 226-227.

Harlow, H.F. (1958): "The nature of love." Amer. Psychol., 13, 673-685.

Harlow, H.F. (1959): "Love in infant monkeys." Sci. Amer., 200, 68-74.

Harlow, H.F. (1962): " The heterosexual affectional system in monkeys." Amer. Psychol., 17, 1-9.

Harlow, H.F. and Harlow, M.K. (1965): "The affectional systems." In: The Behaviour of Non-human Primates. Vol. 2. (Eds., A.M. Schrier, H.F. Harlow and F.S. Stollnitz), Academic Press, Lond., pp. 287-334.

Harrington, J.E. (1976): "Discrimination between individuals by scent in Lemur fulvus." Anim. Behav., 24, 207-212.

Harris, M.A. and Lemon, R.E. (1976): "Responses of male song sparrows Melospiza melodia to neighbouring and non-neighbouring individuals." Ibis, 118, 421-424.

Harvey, P.H., Baker, M.C., Bateson, P., Bischof, N., Emlen, S.T., Holldobler, B. Kramer, B., Linsenmair, K.E., Markl, H, Marler, P., Menzel, E.W., Michener, C.D., Milinski, M. and Trillmich, F. (1980): "Mechanisms of kin-correlated behaviour." In: Evolution of Social Behaviour: Hypotheses and Empirical Tests. (Ed., H. Markl), Verlag Chemie, Weinheim, pp. 183-202.

Hayashi, S. and Kimura, T. (1983): "Degree of kinship as a factor regulating preferences among conspecifics in mice." Anim. Behav., 31, 81-85.

Hazlett, B.A. (1969): "Individual recognition and agonistic behaviour in Pargurus bernhardus." Nature, 222, 268-269

Hess, E.H. (1973): Imprinting. Van Nostrand Reinhold, London.

Hill, J.L. (1974): "Peromyscus: Effect of early pairing on reproduction." Science, 186, 1042-1044.

Hinde, R.A. and Spencer-Booth, Y. (1971): "Effects of brief separations from mother on rhesus monkeys." Science, 173, 111-118.

Hofer, M.A. (1975): "Studies on how early maternal separation produces behavioural change in young rats." Psychosom. Med., 37, 245-264.

Hold, B. and Schleidt, M. (1977): "The importance of human odour in non-verbal communication." Z. Tierpsychol., 43, 225-238.

Holinka, C.F. and Carlson, A.D. (1976): "Pup attraction to lactating Sprague-Dawley rats." Behav. Biol., 16, 489-505.

Holldobler, B. and Michener, C.D. (1980): "Mechanisms of identification and discrimination in social Hymenoptera." In: Evolution of Social Behaviour: Hypotheses and Empirical Tests. (Ed., H. Markl), Verlag Chemie, Weinheim, pp. 35-58.

Hollingsworth, M.J. and Maynard-Smith, J. (1955): "The effects of inbreeding on rate of development and on fertility in Drosophila obscura." J. Genet., 53, 295-314.

Holmes, W.G. and Sherman, P.W. (1982): "The ontogeny of kin recognition in two species of ground squirrels." Amer. Zool., 22, 491-517.

Holmes, W.G. and Sherman, P.W. (1983): "Kin recognition in animals." Amer. Sci., 71, 46-55.

Hoogland, J.L. (1982): "Prairie dogs avoid extreme inbreeding." Science, 215, 1639-1641.

Huck, V.W. and Banks, E.M. (1979): "Behavioural components of individual recognition in the collared lemming (Dicrostonyx groenlandicus)." Behav. Ecol. Sociobiol., 6, 85-90.

Hull, D. (1972): "Thermoregulation in young mammals." In: *Comparative Physiology of Thermoregulation*. Vol. 2. (Ed., G.C. Whittow), Academic Press, N.Y.

Humphreys, A.P. (1982): "The Behavioral Significance of Animal Play." Unpubl. Ph.D. thesis, Uni. of Durham.

Humphreys, A.P. and Einon, D.F. (1981): "Play as a reinforcer for maze-learning in juvenile rats." *Anim. Behav.*, *29*, 259-270.

Husted, J.R. and McKenna, F.S. (1966): "The use of rats as discriminative stimuli." *J. Exp. Anal. Behav.*, *9*, 677-679.

Hutchinson, R.E., Stevenson, J.G. and Thorpe, W.H. (1968): "The basis for individual recognition by voice in the sandwich tern (*Sterna sandvichensis*)." *Behav.*, *32*, 150-157.

Huxley, C.R. and Wilkinson, R. (1979): "Duetting and vocal recognition by Aldabra white-throated rails, *Dryolimnas cuvieri aldabranus*." *Ibis*, *121*, 265-273.

Immelmann, K. and Suomi, S.J. (1981): "Sensitive phases in development." In: *Behavioral Development: The Bielefeld Interdisciplinary Project*. (Eds., K. Immelmann, G.W. Barlow, L. Petrinovich and M. Main), Cambridge Uni. Press, Cambridge, pp. 395-431.

Jaeger, R.G. and Gergits, W.F. (1979): "Intra and interspecific communication in salamanders through chemical signals on the substrate." *Anim. Behav.*, *27*, 150-156.

Jay, P.C. (1963): "Mother-infant relations in langurs." In: *Maternal Behaviour in Mammals*. (Ed., H.L. Rheingold), Wiley, N.Y., pp. 282-304.

Jensen, G.D. (1965): "Mother-infant relationship in the monkey, *Macaca nemestrina*: Development of specificity of response to own infant." *J. Comp. Physiol. Psychol.*, *59*, 305-308.

Jensen, G.D. and Tolman, C.W. (1962): "Mother-infant relationship in the monkey, *Macaca nemestrina*: The effect of brief separation and mother-infant specificity." *J. Comp. Physiol. Psychol.*, *55*, 131-136.

Johanson, I.B. and Hall, W.G. (1979): "Appetitive learning in 1-day-old rat pups." Science, 205, 419-421.

Johanson, I.B. and Hall, W.G. (1982): "Appetitive conditioning in neonatal rats: Conditioned orientation to a novel odour." Develop. Psychobiol., 15, 379-397.

Johanson, I.B. and Teicher, M.H. (1980): "Classical conditioning of an odor preference in 3-day-old rats." Behav. Neur. Biol., 29, 132-136.

Johnson, V.R. (1977): "Individual recognition in the banded shrimp (Stenopus hispidus OLIVIER)." Anim. Behav., 25, 418-428.

Kagan, J. and Beach, F.A. (1953): "Effects of early experience on mating behavior in male rats." J. Comp. Physiol. Psychol., 46, 204-208.

Kalela, O. (1954): "Uber den revierbesitz bei volgen und saugetieren als populationsokologischer faktor." Ann. Zool. Soc. Zool. Bot. Fennicae 'Vanamo', (Helsinki), 16, 1-48.

