



# Free mutual mate preferences in house mice affect reproductive success and offspring performance

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When social constraints on the expression of mate preferences are absent, variation in offspring viability is predicted to favour females and males that display mate preferences. Earlier studies showed that female and male house mice, *Mus domesticus*, tested individually and mated with preferred (P) partners had higher reproductive success and better progeny performance than individuals mated with nonpreferred (NP) partners. Here we tested the effects of mutual mate preferences on reproductive success, offspring viability and performance. We conducted mate preference tests and created four types of reproductive pairings. One involved females and males that preferred each other (P–P); the second type had females that preferred the male but the male did not prefer the female (P–NP); the third had females that did not prefer the male but the male did prefer the female (NP–P). The last set consisted of females and males that did not prefer each other (NP–NP). We measured components of fitness for breeders (reproductive success) and offspring viability (birth-to-weaning viability and weight variation) as well as measures of offspring performance. There were no statistical differences in reproductive success of breeders or offspring viability and quality (weight variation) among the four types of pairings. There were, however, consistent differences between P–P versus NP–NP matings. The number of pups weaned, time to first litter, birth-to-weaning viability, pup body weight at birth and weaning, and the growth rates for pups of both sexes were consistently greater for progeny from P–P matings than NP–NP matings. Significant differences occurred among the four mating types in dominance of sons during aggression trials, nest construction and predator avoidance. Progeny from P–P matings displayed behaviour associated with higher fitness more often than progeny from NP–NP matings. These data show that breeders produce more highly competent progeny, most likely to survive, when social constraints on the expression of mate preferences in both sexes are relaxed.

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Darwin (1871) posited mate choice as a mechanism of sexual selection. Ever since Fisher (1958), considerable evidence has accumulated for the influence of female mate choice on the evolution of traits in sons, and most studies have begun with consideration of variation in males (Andersson 1994). It has proven relatively difficult to demonstrate unequivocal fitness effects of female choice for male traits, and despite notable exceptions (e.g. Petrie 1994) demonstrations of enhanced fitness effects of female mate choice have been controversial and difficult to replicate (e.g. Partridge 1980). There have been almost no studies of how variation among choosing females affects their preferences for mates or of the consequences

of such variation on mothers' fitness through both sexes of offspring (Gowaty 1998). In addition, few studies of male mate choice exist, except in species with high levels of male parental care (Ryan & Altmann 2001). Recently, Altmann (1997) argued that if there is variation among females, any time a male has a choice between females, selection should favour males that also discriminate.

In nature, it is likely that mate preferences are seldom expressed free of constraints. For example, social constraints arise from male–male interactions, female–female interactions, and coercive and manipulative interactions between the sexes. If these sorts of social interactions are common, tests of the consequences of mate preferences must take into account whether individuals are reproducing under constraints (Gowaty 1996, 1997; Gowaty & Buschhaus 1998; P. A. Gowaty & S. P. Hubbell, unpublished data) that affect the likelihood that females (and males) reproduce with individuals they do not prefer.

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Because the signals that choosers receive from to-be-discriminated individuals may be manipulative, we also argued that studies of female mate preferences and fitness variation should be free of investigator bias about the cues that choosers may use.

P. A. Gowaty & S. P. Hubbell (unpublished data) argue, as do others (Hamilton & Zuk 1982; Brown 1997; Wedekind 1999), that mate preferences are affected by dynamical host–pathogen interactions (Jaenike 1978; Dybdahl & Lively 1998; Lively & Dybdahl 2000). In offspring viability and constraints theory (P. A. Gowaty & S. P. Hubbell, unpublished data) viability selection acting through both sons and daughters, rather than just sons, is the critical selective force on mating preferences of potential parents. Because pathogens reproduce much faster than their hosts, mate preferences that provide progeny with adequate genetic defences against parasites and pathogens are likely to evolve. Thus, mate preferences should favour dissimilarity or immune complementarity, as has been shown for house mice, *Mus domesticus* (Potts et al. 1991, 1994; Brown 1997; Penn & Potts 1999). If offspring viability is the critical component of fitness affecting mating preferences, selection should act not just on females, but on males as well, whether or not they invest in offspring.

