

The Effect of Familiarity on Mate Choice

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Abstract The ability to recognize familiar conspecifics appears to be widespread among vertebrates and influences a variety of behavioural interactions including mate selection. Female choice of males has been shown to vary according to male familiarity, but interestingly in some species this favours familiar males, while in others unfamiliar males are preferred. Preference for unfamiliar partners might result from the attempt to minimise inbreeding costs by avoiding mating with individuals encountered during development, or with those sharing relatedness cues. Conspecifics that are familiar through prior mating experience might be avoided in species that benefit from a promiscuous mating system, again resulting in preference for unfamiliar mates. Conversely, familiar mates may be favoured in monogamous species where formation of a pair bond is important for parental investment, and when familiarity provides an opportunity for females to assess the quality and compatibility of potential mates. Thus different types of familiarity may have differing effects on mate choice, with the direction of preference being determined by other aspects of life history, such as the likelihood of inbreeding, the importance of polyandry, and the role of social dominance and territoriality in reproductive success.

1 Introduction

The ability to recognize familiar conspecifics has been found in many vertebrate species, and this capacity to remember previously-encountered individuals is likely to modify subsequent behavioural interactions. For example, familiarity has long been thought to play an important role in mediating competitive behaviour, allowing animals to learn about the abilities of their competitors and to establish recognised territory borders so that direct conflicts can be reduced (Gosling 1990). Animals may also gain advantages from prior familiarity with individuals when selecting mates. There is some evidence that females can recognize familiar males using

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01 a variety of signals, including those in the acoustic (ungulates: Reby, Hewison,
02 Izquierdo and Pepin 2001), visual (fish: Zajitschek, Evans and Brooks 2006) and
03 olfactory (rodents: Hurst 1990) modalities. Females sometimes use the ability to dis-
04 criminate familiar from unfamiliar males to adjust their mating preferences. Intrigu-
05 ingly, however, the direction of this effect is not consistent: while some authors have
06 found that females are more likely to mate with familiar males (e.g. Fisher, Swais-
07 good and Fitch-Snyder 2003), others report female preference for unfamiliar males
08 (e.g. Kelley, Graves and Magurran 1999). Here we consider the ways in which famil-
09 iarity might affect mate choice, and how this might be influenced by social context.

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13 ***1.1 What is Familiarity, and How is it Recognized?***

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15 Familiarisation through direct association is perhaps the most obvious means by
16 which animals can discriminate familiar from unfamiliar conspecifics (Porter 1988).
17 This describes the process whereby familiarity is established through direct associ-
18 ation with an animal or its odours, mediated by the formation of a memory trace or
19 template of the animal (Tang-Martinez 2001) which can subsequently be matched
20 to the current phenotype of the familiar individual. Template formation can be facil-
21 itated through imprinting, habituation and associative learning (Mateo 2004), with
22 learning at different stages of life potentially leading to divergent outcomes.

23 The process of becoming familiar with an individual can occur either through
24 short-term or long-term contact, and both can influence mate choice. Long-term
25 social contact can occur through early social experience, e.g. between those sharing
26 the same nest, and appears to affect adult sexual preferences (discussed below).
27 Short term familiarity can occur during mate assessment, or when an individual's
28 scent is encountered in the environment and provides information about the owner
29 before animals meet. To recognise and discriminate between individuals on the
30 basis of their odours requires, at minimum, the ability to determine whether a new
31 odour matches (familiarity) or does not match (novelty) a previously encountered
32 odour. Such recognition by association involves the animal learning individually
33 distinctive cues to be able to recognise specific individuals. The term "familiarity"
34 is therefore sometimes used to describe individual recognition, but it is important to
35 recognize that discrimination of familiarity is insufficient evidence for the ability to
36 identify individuals. Animals may respond to familiarity without having the ability
37 to identify the individual scent owner from a range of familiar conspecifics. When
38 animals first meet an unfamiliar scent, they usually spend some time investigating
39 and extracting information from the novel odour, but then reduce investigation on
40 future encounters because most of the information contained in the cue has already
41 been obtained. This reliable response to novelty and familiarity is the basis of the
42 widely-used habituation—dishabituation test (Gregg and Thiessen 1981). More pro-
43 longed investigation when animals encounter a new scent indicates that animals
44 have recognised some novelty in the new scent that requires further investigation,
45 i.e. they can discriminate a difference between a familiar and unfamiliar scent

