



Male house mice produce fewer offspring with lower viability and poorer performance when mated with females they do not prefer

PATRICIA ADAIR GOWATY*, LEE C. DRICKAMER† & SABINE SCHMID-HOLMES‡

*Institute of Ecology, University of Georgia

†Department of Biological Sciences, Northern Arizona University

‡Department of Wildlife, Fish & Conservation Biology, University of California, Davis

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We report experimental results consistent with the hypothesis that constraints on the expression of male mating preferences affect breeder fitness, offspring viability and performance. If constraints on the expression of mating preferences are common, tests of fitness variation associated with mate preferences must eliminate as many constraints on mate preferences as possible. We tested whether male mate preferences influenced breeder fitness, offspring performance and viability in typically polygynous house mice, *Mus domesticus*, from a feral source population. Our 'free mate choice' trials not only eliminated female preferences, male–male and female–female competition, but also our best guesses of the traits mediating choosers' preferences. Males mated with their preferred (P) females sired more litters than males mated with their nonpreferred (NP) females. Offspring viability was significantly lower when males reproduced with females they did not prefer compared with females they did prefer. Adult sons of males that mated with their P females were socially dominant to sons of males that mated with their NP females. Adult offspring from P pairings built better nests than offspring from NP pairings. The slope of the survivorship curve for P offspring was significantly higher than for NP offspring. These results showed (1) males' mate preferences affected their fitness, (2) males that mated with females they preferred produced more litters than males that mated with females they did not prefer, and (3) their offspring were significantly more viable and performed significantly better on standardized performance tests. This is the first demonstration of fitness benefits of male choice behaviour in a mammal species with typical paternal investment.

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Darwin (1871) posited mate choice as a mechanism of sexual selection. He argued that female discrimination among potential mates could explain the evolution of bizarre and elaborate traits in males. Despite early controversy, Fisher (1958) showed how female choice could arise and favour arbitrary traits in males through a 'run away' process. Hamilton & Zuk (1982) argued that female mate choice favoured the evolution of indicator traits demonstrating the health of males. Trivers (1972), building on Bateman (1948) and Williams (1966), argued that differences in parental investment of the sexes mould typical sex roles of female mate choice and male–male

contests. 'Discriminating females' and 'indiscriminant males' have come to dominate collective views of sex-role behaviour in many organisms, but particularly in mammals, in which parental investment by females is greater than by males. Today few doubt the importance of female mate choice for the evolution of traits in males (Andersson 1994). Consistent with expectations from parental investment theory, studies of female choice are common (Wagner 1998). In contrast, except for studies of 'role-reversed' species, relatively few studies of male mate choice exist (Gowaty 1998).

Altmann (1997) recently challenged the idea that selection favoured indiscriminate males. She characterized the common view with a quote from a close colleague: 'Why could one possibly think that males would have to choose mates? Surely a male with priority of access can have all mates at little or no cost, unless the mating systems are monogamous or polyandrous, situations that are quite rare in mammals' (page 325). Altmann made the point that if females vary, any time a male has a choice

Correspondence: P. A. Gowaty, Institute of Ecology, University of Georgia, Athens, GA 30602-2602, U.S.A. (email: gowaty@ecology.uga.edu). L. C. Drickamer is at the Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011-5640, U.S.A. S. Schmid-Holmes is at the Department of Wildlife, Fish & Conservation Biology, University of California, Davis, CA 95616, U.S.A.

between two females, selection should favour male mate discrimination.

Earlier, [Hubbell & Johnson \(1987\)](#) made a related point to Altmann's with an absorbing Markov approach that modelled the means and variances in fitness for choosy versus indiscriminate strategists. Their sex-neutral model showed that selection would favour facultative choosy or indiscriminate strategists depending on stochastic variation in environmental and life-history traits independent of past selection for choosy or indiscriminate behaviour. An important implication of their model is the hypothesis that selection has acted so that individuals are sensitive to environmental and social variation that could affect their fitness from choosy or indiscriminate mating. Among the critical parameters of their model is the distribution of fitness differences among potentially mating opposite-sex individuals. Their model showed that even in polygynous species, stochastic environmental variation would sometimes select against choosy females and indiscriminate males (and, contra Altmann, sometimes against choosy males even when fitness differences among potential mates exist). Thus, theoretical predictions of choosy males even in species with no or very little paternal investment in offspring have been available for at least 15 years, but seldom or never tested.

