

COMMENTARY

Experimental tests of mate choice in nonhuman mammals: the need for an integrative approach

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Summary

Experimental studies of mate choice have normally focused on non-mammal animal species, in which female mating preferences are based on clearly defined male traits. Because mammals are invariably larger and behaviourally more complex, they are less suited to this type of experimentation. Nevertheless, numerous studies on nonhuman mammals have shown that females appear to actively choose their mates. In this Commentary, I review the current literature to reveal that most experimental tests of mate choice in mammals are unable to reveal the actual male phenotypic trait(s) of female preference, which is crucial for identifying male characteristics under sexual selection. In addition, very few studies take into account female oestrous stage, or quantify the fitness benefits to discriminating females. Future work should concentrate on demonstrating female preferences for specific male traits that are shown by genetic paternity analysis to be correlated with male reproductive success, using setups that control for the effects of male and female mating strategies and in which the actual experiments are performed during the female's peak oestrous period.

Key words: mammals, mate choice, sexual selection.

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Introduction

Females are predicted to choose particular categories of males in mate-choice contexts either because these preferences result in direct fitness benefits to the females themselves, indirect fitness benefits that increase offspring viability, i.e. 'good genes' (Neff and Pitcher, 2005), or because pre-existing sensory biases make male display characteristics more conspicuous and attractive to females (Ryan, 1998). However, demonstrating female mating preferences, particularly in natural conditions, can be problematic. For example, in territorial species it is difficult to be certain whether females are attracted to individual males or the territory they currently occupy. A further complication is that free-ranging females may copy the preferences of other individuals, or even be attracted to each other in order to reduce predation risk or harassment (Clutton-Brock and McComb, 1993). In addition, female mating strategies may fulfil non-procreative roles, such as the need to confuse paternity in mammals where infanticide is common (Wolff and Macdonald, 2004), and male strategies may force females to mate with certain individuals whatever their preference criteria (Muller et al., 2011). Hence, in order to determine female mating preferences it is imperative to use appropriate experimental setups that control for male–male competition and other female mating strategies.

Experimental studies of female mating preferences

Some studies on small mammals report direct female mate choice for dominant males whilst controlling for male competition using either laboratory [house mice, *Mus musculus* (Rolland et al., 2003)] or field experiments [golden hamsters, *Mesocricetus auratus* (Lisk et al., 1989); brown lemmings, *Lemmus trimucronatus* (Huck and Banks, 1982); voles, *Microtus ochrogaster* and *Microtus montanus* (Shapiro and Dewsbury, 1986); bank voles, *Clethrionomys*

glareolus (Horne and Ylonen, 1996); and brown capuchins, *Cebus apella* (Janson, 1984)]. However, in all these cases, the exact male phenotypic trait(s) of female preference are not known. A recent experiment on domestic goats (*Capra hircus*) allowed females to choose between separately caged males, thus controlling for male–male competition (Longpre and Katz, 2011). The authors report a consistent spatial preference in oestrous females for males with higher testosterone levels. In this case, males did not actively interfere with the mating attempts of other individuals and, therefore, females may have been able to exercise relatively free choice. However, it is not known how females discriminate between males, or whether these preferences translate to increased reproductive success, i.e. whether mating with high-testosterone males actually enhances fertilisation success or increases offspring viability.

Another recent laboratory-based study on prairie voles (*M. ochrogaster*) shows that females prefer males with longer *avpr1* microsatellite alleles that provide more paternal care relative to males with shorter *avpr1a* microsatellite alleles (Castelli et al., 2011). Although these findings suggest that females use phenotypic cues whose expression is correlated with a male's *avpr1a* microsatellite genotype to discriminate among potential mates, the actual phenotypic trait of preference is again not known. Female preferences for heavier and more frequently courting males are also reported in the wild guinea pig (*Galea musteloides*) (Hohoff et al., 2003). Nonetheless, evidence that this female preference results in more viable offspring is lacking. In fact, the only demonstration of increased offspring viability due to free female mate choice in mammals (and hence, empirical evidence of female mate choice for 'good genes') appears to be on house mice (Drickamer et al., 2000). In this study, females that were allowed to choose their mates

produced more viable offspring than those mated at random; however, the actual male phenotypic trait(s) of female preference are again not known.