Kalmus, H. (1955): "The discrimination by the nose of the dog of individual human odours and in particular the odours of twins." Brit. J. Anim. Behav., 3, 25-31.

Kaplan, J. and Schusterman, R.J. (1972): "Social preferences of mother and infant squirrel monkeys following different rearing experiences." Develop. Psychobiol., 5, 53-59.

Kaplan, J.N., Winship-Ball, A. and Sim, L. (1978): "Maternal discrimination of infant vocalisations in squirrel monkeys." Primates, 19, 187-193.

Kareem, A.M. and Barnard, C.J. (1982): "The importance of kinship and familiarity in social interactions between mice." Anim. Behav., 30, 594-601.

Karen, L.M. and Barfield, R.J. (1975): "Differential rates of exhaustion and recovery of several parameters of male rat sexual behavior." J. Comp. Physiol. Psychol., 88, 693-703.

Kincaid, H.L. (1976): "Inbreeding in rainbow trout (Salmo gairdneri)." J. Fish. Res. Bd. Canada, 33, 2420-2426.

King, H.D. (1918a): "Studies on inbreeding: 1. The effects of inbreeding on the growth and variability in body weight of the albino rat." J. Exp. Zool., 26, 1-54.

King, H.D. (1918b): "Studies on inbreeding: 2. The effects of inbreeding on the fertility and on the constitutional vigor of the albino rat." J. Exp. Zool., 26, 55-98.

King, H.D. (1918c): "Studies on inbreeding: 3. The effects of inbreeding with selection on the sex ratio of the albino rat." J. Exp. Zool., 27, 1-35.

King, H.D. (1919): "Studies on inbreeding: 4. A further study of the effects of inbreeding on the growth and variability in body weight of the albino rat." J. Exp. Zool., 29, 134-175.

King, J.A. (1956): "Social relations of the domestic guinea pig living under semi-natural conditions." Ecology, 37, 221-228.

King, J.C. (1980): "The genetics of sociobiology". In: Sociobiology Examined. (Ed. A. Montagu), Oxford Uni. Press, N.Y., pp.82-107.

Kleiman, D.G. (1969): "Maternal care, growth rate and development in the noctule (Nyctalus noctula), pipistrelle (Pipistrellus pipistrellus) and serotine (Eptesicus serotinus) bats." J. Zool., 157, 187-211.

Klein, J. (1975): Biology of Mouse Histocompatibilty-2 Complex. Springer-Verlag. N.Y.

Klingel, H. and Klingel, U. (1966): "Die geburt eines zebras (Equus quagga bohmi MATSCHI)." Z. Tierpsychol., 23, 72-76.

Klopfer, P.H. (1970): "Discrimination of young in galagos." Folia Primatol., 13, 137-143.

Klopfer, P.H. (1981): "Origins of parental care". In: Parental Care in Mammals. (Eds., D.J. Gubernick and P.H. Klopfer), Plenum Press, N.Y., pp. 1-12.

Klopfer, P.H. and Gamble, J. (1966): "Maternal 'imprinting' in goats: The role of chemical senses." Z. Tierpsychol., 23, 588-592.

Klopfer, P.H. and Gilbert, B.K. (1966): "A note on retrieval and recognition of young in the elephant seal, Mirounga angustirostris." Z. Tierpsychol., 23, 757-760.

Klopfer, P.H. and Klopfer, M.S. (1968): "Maternal 'imprinting' in goats: fostering of alien young." Z. Tierpsychol., 25, 862-866.

Koenig, W.D. and Pitelka, F.A. (1979): "Relatedness and inbreeding avoidance: Counterploys in the communally nesting acorn woodpecker." Science, 206, 1103-1105.

Kok, O.B. (1971): "Vocal behaviour of the great-tailed grackle (Quiscalus mexicanus prosopidicola)." Condor, 73, 348-363.

Krames, L. (1970): "Responses of female rats to the individual body odors of male rats." Psychonom. Sci., 20, 274-275.

Krames, L., Carr, W.J. and Bergman, B. (1969): "A pheromone associated with social dominance among rats." Psychonom. Sci., 16, 11-12.

Krames, L. and Shaw, B. (1973): "Role of previous experience in the male rats reaction to odors from group and alien conspecifics." J. Comp. Physiol. Psychol., 82, 444-448.

Krebs, J.R. (1971): "Territory and breeding density in the great tit, Parus major." Ecology, 52, 2-22.

Krebs, J.R. and Davies, N.B. (1982): An Introduction to Behavioural Ecology, Blackwell Sci. Publ., Oxford.

Kroodsma, D.E. (1971): "Song variations and singing behavior in the Rufous-sided towhee, Pipilo erythrophthalamus oregonus." Condor, 73, 303-308.

Kroodsma, D.E. (1976): "The effect of large song repetoires on neighbor 'recognition' in male song sparrows." Condor, 78, 97-99.

Kuhme, W. (1963): "Chemisch ausgeloste brutpflege -und schwarmreaktionen bei Hemichromis bimaculatus (Pisces)." Z. Tierpsychol., 20, 688-704.

Kuhn, C.M., Butler, S.R. and Schanberg, S.M. (1978): "Selective depression of serum growth hormone during maternal deprivation in rat pups." Science, 201, 1034-1036.

Kumaresan, P., Anderson, R.R. and Turner, C.W. (1967): "Effect of litter size upon milk yield and litter weight gain in rats." Proc. Soc. Exp. Biol. Med., 126, 41-45.

Kunkel, P. (1974): "Mating systems of tropical birds: The effects of weakness or absence of external reproduction-timing factors, with special reference to prolonged pair bonds." Z. Tierpsychol., 34, 265-307.

Kurland, J.A. (1977): "Kin selection in the Japanese monkey." Contrb. Primatol., 12.

Kurland, J.A. (1980): "Kin selection theory: A review and selective bibliography." Ethol. Sociobiol., 1, 255-274.

Kurland, J.A. and Gaulin, S.J.C. (1979): "Testing kin selection: Problems with r." Behav. Ecol. Sociobiol., 6, 81-83.

Lacy, R.C. and Sherman, P.W. (1983): "Kin recognition by phenotype matching." Amer. Natural., 121, 489-512.

Laing, D.G. and Panhuber, H. (1980): "Olfactory sensitivity of rats reared in an odorous or deodorized environment." Physiol. Behav., 25, 555-558.

Lashley, K.S. (1930): "The mechanisms of vision. 3: The comparative visual acuity of pigmented and albino rats." J. Genet. Psychol., 37, 481-484.

Lashley, K.S. and Sperry, R.W. (1943): "Olfactory discrimination after destruction of the anterior thalamic nuclei." Amer. J. Physiol., 139, 446-450.

Lavery, J.J. and Foley, P.J. (1963): "Altruism or arousal in the rat?." Science, 140, 172-173.

Laws, R.M. (1956): "The elephant seal (Mirounga leonina LINA). 2. General, social and reproductive behaviour." Falkland 1st Depend. Surv., Sci. Rep., 13, 18pp.