Indeed, until relatively recently ([Ryan & Altmann 2001](#)) the few studies of male mate choice in non-role-reversed species focused on male mate choice for bigger females (e.g. [Downhower et al. 1983](#); [Johnson & Hubbell 1984](#)). In contrast to studies designed to understand the evolution of traits in females, we designed the current study to test how constraints acting on the expression of mate preferences affect the fitness of choosing males and their offspring independent of the cues in females that mediate male mate preferences.

Constraints on the expression of mating preferences are likely to be common ([Gowaty 1996, 1997, 1999](#); [Gowaty & Buschhaus 1998](#)). If they are, investigators should control or eliminate potential constraints when evaluating fitness correlates of mate preferences for choosing individuals. Although first argued in relation to constraints on the expression of female preferences, constraints on the expression of male preferences are also likely to exist and result in variation in offspring viability for males that reproduce under constraints and males that do not. Although the theory is about social constraints, ecological constraints are also likely to be common and affect variation among sires in offspring viability. This point makes sense if ongoing within-species, between-sex interactions, such as sex, are driven by Red Queen host-pathogen contests ([Dybdahl & Lively 1998](#); [Lively & Dybdahl 2000](#)). If host-pathogen interactions are as powerful as many have argued ([Brown 1997](#); [Wedekind 1999](#)), mating preferences, behaviour and physiology of both sexes will be shaped, at least in part, by variation in offspring viability. Because pathogen populations reproduce much faster than their host populations, host efforts to pass to their offspring adequate defences against parasite attacks are a never-ceasing selection pressure that will operate on mate preferences through offspring viability. If this is so, mate choice should favour immune comple-

mentarity (dissimilarity) between parents, because more genetically diverse offspring are more likely to survive attack by evolving (emerging) pathogens ([Brown 1997](#); [Wedekind 1999](#)). What writers have less often emphasized is that different choosers will seldom prefer the same mate because choosers vary too and what they contribute to immune competence of their offspring will determine what constitutes immune complementarity in potential mates. In other words, mate preferences would be self-referential (P. A. Gowaty & S. P. Hubbell, unpublished data). If host-parasite selective dynamics work as expected, the best host phenotype will change from one generation to the next, so that selection should seldom favour a single male phenotype all females prefer (P. A. Gowaty & S. P. Hubbell, unpublished data). If offspring viability selection works in this way, not only female choice, but male choice must matter to offspring viability, even when reproductive rate ([Sutherland 1985](#)) by males is faster than by females ([Hubbell & Johnson 1987](#)) and even when male investment in offspring is vastly less than female investment. It is this basic assumption of differences in costs to offspring viability for breeders reproducing under constraints compared with those that do not that motivated the design of this and our earlier study ([Drickamer et al. 2000](#)) on females. We stress that the questions in this study were not about traits in the chosen sex, but about the effects of constraints on breeder and offspring fitness independent of the traits in females that mediate male preferences.

If offspring viability selection works as described above and if constraints on the free expression of mate preferences are common, reproduction will more often fail when males or females reproduce with partners they do not prefer (NP). Furthermore, if choosers are unable to avoid reproduction with NP partners, offspring viability will be lower in comparison to reproduction with partners they do prefer (P). Thus, we tested whether males and their offspring had enhanced fitness when males reproduced with females they preferred compared with females they did not.

The subjects were house mice, *Mus domesticus*, a territorial, polygynous rodent ([Brown 1953](#); [Bronson 1979](#)). Multiple females live within a male's territory ([Crowcroft & Rowe 1963](#); [Anderson & Hill 1965](#)), whether they are living commensally or in a feral environment ([Mikesic & Drickamer 1992](#)). Much is known about female mate preferences in house mice ([Yamazaki et al. 1978](#); [Lenington 1983](#); [Coopersmith & Lenington 1992](#); [Eklund 1998](#); [Drickamer et al. 2000](#)). A few have tested for male mate preferences ([Yamazaki et al. 1978](#); [Arcaro & Eklund 1998](#)). As far as we are aware, however, no one has tested the functional significance of male mate preferences in house mouse, nor the effects of constraints on males' reproductive decisions. What we do not know is how often males are choosy, if male mate preferences are functionally significant, and whether male mate preferences yield fitness benefits. No one to our knowledge has ever examined how offspring viability varies with fathers' preferences for mates. We tested males in a mate choice situation free of the usual social complications of female preferences and male-male contests. Because constraints

theory argues that individuals (females and males) often are coerced by ecological or social constraints to reproduce with nonoptimal partners, the experimental protocol explicitly eliminated or randomly controlled social constraints on the expression of choosers' relative preference for one of two females. This allowed examination of the effects of 'freely expressed' male mating preferences on fitness among males and their offspring. We stress that our immediate interest was not in female traits mediating male preferences, but in whether there were deficits to offspring viability when choosers reproduced with non-preferred (not random) partners, which might happen whenever social or ecological constraints interfere with the expression of choosers' mate preferences.