Indeed, revealing the morphological and/or behavioural traits that females base mating preferences on is fundamental for identifying male characteristics under sexual selection. In addition, female preferences in many mammals may only emerge at peak conception times. For example, female harvest mice (*Micromys minutus*) only prefer familiar males over unfamiliar ones when they are in oestrus, spending more time in close proximity to unfamiliar males outside of this time (Brandt and Macdonald, 2011). Female mating preferences in African striped mice (*Rhabdomys pumilio*) are also only apparent during peak oestrus (Pillay, 2000). Thus, appropriate experimental setups are required that control for all other extrinsic (e.g. the social environment) and intrinsic (e.g. hormonal) factors that affect female behaviour. In addition, it is necessary to quantify female responses to specific phenotypic traits that are varied in other aspects of the male phenotype. Only this approach will allow us to adequately reveal how inter-sexual selection is generated on specific aspects of the male phenotype.

Female preferences for male phenotypic traits

Empirical evidence that female mammals prefer males with certain morphological and/or behavioural characteristics comes from experimental setups that are able to isolate specific male traits from other aspects of the male phenotype. Conclusively inferring that behavioural responses to an isolated trait variant are indicative of a mate choice decision, however, can be difficult.

Olfactory displays

Some of the best evidence for mate choice in mammals has been generated using olfactory cues, which are relatively simple to isolate and present to females in controlled conditions (Beauchamp and Yamazaki, 2003). For example, female rodents appear able to discriminate between parasitized and non-parasitized males based on urine odours (e.g. Willis and Poulin, 2000) and show marked preferences for the odours of non-parasitized males (e.g. Kavaliers et al., 2003), possibly to secure resistance genes for their offspring. Preferences for the anogenital odours of older males are also reported in rodents (e.g. Ferkin, 1999) whereas senesced (aged) male mice (*M. musculus*) produce urine odours that are less attractive to females than those produced by younger adult males (Garratt et al., 2011). Whether these female preferences translate to mate choice decisions and increased reproductive success in natural conditions remains to be tested. Female odour preferences for resident males are also reported in rabbits (*Oryctolagus cuniculus*) (Reece-Engel, 1988) and for sexually experienced males in African striped mice (Pillay and Rymer, 2010); however, the adaptive significance of these preferences is again not known.

It has also been suggested that scent frequency and placement may play a role in active mate choice for dominant individuals that mark over subordinates (e.g. Fisher et al., 2003). Another study on meadow voles (*Microtus pennsylvanicus*) reports female preferences for familiar over novel males even when their scents have been over-marked by novel males (Johnston et al., 1997), although the ability of females to discriminate between novel and familiar male scent markings placed on top of each other could be disputed. Indeed, other studies on prairie voles suggest that scent quality may be more important than scent frequency and placement for mate attraction (e.g. Mech et al., 2003). Further work on house mice indicates that both scent quality and placement have a role in mate choice, and that their relative influence depends on the

variability in each trait among available males (Roberts and Gosling, 2003).

Female odour preferences for genetically dissimilar/heterozygous males (e.g. Ilmonen et al., 2009), males of intermediate genetic similarity (e.g. Keane, 1990) and even genetically similar males (e.g. Pillay, 2000) are also reported in mammals, although the semiochemical link to genetic variation remains obscure. This type of mate choice for compatible genes based on olfactory cues may have evolved to avoid the reproductive costs associated with inbreeding and distant outbreeding; however, inbreeding avoidance would appear to offer the highest potential fitness benefits to females. The genes of the major histocompatibility complex (MHC) are thought to function as cues to heterozygosity for mate choice, and convincing evidence for MHC-dependent mating preferences mediated through specific odour cues has been generated by work on captive mice (Beauchamp and Yamazaki, 2003) and bank voles (Radwan et al., 2008).

However, a recent study on wild-derived house mice (*Mus musculus domesticus*) showed that females did not display an odour preference for MHC heterozygotes, but instead appear to use major urinary proteins to assess male heterozygosity (Thom et al., 2008). In addition, work on tuco tuco (*Ctenomys talarum*) (Cutrera et al., 2012) found no support for the hypothesis that MHC-associated mate choice is associated with inbreeding avoidance, further demonstrating the need to test these predictions. MHC-disassortative mating preferences also appear to exist in nonhuman primates (Setchell and Huchard, 2010), but the actual mechanism of mate choice (i.e. how females discriminate between males) is not entirely clear. Indeed, while there is much evidence that MHC-dependent mating preferences exist in house mice (Beauchamp and Yamazaki, 2003), more research is required to determine their generality to other mammal species.