Mutual mate preferences have recently been posited to be important in species with relatively high levels of paternal care. None of the studies of mutual mate preferences of which we are aware examined components of fitness for breeders and offspring. Recently, several studies have shown that both free female and/or free male mate preferences can have significant consequences for offspring viability and progeny performance in mice (Drickamer et al. 2000; Gowaty et al. 2003). Similar studies have shown significant effects of constraints on expression of breeder mate preferences on offspring viability and performance in mallards, *Anas platyrhynchos* (C. K. Bluhm & P. A. Gowaty, unpublished data), in Tanzanian cockroaches, *Nauphoeta cinerea* (Moore et al. 2001) and *Drosophila pseudoobscura* (W. W. Anderson, P. A. Gowaty & Y.-K. Kim, unpublished data). For house mice, free female mate preference followed by mating with either a preferred (P) or nonpreferred (NP) partner resulted in higher reproductive success and offspring viability for females mated with P males than with NP males. In addition, offspring from P matings had higher viability and better performance on aggression and nest construction tests than those from NP matings (Drickamer et al. 2000). In a companion male preference study (Gowaty et al. 2003) males mated to P females sired significantly more litters than those mated to NP females. In addition, sons from P matings won more dominance interactions than sons from NP matings and progeny of both sexes from P matings built better nests than those from NP matings.

With the above results in mind, the present series of experiments was designed to test further the effects of freely expressed mate preferences on reproductive success, offspring viability and progeny performance under conditions involving mutual mate choice. In this set of experiments we did multiple, free mate preference tests so

that eventual matings involved pairs of mice that each preferred one another (P–P pairings) and pairs of mice in which neither preferred the other (NP–NP). We also mated pairs in which the female preferred the male but not vice versa (P–NP), and pairs in which the male preferred the female but not vice versa (NP–P). As in our previous studies, a critical feature of the current one is that we picked to-be-discriminated individuals at random with respect to any investigator-measured phenotypic traits, being careful only to avoid asking choosers to discriminate their known kin. Furthermore, as in other mate choice studies (Johnson 1988; Zuk et al. 1990; Wilkinson 1998), ours was conducted in a situation in which there was no other interaction or competition within or between sexes occurring (i.e. a ‘free’ mate choice context).

From the perspective of offspring viability and constraints theory, which argues both female and male mate preferences are important for offspring viability, it is difficult to predict the pattern of results when one partner is with a preferred mate but the other is not. So, we made no specific prediction about the direction of values for offspring viability and performance from P–NP and NP–P pairs, other than to expect that the values would fall somewhere between P–P and NP–NP. A priori, as in our earlier studies, we predicted that there would be significantly greater offspring viability and performance for P–P pairs than NP–NP pairs.

## METHODS

### Subjects

House mice have a generally polygynous mating system (Brown 1953; Bronson 1979) regardless of whether they are living in a commensal or feral situation. When they live commensally, male house mice are territorial, with several females living primarily within each male’s territory (Crowcroft & Rowe 1963; Anderson & Hill 1965). When living in feral situations, both males and females live in overlapping home ranges (Mikesic & Drickamer 1992). Wild house mice used in these experiments were derived from a wild-caught stock obtained from the Coconino County Fairgrounds and several farms in the vicinity of Flagstaff, Arizona, U.S.A. Wild-caught mice were bred with one male and one female per cage captured from different locations to produce mice for mate preference tests (F1 mice). Mice were weaned at 24–25 days of age and housed in unisexual groups until they were given mate preference tests. Because house mice discriminate between kin and others in ways consistent with the avoidance of inbreeding, we took care to place choosers in preference tests with two opposite-sex non-relatives. We used a total of 121 females and 122 males in the mate preference tests, of which 120 of each sex were mated; there was no screening for preference performance prior to the tests and virtually all of the mice tested were used as mates in one of the four treatments. Where retesting of some mice occurred on the same day, there were no complete shifts in preference.

Progeny from matings born after mate preference pairings (F2 mice) were followed from birth to weaning to assess their viability (percentage surviving) and tested after weaning to assess their relative performance in tests of fitness-associated behaviour. All laboratory procedures involved housing mice in standard polypropylene mouse cages (18 × 30 × 15 cm deep) with wire mesh lids. All mice were provided with *ad libitum* food (LabDiet 5008) and water while in the laboratory. Mice were housed in a single room with a 14:10 h light:dark cycle. The ambient temperature was 22–25 °C in the laboratory, with 40–70% RH. Bedding of wood shavings was changed once per week. All pregnant mice were provided with a cotton square (Nestlet; Ancare Corp., Belmont, New York, U.S.A.) for nesting.

### Mate Preference Procedure

The mate preference test apparatus consisted of four chambers and was constructed of plywood covered with epoxy paint. The overall dimensions were 45 × 30 cm. One chamber, where the mouse making the choice was placed, measured 45 cm long by 15 cm wide, encompassing one entire side of the apparatus. Three chambers for the to-be-discriminated mice were on the other side; each measured 15 by 15 cm. The entire apparatus was 50 cm high. At ground level, there were openings, measuring 12 × 12 cm, covered by wire mesh between the chamber where the choosing mouse was placed and the three chambers for the to-be-discriminated mice. This apparatus was cleaned thoroughly with water and paper towels and allowed to air dry after each preference test was completed.