MATERIALS AND METHODS

Drickamer et al. (2000) thoroughly describe the subjects, their sources, methods of culturing, raising, handling and testing procedures. Therefore, we briefly summarize the methods here.

The current study differs from the earlier one primarily in terms of the sex of the choosing individual, and in timing. In Drickamer et al. (2000) we reported tests of female preferences conducted during 1997. Here we report tests of male preferences conducted during 1998. Parents (40 males and 40 females) of breeders (F1s) used in this study were collected in 1997 from wild populations at the Swine Center, Southern Illinois University, Carbondale, Illinois, U.S.A.

We used a three-celled mate choice arena for preference testing. The arenas had a central chamber through which focal males travelled to observe two females that occupied cells at each end of the central chamber. The females could not see each other, nor could males touch them. Males could observe females through a mesh wall, and could smell and hear them. The preference tests lasted for 10 min. For a male to be included in the subsequent reproductive trials he had to display a behavioural preference, because our question is explicitly about comparative fitness for males that reproduce with females they prefer versus those they do not. We emphasize that our experimental breeders were males paired with females they preferred and did not prefer, which differs from designs that compare choosers with preferred versus random mates. We defined a male as having shown a preference if he spent half of the test time in front of either or both females and 60% of his time in front of one of the females. Of the 104 males we tested, 101 met the behavioural criteria for displaying a preference. Of these, we randomly assigned 50 to mate with their P female and 51 to mate with their NP female. We held progeny (1) exclusively in the laboratory, or (2) in the laboratory until about 35 days of age, when we released them into outdoor field enclosures and observed them (as described in Drickamer et al. 2000).

Observers scored performance and fitness blind to the preference status of breeding pairs. We measured the following components of fitness of choosing males: the number that sired litters (fertility), the time to first litter, the number of pups born per litter (fecundity), the

number of litters weaned, the number of pups weaned per litter, and the number surviving to 60 days old in the laboratory. Overall number of offspring surviving to reproductive age is commonly estimated using values from separate sets of observations; for example, the number surviving to some arbitrary age, a , in one observational set, multiplied by the percentage surviving from a to $a+1$, observed in a subset of the total experimental set. We did not place all offspring in outdoor field enclosures. Therefore, we estimated the overall number of offspring that would have survived in the outdoor enclosures had all offspring reaching 35 days of age been placed in the outdoor enclosures as the product of the number surviving to 35 days times the proportion surviving 3 days postrelease to the outdoor field enclosures. This is our ultimate measure of breeder reproductive success as it is the best estimate of the number of offspring surviving to the age of first reproduction. We report offspring viability as the percentage of offspring surviving from birth to weaning, from introduction to the field enclosures to 3 days postintroduction, and to 30 and 60 days postintroduction.

We measured three components of offspring performance: offspring quality as evidenced by weight gain and weight at birth and weaning; offspring performance in dominance and nest-building trials, and in their trappability. We examined interactions between sex and mating type on performance and survivorship because Trivers & Williard (1973) and Burley (1986) have associated variation in parental sex allocation of polygynous animals with fitness interests of parents.

We measured performance of sons in dominance trials. We measured nest construction ability of sons and daughters using a standardized testing protocol. We followed survival of mice in the field for 60 days postrelease. As in our previous study (Drickamer et al. 2000), after placing the mice in the field enclosures, we trapped them twice a week during 1-h sessions using live traps in each of 54 baited stations within each of the three outdoor enclosures. We scored mice as having been alive in the last trapping session that we caught them. We caught all mice remaining on day 60 postintroduction using live traps or death traps and removed them from the field enclosures.