Vocal displays

Numerous mammal studies have suggested that male calls function directly to advertise male quality and attract females without testing experimentally whether this is the case (e.g. Bradbury, 1977; Craul et al., 2004). Indeed, it is crucial to test predictions about mate choice based on vocal signals using systematic playback experiments. For example, although the structurally complex songs of lone humpback whales (*Megaptera novaeangliae*) and the long calls of male orangutans (*Pongo pygmaeus*) were both thought to function in mate attraction (Tyack, 1983; Mitani, 1985), playback experiments designed to test these predictions reported no female attraction to male vocal signals.

A recent playback study on house mice showed that females approach male ultrasonic vocalizations (Hammerschmidt et al., 2009); however, because female responses did not vary according to oestrous stage, it is difficult to interpret these results as reflecting a true mating preference. In addition, whether these ultrasonic calls signal any aspect of the male phenotype of potential importance in female mate choice contexts is unknown. Further playback work on neotropical singing mice (*Scotinomys teguina*) revealed a female preference for experimentally manipulated male trill vocalisations representing callers with high androgen levels (Pasch et al., 2011). Whereas this provides preliminary evidence in this species' that male vocal signals may be used in female mate choice contexts, the study did not exclusively target oestrous females or identify the specific acoustic features of male calls that females base their preferences on.

Indeed, although female mate choice is very likely to be a significant selection force on the vocal signals of many male mammals, currently, the only mammal studies that systematically demonstrate a female preference for a vocal characteristic have been carried out on red deer (*Cervus elaphus*) (McComb, 1991; Charlton et al., 2007; Reby et al., 2010). Playback experiments of resynthesized vocal stimuli conducted during the breeding season have shown that female red deer are more likely to look at and approach speakers playing male roars delivered at higher rates (McComb, 1991). More recent work on oestrous female red deer demonstrated a preference for male roars with lower formant frequencies, simulating larger callers (Charlton et al., 2007), a trait positively correlated to male reproductive success in this species (Reby and McComb, 2003). To date, this study remains the only definite example of a mating preference for a vocal trait signalling 'good genes' (larger body size) in mammals, i.e. whilst controlling for female oestrous stage and male-male competition. Oestrous female red deer also prefer higher pitched male roars (Reby et al., 2010), although the adaptive significance of this preference is unclear. However, since previous studies on female red deer failed to reveal a differential response to playbacks of different male pitch variants (McComb, 1991; Charlton et al., 2008), these findings do further emphasize that experimental investigation of female choice in mammals should be conducted during the female's peak conception times.

Visual displays

Nonhuman primates often have brilliant secondary sexual colouration that may serve to advertise the bearer's quality to potential mates. Examples include the brightly coloured faces of male mandrills (*Mandrillus sphinx*) (Setchell and Dixon, 2001) and scrotal colour in vervets (*Cercopithecus aethiops*) (Gerald, 2001). It is not known though whether female mandrills or vervet monkeys attend to these colour differences. Rhesus macaque females (*Macaca mulatta*) gaze for longer at computer-manipulated red male faces than pale versions of male faces (Waite et al., 2003), indicating that male colouration might provide a cue to male quality in sexual contexts. Determining whether these visual preferences indicate sexual preferences, rather than constituting a more general response, requires further research. In African lions (*Panthera leo*), males with dark manes have higher testosterone levels and are more competitive than individuals with light manes, and experiments have shown that female lions preferentially approach life-size models of males with darker manes (West and Packer, 2002). Thus, females that prefer to mate with darker-maned males could gain the indirect genetic benefits of superior survival and competitive abilities for their offspring, and possibly secure greater protection from infanticide for their cubs. It appears likely then that female mammals use male colouration in mate-choice contexts. Nevertheless, controlled mate-choice experiments still need to be conducted on oestrous female mammals to conclusively determine whether male visual displays play a role in adaptive female mate choice.