Leach, C. (1979): Introduction to Statistics. J. Wiley, London.

Lemon, R.E. (1967): "The response of cardinals to songs of different dialects." Anim. Behav., 15, 538-545.

Lent, P.C. (1966): "Calving and related social behaviour in the barren-ground caribou." Z. Tierpsychol., 23, 701-756.

Leon, M. (1974): "Maternal pheromone." Physiol. Behav., 13, 441-453.

Leon, M. (1975): "Dietary control of maternal pheromone in the lactating rat." Physiol. Behav., 14, 311-319.

Leon, M. (1980): "Development of olfactory attraction by young Norway rats." In: Chemical Signals: Vertebrate and Aquatic Invertebrates. (Eds., D. Muller-Schwarze and R.M. Silverstein), Plenum Press, Lond., pp.193-209.

Leon, M. and Moltz, H. (1971): "Maternal pheromone: Discrimination by pre-weanling albino rats." Physiol. Behav., 7, 265-267.

Leon, M. and Moltz, H. (1972): "The development of the pheromonal bond in the albino rat." Physiol. Behav., 8, 683-686.

Lev, R. and Orlic, D. (1972): "Protein absorption by the intestine of the fetal rat in utero." Science, 177, 522-524.

Levin, R. and Stern, J.M. (1975): "Maternal influences on ontogeny of suckling and feeding rhythms in the rat." J. Comp. Physiol. Psychol., 89,711-721.

Levins, R. (1970): "Extinction." In: Some Mathematical Questions in Biology. Lectures on Mathematics in the Life Sciences. (Ed. M. Gerstenhaber), American Mathematical Soc., Prov., Rhode Island, pp. 77-107.

Liechti, P.M. and Bell, W.J. (1975): "Brooding behavior of the Cuban burrowing cockroach, Byrsotria fumigata (Blaberidae,Blattaria)." Insectes. Soc., 22, 35-46.

Lillehei, R.A. and Snowdon, C.T. (1978): "Individual and situational differences in the vocalisations of young stumptail macaques (Macaca arctoides)." Behav., 65, 270-281.

Lindsay, D.R. and Fletcher, I.C. (1968): "Sensory involvement in the recognition of lambs by their dams." Anim. Behav., 16, 415-417.

Linsenmair, K.E. (1972): "The importance of family-specific 'badges' for the cohesion of families in the social desert woodlouse, Hemilepistus reamuri." Z. Tierpsychol., 31, 131-162.

Linsenmair, K.E. and Linsenmair, C. (1971): "Pair formation and pair maintenance in the momogamous desert woodlouse, Hemilepistus reamuri." Z. Tierpsychol., 29, 134-155.

Lore, R. and Flannelly, K. (1977): "Rat societies." Sci. Amer., 236, 106-116.

Lorenz, K. (1935): "Der kumpan in der Unwelt des vogels." J. Ornithologie, 83, 137-213, 289-413.

Lorenz, K. (1938): "A contribution to the comparative sociology of colonial-nesting birds." Proc. 8th Ornithol. Congr., Oxford, 1934, pp. 204-218.

Lorenz, K. (1956): "Plays and vacuum activities." In: L'instinct dans le Comportement des Animaux et de l'homme. (Eds., M. Autuori et al.), Masson, Paris, pp. 633-645.

Lytle, L.D. and Keil, F.C. (1974): "Brain and peripheral monoamines: Possible role in the ontogenesis of normal and drug-induced responses in the immature mammal." In: Dynamics of Degeneration and Growth in Neurones. (Eds., K. Fuxe, L. Olsen and Y. Zotterman), Pergammon Press, N.Y.

Macfarlane, A. (1975): "Olfaction in the development of social preferences in the human neonate." Ciba Found. Symp., 33, 103-117.

Macfarlane Burnet, F. (1976): "The evolution of receptors and recognition in the immune system." In: Receptors and Recognition. Series A.(1). (Eds., P. Cuatrecasas and M.F. Greaves), Chapman Hall, Lond., pp.33-58.

MacGinitie, G.E. (1939): "The natural history of the blind goby, Typhlogobius californiensis (Steindachner)." Amer. Mid. Natural., 21, 489-505.

Mackay-Sim, A. and Laing, D.G. (1980): "Discrimination of odors from stressed rats by non-stressed rats." Physiol. Behav., 24, 699-704.

Madison, D.M. (1975): "Intraspecific odor preferences between salamanders of the same sex: Dependence on season and proximity of residence." Can. J. Zool., 53, 1356-1361.

Maier, R.A. (1964): "The role of the dominance-submission ritual in social recognition of hens." Anim. Behav., 12, 59.

Mamman, D.L. and Nowicki, S. (1981): "Individual differences and within flock convergence in chickadee calls." Behav. Ecol. Sociobiol., 9, 179-186.

Marasco, E., Cornwell-Jones, C. and Sobrian, S.K. (1979): "6-hydroxydopamine reduces preference for conspecific but not other familiar odors in rat pups." Pharm. Biochem. Behav., 10, 319-323.

Marler, P. and Hobbett, L. (1975): "Individuality in a long-range vocalisation of a wild chimpanzee." Z. Tierpsychol., 38, 97-109.

Marr, J.N. and Gardner, L.E. (1965): "Early olfactory experience and later social behaviour in the rat: Preference, sexual responsiveness and care of young." J. Genet. Psychol., 107, 167-174.

Marr, J.N. and Lilliston, L.G. (1969): "Social attachment in rats by odor and age." Behav., 33, 277-282.

Materazzi, G. (1967): "Osservazioni sulla funzione dei 'Tubuli a grani' della ghiandola sottomandibolare del ratto." Riv. Biol. Suppl., 60, 73-84.

Mather, K. (1955): "The genetical basis of heterosis." Proceed. Royal. Soc. B., 144, 143-150.

Mathison, O.A., Beade, R.T. and Lopp, R.J. (1962): "Breeding habits, growth and stomach contents of the Stellar sea lion in Alaska." J. Mammol., 43, 469-477.

Maynard Smith, J. (1956): "Fertility, mating behaviour and sexual selection in Drosophila subobscura." J. Genet., 54, 261-279.

Maynard Smith, J. (1964): "Group selection and kin selection." Nature, 201, 1145-1147.

Maynard Smith, J. (1980): "Models of the evolution of altruism." Theoret. Pop. Biol., 18, 151-159.

Maynard Smith, J. and Ridpath, M.G. (1972): "Wife sharing in the Tasmanian Native hen, Tribonyx mortierii: A case of kin selection." Amer. Natural., 106, 447-452.

McClintock, M.K. (1974): "Sociobiology of Reproduction in the Norway Rat (Rattus norvegicus). Estrous Synchrony and the Role of the Female in Copulatory Behavior." Unpubl. Ph.D. thesis, Uni. of Pennslyvania.

