Manipulation of Olfactory Signaling and Mate Choice for Conservation Breeding: a Case Study of Harvest Mice

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Abstract: *Mate choice by females can introduce difficulties to captive breeding programs because there may be a conflict between the conservation manager's choice of mate (based on random allocation or maximizing heterogeneity) and the females' own preferences, often resulting in incompatibility and aggression. Similar effects are caused by inappropriate social contexts at the time of pairing. We manipulated the social experience of male and female harvest mice (Micromys minutus) to investigate whether we could enhance compatibility between randomly allocated mates by altering female preferences. In one experiment, we used a choice test to identify female preferences between two males and then varied the competitive context of unpreferred males by transferring competitor's scent marks into their cages. The manipulation caused them to increase their investment in a form of olfactory signaling (scent marking), which female rodents use as an indicator of male quality when choosing mates. The manipulation increased their attractiveness relative to the initially preferred male when the choice test was repeated. In a second experiment, we tested the effect of females' familiarity with the odor of males by transfer of male scent marks to female cages. Females preferred familiar males in choice tests and were less aggressive toward them when pairs were introduced than females paired with unfamiliar males. This kind of approach can influence mate choice, and transferring scent marks between cages or collections is an effective and practical behavioral means of improving success in conservation breeding programs.*

Key Words: captive breeding, mate choice, olfaction, scent mark, sexual selection

Manipulación de la Señalización Olfativa y Selección de Pareja para la Reproducción con fines de Conservación: un Estudio de Caso de *Micromys minutus*

Resumen: *La elección de pareja por hembras puede provocar dificultades a los programas de reproducción en cautiverio porque puede haber conflicto entre la selección de la pareja por el conservacionista (basada en asignación aleatoria o maximización de heterogeneidad) y las preferencias de la propia hembra, que a menudo resulta en incompatibilidad y agresividad. Efectos similares son causados por contextos sociales inapropiados al momento del apareamiento. Manipulamos la experiencia social de machos y hembras de Micromys minutus para investigar si alterando las preferencias de las hembras podíamos incrementar la compatibilidad entre parejas formadas aleatoriamente. En un experimento utilizamos una prueba de selección para identificar las preferencias de hembras entre dos machos y luego variamos el contexto competitivo de machos no preferidos mediante la transferencia a sus jaulas de las marcas aromáticas de sus competidores. La manipulación hizo que incrementaran su inversión a manera de la señalización olfativa (marcaje aromático), que utilizan los roedores hembras como un indicador de la calidad del macho al seleccionar pareja. La manipulación incrementó su atracción en relación con el macho preferido inicialmente cuando fue repetida la prueba de selección. En un segundo experimento, con transferencia de marcas aromáticas de machos a jaulas de hembras*

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probamos el efecto de familiaridad de las hembras con el olor de los machos. Las hembras prefirieron machos conocidos en pruebas de selección y fueron menos agresivas hacia ellos que las hembras apareadas con machos desconocidos. Este enfoque puede influir la selección de pareja y la transferencia de marcas aromáticas entre jaulas o colecciones es un método conductual efectivo y práctico de incrementar el éxito en programas de reproducción con fines de conservación.

Palabras Clave: marca aromática, reproducción en cautiverio, selección de pareja, selección sexual

Introduction

Sexual selection theory asserts that mate choice by females leads to fitness benefits, either through more offspring or through offspring that are better at surviving and reproducing (Darwin 1871; Hamilton & Zuk 1982; Andersson 1994). Although the precise nature and extent of the benefits may be diverse and remain open to debate (e.g., Kirkpatrick & Ryan 1991; Pomiankowski & Møller 1995), evidence for female choice and its associated benefits has been rapidly accumulating in recent years (reviews in Bateson 1983; Andersson 1994; Jennions & Petrie 2000). Females allowed to choose between males produce offspring with higher fitness than those with limited choice (Partridge 1980; Drickamer et al. 2000). Other studies show that differential expression of a male phenotypic trait (e.g., bird plumage or song repertoire) can lead to female preferences for particular males and higher offspring viability as a result of mating with them (e.g., Petrie 1994; Hasselquist et al. 1996).