Our experimental design was conservative relative to our main questions about the fitness consequences for males and their offspring of mating with P versus NP partners for the following reasons. (1) Males discriminated between only two females rather than among three or more. Had males discriminated among more females, the differences between most preferred and least preferred probably would have been larger. Thus, a priori, the experimental design decreased the likelihood of observation of differences between males paired with their P and NP females and their offspring. (2) Individuals from a feral population comprised source breeders for our experimental subjects so that differences due to rare male mating advantages, interdemec mixing, or other outbreeding advantages were likely to be small, perhaps nonexistent. Thus, if differences resulted from outbreeding or from maximizing differences at immune system

Table 1. Tests for differences in components of fitness for choosing males experimentally paired with either their preferred or nonpreferred female

Trait	Preferred mating	Nonpreferred mating	Test	<i>P</i> *
Litters born	44/50	37/51	$\chi^2_1=3.887$	<0.05
Pups born/male	4.8±0.3	3.8±0.3	$t_{99}=-2.078$	<0.041
Mean size of litters born	5.5±0.2	5.3±0.2	$t_{79}=0.732$	0.4662
Litters born that weaned	39/44	28/37	$\chi^2_1=2.37$	0.1239
Litters weaned/pair (including pairs that did not produce offspring)	39/50	28/51	$\chi^2_1=6.13$	<0.01
Pups weaned/litter	4.6±0.3	4.2±0.4	$t_{79}=0.678$	0.4998
Pups weaned/pair	4.0±0.4	3.0±0.4	$t_{99}=-1.783$	<0.078
% Females born	50.1±3.0	46.0±3.6	$t_{79}=0.882$	0.38
Time to first litter (days)	26.8±0.8	28.4±1.1	$t_{79}=-1.190$	0.2376
Mother's age at mating (days)	66.0±2.0	63.4±1.9	$t_{99}=0.917$	0.3617
Second litters born	30/44	25/37	$\chi^2_1=0.003$	>0.90

Values are either the number of offspring that survived/did not survive, or means±SEs for each mating type.
**P* values are from Student's *t* tests or chi-square tests.

components, our use of a single source population a priori decreased the probability of observation of differences. In addition, we were careful not to present male choosers with any of their known siblings or other first-degree relatives, thus differences we report are unlikely due to fitness costs of breeding with close kin. (3) We used a 60% bias for assigning preference because it too was conservative. It allowed us to systematically determine whether a given male had a minimal preference for either female. Because we used a low difference in determining preference, we a priori reduced the likelihood of observing differences in offspring viability. (4) We tested offspring performance and viability in two situations expected to differ in the likelihood of exposure to naturally occurring pathogens and predators, and thus in terms of the stress that offspring might have experienced. We suspected that any differences in viability and performance that we might have observed would have been due to effects acting differently on progeny from P and NP pairs. Because the laboratory environment was relatively free of pathogens and entirely free from predators, we a priori reduced the likelihood of observation of viability and performance differences in laboratory tests. Because we provided shelter and ad libitum food in outdoor field enclosures, we reduced the likelihood of observing differences in our experimental categories, even if they existed.

RESULTS

Breeder Reproductive Success

The percentage of pairs in which litters were born was significantly higher (Table 1) when males were mated to their P females (88%) than to their NP females (72.5%). Males mated to their P females sired 242 pups and those mated to their NP females sired 195, however, the mean number of offspring born per pair (litter size) was not significantly different (Table 1). For pairs with any offspring born, there was no significant difference in the number of litters weaned. The number of pups weaned

per litter born was also nonsignificant (Table 1). Some pairs had more than one litter. The number of pups weaned per pair did not differ for P matings (four pups/pair) and NP matings (three pups/pair) (Table 1). There was a total of 200 weaned pups sired by males mated to their P females and 155 pups sired by males mated to their NP females. When we calculated the number of litters weaned over all pairs in each treatment (including those without any litters born), 78% of the males mated to their P females had weaned litters, versus 54.9% of males mated to their NP females, a significant difference (Table 1). Males mated to their P females had a total of 74 litters born (1.48 litters per each of 50 males) and those mated to their NP females had 62 (1.2 litters per each of 51 males), however, there was no significant difference in whether a second litter was born once a first litter was born (Table 1). Had we placed all offspring from P and NP pairs surviving to the time of release in the outdoor field enclosures, by 3 days postintroduction, 150 offspring (75% of 200) from males mated to their P females would have survived versus only 98 offspring (63% of 155) from males mated to their NP females. Thus, the estimated average overall productivity of a male mated to a P female was 2.9 offspring, and that for a male mated to an NP female was 1.9 offspring.