At 60–70 days of age, F1 mice were used in mate preference tests. We selected four males and four females, all from different litters, opportunistically and at random with respect to phenotypic variation. These mice were then used in a partial round-robin set of preference tests. All of the mate preference testing for a group of four males and four females was carried out on the same day. First we tested with two males (designated A and B) in the side chambers and a female (designated W) as the chooser. This procedure was repeated with a second female (designated X) as the chooser and using the same two males (A and B). We next tested two other males (designated C and D), first with a third female (designated Y) and then with a fourth female (designated Z). This entire scheme was then carried out with pairs of females as test mice and individual males as choosers. Once these initial mate choice tests were completed, we examined the preferences of males and females in an attempt to find pairings of one male with one female to represent the four possible mating categories. There were four categories for matings. (1) Both mice preferred each other ('P–P' indicates that the male was preferred by the choosing female and the female was preferred by the choosing male; here and throughout the text and tables we designate the female as chooser first and the male as chooser second); (2) the female preferred the male, but the male did not prefer the female (P–NP); (3) the female did not prefer the male, but the male did prefer the female

(NP–P); and (4) neither the female nor the male preferred each other (NP–NP). If an initial examination of the data did not result in one possible mating for each of these four categories from the four males and four females, then additional testing occurred among other possible pairings. For example, we tested to-be-discriminated males designated as A and B in the side chambers with the female designated as Y or Z as the chooser, and so forth. When choosers did not meet our criteria for having displayed a preference, we conducted additional tests with different individuals or repeated the test with the same animals later in the day. During the course of the study only 38 of 340 (11.2%) preference tests resulted in the choosing mouse failing to show a preference.

For each mate preference trial, one test mouse was placed, randomly by a coin flip, in each of the end preference chambers; the centre preference chamber was left vacant because house mice, being thigmotactic, will not spend time in front of a central chamber with no side walls nearby. The choosing mouse was placed in the larger chamber, with the ability to smell, hear and make some tactile contact through the wire mesh with each of the two test mice. We placed the two test males or females in the side chambers of the apparatus first, followed by the choosing mouse of the opposite sex placed in the larger chamber. When the choosing mouse had explored to the extent that it had made contact through the wire mesh with both test mice, the test began. The preference test lasted 10 min. This mate preference procedure is similar to that used by Dewsbury *et al.* (1986). We used two criteria to determine whether a preference was made. First, the choosing mouse had to spend at least 300 s of the 600-s test in front of the two test mice combined. Second, the choosing mouse had to spend at least 60% of the time that it was in front of the two test mice in front of one of those mice. If the choosing mouse met these criteria, then we designated it as having selected a preferred mate. If the choosing mouse failed the test on either of these criteria, then all three mice were returned to their home cages and a new test was initiated.

Prior to testing a group of males and females for mate preferences, they were each weighed to the nearest 0.1 g, and their body length and tail length were measured to the nearest 0.1 cm. We used these measures to test whether these morphological traits were cues associated with preference by the opposite sex.

### Breeding Procedure and Breeder Reproductive Success

From sets of four female and four male mice that met criteria for showing a preference, we generated four pairs of mated mice, with one mating being of each of the four possible types. We completed this mate selection procedure 30 times (approximately 3 times/week for 10 weeks). These enforced monogamous matings were maintained throughout the litter production phase of the experiment. We waited up to 60 days to determine whether a litter was born. Matings where no litters were produced after 60 days were scored as not having a litter. When a litter was born, we recorded the time from

mating to birth of the litter, and the sexes, total body weight, and body weight by sex of the pups born. We weaned all pups at 24–25 days of age, weighed them individually, and gave them unique toe-clip and ear-punch numbers.

Mice were housed in unisexual groups until tested as described below. At this time a separate data record was established for each of these progeny mice, using its individual identification number. Mated pairs were retained together for an additional 60 days to determine whether they would produce second litters. We recorded the presence or absence of such litters and the time between birth of the first and second litters. Only progeny from the first litters were used in subsequent offspring performance tests.

#### *Ethical note*

We used the toe-clip and ear-punch method for identifying individual mice for several reasons. The size of the smaller individuals generally precluded the use of passive integrated transponder (PIT) tags. The use of fingerling tags on the ears results in infections and mice being caught by the tags on wire mesh as well as occasionally on plants. When mice were toe-clipped we spread a layer of antibacterial cream on their toes. In 9 years of field work at the mouse pens we never encountered a death due to toe clipping. We also never recorded any alterations in behaviour; a maximum of four toes, each on different feet are clipped with our method. This procedure was approved by the Institutional Animal Care and Use Committee at Southern Illinois University (Protocol No. 95-161).