In the light of mate choice theory, it is not difficult to see how attempts to breed animals in captivity sometimes fail because animals selected as potential mates may not accept each other. Incompatibility between potential mates can thwart the efforts of carefully designed captive breeding programs (Wielebnowski 1998; Sutherland & Gosling 2000), which often aim to maximize genetic variation in the managed population (Montgomery et al. 1997). At best, this may delay a suitable match; at worst, it may result in fighting, injury, and even death (e.g., in endangered clouded leopards [*Neofelis nebulosa*]; Yamada & Durrant 1989). In some cases—depending on population size, breeding seasonality, interbirth interval, and other factors—even small delays in obtaining compatible pairs may have substantial effects on the success of a breeding program. In the face of such behavioral incompatibility between mates, one current alternative is to use invasive reproductive techniques, such as artificial insemination (Ballou & Cooper 1992), but these techniques are not always desirable and require substantial resources and expertise (Conway 1995). For these reasons, and in order to preserve natural behavior within captive populations (Lyles & May 1987; May 1991; Wallace 2000), developing noninvasive methods of breeding these difficult species is a priority. Advances in behavioral ecology over the past 25 years have laid a foundation on which we can begin to

confront such issues in conservation biology (e.g., Clemmons & Bucholz 1997; Caro 1998; Gosling & Sutherland 2000). In particular, Sutherland and Gosling (2000) highlight the potential for increased understanding of processes underlying mate choice in overcoming behavioral incompatibility and extreme intrapair aggression.

We describe an attempt to apply principles derived from basic behavioral ecology to improve the chance of successful breeding in the harvest mouse (*Micromys minutus*). Although harvest mice do breed in captivity, obtaining compatible pairs is often difficult and characterized by high levels of female aggression toward males (Trout 1978; P. Rudd, personal communication). We sought to test whether it is possible to manipulate, in a specific direction, the preference of females for males. That is, could we make unpreferred males more attractive (cf. Sutherland & Gosling 2000; see also Wedekind 2002)?

Tackling the issue of mate incompatibility requires an understanding of the basis of mate quality and, in particular, how males communicate this information to females and how females make their choice. This information is generally not available in sufficient detail for threatened species, but useful progress may be achieved through careful comparison with better-known, related species and through application of theoretical principles to particular problems. In our case study, we drew upon (1) the large body of knowledge concerning reproduction in small rodents, especially the role of olfactory signaling, and (2) the theoretical principle of "honest signaling," in which costly traits might be used by females as a reliable (i.e., honest) indicator of quality (Zahavi 1975).

Olfaction is the dominant sensory modality in mammalian reproduction, and olfactory signaling can be seen as a handicap because it may be costly for males on several levels. First, signal production is energetically expensive (Gosling et al. 2000), especially where the scent secretion used contains constituents of large molecular weight (Alberts 1992; Gosling et al. 2000). Second, it requires time and energy to place signals in strategic positions where receivers are most likely to detect them (Gosling 1981; Roberts & Lowen 1997; Roberts & Gosling 2001). Third, signals may alert eavesdropping predators to the signaler (Gosling & Roberts 2001; Roberts et al. 2001).

Evidence for condition dependence in the expression of olfactory signals, especially in rodents, suggests that these costs are prohibitive for poor-quality males. Territorial

or dominant males signal at higher rates (Gosling et al. 2000; Gosling & Roberts 2001), and these rates measured in youngsters predict dominance in adulthood (Collins et al. 1997). As predicted, females choose between males using such olfactory cues. Scents differ between individuals (e.g., Johnston et al. 1993), and females prefer males whose patterns or frequencies of scent marking indicate that they are of high quality (Clark et al. 1992; Rich & Hurst 1999; Fisher et al. 2003). Experiments showing positive influences of odor familiarity on female preferences (e.g., Tang-Martinez et al. 1993; Swaisgood et al. 2000) may also fit within this theoretical framework, because it is likely that, under natural conditions, familiarity correlates with male quality: females may be most familiar with locally territorial or dominant males.

Against this theoretical and empirical background, we attempted to alter female preferences for males in two experiments. First, we used a longitudinal design to measure changes in preferences in relation to a desired and predicted direction. Second, we tested the effect of odor familiarity on both female preferences and the level of aggression between mates when they were paired.

