



Monogamous male mice bias behaviour towards females according to very small differences in kinship

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To the extent that relatedness between mates predicts their reproductive success, individuals are expected to bias their behaviours towards opposite-sex conspecifics according to differences in kinship. Here we show that monogamous male oldfield mice, *Peromyscus polionotus rhoadsi*, bias their social behaviour towards unfamiliar, distantly related females according to an average 1.3% difference in their kinship to these potential mates. Males in the present study favoured less-related females. Previous empirical investigations have not demonstrated behavioural biases based on such small kinship differences. Consequently, these small differences in kinship have been considered inadequate to drive the evolution of mate choice, particularly by males. Even a small incremental difference in mate quality, however, may significantly affect male reproductive success, especially for monogamous species or those that require maternal care. This study has demonstrated that the social preferences of male oldfield mice are distributed between females according to small differences in their kinship to these potential mates.

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Among sexually reproducing species, an individual's fitness is partially determined by the phenotypic and genetic qualities of its mate(s). Consequently, individuals may enjoy a fitness advantage by choosing between potential mates based on differences in quality (e.g. Trivers 1972; Halliday 1983; Kirkpatrick et al. 1990; reviewed by Andersson 1994, pp. 157–160, 184–206). Mate quality is defined here as the relative impact of an individual on the fitness of its partner(s); higher-quality mates improve the relative fitness of their partners. Mate quality may depend on phenotypic and genetic traits of potential mates, as well as the degree to which such traits complement traits possessed by the choosy individual (Trivers 1972; Zeh & Zeh 1996, 1997; Ryan & Altmann 2001). This benefit of mate choice is predicted to vary among species and between the sexes according to mating system and life-history characteristics. Benefits of choosiness are predicted to increase with greater parental investment per mate and greater variance in mate quality (Trivers 1972; Parker 1983).

For species in which both sexes exhibit significant parental investment, reproductive success of both males and females is limited by the costs of those investments

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and by mate quality. To the extent that potential mates vary in quality, choosy individuals of both sexes will be favoured (Trivers 1972; Parker 1983). For monogamous species, therefore, males as well as females are predicted to bias their behaviour between potential mates according to differences in quality. This study investigated male preferences in the socially and reproductively monogamous oldfield mouse, *Peromyscus polionotus rhoadsi*.

Relatedness between mates may influence both the number of offspring they produce and the fitness of those offspring (Charlesworth & Charlesworth 1987; Pusey & Wolf 1996; reviewed by Thornhill 1993), making it a potentially important component of mate quality. When mates are related, they risk inbreeding depression, a reduced reproductive success due to increased expression of deleterious recessives or to the loss of general heterozygote vigour (Charlesworth & Charlesworth 1987). Evidence for inbreeding depression dates back at least to Darwin (1868) and encompasses a variety of taxa (reviewed by Thornhill 1993), including *P. polionotus* (Brewer et al. 1990; Lacy et al. 1996; Lacy & Ballou 1998; Margulis 1998a). Conversely, mates that are too distantly related may risk outbreeding depression, a reduction in reproductive success due to the break-up of coadapted gene complexes (Shields 1982; Bateson 1983). Outbreeding depression has been less extensively documented, and is most likely to occur when mates come

from ecologically different or isolated populations. A recent study found substantial outbreeding enhancement when *P. p. rhoadsi* were crossed with the geographically closest subspecies, *P. p. subgriseus*. First-, second- and third-generation intercrosses showed 30, 66 and 56% increases in reproductive success relative to the mean within-population pairings (R. C. Lacy, unpublished data). These potential effects of kinship on reproductive success predict that many animals, including oldfield mice, should bias behaviours between potential mates according to differences in kinship (Shields 1982; Bateson 1983).