Offspring Quality

There were no significant differences in the phenotypic measures of offspring quality (Table 2). There were no differences in pup weights at birth or at weaning or in weight gained per pup for the two groups of sires.

Offspring Viability

There were no differences in survival of adult offspring when we held them in the laboratory until 95 days of age. The percentage of offspring surviving at four intervals were each nonsignificant: birth to weaning (Table 2), from introduction to outdoor field enclosures to 3 days,

Table 2. Tests for differences in offspring viability and quality (numbers or means±SE) for males mated to their preferred or nonpreferred female

Trait	Preferred mating	Nonpreferred mating	Test	<i>P</i> *
Average birth to weaning viability (% surviving to weaning/litter)	85.0±5.7	73.9±6.3	$t_{79}=0.194$	0.1935
Average pup weight				
At birth (g)	1.34±0.03	1.37±0.04	$t_{79}=-0.773$	0.4413
At weaning (g)	10.4±0.2	10.7±0.2	$t_{65}=-1.105$	0.2732
Average weight gain/pup (g)	8.9±0.2	9.3±0.26	$t_{65}=-0.991$	0.3252

Values are means±SEs for each mating type.

**P* values are from Student's *t* tests or chi-square tests.

Table 3. Survival in field enclosures of offspring sired by males that were mated to their preferred and nonpreferred females

	Survived introduction	Survival to 30 days	Survival to 60 days
Combined over sex of offspring			
Nonpreferred, <i>N</i> =53	33/20 (62)	21/32 (40)	9/44 (17)
Preferred, <i>N</i> =51	38/13 (75)	26/25 (51)	8/43 (16)
G_1	1.81	1.356	0.32
P	0.1785	0.2442	0.8583
Sons			
Nonpreferred, <i>N</i> =28	18/10 (64)	12/16 (42.8)	4/24 (14)
Preferred, <i>N</i> =25	19/6 (76)	14/11 (56)	3/22 (12)
χ^2_1	0.868	0.915	0.035
P	0.39	0.34	0.85
Daughters			
Nonpreferred, <i>N</i> =25	15/10 (60)	9/16 (36)	5/20 (20%)
Preferred, <i>N</i> =26	19/7 (73)	12/14 (46.2)	5/21 (19.2%)
χ^2_1	0.98	0.54	0.005
P	0.32	0.4608	0.94

Values are the number of offspring that survived/did not survive (percentages are given in parentheses).

from introduction to 30 days, and from introduction to 60 days (Table 3). In the test of the effects of mating type on the slopes of the curves in the percentage of offspring surviving with age as the covariate, both age and mating type were significant (Fig. 1). Birth to weaning viability had a greater effect on the slopes than the other viability estimates (age: $SS=8228.9$, F_1 ratio=372.3, $P>F<0.0001$). Offspring whose sires reproduced with P partners had significantly higher overall viability (mating type: P versus NP: $SS=119.03$, F_1 ratio=5.39, $P>F=0.05$).

Offspring Performance

In social dominance tests, male progeny sired by fathers mated to their P females defeated sons sired by fathers mated to their NP females in 19 of 26 trials (chi-square test: $\chi^2_1=5.538$, $P<0.025$). Body mass did not influence the outcomes of the social dominance trials. In five of the 26 trials, the mice weighed the same. The heavier mouse won 11 and lost nine of the remaining 21 trials.

Nests built by mice in laboratory cages varied significantly by sex and mate preference category of their parents; the interaction term was not significant

(ANOVA: $F_{1,112}=0.459$, $P=0.4993$). Sex of offspring was significant ($F_{1,112}=11.7$, $P=0.0009$), with daughters (mean ± SE=2.70 ± 0.08) building better nests than sons did (2.21 ± 0.12). Mice from P matings (2.64 ± 0.09) built significantly ($F_{1,112}=7.1$, $P<0.009$) better nests than mice from NP matings did (2.24 ± 0.12). Nests built by progeny in the field enclosures differed significantly by mate choice treatment ($F_{1,69}=9.684$, $P=0.0027$), but not by sex ($F_{1,69}=0.099$, $P=0.7545$); the interaction term was not significant. Nests built by offspring sired by fathers mated to their P females (2.37 ± 0.10; *N*=38) were significantly better than those built by progeny sired by fathers mated to their NP females (1.93 ± 0.11; *N*=33).