Methods

Husbandry

We used harvest mice from the captive breeding program at Chester Zoological Gardens (United Kingdom). Seventeen pairs of mice were used in the two experiments, which were carried out in two batches (June-August 1999 and April-May 2000) because of the small number of animals available. Each mouse was isolated for 4 weeks before the experiments in a plastic tank ($37 \times 22 \times 23$ cm)

with a wire mesh lid and a substrate of approximately 8 cm of wooden shavings. Tanks were held at $21 \pm 2°$ C with a 12:12–hour cycle of light and dark. Observations and video recording were carried out in darkness with a dim red light. Mice were fed ad libidum with a diet of mixed seeds (black and white millet, sunflower seeds), and water was provided with a dropper suspended from the lid. A dried millet spray was suspended from the lid to provide additional food and enrichment.

Little is known about the scent-marking behavior of harvest mice, but Frank (1952) concluded that urine is used as a scent mark, and urine and feces usually accumulate in specific areas of the cage, often on aerial routes such as branches (Trout 1978; S.C.R., personal observation). To measure and collect scent marks, we constructed an artificial "branch," which was a 15-cm wooden rod (2 cm in diameter) suspended 10–15 cm above the substrate and sloped at an angle of 18°. The rods were removable for the transfer of scent marks between tanks. Rods were wrapped in clean filter paper (Benchkote, Merck UK, Lutterworth) to promote absorption and enable measurement of marking rates.

Prior to female preference tests, females were checked for estrus condition by vaginal smears. We used a tight hoop of 0.46-mm platinum wire (BDH Chemicals, Poole, United Kingom) smeared on a slide with a droplet of distilled water and stained in 0.04% methylene blue. We examined slides for the presence of cornified epithelial cells and absence of leucocytes, which characterize estrus.

Experimental Design

The design of two experiments that aimed to alter female preferences for selected males is summarized in Fig. 1.

1) Altering male signaling context
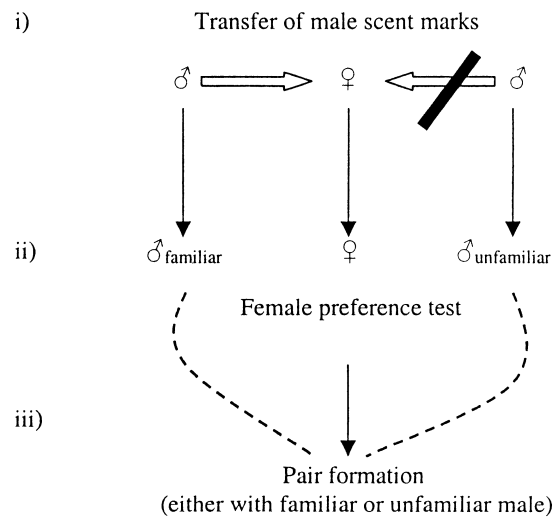
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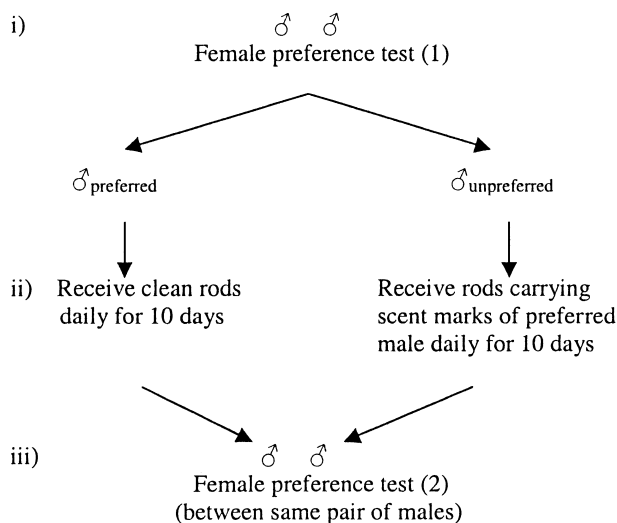
2) Altering male familiarity

i)

Figure 1. Design of two experiments aimed at manipulating preferences of female harvest mice for males.