Indeed, empirical studies have provided abundant evidence for kin-biased behaviour by a variety of vertebrate taxa (reviews by Fletcher & Michener 1987; Hepper 1991). However, these empirical investigations have generally divided individuals into only a few discrete classes of very different kinship. Many have considered just two classes, designated as kin and nonkin. Kin typically refers to a small group of first-order (e.g. offspring, full siblings) or second-order (e.g. aunts/uncles, half-siblings) relatives, while nonkin refers to the rest of the population. Fewer studies have included classes of intermediate kinship (e.g. cousins). Several of these have demonstrated kin bias towards unfamiliar first-cousins compared to unrelated conspecifics (Slater & Clements 1981; Bateson 1982; Keane 1990), the finest discrimination previously demonstrated for unfamiliar individuals. Kinship in natural populations, however, varies continuously. Moreover, relatedness to conspecifics that are encountered as potential mates will often vary within, rather than between, extreme classes. The ability of animals to distinguish these small, but potentially important, differences has not previously been demonstrated. Using a continuous measure of kinship, we show here that monogamous male oldfield mice bias their behaviour towards unfamiliar, distantly related females according to very small differences in their kinship to these potential mates.

METHODS

Species and Population

Peromyscus polionotus is a small, nocturnal mouse found in the southeastern U.S.A. Genetic evidence indicates that oldfield mice are reproductively monogamous. There is no multiple paternity of litters; pairs mate for life, together raising several litters of offspring (Foltz 1981). Males as well as females exhibit extensive parental care (Margulis 1997). Consequently, mate quality will significantly impact reproductive success, and mate choice should be important for both sexes.

The subjects were drawn from a large research colony of oldfield mice housed at the Brookfield Zoo, Brookfield, Illinois, U.S.A. This colony was founded by 52 *P. p. rhoadsi* trapped at field sites in Lake Placid, Florida, U.S.A. in 1990 and 1991, and it has since been the subject of several long-term studies of inbreeding and outbreeding (Lacy et al. 1996; Margulis 1997, 1998a, b; Lacy & Ballou 1998). Known pedigrees date back 14 generations to the colony's founding, facilitating a precise and continuous measure

of relatedness, the kinship coefficient (k). Kinship coefficient between two diploid individuals is the probability that a pair of alleles chosen at random from the same locus in the two individuals are identical by descent (Michod 1993). The inbreeding coefficient (f) of an individual is the probability that the maternally derived allele and the paternally derived allele at a genetic locus in an individual are identical by descent. The inbreeding coefficient of an offspring is therefore mathematically the same as the kinship coefficient between its parents. The kinship coefficient of full siblings=0.25, half-siblings=0.125, first-cousins=0.0625 and second-cousins=0.015625.

The kinship coefficients used in this study were calculated relative to the 52 founders, which we assumed were unrelated to each other. It is possible, however, that some of the wild-caught mice used to establish the colony were related and that kinships among their descendants could have been underestimated. This is a potential problem with all studies of wild populations or animals derived from wild populations. However, the founders were trapped over a fairly extensive area of habitat (traplines were dispersed over an area about 1 km²), and rarely were two founder mice trapped on the same 100-m trapline. Moreover, the effect on kinship calculations of any initial kinships among some founders would have been greatly diminished during the 14 subsequent generations of the pedigree. Regardless, any resulting discrepancy in the kinship coefficients would have been randomly distributed among individuals and would not bias the outcome of our study.

All animals were housed in the same colony room in polycarbonate cages (26 × 15 × 12 cm), on corn-cob bedding, with Purina mouse chow and water provided ad libitum, under a 12:12 h light:dark cycle. Mice were weaned at 20 days old and were housed with same-sex age peers until testing.

Social Preference Tests

Previous studies in this population (Lacy et al. 1996; Margulis 1997) demonstrated that female traits such as parental behaviour have a greater impact on the reproductive success of a pair than do male traits. In this specific captive population, therefore, male oldfield mice would gain a greater benefit from choosing carefully between potential mates. Consequently, this study investigated male preferences.

Male preference was assessed using a Y-maze-type apparatus. This consisted of a 38-litre (10-gallon) glass aquarium divided by opaque Plexiglas and hardware cloth. The females were separated from each other by opaque Plexiglas, prohibiting visual and physical interaction. The male was separated from each female by hardware cloth, a large wire mesh that facilitated visual and physical interaction but prohibited mating. A 14-cm extension of the Plexiglas divider required the male to move around this extension in order to move from one female to the other (see Ryan & Altmann 2001, for a figure).