We also tested the possibility that mice would respond differently to the live traps depending on sex or mating type using a two-way ANOVA. We calculated the dependent variable as the proportion of times that we caught each individual mouse in the live traps in relation to the number of times that we could have caught it. Trappability varied by mate choice treatment ($F_{1,61}=5.665$, $P=0.0204$), but not by sex ($F_{1,61}=0.852$, $P=0.3597$). We caught progeny of males mated to their P females (41.2 ± 3.3%), on average, a greater proportion of time than those of males mated to their NP females

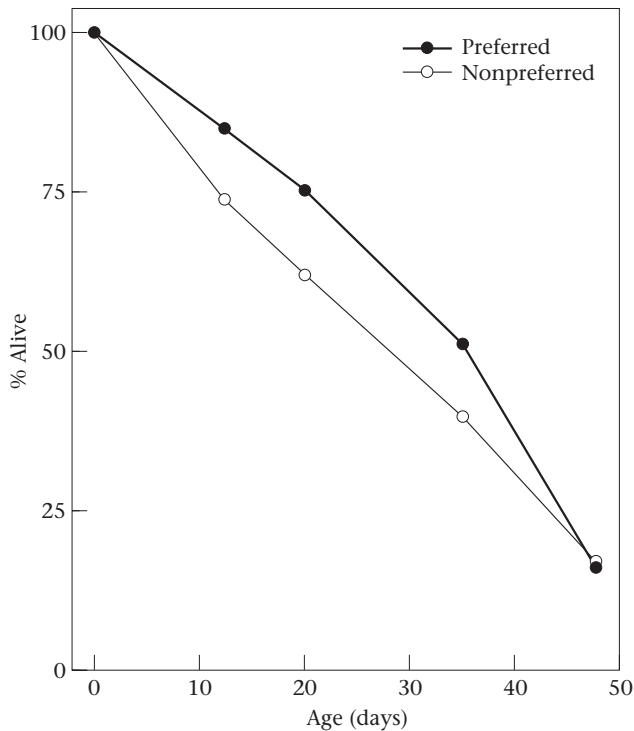


Figure 1. Survivorship curve of offspring whose fathers were paired with preferred and nonpreferred females. Data on age at death were plotted from the midpoint of the age interval over which survivorship was assessed.

($30.2 \pm 3.9\%$). The interaction term was significant ($F_{1,61}=5.083$, $P=0.0278$): trappability was associated with the interaction of offspring sex with sire's mating type. The effect of sire's mating type was significant only for daughters; we caught daughters from NP pairs significantly less often than daughters from P pairs. We caught daughters of P pairs $44.2 \pm 5.5\%$ of the time and sons $37.6 \pm 2.8\%$ of the time. We caught daughters of NP pairs $21.4 \pm 3.2\%$ of the time and sons $37.0 \pm 6.0\%$ of the time.

DISCUSSION

Choosy Males

Male house mice display preferences when given a choice between two females. The choosiness of the males could be more apparent than real if choosing males merely respond to females that prefer them. Although this is a possibility, we suspect it does not account for the overall differences we observed, because in a later series of experiments (Drickamer et al. 2003) measuring mutual mate preferences, males preferred females even when females did not prefer them, and vice versa. If the choosers and chosen in this study behaved similarly to those in the later study, then males in the present study should have been as likely as not to prefer females that did not prefer them, and vice versa.

Parental investment theory (Trivers 1972) does not predict choosy males in species like house mice with greater maternal than paternal investment. Theories that

do predict choosy males also assume that offspring viability favours mate preferences (P. A. Gowaty & S. P. Hubbell, unpublished data), even in species with asymmetric parental investment (Hubbell & Johnson 1987; Altmann 1997). A study (W. W. Anderson, P. A. Gowaty & Y. K. Kim, unpublished data) using mate preference protocols like the ones reported here showed that in *Drosophila pseudoobscura*, a species with highly biased female parental investment, male mate preferences significantly enhance breeder productivity and offspring viability.

Traits of Preferred Females

The females in our trials were included at random with respect to phenotypic variation, and we did not measure female traits in this study. Thus, we do not know what female traits cued males' preferences, or if female traits alone could account for the fitness variations we observed. It is possible, of course, that the fitness differences we report may have arisen as an effect of size variation in females. In a later series of trials (Drickamer et al. 2003) using protocols identical to the ones we used here, female morphological traits including weight did not vary systematically for females that were either preferred or nonpreferred. Therefore, we doubt that systematic size differences among mothers accounted for the differences in breeder fitness and offspring viability that we report here.