McClintock, M.K., Toner, J.P., Adler, N.T. and Anisko, J.J. (1982): "Postejaculatory quiescence in female and male rats: Consequences for sperm transport during group mating." J. Comp. Physiol. Psychol., 96, 268-277.

McHugh, T. (1958): "Social behaviour of the American buffalo (Bison bison bison)." Zoologica, 43, 1-40.

McIntosh, T.K. and Barfield, R.J. (1980): "The temporal patterning of 40-60 KHz ultrasonic vocalisations and copulation in the rat (Rattus norvegicus)." Behav. Neur. Biol., 29, 349-358.

McKaye, K.R. and Barlow, G.W. (1976): "Chemical recognition of young by the Midas cichlid, *Cichlasoma citrinellum*." *Copeia*, *2*, 276-282.

Meany, M.J. and Stewart, J. (1981): A descriptive study of social development in the rat (*Rattus norvegicus*)." *Anim. Behav.*, *29*, 34-45.

Meese, G.B., Connor, D.J. and Baldwin, B.A. (1975): "Ability of the pig to distinguish between conspecific urine samples using olfaction." *Physiol. Behav.*, *15*, 121-125.

Meikle, D.B. and Vessey, S.H. (1981): "Nepotism among rhesus monkey brothers." *Nature*, *294*, 160-161.

Mertl, A.S. (1975): "Discrimination of individuals by scent in a primate." *Behav. Biol.*, *14*, 505-509.

Metcalf, R.A. (1980): "Measuring fitness in social insects." In: *Evolution of Social Behaviour: Hypotheses and Empirical Tests*. (Ed., H. Markl), Verlag Chemie, Weinheim, pp. 81-95.

Michener, G.R. and Sheppard, D.H. (1972): "Social behaviour between adult female Richardson's ground squirrels (*Spermophilus richardsonii*) and their own and alien young." *Can. J. Zool.*, *50*, 1343-1349.

Michod, R.E. (1982): "The theory of kin selection." *Ann. Rev. Ecol. Systemat.*, *13*, 23-55.

Michod, R.E. and Hamilton, W.D. (1980): "Coefficients of relatedness in sociobiology." *Nature*, *288*, 694-697.

Miller, D.B. (1979): "The acoustic basis of mate recognition by female zebra finches (*Taeniopygia guttata*)." *Anim. Behav.*, *27*, 376-380.

Miller, D.E. and Emlen, J.T. (1975): "Individual chick recognition and family integrity in the ring-billed gull." *Behav.*, *52*, 124-144.

Miller, S. (1973): "Ends, means, and gallumphing: some leitmotifs of play." *Amer. Anthropol.*, *75*, 87-98.

Moltz, H. and Lee, T.M. (1981): "The maternal pheromone of the rat: Identity and functional significance." *Physiol. Behav.*, *26*, 301-306.

Montgomery, K.C. (1952): "A test of two explanations of spontaneous alternation." *J. Comp. Physiol. Psychol.*, *45*, 287-293.

Moran, T.H., Lew, M.F. and Blass, E.M. (1981): "Intracranial self-stimulation in 3-day-old rat pups." Science, 214, 1366-1368.

Morgan, M.J. (1973): "Effects of postweaning environment on learning in the rat." Anim. Behav., 21, 429-442.

Morgan, P.D., Boundy, C.A.P., Arnold, G.W. and Lindsay, D.R. (1975): "The roles played by the senses of the ewe in the location and recognition of lambs." Appl. Anim. Ethol., 1, 139-150.

Morrison, R.R. and Ludvigson, H.W. (1970): "Discrimination by rats of conspecific odors of reward and non-reward." Science, 167, 904-905.

Moseley, L.J. (1979): "Individual auditory recognition in the least tern (Sterna albifrons)." Auk, 96, 31-39.

Mozell, M.M. (1971): "Spatial and temporal patterning." In: Handbook of Sensory Physiology: 4. Olfaction. (Ed., L.M. Beidler), Springer-Verlag, Berlin, pp. 205-215.

Muller-Schwarze, D. (1968): "Play deprivation in deer." Behav., 31, 144-162.

Muller-Schwarze, D. (1971): " Pheromones in black-tailed deer (Odocoileus hemionus columbians)." Anim. Behav., 19, 141-152.

Muller-Schwarze, D., Quay, W.B. and Brundin, A. (1977): "The caudal gland in reindeer (Rangifer tarandus L.): its behavioural role, histology and chemistry." J. Chem. Ecol., 3, 591-602.

Mundinger, P.C. (1970): "Vocal imitation and individual recognition of finch calls." Science, 168, 480-482.

Munn, N.L. (1950): Handbook of Psychological Research on the Rat. Riverside Press, Mass.

Myberg, A.A. (1975): "The role of chemical and visual stimuli in the preferential discrimination of young by the cichlid fish Cichlasoma nigrofasciatum (Gunther)." Z. Tierpsychol., 37, 274-297.

Mykytowycz, R. and Ward, M.M. (1971): "Some reactions of nestlings of the wild rabbit, Oryctolagus cuniculus (L.), when exposed to natural rabbit odours." Forma et Functio, 4, 137-148.

Narayanan, C.H., Fox, M.W. and Hamburger, V. (1971): "Prenatal development of spontaneous and evoked activity in the rat (Rattus norvegicus albinus)."

Behav., 40, 100-134.

Nash, L.T. (1978): "Kin preference in the behaviour of young baboons." Rec. Adv. Primatol., 1, 71-73.

Neal, M.V. (1968): "Vestibular stimulation and developmental behaviour of the small premature infant." Nurse Res. Rep., 3, 1-5.

Nicolaides, N. (1974): "Skin lipids: Their biochemical uniqueness." Science, 186, 19-26.

Noble, G.K. and Clausen, H.J. (1936): "The aggregation behaviour of Storeria dekayi and other snakes with especial reference to the sense organs involved." Ecol. Monogr., 6, 269-316.

Noble, G.K. and Curtis, B. (1939): "The social behaviour of the Jewel fish; Hemichromis bimaculatus GILL." Bull. Amer. Mus. Nat. Hist., 76, 1-46.

Nyakas, C. and Endroczi, E. (1970): "Olfaction guided approaching behaviour of infantile rats to the mother in maze box." Acta Physiol. Acad. Sci. Hung., 38, 59-65.

O'Hara R.K. and Blaustein, A.R. (1981): "An investigation of sibling recognition in Rana cascadae tadpoles." Anim. Behav., 29, 1121-1126.

Okon, E. (1972): "Factors affecting ultrasound production in infant rodents." J. Zool., 168, 139-148.

Oster, G.F., Bradbury, J.W., Charlesworth, B., Curio, E., Feldman, M.W., Hammerstein, P., Hausfater, G., Heller, R., Lumsden, C.J., May, R.M., Maynard Smith, J., Sherman, P.W. and Wickler, W. (1980): "Methodology and sociobiology modelling group report." In: Evolution of Social Behaviour: Hypotheses and Empirical Tests. (Ed., H. Markl), Verlag Chemie, Weinheim, pp. 165-180.