#### **Laboratory Performance Measures**

The progeny from the four types of matings were subjected to three types of behavioural performance tests under laboratory conditions. We designed these tests to explore further the differences in progeny from the different mating types. We used dominance encounters, because social dominance in house mice is related to reproductive success (Oakeshott 1974). We also used a test of nest-building skill, because nest-building skills in house mice are associated with survival (Lynch & Hegmann 1972). We designed a test of behaviour in the potential presence of a predator, because predator avoidance is critical for survival of young mice as they leave their natal sites to disperse and establish ranges of their own.

The dominance trials used male mice only. These involved an encounter test to assess social dominance, conducted when the males were 75–90 days of age. We placed pairs of male mice from two mating types in a standard laboratory mouse cage. We weighed the mice prior to pairing and marked them on the back and flanks with powdered chalk for identification. We observed them until one mouse attacked the other four times in succession (Lenington et al. 1996). At that point the attacking mouse was declared the winner and the other was designated as the loser. No aggressive encounters

resulted in any visible injuries to any participants. We conducted 15 encounters between pairs of males for each of the six possible combinations of the four mating types. No males were used in more than one encounter. No more than two males were used from any particular litter for these tests.

The nest-building trials used both female and male mice. Twenty females and 20 males from each mating type were given a 24-h nesting test when they were  $35 \pm 5$  days of age. We placed each mouse in a standard laboratory cage without any bedding or wood shavings, but with only a Nestlet. Food and water were available ad libitum. After 24 h, we scored the nests on a scale of 0–4. An individual was given a score of 0 if it failed entirely to alter the cotton square. If the mouse only made small tears in the Nestlet it was scored a 1. If the mouse tore apart more than half of the Nestlet and made some attempt to construct a nest, it was scored 2. If it tore the entire Nestlet apart and constructed a solid platform nest, it received a score of 3. Mice that tore apart the entire Nestlet and constructed a complete domed nest received a score of 4.

We gave 20 female and 20 males from each mating type a ‘predator avoidance’ test when they were 30–44 days old. Mice (and other rodents) confronted with a situation involving potential danger, particularly as exemplified by a predator’s presence, have a tendency to freeze as a means of avoiding detection. Also, in such a situation, a mouse that reaches a refuge, as for example, a nestbox as we used in this experiment would be at an advantage in terms of avoiding predators. Similarly, a mouse that remained in that refuge for an extended period would presumably have an advantage over a mouse that exited from the refuge while the predator was still present. We used this sort of logic to design the predator avoidance test. We used no more than two mice from the same litter in this test, and in those cases where two mice from the same litter were used, they were of opposite sex. The test was a modification of the open-field testing used on many rodents including mice (Willingham 1956; Streng 1971). The test apparatus consisted of a 40-litre aquarium measuring  $46 \times 24 \times 28$  cm deep with clear glass on all four sides. A wooden nestbox measuring 10 cm on each side and with an opening 2.5 cm in diameter was placed at the centre of one of the shorter side walls with the opening facing the centre of the aquarium. Prior to starting a trial, the mouse was placed in the nestbox using the birthing forceps that we customarily used to handle all mice. This was to ensure that each mouse knew of the presence of the nestbox. After 10–15 s we removed the mouse from the nestbox if it had not exited on its own. We then began the trial by picking up the mouse with the forceps and dropping it from 30 cm to the centre of the floor of the aquarium. Our first measure consisted of the mouse either adopting a freezing posture within 5 s of the start of the trial, or not freezing. As soon as a mouse froze, we started a stopwatch to measure the latency to begin moving after freezing. Either as the test started for those mice that did not freeze, or as soon as it had ceased freezing, we started a stopwatch to measure the latency to enter the nestbox. Once the mouse had entered the

nestbox we restarted the stopwatch to time the latency until the mouse left the nestbox and again had all four feet on the floor of the aquarium, at which point the trial was terminated. After a trial had started the observer and stopwatches were 2 m from the aquarium and the observer remained essentially motionless throughout the trial. Because those individuals remaining frozen the longest and those with a higher latency to leave the box shelter after predator exposure would be most successful at avoiding predation, we predicted that progeny from P-P pairings would freeze for longer times and exit the box after predator exposure more slowly. The aquarium and nestbox were cleaned with water and paper towels after each test and were then air dried before beginning another trial.

## Analyses

For the morphological measures taken at the time of the mate preference tests we followed a multi-step procedure. First, we classified each mouse as having been preferred, not preferred, or neither. This was accomplished by examining the data from the preference tests where individual mice were tested a minimum of two times and a maximum of five times in order to establish the mating pairs of the four types. We classified mice as preferred if their ratio of P to NP results was 0.67 or greater. Similarly, we classified mice as not preferred if their ratio of P to NP results was 0.33 or lower. All remaining mice had preferences that were intermediate. For each sex we conducted one-way analyses of variance (ANOVAs) on five different dependent variables: body weight, body length, tail length, body weight/body length and body length/tail length. These analyses were followed by Scheffe's post hoc tests for mean differences.