First, we compared female preferences between pairs of males in two choice tests spaced 2 weeks apart. In each test, estrus females ($n = 16$) were introduced to the central chamber of the test arena, from which two plastic tubes, at opposite ends of the chamber, each led toward an additional chamber containing a male, constrained behind a perforated, transparent plastic cage divider. During the first 10 minutes of the test, entry into the male chambers was prevented by wire mesh barriers, so females were in olfactory contact with males but prevented from approaching and inspecting them at close range. The amount of time spent in the tubes leading toward each male was recorded. After 10 minutes, the barriers were removed and female movements between chambers were recorded over the following 30 minutes to obtain a further measure of female preference when females could both smell and see males.

At the end of the first test, the amount of time each female spent with each male was calculated. There was a high degree of agreement between females exposed to the same male pairs. Only one of eight pairs of females exposed to the same males preferred different individuals. For this reason, in this one pair we chose to (randomly) discard one female from the experiment so that males in the unpreferred group would be genuinely unpreferred in every case. Because of the small numbers of animals available, pairs of males were normally used twice (2 of 9 pairs were used once). To avoid pseudoreplication in our analyses, we averaged the times spent with each male across the two females.

Between the first and second choice tests, we manipulated the social context of the unpreferred males. We first replaced the rods in each cage with new rods coated in clean Benchkote paper. After 24 hours, the paper-covered rods from each of the preferred males were transferred to the tank of the unpreferred male of the pair and replaced with new rods covered in clean paper. Rods from unpreferred males were removed and discarded, thus controlling for disturbance effects between the two groups. We repeated this procedure for the following 7 days. At the end of this period of scent-mark manipulation, we carried out a second choice test in which females were presented with the same pair of males as before. Females were again checked for estrus condition before the test. We did this to ensure that females were likely to be searching for mates during the preference tests and because variation in the stage of the estrus cycle is known to alter female preferences for male traits (e.g., Schulte & Rasmussen 1999). Although this unavoidably introduced a slight variance in the interval between the two preference tests (range, 13–16 days) and between the last transfer of male scent and the second preference test (range, 1–4 days), our results are conservative with respect to this variance.

We also measured male scent-marking rates before each preference test. We placed rods, wrapped in clean paper, in male tanks for 24 hours on 3 consecutive days leading up to the beginning of the tests. The paper was then removed and sprayed with ninhydrin to stain the scent marks. We quantified percent cover of the marks with an overlaid transparent grid and calculated means for each male before and after the manipulation.

In the second experiment, we varied the degree of familiarity between females ($n = 16$) and potential mates. We randomly allocated males to females and established female familiarity with the odor of their allocated males by daily transferral of male scent marks to female tanks over 10 days. Scent marks were collected by placing rods in male tanks for 24 hours, as in the first experiment. After 10 days, we carried out a female preference test, following the same procedure as before, between the male whose odor was familiar and another male whose odor was unfamiliar. The scent marks of this unfamiliar male had been collected and transferred to another female during the period prior to the test, thus standardizing the males' experience prior to the experiment. Males were each used in two separate preference tests, as a familiar and an unfamiliar male.

Three days after the preference tests, females were paired with either the familiar or the unfamiliar male (eight familiar and seven unfamiliar pairings; one female died between the preference test and pairing). Females were placed in a clean tank immediately before pairing to ensure that neither individual's odor was present when pairs were established. The male was introduced and interactions were video recorded for the following 40 minutes. The number and initiator of aggressive interactions were noted. Measures of the level of investigation were also recorded, including the number of approaches by each sex to within one body length of the other (and number of departures beyond one body length) and the frequency of nose-nose sniffs (by one-zero sampling [Martin & Bateson 1986] for each minute). Data on the number of approaches and departures were used to calculate an index (Hinde & Atkinson 1970) that evaluates responsibility for maintaining proximity within pairs, calculated as

$$\text{index} = A_M/(A_M + A_F) - D_M/(D_M + D_F),$$

where A is the number of approaches, D is the number of departures, and M and F are male and female, respectively. Mating and courtship behavior would have been recorded, but none was observed. We intended to record variations in reproductive success resulting from these matings, but unfortunately no litters were born in the second batch of pairings. We do not know the reason for this, but it may have been a seasonal effect. Sample sizes from the first batch of pairings were too small for statistical analysis, so we do not present these data.