Ostermeyer, M.C. and Elwood, R.W. (1983): "Pup recognition in Mus musculus: Parental discrimination between their own and alien young." Develop. Psychobiol., 16, 75-82.

Owens, N.W. (1975): "Social play behaviour in free living baboons Papio Anubis." Anim. Behav., 23, 387-408.

Packer, C. (1975): "Male transfer in olive baboons." Nature, 255, 219-220.

Packer, C. (1979): "Male dominance and reproductive activity in Papio anubis." Anim. Behav., 27, 37-45.

Pager, J. (1974): "A selective modulation of the olfactory bulb electrical activity in relation to the learning of palatability in hungry and satiated rats." Physiol. Behav., 12, 189-195.

Panksepp, J. (1981): "The ontogeny of play in rats." Develop. Psychobiol., 14, 327-332.

Pearson, O.P., Koford, M.R. and Pearson, A.K. (1952): "Reproduction in the lump-nosed bat (Corynorhinus rafinesquei) in California." J. Mammol., 33, 273-320.

Pederson, P.E., Williams, C.L. and Blass, E.M. (1982): "Activation and odor conditioning of suckling behavior in 3-day-old albino rats." J. Expt. Psychol.: Anim. Behav. Process., 8, 329-341.

Petrinovich, L. (1974): "Individual recognition of pup vocalisations by Northern elephant seal mothers." Z. Tierpsychol., 34, 308-312.

Pettijohn, T.F. (1981): "Conditioned social aversion in the male mongolian gerbil (Meriones unguiculatus)." J. Comp. Physiol. Psychol., 95, 228-239.

Pietras, R.J. and Moulton, D.G. (1974): "Hormonal influences on odor detection in rats: Changes associated with the estrous cycle, pseudopregnancy, ovariectomy, and administration of testosterone propionate." Physiol. Behav., 12, 475-491.

Pinching, A.J. and Doving, K.B. (1974): "Selective degeneration in the rat olfactory bulb following exposure to different odours." Brain Res., 82, 195-204.

Poirier, F.E. and Smith, E.O. (1974): "Socialising functions of primate play." Amer. Zool., 14, 275-287.

Poole, T.B. and Fish, J. (1975): "An investigation of playful behaviour in Rattus norvegicus and Mus musculus (Mammalia)." J. Zool., 175, 61-71.

Porter, R.H., Fullerton, C. and Berryman, J.C. (1973): "Guinea-pig mother-young attachment behaviour." Z. Tierpsychol., 32, 489-495.

Porter, R.H. and Moore, J.D. (1981): "Human kin recognition by olfactory cues." Physiol. Behav., 27, 493-495.

Porter, R.H., Moore, J.D. and White, D.M. (1980): "Foodsharing by sibling vs nonsibling spiny mice (Acomys cahirinus)." Behav. Ecol. Sociobiol., 8, 207-212.

Porter, R.H., Tepper, V.J. and White, D.M. (1981): "Experiential influences on the development of huddling preferences and 'sibling' recognition in spiny mice." Develop. Psychobiol., 14, 375-382.

Porter, W.H. and Wyrick, M. (1979): "Sibling recognition in spiny mice (Acomys cahirinus): influence of age and isolation." Anim. Behav., 761-766.

Porter, R.H., Wyrick, M. and Pankey, J. (1978): "Sibling recognition in Spiny mice (Acomys cahirinus)." Behav. Ecol. Sociobiol., 3, 61-68.

Pruitt, W.O. (1960): "Behaviour of the barren-ground caribou." Biol. Pap. Uni. Alaska, 3, 1-43.

Pusey, A.E. (1980): "Inbreeding avoidance in chimpanzees." Anim. Behav., 28, 543-552.

Ralls, K., Brugger, K. and Ballow, J. (1979): "Inbreeding and juvenile mortality in small populations of ungulates." Science, 206, 1101-1103.

Rappolt, G.A., John, J. and Thompson, M.S. (1979): "Canine reponses to familiar and unfamiliar humans." Aggress. Behav., 5, 155-161.

Rasa, A. (1973): "Marking behaviour and its social significance in the African dwarf mongoose, Helogale undulata rufula." Z. Tierpsychol., 32, 293-318.

Rice, G.E. and Gainer, P. (1962): "'Altruism' in the albino rat." J. Comp. Physiol. Psychol., 55, 123-125.

Richards, D.G. (1979): "Recognition of neighbours by associative learning in rufous-sided towhees." Auk, 96, 688-693.

Richards, I.S. (1974): "Caudal neurosecretory system: Possible role in pheromone production." J. Exp. Zool., 187, 405-408.

Ridley, M. and Grafen, A. (1981): "Are green beard genes outlaws?." Anim. Behav., 29, 954-955.

Ritzema-Bos, J. (1894): "Untersuchungen uber die Folgen der zucht in engster Blutverwandtschaft." Biol. Cent., 14, 75-81.

Robson, C. (1975): Experiment, Design and Statistics in Psychology. Penguin, Harmondsworth.

Roeder, J.J. (1980): "Marking behaviour and olfactory recognition in genets. (Genetta genetta L., Carnivora-Viverridae)." Behav., 72, 200-210.

Romanes, G.J. (1883a): Mental Evolution in Animals. Kegan, Paul and Trench, Lond.

Romanes, G.J. (1883b): Animal Intelligence. Kegan, Paul and Trench, Lond.

Rosenblatt, J.S. (1969): "The development of maternal responsiveness in the rat." Amer. J. Orthopsychiat., 39, 36-56.

Rosenblatt, J.S. and Lehrman, D.S (1963): "Maternal behaviour of the laboratory rat." In: Maternal Behaviour in Mammals. (Ed., H.L. Rheingold), J. Wiley, Lond., pp. 8-57.

Roth, L.L. and Rosenblatt, J.S. (1967): "Changes in self-licking during pregnancy in the rat." J. Comp. Physiol. Psychol., 63, 397-400.

Roth-Kolar, H. (1957): "Beitrage zu einen Aktionssystem des Aguti (Dasyprocta aguti aguti L." Z. Tierpsychol, 14, 362-375.

Rothstein, S.I. (1975): "Mechanisms of avian egg-recognition: Do birds know their own eggs?." Anim. Behav., 23, 268-278.

Rothstein, S.I. (1980): "Reciprocal altruism and kin selection are not clearly separable phenomena." J. Theoret. Biol., 87, 255-261.

Rowell, T.E. (1960): "On the retrieving of young and other behaviour in lactating golden hamsters." Proc. Zool. Soc. Lond., 135, 265-282.

Rowley, I. (1980): "Parent-offspring recognition in a cockatoo, the Galah, Cacatua rosekapilla." Aust. J. Zool., 28, 445-456.