Future perspectives

Female mate choice in mammals is a challenging research area and there are still many questions to be answered. Experimental studies often rely on indirect methods to determine mating preferences such as increased attention towards an isolated male trait, which does not necessarily indicate attraction. It is also worth noting that females are likely to use a combination of cues across sensory modalities to assess mating partners in natural conditions. In

addition, many observational studies only record mating success as individuals gaining copulations or proximity to members of the opposite sex, and do not necessarily record the reproductive success of individuals with preferred characteristics using genetic paternity analyses, which is essential to determine any reproductive benefits to choice. Studies of female choice in mammals, in which female preferences may only emerge during the period of peak conception, also emphasize the importance of considering the timing of female ovulation (Pillay, 2000; Brandt and Macdonald, 2011).

Hence, future work should concentrate on demonstrating female preferences for specific male traits that are shown by genetic paternity analysis to be correlated with male reproductive success, using setups that control for the effects of male and female mating strategies and in which the actual experiments are performed during the female's peak oestrous period (*sensu* Charlton et al., 2007). In particular, I suggest that experimental examination of female preferences is carried out in conjunction with long-term studies that examine whether preferences for specific male characteristics actually result in direct fitness benefits to females (i.e. impact on female survival or fecundity) or yield indirect fitness benefits *via* increased offspring viability and/or attractiveness. Although this type of multidisciplinary research approach can be difficult to implement, involving biologists from different fields of expertise, it is crucial to interpret any female mating preferences in light of their potential adaptive significance.

It is also important to consider that variation in mating preferences among females can arise due to genetic differences and environmental influences (Jennions and Petrie, 1997), and this can affect the intensity of selection on male traits. Furthermore, studies that focus on the variability of individual responses, as well as the overall female response, would shed light on how heritable variation in female preferences is maintained, and provide information on the magnitude of any potential indirect fitness benefits associated with mate choice. In addition, population-level choice tests in which females are tested only once with a set of stimuli do not evaluate within-female variation in preference. Accordingly, I suggest that future studies test females multiple times to build up preference functions for individuals. This would allow researchers to examine how consistent mating preferences are both within and across females and, in doing so, help us to better understand the evolutionary history of female mating preferences and preferred traits

Concluding remarks

In conclusion, female mate choice in nonhuman mammals is a complex research area that requires controlled experiments to reveal female preferences that often only become apparent during oestrus. Technological advances in digital sound production now allow researchers to manipulate vocal characteristics so that vocal signals can be modified to represent different male phenotypes (Charlton et al., 2007). These re-synthesized calls can then be presented to females in mate choice experiments. Other technological advances now allow digital images to be realistically modified to test for visual preferences (Waite et al., 2003). In addition, once the chemical correlates of male traits have been isolated, olfactory signals could also theoretically be synthesized and manipulated to simulate different male trait variants. This experimental work should be combined with genetic paternity analyses on free-ranging animals to determine the reproductive success of individuals with preferred characteristics. An integrative approach such as this promises to advance our knowledge of female mate choice in nonhuman mammals, and will shed light on how

inter-sexual selection pressures lead to the evolution of specific male traits.

Glossary

Disassortative mating

A non-random mating pattern where individuals with dissimilar genotypes and/or phenotypes mate with one another more frequently than would be expected by chance.

Fitness

The ability to both survive and reproduce, measured as the number of offspring produced by an individual that survive to reproductive age.

Semiochemical

A chemical substance emitted by a plant or animal that evokes a behavioural or physiological response in another organism.

Sexual selection theory

The theory of sexual selection was first proposed by Charles Darwin, and posits that certain morphological and behavioural characteristics evolve because they enhance an individual's ability to acquire mates. Broadly speaking there are two processes: intra-sexual selection, favouring traits that give an advantage to individuals when competing with members of the same sex, and inter-sexual selection, favouring the evolution of characteristics attractive to the opposite sex.

Trait/phenotypic traits

The observable expression of an organism's underlying genes. Traits can be physical or behavioural characteristics of individuals, whereas phenotypic traits are purely physical characteristics.

Two-way mate choice experiment

A mate choice experiment that provides females with a choice between two trait variants, e.g. a large *versus* a small male.

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