Data for breeder fitness and offspring viability and performance were analysed by chi-square tests with four mating types cross-classified with the production or lack of production of the first litter (Zar 1996). From the sexes of the pups at birth, we calculated the proportion of each litter that was female and used this as a dependent variable. Using the numbers of each sex at birth and weaning, we calculated the proportion of each sex that was weaned from each litter as well as the overall proportion of the litter that was weaned. Using the body mass information at birth and weaning, we calculated the average pup weight by sex at weaning and the average growth in weight from birth to weaning by sex for each litter. All of these litter characteristics were analysed using one-way ANOVAs with a single factor with the four mating types as treatment. The ANOVAs were followed by Scheffe's post hoc tests to examine mean differences between treatments.

Aggression data were analysed using a chi-square test with the four mating types cross-classified with the numbers of encounters won and lost. Data for nest construction were analysed using a two-way ANOVA with sex and treatment, with the latter consisting of the four mating types. Some males that were used in nest-building tests were also used again either in the aggression test or the predator avoidance test, but not both. Since there is little

**Table 1.** Results from one-way ANOVAs carried out on data for three measured and two derived morphological traits for each sex at the time of the mate choice trials

Trait	Females choosing males		Males choosing females	
	<i>F</i> ratio	<i>P</i>	<i>F</i> ratio	<i>P</i>
Body mass	0.136	0.873	0.525	0.593
Body length	0.352	0.704	0.479	0.621
Tail length	0.344	0.710	0.239	0.788
Body mass/tail length	0.396	0.674	0.394	0.676
Body length/tail length	0.006	0.994	0.107	0.899

All *F* ratios had *dfs*=2,117.

connection between a nest-building test where the animal is alone in a cage and either of the other two tests we do not feel that there should be any problem with reusing the mice. A chi-square test and three two-way ANOVAs with sex cross-classified with four mating types were used to analyse the four dependent variables from the predator avoidance test. All analyses were run using Statview for MacIntosh version 4.5 (Abacus Concepts 1995).

## RESULTS

### Mouse Morphology and Mate Preferences

None of the measured or derived morphological traits was significantly different for either sex when their preference status was most often preferred, least often preferred, or intermediate (Table 1).

### Components of Fitness for Breeders and Offspring

Table 2 presents tests for differences among the four mating types in components of breeder fitness. There were no significant differences across the four mating types in whether they produced a litter, the number of pups per litter, the sex ratio of progeny, whether the litter was weaned, the numbers of litters weaned, or the number of pups weaned. There was no significant difference in the age of the females at the time of pairing for the four mating types, and no significant difference in the number of females producing second litters. There was, however, significant heterogeneity in the latency to litter production with the longest latency being for NP-NP pairs. Post hoc analyses indicated that there were significant differences for the comparison between P-P and NP-NP pairs for the number of pups weaned and the proportion of females in the litter; P-P pairs weaned significantly more pups and produced more sons than NP-NP pairs.

Table 3 presents tests for differences among the four mating types in components of fitness of offspring. There was no significant heterogeneity among the four mating types in birth-to-weaning viability, in mean pup weights at birth or weaning, or in average weight gains.

Despite the lack of statistically significant results when all four treatment groups were considered, there was an

**Table 2.** Components of breeder fitness by mating type

Trait	Mating type				Test	P
	P-P	P-NP	NP-P	NP-NP		
Litters produced	26	28	28	28	$\chi^2_3=1.309$	>0.40
Mean litter size	6.3 (0.3)	6.7 (0.3)	6.6 (0.3)	6.5 (0.2)	$F_{3,106}=1.696$	0.803
% Female born	45.3 (4.7) <sup>a</sup>	50.2 (3.2) <sup>ab</sup>	45.4 (3.1) <sup>a</sup>	54.2 (2.6) <sup>a</sup>	$F_{3,106}=1.546$	0.207
Litters weaned	26	28	28	28	$\chi^2_3=1.309$	>0.40
Pups weaned	5.8 (0.4) <sup>b</sup>	5.8 (0.5) <sup>b</sup>	5.9 (0.4) <sup>b</sup>	4.9 (0.5) <sup>a</sup>	$F_{3,106}=1.122$	0.344
Time to first litter (days)	25.3 (0.7) <sup>a</sup>	24.6 (0.5) <sup>a</sup>	24.9 (1.1) <sup>a</sup>	28.5 (1.6) <sup>b</sup>	$F_{3,106}=2.835$	0.042
Mother's age at mating (days)	76.7 (1.6)	75.5 (1.7)	72.7 (1.8)	75.2 (1.9)	$F_{3,116}=0.986$	0.402
Produced second litter	24	24	25	25	$\chi^2_3=0.223$	>0.90

Numbers or mean values ( $\pm 1$  SE), chi-square tests or ANOVAs, and *P* values for various traits related to litter production by females that were mated with either a preferred (P) or nonpreferred (NP) male. For each mating type, the female's choice of mate (P or NP) is given first, followed by the male's choice of mate. Superscript letters indicate significant differences ( $P < 0.05$ ) for means using a Scheffe's post hoc test.