Rowley, J. (1929): "Life history of the sea-lions of the California coast." J. Mammol., 10, 1-36.

Ruddy, L.L. (1980): "Discrimination among colony mates' anogenital odors by guinea-pigs (Cavia porcellus)." J. Comp. Physiol. Psychol., 94, 767-774.

Rudy, J.W. and Cheatle, M.D. (1977): "Odor-aversion learning in neonatal rats." Science, 198, 845-846.

Rudy, J.W. and Cheatle, M.D. (1979): "Ontogeny of associative learning: Acquisition of odor aversions by neonatal rats." In: The Ontogeny of Learning and Memory. (Eds., N.E. Spear and B.A. Campbell), Erlbaum, Hillsdale,N.J., pp. 157-188.

Rudy, J.W. and Cheatle, M.D. (1980): "Odor aversion learning by neonatal rats: Ontogeny of osmic memory." In: Chemical Signals: Vertebrate and Aquatic Invertebrates. (Eds., D. Muller-Schwarze and R.M. Silverstein), Plenum Press, Lond., pp. 221-228.

Ryan, C.M.E. (1982): "Concept formation and individual recognition in the domestic chicken (Gallus gallus)." Behav. Anal. Lett., 2, 213-220.

Sachs, B.D. and Barfield, R.J. (1976): "Functional analysis of masculine copulatory behavior in the rat." Adv. St. Behav., 7, 91-154.

Sales, G.D. (1972): "Ultrasound and aggressive behaviour in rats and other small mammals." Anim. Behav., 20, 88-100.

Sales, G.D. and Smith, J.C. (1978): "Comparative studies of the ultrasonic calls of infant murid rodents." Develop. Psychobiol., 11, 595-619.

Schapiro, S. and Salas, M. (1970): "Behavioural response of infant rats to maternal odor." Physiol. Behav., 5, 815-817.

Schenkel, R. (1966): "Play, exploration and territorality in the wild lion." Symp. Zool. Soc. Lond., 18, 11-22.

Schneirla, T.C., Rosenblatt, J.S. and Tobach, E. (1963): "Maternal behaviour in the cat." In: Maternal Behaviour in Mammals. (Ed., H.L. Rheingold), Wiley, N.Y., pp. 122-168.

Schumacher, S.K. and Moltz, H. (1982): "The maternal pheromone of the rat as an innate stimulus for pre-weanling young." Physiol. Behav., 28, 67-71.

Scofield, V.L., Schlumpberger, J.M., West, L.A. and Weissman, I.L. (1982): "Protochordate allorecognition is controlled by a M.H.C.-like gene system." Nature, 295, 499-502.

Scudder, K.M., Stewart, N.J. and Smith, H.M. (1980): "The response of neonate water snakes (Nerodia sipedon sipedon) to conspecific chemical cues." J. Herpetol., 14, 196-198.

Sczerzenie, V. and Hsiao, S. (1977): "Development of locomotion towards home nesting material in neonatal rats." Develop. Psychobiol., 10, 315-321.

Seger, J. (1976): "Evolution of responses to relative homozygosity." Nature, 262, 578-580.

Seligman, M.E.P. (1970): "On the generality of the laws of learning." Psychol. Rev., 77, 406-418.

Seligman, M.E.P. and Hager, J.L. (1972): Biological Boundaries of Learning. Appleton Century Crofts, N.Y.

Sharpe, L.G. and Cooper, J.B. (1966): "Individual recognition in albino rats." J. Genet. Psychol., 109, 151-161.

Shepher, J. (1971): "Mate selection among second generation kibbutz adolescents and adults: Incest avoidance and negative imprinting." Arch. Sex. Behav., 1, 293-307.

Sheppard, D.H. and Yoshida, S.Y. (1971): "Social behaviour in captive Richardson's ground squirrel." J. Mammol., 52, 793-799.

Siegel, S. (1956): Nonparametric Statistics for the Behavioural Sciences. McGraw Hill. Lond.

Silk, J.B. (1982): "Altruism among female Macaca radiata: Explanations and analysis of patterns of grooming and coalition formation." Behav., 79, 162-188.

Silk, J.B., Samuels, A. and Rodman, P.S. (1981): "The influence of kinship, rank and sex on affiliation and aggression between adult female and immature bonnet macaques (Macaca radiata)." Behav., 78, 111-137.

Simons, R.C., Bobbitt, R.A. and Jensen, G.D. (1968): "Monkey mothers (Macaca nemestrina) responses to infant vocalisations." Percept. Mot. Skills, 27, 3-10.

Sittman, K., Abplanalp, H. and Fraser, R.A. (1966): "Inbreeding depression in the Japanese quail." Genetics, 54, 371-379.

Small, W.S. (1899): "Notes on the psychic development of the young white rat." Amer. J. Psychol., 11, 80-100.

Smith, E.O. (1978): "A historical view of the study of play: statement of the problem." In: *Social Play in Primates*. (Ed., E.O.Smith), Acad. Press, N.Y.,

Smith, F.V., Van-Toller, C. and Boyes, T. (1966): "The 'critical period' in the attachment of lambs and ewes." *Anim. Behav.*, *14*, 120-125.

Smith, G.J. and Spear, N.E (1980): "Facilitation of conditioning in 2-day-old rats by training in the presence of conspecifics." *Behav. Neur. Biol.*, *28*, 491-495.

Smith, P.K. (1982): "Does play matter? Functional and evolutionary aspects of animal and human play." *Behav. Brain Sci.*, *5*, 139-184.

Smotherman, W.P. (1982a): "In utero chemosensory experience alters taste preferences and corticosterone responsiveness." *Behav. Neur. Biol.*, *36*, 61-68.

Smotherman, W.P. (1982b): "Odor aversion learning by the rat fetus." *Physiol. Behav.*, *29*, 769-771.

Smotherman, W.P., Bell. R.W., Starzec, J., Elias, J. and Zachman, T.A. (1974): "Maternal responses to infant vocalizations and olfactory cues in rats and mice." *Behav. Biol.*, *12*, 55-66.

Snowdon, C.T. and Cleveland, J. (1980): "Individual recognition of contact calls by Pygmy marmosets." *Anim. Behav.*, *28*, 717-727.

Sobrian, S.K. and Cornwell-Jones, C.A. (1977): "Neonatal 6-hydroxydopamine alters olfactory development." *Behav. Biol.*, *21*, 329-340.

Sokolov, V.E. and Lyapunova, K.L. (1979): "Reactions of Norway rats (*Rattus norvegicus*) to conspecific olfactory cues with respect to sex and social rank." *Zool. Zh.*, *58*, 218-229.

Solkoff, N., Yaffe, S., Weintraub, D. and Blase, B. (1969): "Effects of handling on the subsequent development of premature infants." *Develop. Psychobiol.*, *1*, 765-768.