Analyses

We used nonparametric tests throughout. Wilcoxon signed-ranks tests and sign tests were used to compare

within-female variations in preference for male pairs and scent-marking rates of paired males. We used Spearman's rank correlations to compare variation in male scent-marking rates and Mann-Whitney *U* tests to compare behavior in familiar and unfamiliar pairs. Analyses were carried out with SPSS (version 9, SPSS Inc., Chicago), and all tests were nondirectional.

Ethical Note

Intersexual aggression, particularly by females toward males, is common in harvest mice (Trout 1978; P. Rudd, personal communication). Our familiarity experiment was designed to test whether simple manipulation of male signals could potentially be used to minimize such aggression. We therefore expected a certain amount of aggression, at least with unfamiliar males. However, we reasoned that introducing pairs in a clean tank, rather than the female's home tank, would help reduce this aggression, and we provided opportunities for escape (the wooden frame and rod, millet spray, and a plastic tube). Interactions were observed during video recording, and pairs would have been separated if sustained fighting and serious injuries occurred, but this did not happen.

Results

Manipulation of Male Social Context

Our manipulation of males' social context, by introducing a competitor's odor into the enclosure of initially unpreferred males, resulted in a significant alteration in the degree of preference expressed by females within pairs of males. Females spent more time with initially unpreferred males in the second trial (after manipulation) than they had in the first (Fig. 2). This was true both when preferences were based on odor alone ($T = 2, p < 0.05, n = 8$, because females choosing between one male pair did not leave the central chamber during the first 10 minutes) and, especially, when females could see and smell the males ($T = 1, n = 9, p < 0.01$). In total, time spent with initially unpreferred males increased after manipulation in every male pair, suggesting the manipulation had a significant effect on the relative attractiveness of the males (sign test: $p = 0.004$). However, the manipulation did not completely reverse female preferences (preferences were reversed in 2 of 9 male pairs): initially unpreferred males were, on average, still unpreferred.

Two alternative explanations are possible for the increase in time spent with initially unpreferred males. First, these changes could have been due to a change in female behavior between tests (specifically, switching time near males with time in the central chamber). This was not important, however, because the amount of time spent in the central chamber did not differ between the two pref-
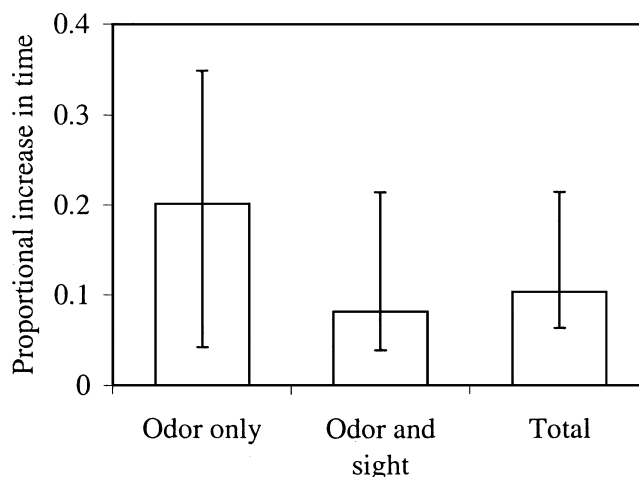

Figure 2. Increase in the proportion of time female harvest mice spent with initially unpreferred males following manipulation of the males' social context, in the initial 10-minute period (when females could only smell the males), the following 30 minutes (when they could see and smell them), and the total increase. Data are medians ± quartiles.

erence tests (odor: medians 346 and 411 seconds, $T = 21$, not significant; odor and vision: medians 491.5 and 471.5 seconds, $T = 15$, not significant). A second possibility is that females choose randomly among male pairs in both tests. This could lead to an increase in time spent with initially unpreferred males in the second test, independent of any experimental manipulation. However, the proportion of time spent with unpreferred males by each female was positively correlated across the two tests ($r_s = 0.526, n = 16, p = 0.036$), indicating that females did not choose randomly in these tests.