**Table 3.** Components of offspring fitness when their parents had reproduced with a preferred or a nonpreferred partner

Trait	Mating type				ANOVA	P
	P-P	P-NP	NP-P	NP-NP		
% Pups weaned	91.9 (4.7) <sup>b</sup>	86.3 (4.9) <sup>b</sup>	89.6 (4.5) <sup>b</sup>	76.1 (6.9) <sup>a</sup>	$F_{3,106}=1.678$	0.176
Males	92.2 (4.5) <sup>b</sup>	91.5 (4.2) <sup>b</sup>	89.3 (5.5) <sup>b</sup>	78.0 (7.1) <sup>a</sup>	$F_{3,105}=1.472$	0.226
Females	89.6 (6.0)	81.6 (6.2)	90.2 (4.1)	74.9 (7.2)	$F_{3,104}=1.479$	0.225
Average weight/pup (g)						
At birth	1.82 (0.06)	1.78 (0.05)	1.72 (0.06)	1.74 (0.53)	$F_{3,106}=0.622$	0.602
At weaning	11.4 (0.4) <sup>b</sup>	10.7 (0.3) <sup>ab</sup>	10.9 (0.3) <sup>ab</sup>	10.4 (0.3) <sup>a</sup>	$F_{3,98}=1.951$	0.126
Males	11.6 (0.4)	11.2 (0.4)	11.3 (0.3)	10.9 (0.3)	$F_{3,96}=0.668$	0.574
Females	11.0 (0.4) <sup>b</sup>	10.1 (0.3) <sup>a</sup>	10.4 (0.3) <sup>ab</sup>	10.1 (0.2) <sup>a</sup>	$F_{3,93}=1.781$	0.156
Average weight gain/pup (g)	9.4 (0.4) <sup>b</sup>	8.3 (0.4) <sup>a</sup>	8.9 (0.3) <sup>ab</sup>	8.4 (0.2) <sup>a</sup>	$F_{3,98}=1.946$	0.127
Males	9.7 (0.4)	9.3 (0.3)	9.4 (0.3)	9.0 (0.3)	$F_{3,96}=0.766$	0.516
Females	9.1 (0.4) <sup>b</sup>	8.0 (0.3) <sup>a</sup>	8.5 (0.3) <sup>ab</sup>	8.1 (0.2) <sup>a</sup>	$F_{3,93}=2.650$	0.053

Numbers or mean values ( $\pm$ SE). Superscript letters indicate significant differences ( $P < 0.05$ ) using a Scheffe's post hoc test. Mating types as defined in Table 2.

overall pattern, consistent with our original prediction. Number of pups weaned, proportion of the birth litter that was weaned (and the proportions of males and females weaned), average pup mass at birth, average pup mass at weaning (and average male and female pup masses at weaning) and mean mass growth from birth to weaning (and average male and female pup mass growth from birth to weaning) were all greater for litters from P-P matings than for litters from NP-NP matings (Table 3, post hoc analyses).

### Offspring Performance

For the aggression tests, there was a significant overall effect for pairings of males from the four different mating types (chi-square test:  $\chi^2_3=16.590$ ,  $P < 0.001$ ). Male progeny from P-P matings won 71.1% of their encounters with males from the other three mating types (Table 4). By contrast, male progeny from NP-NP matings won only 31.1% of their encounters with other males. Males from the other two mating types were intermediate with respect to the proportion of encounters they won. An ANOVA of the body weight data at the time of their

encounters revealed no significant differences for males from the four mating types ( $F_{3,176}=1.694$ ,  $P=0.170$ ). Of the 90 encounters, males that were heavier than their opponent won 39, 39 were won by males that were lighter, and 12 involved males of the same body weight.

For nest construction trials, the ANOVA revealed no significant sex differences ( $F_{1,152}=1.914$ ,  $P=0.169$ ) and no significant interaction between sex and the four mating

**Table 4.** Matrix of winners and losers for encounters between adult sons from the four mating types

Loser	Winner			
	P-P	P-NP	NP-P	NP-NP
P-P		4	4	5
P-NP	11		4	5
NP-P	11	11		4
NP-NP	10	10	11	

There were 15 encounters for each of the possible six pairwise combinations of the four mating types. Mating types as defined in Table 2.