Spencer, H. (1878): *The Principles of Psychology*, Vol. 2. Appleton, N.Y.,

Stehn, R.A. and Richmond, M.E. (1975): "Male induced pregnancy termination in the prairie vole, *Microtus ochrogaster*." *Science*, *187*, 1210-1211.

Stern, J.J. (1970): "Responses of male rats to sex odours." Physiol. Behav., 5, 519-524.

Stevenson, J.G., Hutchinson, R.E., Hutchinson, J.B., Bertram, B.C.R. and Thorpe, W.H. (1970): "Individual recognition by auditory cues in the common tern (Sterna hirundo)." Nature, 226, 562-563.

Stickrod, G., Kimble, D.P. and Smotherman, W.P. (1982): "In utero taste/odour aversion conditioning in the rat." Physiol. Behav., 28, 5-7.

Stoddart, D.M. (1980): The Ecology of Vertebrate Olfaction. Chapman Hall, Lond.

Suarez, S.D. and Gallup, G.G. (1981): "Self-recognition in chimpanzees and orangutans, but not gorillas." J. Hum. Evol., 10, 175-188.

Svare, B.B. (1981): "Maternal aggression in animals." In: Parental Care in Mammals. (Eds., D.J. Gubernick and P.H. Klopfer), Plenum Press, Lond., pp. 179-210.

Swann, H.G. (1933): "The function of the brain in olfaction: 1. Olfactory discrimination and an apparatus for its test." J. Comp. Psychol., 15, 229-241.

Swartz, K.B. (1977): "Species and Individual Recognition in Infant Macaques." Unpubl. Ph.D. Thesis, Brown Uni.

Symons, D. (1978): Play and Aggression: A Study of Rhesus Monkeys. Columbia Uni. Press. N.Y.

Talbot, L.M. and Talbot, M.H. (1963): "The wildebeest in Western Masailand, East Africa." Wildlf. Monogr., 12, 1-88.

Taruski, A.G. (1979): "The whistle of the North Atlantic pilot whale (Gloicephala melaena) and its relationship to behaviour and environment." In: Behaviour of Marine Animals. Current Perspectives in Research. Vol. 3. Cetaceans. (Eds., H.E. Winn and B.L. Olla), Plenum Press, N.Y., pp. 345-368.

Tavolga, M.C. and Essapian, F.S. (1957): "The behaviour of the bottle-nosed dolphin (Tursiops truncatus): Mating, pregnancy, parturition and mother-infant behaviour." Zoologica, 42, 11-31.

Taylor, P.M. (1960): "Oxygen consumption in new-born rats." J. Physiol., 154, 153-168.

Taylor, R.D. and Ludvigson, H.W. (1980a): "Selective removal of reward and nonreward odors to assess their control of patterned responding in rats." Bull. Psychon. Soc., 16, 101-104.

Taylor, R.D. and Ludvigson, H.W. (1980b): "Selective removal of alleyway paper flooring or air to assess locus of nonreward odor." Bull. Psychon. Soc., 16, 105-108.

Telle, H.J. (1966): "Contribution to the knowledge of behavioural patterns in two species of rats, Rattus norvegicus and Rattus rattus." Z. angewandte Zool., 53, 129-196.

Terhune, J.M., Terhune, M.E. and Ronald, K. (1979): "Location and recognition of pups by adult female Harp seals." Appl. Anim. Ethol., 5, 375-380.

Thompson, D.H. and Emlem, J.T. (1969): "Parent-chick individual recognition in the Adelie penguin." Antact. J., 3, 132.

Thompson, N.S. (1969): "Individual identification and temporal patterning in the cawing of common crows." Commun. Behav. Biol., No. 09690044.

Thompson, T.J., Winn, H.E. and Perkins, P.J. (1979): "Mysticete sounds." In: Behaviour of Marine Animals. Current Perspectives in Research. Vol 3. Cetaceans. (Eds., H.E. Winn and B.L. Olla), Plenum Press, N.Y., pp. 403-428.

Thompson, W.R., Watson, J. and Charlesworth, W.R. (1962): "The effects of prenatal maternal stress on offspring behaviour in rats." Psychol. Monogr., 76, 1-26.

Thor, D.H. (1979): "Olfactory perception and inclusive fitness." Physiol. Psychol., 7, 303-306.

Thorpe, W.H. and North, M.E.W. (1965): "Origin and significance of the power of vocal imitation: with special reference to the antiphonal singing of birds." Nature, 208, 219-222.

Thorpe, W.H. and North, M.E.W. (1966): "Vocal imitation in the tropical bou-bou shrike, Laniarius aethiopicus major, as a means of establishing and maintaining social bonds." Ibis, 108, 432-435.

Todd, J.H., Atema, J. and Bardach, J.E. (1967): "Chemical communication in social behaviour of a fish, the yellow bullhead (Ictalurus natalis)." Science, 158, 672-673.

Tolman, C.W. (1961): "Social preference in the albino rat pup." Psychol. Rep., 8, 522.

Tolman, E.C. (1925): "Purpose and cognition: The determiners of animal learning." Psychol. Rev., 32, 285-297.

Trillmich, F. (1976): "Learning experiments on individual recognition in budgerigars (Melopsittacusundulatus). Z. Tierpsychol., 41, 372-395.

Trillmich, F. (1981): "Mutual mother-pup recognition in Galapagos fur seals and sea-lions: Cues used and functional significance." Behav., 78, 21-42.

Trivers, R.L. (1971): "The evolution of reciprocal altruism." Quart. Rev. Biol., 46, 35-57.

Trivers, R.L. (1972): "Parental investment and sexual selection." In: Sexual Selection and the Descent of Man. (Ed., B. Campbell), Aldine, Chicago, pp. 136-179.

Tsai, L.S. (1950): "Rivalry and cooperation in white rats." Amer. Psychol., 5, 262.

Tucker, D. (1963): "Physical variables in the olfactory stimulation process." J. Gen. Physiol., 46, 453-489.

Uyenoyama, M.K. and Feldman, M. (1982): "Population genetic theory of kin selection. 2. The multiplicative model." Amer. Natural. 120, 614-627.

Valenta, J.G. and Rigby, M.K. (1968): "Discrimination of odor by stressed rats." Science, 161, 599-601.

Vandenberg, B. (1978): "Play and development from an ethological perspective." Amer. Psychol., 33, 724-738.

Vaz-Ferreira, R. and Achaval, F. (1979): "Mother-infant recognition and the relationship in Otaria flavescens (Shaw) and reactions of subadult males to the pups." Acta Zool. Lilloana, 35, 295-302.

Victoria, J.K. (1972): "Clutch characteristics and egg discriminative ability of the African village weaverbird, Ploceus cucullatus." Ibis, 114, 367-376.

Voland, E. (1977): "Social play behaviour of the common marmoset (Callithrix jacchus Erxl, 1777) in captivity." Primates, 18, 883-901.