Although we expected preferred males to scent-mark at higher intensities than unpreferred males, the two groups did not differ significantly before the manipulation of the males' social context (Fig. 3; $T = 20, n = 9$, not significant). After the manipulation, however, the scent-marking rates of initially unpreferred males increased ($T = 1, p < 0.01$) and were now higher than those of initially preferred males ($T = 0, p < 0.01$). This increase was not due simply to change over time because there was no change in marking rates of preferred males over the same time period ($T = 10.5$, not significant). Indeed, individual marking rates before and after manipulation were positively correlated ($r_s = 0.700, n = 9, p = 0.036$) in preferred males but not in unpreferred males ($r_s = -0.410, n = 9$, not significant).

Manipulation of Familiarity

As predicted, the degree of familiarity between females and the scent of potential mates influenced the likely success of pairing. In a single two-way preference test,
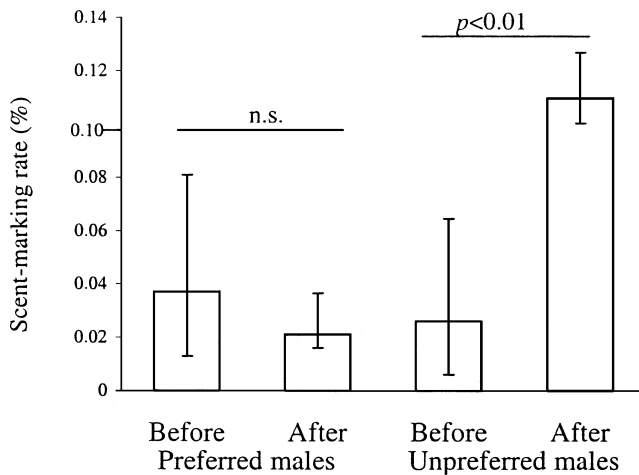
Figure 3. Scent-marking rates of harvest mouse males before and after manipulation of the males' social context. Data are medians ± quartiles (Wilcoxon signed-ranks tests; n.s., not significant).

females spent more time, when they could only smell males, with the male whose odor was familiar (Fig. 4; $T = 11$, $n = 14$, $p < 0.01$), although there was no difference when females could both smell and see males (Fig. 4; $T = 53$, $n = 16$).

Familiarity also had an effect on levels of aggression between mates when they were first introduced to each other. Females paired with males with familiar odor initiated fewer bouts of aggression (including fights, isolated bites, or aggressive lunges) and bit males less often than females paired with males whose odor was unfamiliar (Table 1). Although males were equally unfamiliar with
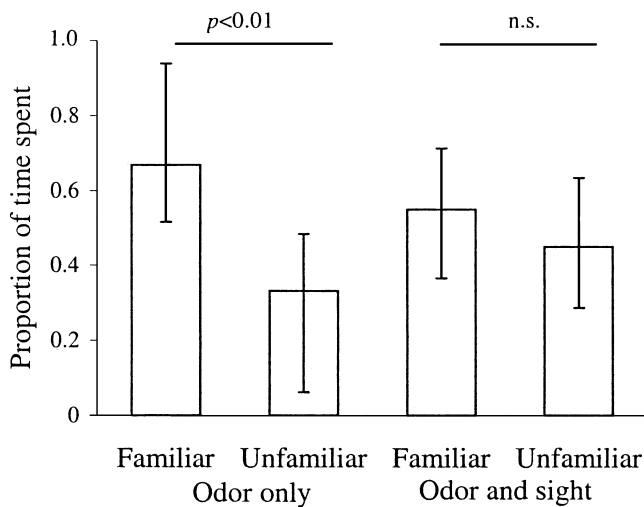

Figure 4. Median (±quartiles) proportion of time spent by female harvest mice in two-way choice tests with males whose odor was familiar or unfamiliar(Wilcoxon signed-ranks tests; n.s., not significant).

females, they initiated more aggressive bouts toward females when females had not been exposed to their scent marks before pairing. Odor familiarity had no effect on the amount of investigation by either sex, measured either by the number of approaches to each other or, more directly, by the frequency of close-proximity sniffing. There were no overall differences in the number of approaches or withdrawals by either sex or in the number of sniffs or bites, but females initiated more bouts of aggression than males did (females: mean ± SE, $3.13 ± 0.93$; males: $1.13 ± 0.38$; Wilcoxon signed-ranks test, $T = 6$, $n = 15$, $p < 0.01$).