**Table 5.** Frequency of freezing behaviour and mean $\pm$ SE for three dependent variables in a predator avoidance test for female and male progeny from each of the four mating types

Variable	Mating type			
	P-P	P-NP	NP-P	NP-NP
Freezing behaviour (froze/did not freeze)				
Female	16/4	11/9	11/9	6/14
Male	16/4	12/8	10/10	6/14
Latency to break from freezing (s) ( $\pm$ SE)				
Female	112 (11)	90 (13)	74 (10)	69 (14)
Male	139 (8)	82 (17)	96 (15)	120 (19)
Latency to enter nestbox (s) ( $\pm$ SE)				
Female	133 (15)	213 (16)	190 (17)	219 (17)
Male	125 (15)	186 (15)	203 (16)	201 (16)
Latency to leave nestbox (s) ( $\pm$ SE)				
Female	137 (19)	86 (15)	119 (19)	75 (12)
Male	179 (18)	66 (9)	59 (12)	98 (15)

$N=20$  mice of each sex from each mating type were tested. Mating types as defined in Table 2.

treatments ( $F_{3,152}=1.327$ ,  $P=0.268$ ). The main treatment effect for mating types was significant ( $F_{3,152}=15.872$ ,  $P<0.001$ ). Differences between means, obtained from a Scheffe's post hoc analysis, revealed that the mean nest score, with sexes combined, for progeny from P-P matings was 2.1 ( $\pm 0.1$ ), significantly greater than the scores for P-NP ( $0.8 \pm 0.1$ ), NP-P ( $1.2 \pm 0.2$ ), or NP-NP ( $1.0 \pm 0.1$ ) matings.

In the predator avoidance test, the overall analysis for the tendency to adopt freezing behaviour at the start of the trial was significant (chi-square test:  $\chi^2_3=20.404$ ,  $P<0.001$ ). The cells contributing the most to this significant effect were those for male and female progeny from P-P matings. More offspring from P-P matings adopted freezing behaviour than expected by chance, while fewer of those from NP-NP matings did so than expected by chance. Progeny from the other two mating types were intermediate in their tendency to freeze. An analysis of the latency to break from this freeze (amount of time the mouse remained in a freeze posture) revealed significant effects for both sex ( $F_{1,80}=5.473$ ,  $P=0.022$ ) and mating type ( $F_{3,80}=5.367$ ,  $P=0.002$ ), but not for the interaction ( $F_{3,80}=1.350$ ,  $P=0.264$ ). Males spent a longer time in the freeze posture than females. A Scheffe's post hoc analysis with the sexes combined revealed that progeny from P-P matings remained in the freeze posture longer on average than progeny from any of the other three mating types (Table 5).

There was a significant treatment effect ( $F_{3,152}=10.806$ ,  $P<0.001$ ) for the time to enter the nestbox, but no significant sex ( $F_{1,152}=0.803$ ,  $P=0.372$ ) or interaction ( $F_{3,152}=0.555$ ,  $P=0.646$ ) effects. A Scheffe's post hoc analysis revealed that the main treatment effect was attributable to a significantly shorter mean latency to enter the nestbox for male and female progeny from P-P matings. Progeny from all of the remaining three mating types took longer to enter the nestbox. The analysis of the latency to leave the nestbox revealed a significant main treatment effect for mating type ( $F_{3,152}=12.099$ ,  $P<0.001$ ) and for the interaction of sex and mating type

( $F_{3,152}=4.364$ ,  $P=0.006$ ), but no sex difference ( $F_{1,152}=0.117$ ,  $P=0.733$ ). The main treatment effect was due to the fact that mice from P-P matings remained in the nextbox for nearly twice as long on average relative to the progeny from the other three mating types (Scheffe's post hoc test). The significant interaction occurred because for P-P and NP-NP matings, the mean latencies were lower for females than for males, whereas for P-NP and NP-P matings, the latencies to leave the nextbox were higher for females than for males.

## DISCUSSION

### Mate Preferences and Variation in Morphology

This study was not designed to measure the cues mediating mate preferences. Because we used only known opposite-sex nonkin in the mate preference trials, we do not believe the preferences in this study can be explained by avoidance of inbreeding. Choosers may have discriminated levels of genetic variation, but we collected no data relevant to a direct evaluation of this possibility. We found no association between preference status and morphological variation. Neither females nor males were apparently selecting their preferred partners based on size indicators (Table 1). We make little of this observation because, as we have stressed, the cues of mate preferences were not the motivation for this study.

### Constraints on Mate Preferences and Components of Fitness

Our results indicate the following. (1) There were few differences in components of fitness for breeders from the four types of pairings of P and NP partners. (2) There was no statistically significant heterogeneity across the four mating types in offspring viability or variation in weight. (3) However, inspection of the data and post hoc tests

indicated enhanced fitness for P–P pairings compared with NP–NP pairings in the number of pups weaned, birth-to-weaning viability and offspring weight variation. (4) There were statistically significant differences in performance measures across all four treatment categories. Progeny from P–P matings displayed behaviour that would probably be associated with higher fitness in nature than did progeny from NP–NP matings.