Pair bonding may be an important aspect of mate choice in this monogamous species. If pair bonds take time to develop, mate preference might be expressed even when females are not fertile. Alternatively, social preference might vary according to female sexual receptivity. To account for these alternatives, we conducted two types of social preference tests. In the first set of tests, we presented each male with two dioestrous females. Dioestrous describes a stage in the oestrous cycle in which females are not sexually receptive and are not fertile ($N=35$ dioestrous tests). In the second set of tests, we presented each male with two pro-oestrous females. During pro-oestrous, females are sexually receptive and fertile ($N=32$ pro-oestrous tests). Oestrous cycles were followed using standard daily vaginal smears. Females were determined to be in dioestrus on days when their vaginal smear was dominated by leukocytes. They were determined to be in pro-oestrus when a smear dominated by cornified and/or nucleated epithelial cells immediately followed a smear dominated by leukocytes.

Each oldfield mouse participated in one dioestrous test and one pro-oestrous test. First, each male and each female participated in one dioestrous test. Approximately 5 weeks later, these same individuals each participated in one pro-oestrous test. However, all of the trios and all of the pairs within the trios were unique. In other words, for every preference test all three of the mice were unfamiliar to each other.

Sexually mature, virgin adult males were observed in the choice apparatus with two unfamiliar (never before encountered) mature, virgin females. Trios were placed together in the apparatus 35–45 min prior to the onset of the dark phase of the light cycle. They were then allowed to acclimate for an additional 20–25 min under red light. This acclimation period was chosen after a pilot study of various alternatives. A 1-h continuous focal observation followed (Altmann 1974). We measured with stop-watches the amount of time males spent associating with either female. A male was scored as associating with a given female if he was on her side of the apparatus, within the area separated by the extension of the Plexiglas divider. Time spent in the undivided rear of the apparatus was considered neutral.

The two females that participated in any given test were chosen primarily because they were in the same stage of their oestrous cycles on the same day (see Ryan & Altmann 2001). We also recorded the value of several traits of the females used in the tests, including their kinship to the male (k), mass, age, and their inbreeding coefficient (f). Variation of these traits is presented in Table 1, for dioestrous tests all $N=35$, for pro-oestrous tests all $N=32$. Kinship between each female and the choosing male was restricted to values of $k < 0.068$; for dioestrous tests mean $k \pm SE = 0.046 \pm 0.002$, among pro-oestrous tests mean $k \pm SE = 0.047 \pm 0.001$. Consequently, the two females in a given test differed only slightly in their kinship coefficients to the male; among dioestrous tests the mean difference was $\Delta k \pm 1 SE = 0.014 \pm 0.002$, among pro-oestrous tests the mean difference was $\Delta k \pm SE = 0.012 \pm 0.001$. The observer knew the mass of

Table 1. Variation in female traits

Trait	Oestrous state	\bar{X}	SE
Kinship coefficient (k)	Dioestrous	0.046	0.001
	Pro-oestrous	0.047	0.001
Difference in k	Dioestrous	0.014	0.002
	Pro-oestrous	0.012	0.001
Mass (g)	Dioestrous	14.99	0.22
	Pro-oestrous	15.79	0.21
Difference in mass	Dioestrous	1.83	0.24
	Pro-oestrous	2.11	0.22
Age (days)	Dioestrous	119.4	5.8
	Pro-oestrous	168.9	3.0
Difference in age	Dioestrous	17.8	10.2
	Pro-oestrous	14.7	2.3
Inbreeding coefficient (f)	Dioestrous	0.094	0.012
	Pro-oestrous	0.086	0.012
Difference in f	Dioestrous	0.110	0.019
	Pro-oestrous	0.081	0.019

In each preference test, one male was allowed to interact with two females. For each trait we first report the variation among all females: for dioestrous females, $N=70$; for pro-oestrous females, $N=64$. We next report variation in the pairwise differences between the two females (i.e. value of the trait for female A – value of the trait for female B): for dioestrous tests, $N=35$; for pro-oestrous tests, $N=32$.

each female, but was blind to the female's age, inbreeding coefficient and kinship to the choosing male.

Statistical Methods

We analysed male preferences using the Wilcoxon matched-pairs signed-ranks test, a nonparametric alternative to the one-sample t test for a paired comparisons design (Sokal & Rohlf 1995, page 440). Separate Wilcoxon statistics were calculated for dioestrous and pro-oestrous data. Because the same individuals participated in both dioestrous and pro-oestrous tests, the two results are not completely independent. Therefore, the latter pro-oestrous tests cannot be considered as independent confirmation of the preferences demonstrated in the dioestrous tests. To assess the effect of oestrous state on male preference, we used both dioestrous and pro-oestrous data from each male in the Friedman's method for randomized blocks, a nonparametric alternative to the two-way analysis of variance (Sokal & Rohlf 1995, page 440).