Discussion

Mate Choice Manipulation in Harvest Mice

Our study demonstrates the potential for subtle alteration of mate preferences, through purely behavioral means, in species that are difficult to breed in captivity. With individual differences in preference (females) and behavior (males) controlled for by our longitudinal experimental design, the results from our first experiment showed that manipulation of sexual signaling characteristics of relatively unattractive males may increase their allure. In addition, manipulation of the degree of familiarity influenced time spent with males in choice tests and reduced the amount of aggression between mates when they were paired.

Introduction of the scent marks of a competitor into the home enclosure of initially unpreferred males caused these males to increase their investment in scent marking. Because scent marking in mammals typically plays a key role in intrasexual competition and in the economics of territory defense (Gosling 1981, 1982, 1990; Gosling & Roberts 2001) and because our manipulation simulates a territorial intrusion by a competitor, such a response is consistent with the need to reassert the male's territorial claims. This effect is not unique to the harvest mouse. Similar effects have been found in marking rates of laboratory mice (*Mus musculus*, L.M.G., unpublished data), other rodents (e.g., Zuri et al. 1997), ungulates (Roberts 1998), and carnivores (Sliwa & Richardson 1998). The strength of the response—nearly a four-fold increase—was remarkable, however, and resulted in initially unpreferred males having significantly higher marking rates than preferred males. Because marking rates of the preferred males did not change, it seems most likely that this increase was caused by our manipulation rather than simply temporal variation or a response to brief exposure to the female (although it remains possible that preferred and unpreferred males might react differently).

Previous empirical work (Johnston et al. 1997; Rich & Hurst 1999; Fisher et al. 2003) indicates that females prefer males who scent mark or countermark at high levels.

Table 1. Effect of familiarity between harvest mouse females and mates on olfactory investigation and levels of aggression after pairing.[a]

Behavior	Familiar	Unfamiliar	Mann-Whitney U	p
Approaches by male	16.8 ± 5.2	11.5 ± 1.7	21.5	0.460
Approaches by female	1.8 ± 0.8	11.8 ± 5.4	19	0.336
Hinde-Atkinson index of proximity[b]	0.15 ± 0.17	0.02 ± 0.10	18.5	0.456
Sniffs by female	2.5 ± 1.1	2.0 ± 1.7	20.5	0.397
Sniffs by male	5.9 ± 2.1	2.7 ± 1.2	19.5	0.336
Mutual sniffs	14.5 ± 4.2	16.0 ± 2.0	16	0.189
Aggressive attacks by male	1.0 ± 1.0	1.8 ± 0.5	10.5	0.040
Aggressive attacks by female	0.5 ± 0.3	7.8 ± 1.5	8.5	0.021
Bites by male	1.3 ± 1.3	0.8 ± 0.3	12	0.072
Bites by female	0.5 ± 0.5	8.5 ± 4.2	10.5	0.040

[a]*Data are from eight familiar and seven unfamiliar pairs (means ± SE), video recorded for 40 minutes after pairing.*
[b]*Hinde-Atkinson index described in Methods.*

In our experiment, however, initial scent-marking rates did not predict female preference in the first choice test. One possible explanation is that isolation prior to the test reduced the incentive to scent-mark, so that initial levels failed to distinguish males of different quality (isolation has this effect in laboratory mice; L.M.G., unpublished data). Thus, although we cannot yet attribute changes in preferences of female harvest mice to changes in marking rates, it remains a strong possibility.

In common with previous studies (Tang-Martinez et al. 1993; Swaisgood et al. 2000), we found that the familiarity of females with the odor of potential mates influenced the amount of time females spent with males and their behavior toward them. Adaptive explanations for the effect of familiarity are not always clear in the absence of paternal care but seem most likely to arise from the interaction between female and male movements under natural conditions. In species whose males are territorial, as harvest mice apparently are (Trout 1978), females will regularly encounter scent marks of locally territorial males. Because scent marking provides a comprehensive and reliable indicator of a male's ability to defend a territory (Gosling 1982, 1990), females might use this information to judge mate quality (whether scent marks are a direct signal to females or an intrasexual signal eavesdropped by females; Gosling & Roberts 2001). Hence, familiarity may, for females, be a proximate cue to male quality. Other effects of familiarity may include reducing stress associated with unfamiliar odors and priming females so that they are more receptive to familiar males (Brown 1985).