### Components of Fitness for Breeders

In this study the only reported statistically significant components of fitness for breeders was that NP–NP pairs had a longer latency to birth of the first litter than P–P pairs. Since house mice almost invariably have a gestation period of 19–20 days, this difference probably results from male or female resistance to mate with a non-preferred partner.

### Offspring Viability and Performance

The patterns of offspring viability, variation in weight and weight gain illustrate a consistent pattern. They were greater for progeny from P–P matings than NP–NP matings. Thus, while none of the individual analyses based on the four treatments were significant, an examination of the results from all of the progeny characteristics (Table 3) and post hoc tests indicated that the mean values for progeny from P–P matings were better than those for progeny from NP–NP matings.

For some progeny characteristics (Table 3) the mean values for progeny from P–P matings and the two intermediate mating types (P–NP and NP–P) did not differ, whereas those for progeny from the intermediate types and NP–NP matings did. In other instances, values for progeny from intermediate mating types differed from those of P–P matings, but did not differ from those of NP–NP matings. Offspring viability and constraints theory makes no prediction about the direction of variation between P–NP versus NP–P. Parental investment theory (Trivers 1972) states that when mothers reproduce with their preferred partners, offspring viability benefits should be more exaggerated than when fathers reproduce with their preferred partners. Differential allocation theory (Burley 1986) makes no predictions about offspring viability for P–NP versus NP–P matings, but does make predictions about the sex of offspring in which parents should invest. When males are with females they prefer, but females are not with males they prefer, differential allocation theory predicts that mothers are more attractive than fathers, so that such pairs would be selected to invest more in daughters. Thus, when females are with males they prefer, but their mates do not prefer them, differential allocation theory predicts that fathers are more attractive than mothers, so that such pairs should invest more in sons. Further experimental work on these intermediate patterns may prove valuable from the perspective of the differential allocation hypothesis (Burley 1986).

### Progeny Performance

The differences in progeny performance among the four treatment groups were all in the predicted direction. Progeny from P–P pairings performed significantly better in all tests than progeny from NP–NP pairings. Thus, sons and daughters that are heavier at weaning and that have grown most rapidly between birth and weaning are more likely to have sufficient resources at the time of dispersal to survive the rigours of leaving the natal area than are mice that are smaller and have fewer reserves.

The tendency of progeny of both sexes from P–P matings to build better nests than progeny from NP–NP matings is also consistent with the potential greater viability for progeny of P–P matings. We specifically tested young mice at about the age that the mice in the wild would be dispersing from their natal area. At this time, the capacity to build an adequate nest to aid with thermoregulation, protection from the elements and possibly evading predators would provide a distinct fitness advantage to wild-living mice. In this particular test, the results for the two mating types involving one preferred partner were about the same as for the NP–NP progeny. Thus, with regard to nest building, it appears that there is a consistent and distinct advantage for progeny born to partners where both prefer each other.

For the performance test involving male aggressive encounters, the overall pattern was more graded. These tests were conducted when the mice were at an age where they are sexually mature and nearly physically mature as well (body mass of 18–20 g). There was, as with nest building, a distinct difference in performance between males born to P–P pairings, where most encounters were 'won', compared with males from NP–NP matings. In this instance, however, the results for the proportions of encounters 'won' by males from P–NP and NP–P mating types were intermediate. Overall, we conclude that being dominant in an aggressive encounter is an advantage, and thus, male progeny from P–P matings would probably have greater access to food, shelter and possibly mates.

We performed simulated-predator avoidance tests on the mice at an age when they would be dispersing from natal sites. For each of the four measures we obtained in this test, there was a clear difference between progeny from P–P matings and those from NP–NP matings. In each instance, the actions of the progeny from P–P matings, regardless of progeny sex, were such that these mice would be more likely to survive the presence of a predator. Both male and female progeny from P–P matings were more likely to freeze and remain in the freeze posture longer, and to enter the refuge more quickly and remain in the refuge longer than male and female progeny from NP–NP matings. For this test, the progeny from the other two mating types were generally intermediate in performance. Nevertheless, as with the latency to enter the refuge, mice from P–NP and NP–P matings did not differ from the progeny from NP–NP matings and were significantly slower than progeny from P–P matings to achieve this shelter.

Taken together, our data are consistent with the predictions that (1) both females and males discriminate between potential reproductive partners, and (2) in ways that favour enhanced offspring performance and perhaps their overall viability. These results further suggest that attention to patterns of mutual mate preferences, even in species with little or no male parental investment, may bring further clarity to our questions about the fitness consequences of mate preferences for breeders and their offspring.

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