These results remain consistent with Altmann's (1997) theory that male mate preferences will be favoured whenever females vary. We experimentally controlled for mating status (all test females were virgins); age (all females were about 60 days old when originally tested) and original source (all were F1 progeny of parents wild-caught from the same farm). We further controlled the tests so males did not discriminate between sisters or other first-degree relatives in the arena trials. We never used sisters simultaneously as test females. However, we made no explicit measurements of phenotypic trait variation of test females. In a later study using identical mate preferences protocols (Drickamer et al. 2003), we examined other morphological correlates besides size of female preference status. In that study we found no consistent size or other morphological correlate of preference status for females. Despite these caveats, we suspect that females probably did vary in other interesting ways (see below).

Breeder Reproductive Success

Free male mate choice enhanced the fitness of fathers. Fertility (number of litters born), observed productivity (number of offspring surviving to reproductive age) and estimated productivity (the product of the number of offspring surviving to 35 days of age and the viability of those released to enclosures that survived for at least 3 days) were greater when males were mated to their P females compared with their NP females. The estimated overall productivity represents a large selection differential (3 versus 2 for males mated to P versus NP females).

These results confirm the prediction of the theory that says individuals should avoid reproduction with NP mates. The expression of male mate preferences free of social constraints enhanced their reproductive success.

Offspring Viability

Offspring of sires mated to NP females had a steeper survivorship curve than offspring of sires mated to P females (Fig. 1). Thus, observations matched the critical prediction that offspring viability is higher when fathers mate with females they prefer than with females they do not prefer. No other theory of which we are aware predicts enhanced offspring viability for male mate preferences in species with typical female-biased parental investment. Not surprisingly, given the differences in offspring performance in dominance and nest-building trials. Offspring of sires mated to P females consistently outperformed offspring of sires mated to NP females.

The differences in overall offspring viability (Fig. 1) and performance occurred despite our conservative experimental approach. Our conservative design may have contributed to the lack of significant differences in offspring survivorship calculated separately at four points: from birth to weaning, and at 3, 30 and 60 days post-introduction to field enclosures (Table 3). First, as we described in the Methods, the design of the preference tests made it unlikely that differences between males mated to P versus NP females would be large. Second, we did not specifically challenge offspring as Partridge (1980) did. Third, we provided supplemental food and water ad libitum in quantities that were never exhausted. Thus, we believe the methods worked against the likelihood of observations of the critical prediction, so we conclude that the offspring viability differences that we do report are robust.

We designed this experiment to evaluate the fitness consequences for offspring of males breeding under constraints. If we knew the exact information about females or female signals that mediate male preferences, we could address Altmann's hypothesis further. However, we explicitly placed females in these trials at random with respect to their phenotypic variation in order to test the key idea that constraints on the expression of mate preferences affect offspring viability. This key idea is that in nature choosers may not achieve reproduction with preferred partners because of ecological and social constraints on mating, for both females and males. We felt that picking 'to-be-discriminated' individuals based on phenotypic variation obvious to us would potentially bias this test. This might be particularly so, if signals from to-be-discriminated individuals manipulate choosers' behaviour, as suggested by terms in the mate choice literature, such as 'exploitation of pre-existing sensory bias'. By placing to-be-discriminated individuals into the mate preference arenas at random means that sometimes, at least, males discriminated between females with similar trait values.

Our observations provide no information on mechanisms of failure to produce litters or to successfully wean