Wackernagal, H. (1965): "Grant's zebra, Equus burchelli boehmi, at Basle zoo - a contribution to breeding biology." Int. Zoo. Ybk., 5, 38-41.

Wade, M.J. (1980): "Kin selection: Its components." Science, 210, 665-667.

Wainwright, P. (1980): "Relative effects of maternal and pup heredity on post-natal mouse development." Develop. Psychobiol., 13, 493-498.

Waldman, B. (1981): "Sibling recognition in toad tadpoles: The role of experience." Z. Tierpsychol., 56, 341-358.

Waldman, B. (1982): "Sibling association among schooling toad tadpoles: Field evidence and implications." Anim. Behav., 30, 700-713.

Waldman, B. and Adler, K. (1979): "Toad tadpoles associate preferentially with siblings.' Nature, 282, 611-613.

Wallace, P. (1977): "Individual discrimination of humans by odour." Physiol. Behav., 19, 577-579.

Walser, E.S. and Hague, P. (1980): "Variation in the structure of bleats from sheep of 4 different breeds." Behav., 75, 22-35.

Walser, E.S., Hague, P. and Walters, E. (1981): "Vocal recognition of recorded lambs voices by ewes of three breeds of sheep." Behav., 78, 260-272.

Ward, I.L. (1972): "Prenatal stress feminizes and demasculinizes the behaviour of males." Science, 175, 82-84.

Waser, P.M. (1977): "Individual recognition, intragroup cohesion and intergroup spacing: Evidence from sound playback to forest monkeys." Behav., 60. 28-74.

Watson, J.B. and Lashley, K.S. (1915): "Homing and related activities of birds." Carnegie Inst., Wash. Publ. 211.

Watts, C.R. and Stokes, A.W. (1971): "The social order of turkeys." Sci. Amer., 224, 112-118.

Waynforth, H.B. (1980): Experimental and Surgical Technique in the Rat. Academic Press, Lond.

Weeden, J.S. and Falls, J.B. (1959): "Differential responses of male ovenbirds to recorded songs of neighboring and more distant individuals." Auk, 76, 343-351.

Weisler, A. and McCall, R.B. (1976): "Exploration and play: Resume and redirection." *Amer. Psychol.*, *31*, 492-508.

Weisner, B.P. and Sheard, N.M. (1933): *Maternal Behaviour in the Rat*. Oliver and Boyd, Edin.

West-Eberhard, M.J. (1975): "The evolution of social behaviour by kin selection." *Quart. Rev. Biol.*, *50*, 1-33.

Westby, G.W.M. (1974): "Further analysis of the individual discharge characteristics predicting social dominance in the electric fish, *Gymnotus carapo*." *Anim. Behav.*, *23*, 249-260.

Westermarck, E. (1921): *The History of Human Marriage*. Macmillan, Lond.

Wheeler, J.W., von Endt, D.W. and Wemmer, C. (1975): "5-thiomethylpentane-2, 3-dione. A unique natural product from the striped hyena." *J. Amer. Chem. Soc.*, *97*, 441-442.

White, P, Fischer, R. and Meunier, G. (1982): "The lack of recognition of lactating females by infant *Octodon degus*." *Physiol. Behav.*, *28*, 623-625.

White, S.J. and White, R.E.C. (1970): "Individual voice production in gannets." *Behav.*, *37*, 40-54.

White, S.J., White, R.E.C. and Thorpe, W.H. (1970): "Acoustic basis for individual recognition by voice in the gannet." *Nature*, *225*, 1156-1158.

Wickler, W. and Seibt, U. (1970): "Behaviour of the starfish killing shrimp, *Hymenocera picta*." *Z. Tierpsychol.*, *27*, 352-368.

Wiley, R.H. and Wiley, M.S. (1977): "Recognition of neighbors duets by stripe-backed wrens, *Campylorhynchus nuchalis*." *Behav.*, *62*, 10-34.

Wilson, D.S. (1980): *The Natural Selection of Populations and Communities*. Benjamin Cummings, Californ.

Wilson, E.O. (1973): "Group selection and its significance for ecology." *Bioscience*, *23*, 631-638.

Wilson, E.O. (1975): *Sociobiology: The New Synthesis*. Belknap Press, Camb., Mass.

Winer, B.J. (1962): *Statistical Principles in Experimental Design*. McGraw Hill, N.Y.

Winn, H.E. and Olla, B.L., Eds. (1979): Behaviour of Marine Animals. Current Perspectives in Research. Vol. 3. Cetaceans. Plenum Press, N.Y.

Wolf, A.P. (1966): "Childhood association, sexual attraction, and the incest taboo: A Chinese case." Amer. Anthropol. 68, 883-898.

Wolf, A.P. (1970): "Childhood association and sexual attraction: A further test of the Westermarck hypothesis." Amer. Anthropol., 72, 503-515.

Wooler, R.D. (1978): "Individual vocal recognition in the kittewake gull, Rissa tridactyla (L.)." Z. Tierpsychol., 48, 68-86.

Wright, R.H. (1977): "Odor and molecular vibration: Neural coding of olfactory information." J. Theor. Biol., 64, 473-502.

Wright, S. (1945): "Tempo and mode in evolution: a critical review." Ecology, 26, 415-419.

Wright, S. (1969): Evolution and the Genetics of Populations. Vol. 2. The Theory of Gene Frequencies. Uni. of Chicago Press, Chicago.

Wright, S. (1977): Evolution and the Genetics of Populations. Vol. 3. Experimental Results and Evolutionary Deductions. Uni. of Chicago Press, Chicago.

Wu, H.M.H., Holmes, W.G., Medina, S.R. and Sackett, G.P. (1980): "Kin preference in infant Macaca nemestrina." Nature, 285, 225-227.

Wunderle, J.M. (1978): "Differential response of territorial yellowthroats to songs of neighbors and non-neighbors." Auk, 95, 389-395.

Wynne-Edwards, V.C. (1962): Animal Dispersion in Relation to Social Behaviour. Oliver and Boyd, Edin.

Yamazaki, K., Boyse, E.A., Mike, V., Thaler, H.T., Mathieson, B.J., Abbott, J., Boyse, J., Zayas, Z.A. and Thomas, L. (1976): "Control of mating preferences in mice by genes in the major histocompatibility complex." J. Exp. Med., 144, 1324-1335.

Yamazaki, K., Yamaguchi, M., Baronoski, L., Bard, J., Boyse, E.A. and Thomas, L. (1980): "The major histocompatibility complex as a source of odors imparting individuality among mice." In: Chemical Signals: Vertebrates and Aquatic Invertebrates. (Eds., D. Muller-Schwarze and R.M. Silverstein), Plenum Press, Lond., pp. 267-273.

Yamazaki, K., Yamaguchi, M., Boyse, E.A. and Thomas, L. (1979): "M.H.C. associated recognition among mice: Evidence from the use of a Y maze differentially scented by congenic mice of different major histocompatibility types." J. Exp. Med., 150, 755-760.