RESULTS

In both dioestrous and pro-oestrous tests males spent significantly more time associating with less-related females than with more-related females (Table 2). Among dioestrous tests, the median preference for the less-related female (minutes with the less-related female minus minutes with the more-related female) was 6.8 min (Wilcoxon matched-pairs signed-ranks test: $Z=444.5$, $N=35$, $P=0.035$). Among pro-oestrous tests, the median preference for the less-related female was 7.5 min,

Table 2. Male preferences for female traits

Oestrous state	Trait	Median preference (min)	P
Dioestrus	Kinship (<i>k</i>)	-6.8	0.035*
	Mass	-4	0.258
	Age	5	0.286
	Inbreeding coefficient (<i>f</i>)	3	0.647
Pro-oestrus	Kinship (<i>k</i>)	-7.5	0.022*
	Mass	3	0.213
	Age	-1.5	0.13
	Inbreeding coefficient (<i>f</i>)	1	0.724

For each trait we calculated the male preference as follows: (minutes the male spent with the female having a greater value of the trait minus minutes he spent with the female having a lesser value of the trait). All *P* values were calculated using the Wilcoxon matched-pairs signed-ranks test. Among dioestrous tests, *N*=35; among pro-oestrous tests, *N*=32.

($Z=365.5$, $N=32$, $P=0.022$). These pairwise comparisons provide strong evidence that oldfield mice in this study biased their behaviour towards unfamiliar, distantly related females according to kinship differences that are five-fold smaller than those any other species is known to distinguish.

Males did not bias their social behaviour according to differences in the mass, age, or inbreeding coefficient of the females. Male preferences for these traits are listed in Table 2. All *P* values were calculated using the Wilcoxon matched-pairs signed-ranks test. Among dioestrous tests, *N*=35; among pro-oestrous tests, *N*=32.

Female oestrous state was not a significant factor influencing male preference (Friedman two-way analysis of variance (ANOVA) by ranks, $N=25$, $\chi^2_1=0.04$, $P<0.841$). In other words, males favoured less-related females regardless of their sexual receptivity. For polygynous species, social preferences expressed when females are in pro-oestrus have traditionally been interpreted as mating preferences. Conversely, social preferences expressed when females are in dioestrus have been interpreted as not being related to mating. In this monogamous, pair-bonded species, however, mate preferences might be expressed even when females are not fertile.

DISCUSSION

Inferring mate preference from social preference in the absence of actual mating behaviour can be problematic. As Real (1990) has proposed, however, adaptive mate choice is supported when we can demonstrate its consequences. Such a study (Ryan & Altmann 2001) has demonstrated the positive reproductive consequences of the social preferences exhibited by these male oldfield mice. Those males that were subsequently paired with the female they had preferred in the pro-oestrous social preference tests sired more offspring than those males that were subsequently paired with the female they had rejected, suggesting that these social preferences reflect adaptive male mate choice. Similarly, adaptive consequences of female mate choice have been demonstrated for house mice (Drickamer et al. 2000) and stink bugs (McLain 1998).

Kin-biased social preferences between potential mates have traditionally been interpreted as a means for optimizing the relatedness between mates, which is equivalent to optimizing the inbreeding of their offspring. Previous studies using this laboratory population of *P. polionotus* have shown that kinship between mates and the consequent inbreeding of the progeny have deleterious consequences for a variety of components of reproductive success, although the magnitude of the impacts varies among populations (Brewer et al. 1990; Lacy et al. 1996; Lacy & Ballou 1998; Margulis 1998a). The regression of reproductive success on kinship between mates reported by Lacy et al. (1996) would predict a 2.43% decrease in reproductive success at the mean (0.046) level of kinship between potential mates in the present study. The laboratory population used in the present study was derived from a large mainland population with apparently continuous habitat. Experimental crosses of this population to the geographically adjacent subspecies (*P. p. subgriseus*) led to enhanced reproductive success (R. C. Lacy, unpublished data), so it would seem that outbreeding depression is not a problem for this population and the populations with which it could interbreed in the wild. Consequently, if the kin-biased social preferences of oldfield mice males functioned to optimize inbreeding/outbreeding, they would be predicted to favour less-related females.