litters sired by males mated to their NP females. However, they are consistent with other studies of reproductive success variation in house mice mated to partners with MHC alleles similar and dissimilar from their own (Potts et al. 1991, 1994; Potts & Wakeland 1993). Females more often abort offspring when mated to males with MHC alleles similar to their own, which may or may not explain the failure of males mated to their NP females to produce and successfully wean litters in this experiment. Furthermore, in preference tests that explicitly varied the degree of MHC dissimilarity between choosers and to-be-discriminated individuals, house mice preferred partners with MHC variants dissimilar to their own (Egid & Brown 1989). Indeed, if this is the underlying mechanism explaining the differences we report, male mate preferences may be self-referential, and the important differences between P and NP females may not be absolute differences, but differences relative to the choosing male. Because constraints theory pivots on mate choice advantages accruing through offspring viability, the immune complementarity (at MHC coding loci and other immune system loci as well) of choosy males with their P and NP partners may deserve further experimental examination. Females paired to males that did not prefer them and that did not produce any litters may have resisted copulation, aborted broods, or cannibalized recently born young. If males inseminated them, NP females may have physiologically inhibited fertilization or implantation. If pregnancy occurred, NP females may have aborted fetuses. Whatever mechanisms underlie observations of significantly reduced litter production for offspring of males that mated with their NP females, they are also consistent with flexible adjustment of reproduction by females in response to the probability of producing less competitive and/or less viable offspring. Of course, some males simply may not have copulated with some of their NP females. This possibility also deserves further experimental scrutiny.

Others have reported variation in fitness of offspring as a function of reproducing with more or less attractive partners (Reynolds & Gross 1992; Nicoletto 1995). Our experiment differed from these in that we were not asking whether particular traits in potential mates indicated health; nor were we asking whether particular traits correlated with absolute or among-male attractiveness averaged over a population of females. Ryan & Altmann's (2001) germinal study was different from and similar to ours in several important design features. They manipulated the degree of kinship differences between the to-be-discriminated females and the choosing males, something we did not do. Unlike our design, theirs did not measure fitness consequences for the progeny of male choices. Their study was free of between-sex coercion and within-sex contests, as ours were. They asked whether the degree of relatedness between choosing males and the chosen-between females determined male mate preferences in a socially monogamous rodent, in which parental investment patterns between the sexes are more equitable than in typically polygynous mammals. In other words, their study, like ours, tested an idea associated with self-referential mate choice. We noted with

interest Ryan & Altmann's definitive demonstration that there existed no absolutely 'best female' in their population, a result consistent with mate preferences for offspring viability, but not with most other mate choice theories. Thus, we suspect that in mate preference trials of many other species, including those with and without paternal investment that eliminate a priori any possibility of inbreeding, that males and females reproducing with their P and NP mates will produce offspring with enhanced offspring viability.

Offspring Performance

Cold stress induces mice to build better nests (Lynch *et al.* 1976), nests are 'required' barriers against thermal stress, and there are heritable differences in nest-building ability (Lynch & Hegmann 1972). The fitness consequences of variation in nest-building ability are unevaluated as far as we know; nevertheless, female house mice usually deposit newborn pups into nests, and both males and females build nests for their own use, suggesting that these nests have adaptive significance. Obviously, therefore, the differences in nest-building performance by offspring sired by males mated to their P and NP females ultimately may have contributed to differences in long-term viability and reproductive success.

Dominance among males in polygynous species increases male mating success in mice (Oakeshott 1974), other mammals (e.g. Byers 1998) and in insects (Moore & Moore 1999), so it is likely that more dominant sons may enhance fitness benefits for fathers that mate with their P females in natural settings.

The significant interaction between offspring sex and trappability may indicate differential allocation to or quality (Burley 1986) of daughters and sons in this polygynous species. We caught sons and daughters from P pairings equally often, but we caught daughters from NP pairings significantly less often than sons. This interaction may represent differences in the relative quality of daughters and sons from P and NP pairings, but this is something that cannot be resolved without further study.

Constraints Theory

If variation in parental investment patterns between the sexes is the 'key variable controlling sexual selection' (Trivers 1972) in house mice, we should have observed no differences in fitness of males when mated to their P or NP females, or in the viability and performance of their progeny. We do not deny that parental investment patterns may affect variation between the sexes in mate choice behaviour. However, variation in parental investment is unlikely to be the 'key variable' explaining sexual selection via choosy males in house mice.

The experiment confirmed two crucial predictions relative to male mate preferences. (1) Males are choosy, even in polygynous species with 'typical' female-biased patterns of parental investment and (2) sires' mate preferences enhance their own fitness and the viability of their offspring. If constraints act on males so that they

commonly reproduce with NP females, constraints theory argues, as it does for females reproducing under constraints, that selection should act on males to attempt to compensate fitness losses (P. A. Gowaty & S. P. Hubbell, unpublished data). Reproductive compensation could occur by an increase in the number of offspring sired by such males or increasing paternal investment in forms associated with increased survivorship of pups. We expect compensation under constrained reproduction to be common among females; further evaluation of the conditions under which male compensation occurs may be profitable.

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