Familiarity had an effect on female behavior only in the initial phase of the choice tests. The absence of an expressed preference in the second phase, when females could both smell and see males, suggests that familiarity had a relatively weak influence and that visual characteristics perhaps played a more important role. Despite this, when pairs were formed, females were significantly less aggressive toward males with familiar odor than toward males with unfamiliar odor. Females were also the target of more aggression if they were paired with males whose odor was unfamiliar, although this was probably due prin-

cipally to male self-defense or retaliation, because males were equally unfamiliar with their mate and females were generally more aggressive than males.

Although our results indicate that female harvest mice are more likely to mate with familiar males (as in other species), this is not a universal finding. For example, unfamiliar males are preferred in eusocial naked mole-rats (*Heterocephalus glaber*), which are highly inbred (Clarke & Faulkes 1999). Care needs to be taken in generalizing results across species.

Applicability of the Approach

A common criticism of behavioral research in zoos is that much of it is descriptive or anecdotal, rather than based on a hypothesis-testing approach (Berger 1990; Kleiman 1994; Wielebnowski 1998). One of the main obstacles to such an approach is the small sample sizes with which most studies have to contend. Even if considerable effort is expended to include subjects from a number of disparate collections, the lack of control over (for example) environmental variables, enclosure sizes, husbandry regimes, and social experience makes the process difficult to standardize. Furthermore, the ethical issues involved with such studies of threatened species are considerable and often prohibitive. One solution to these obstacles is to make use of commonly available, easily managed species as models on which to test ideas and develop principles that can later be tailored to specific conservation problems. In this study, for example, we used the wealth of knowledge on olfactory signaling and mate choice in small rodents (notably laboratory mice) and general theoretical principles from behavioral ecology to help plan and inform our experiments. Our choice of harvest mice was a deliberate one that allowed us to develop the ideas arising from studies of different but closely related species.

Grahn et al. (1998) and Wedekind (2002) argue convincingly that incorporating the possibility for mate choice within the design of conservation breeding programs may substantially improve the viability of captive

animal populations. Active mate choice, as opposed to mate allocation by managers, may select out deleterious alleles and promote beneficial ones. For example, it may result in elevated resistance to pathogens through selection at the major histocompatibility complex, or MHC (Brown & Eklund 1994; Penn & Potts 1999). For such reasons, manipulating mate choice to maximize heterozygosity may not always be desirable, whether it be through biotechnological or behavioral means. The appropriateness of such methods should thus be carefully assessed before they are implemented. Nonetheless, apparent incompatibility does not necessarily imply genetic unsuitability, or poor quality, of potential mates and may rather be due to disruption of natural behavior by (sometimes unavoidable) captive conditions. Our approach is valid in such cases and in those where the number of suitable mates is limited or the population is small enough that outbreeding becomes an urgent priority (see also Wedekind 2002).

How useful might this kind of approach be for improving success in conservation breeding? We believe the advantages are numerous and diverse. Practicality is the key to achieving widespread adoption of such approaches, and the ideas we present are noninvasive and cheap and can be carried out by trained zoo personnel. Scent marks appear to be ideal in this respect because they are usually visible and long-lasting and can be collected, stored (usually frozen), and moved. As our experiments demonstrate, these properties create a powerful tool for manipulating the social environment of animals in captivity (principally mammals, but also amphibians, reptiles, and some invertebrates), with implications for behavioral enrichment, captive breeding, and preparation for reintroduction. Scent marks switched between cages might be routinely used to establish familiarity with potential mates, for example, or to simulate a complex network of territorial neighbors. Recent work on the effect of odor on mate compatibility in pandas (*Ailuropoda melanoleuca*; Swaisgood et al. 2000) advocates switching animals between cages so they are exposed to "the complex gestalt of odors" produced by others. This is probably preferable where practical constraints permit, but the advantage of collecting and moving scent marks is that social-context manipulations can be achieved with minimal disruption and irrespective of the actual proximity of the cages. Delivery of such "scent postcards" can be easily achieved between collections, even on an international basis and over considerable lead-in periods, for the price of a postage stamp.

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