Genetic compatibility between mates has long been recognized as a potentially important component of mate quality (e.g. Trivers 1972; Zeh & Zeh 1996, 1997; Brown 1999). It has received little attention, however, because the ability of choosy individuals to match their own genotype against the genotypes of potential mates has been questioned (Parker 1992; Zeh & Zeh 1997). The present study adds to growing evidence (Drickamer & Lenington 1987; Brown & Eklund 1994; Penn & Potts 1999; Ryan & Altmann 2001) that mate preferences for genetically compatible partners may be more precise than we have previously suspected.

Male oldfield mice in this study may either be discriminating differences in kinship, per se, or they may be discriminating differences in genetic similarity that are closely correlated with kinship (Grafen 1990; Barnard

et al. 1991). The functional implications for adaptive mate choice are the same, however, regardless of the specific mechanism. Inbreeding depression does not result from the genealogical relationships between individuals, per se. Rather it is a consequence of the genetic similarity between individuals that is predicted by these genealogical relationships.

Indeed, these data raise numerous questions regarding the mechanism of this finely tuned kin bias. The mechanism of kin bias has been described (Grafen 1990; Barnard et al. 1991) as having three components: (1) labels: phenotypic or environmental cues that allow the degree of relatedness between the discriminator and another individual to be assessed; (2) templates: internal models (learned, encoded, or both) against which labels can be compared; and (3) decision rules: rules for evaluating the fit between labels and templates and for determining responses on the basis of perceived similarity. This study addresses only one of these components, the decision rules. Males respond to the perceived similarities by spending more time associating with less-similar females.

Both because all individuals were unfamiliar, and because of the small difference in relatedness, the label involved must be very tightly correlated with kinship. Because of the homogeneity of the laboratory environment, it must be a phenotypic, rather than an environmental, cue. Congenic strains of *Mus* are known to discriminate conspecifics according to differences in major histocompatibility (MHC) haplotype (Yamazaki et al. 1976; Eklund et al. 1991; Potts et al. 1991; Brown & Eklund 1994; Penn & Potts 1999). If dissimilarity at this hypervariable site correlates with overall genetic dissimilarity, it provides a good candidate for the recognition cue. The animals that participated in this study have been genotyped for several MHC loci and analysis of these data is underway (A. Eklund, unpublished data).

It is likely that family members provide a template of family labels that is learned by the males prior to weaning. The choosing males in this study were housed until weaning with their mothers and their littermates. At weaning, each male was separated from his mother and sisters, and was housed with as many as three brothers until testing. This approximates the wild condition, in which litters remain at the nest with their parents and siblings for up to several weeks after weaning until both sexes disperse and find mates. (In our field collections, we have found that subadult, postweaning offspring often occupy nest burrows with their parents, littermates and siblings from a subsequent litter.) After dispersal, when faced with a choice between two potential mates, males might prefer females that are less similar to this learned template. Note that this proposed template of several first-order relatives would allow for a more finely tuned discrimination of kinship than a self-only template (Lacy & Sherman 1983). Furthermore, given the social structure of wild *P. polionotus*, such a mechanism would never result in learning labels from nonrelatives prior to dispersal.

Considerable controversy exists regarding the prevalence of inbreeding in natural animal populations

(reviewed by Thornhill 1993; Pusey & Wolf 1996; Keane et al. 1997), due in large part to a scarcity of data. As for most species, there have been no studies of inbreeding depression for in situ wild populations of *P. polionotus*. However, the deleterious consequences of inbreeding in wild-derived laboratory populations of *P. polionotus* are well documented (Brewer et al. 1990; Lacy et al. 1996). Furthermore, in a study of the congeneric *P. leucopus*, Jiménez et al. (1994) found that the deleterious impact of inbreeding can be much greater when measured in a natural habitat than when assessed in the laboratory. The kin-biased behaviour by oldfield mouse males, favouring less-related females even among distant relatives, suggests that oldfield mice avoid inbreeding when possible in large wild populations. As the wild populations of this subspecies become increasingly isolated and fragmented by human development of their sand pine scrub habitats (Humphrey 1992), however, this well-developed ability to avoid inbreeding can slow, but not eliminate, negative effects of inbreeding on survival and reproduction.

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