01 (or animals), but this tells us nothing about the information, if any, gained on investigat-
02 ating the source. The novel scent could be from a previously familiar individual
03 whose scent has changed (e.g. due to a change of status) or has been forgotten, or
04 from an unfamiliar individual. To understand whether animals recognise individuals
05 or other information from familiar scents requires a test of their subsequent response
06 indicating that they have gained specific information from investigating the scent
07 (Thom and Hurst 2004).

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11 **2 Avoidance of Familiar Individuals as Mates**

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13 In many vertebrate species, familiarity effects on adult sexual preferences begin
14 early in life. During development, offspring may imprint on the odours of their
15 parents and siblings and use this information as adults when choosing a mating
16 partner. While immature animals may prefer the odours of their opposite sex sib-
17 lings (Kruczek 2007), in many species the adults of both sexes tend to reject close
18 kin as mates to avoid the substantial fitness costs associated with inbreeding (Thom,
19 Stockley, Beynon and Hurst this volume). This behaviour is frequently modulated
20 through odour cues. For example, female bank voles prefer the novel odour of unre-
21 lated over related males (Kruczek and Golas 2003), regardless of whether they were
22 reared in the presence of the related subject (Kruczek 2007); mature pine voles
23 of both sexes are more attracted to the chemical cues of unrelated opposite-sex
24 conspecifics (Solomon and Rumbaugh 1997) and when given a choice between a
25 sibling and non-sibling male, female prairie voles choose the non-sibling's odour
26 (Smale, Pedersen, Block and Zucker 1990). This behaviour can be mediated by
27 familial imprinting, as demonstrated by cross-fostering studies. For example, inbred
28 laboratory strain male mice reverse their mate preference following cross-fostering
29 (Yamazaki, Beauchamp, Kupniewski, Bard, Thomas and Boyse 1988). Familial
30 imprinting can also influence the reproductive priming effects of scents. While
31 puberty in juvenile female rodents can be accelerated by exposure to the scents
32 of unfamiliar adult males, they do not show this response to the scents of familiar
33 males with which they are reared (e.g. Berger, Negus and Day 1997). Penn and
34 Potts (1998) have argued that familial imprinting may provide a more effective
35 means of recognizing close relatives and avoid inbreeding than self-inspection alone
36 because this mechanism allows animals to recognise a greater range of close rela-
37 tives than just those bearing their own genotype. While imprinting on the genotypes
38 of other animals during rearing would allow recognition of a much greater range
39 of genotypes than self-referent matching, it is also likely to mean greater recogni-
40 tion and rejection of potential mates that may not be close kin. Imprinting is likely
41 to be error-prone in species where multiple paternity is common or offspring are
42 reared communally by females, when self-referent matching may be a much more
43 reliable mechanism (Mateo 2004). However there is currently insufficient evidence
44 to determine whether self-referent phenotype matching of odour cues is used to
45 avoid inbreeding.

01 In many species, female choice does not involve simply mating with a single pre-
02 ferred male and rejecting all alternatives; instead, females often mate with multiple
03 males in a single reproductive event. The many explanations for polyandry include:
04 direct benefits associated with avoiding the costs of resisting mating or acquisition
05 of material resources (Andersson 1994), or indirect genetic benefits result-
06 ing from genetic diversification of litters or facilitation of post-copulatory choice
07 mechanisms to overcome females' inability to correctly identify the most geneti-
08 cally superior or genetically compatible male through pre-copulatory mate choice
09 (Jennions and Petrie 2000). Under all these hypotheses except the first, females
10 should improve their fitness by mating with multiple males. Similar behaviour is
11 expected in males, where advantages of multiple mating are more straightforward:
12 there is generally a positive relationship between the number of females mated and
13 male reproductive success (Andersson 1994). We might thus expect males in gen-
14 eral, together with females of polyandrous species, to actively discriminate against
15 previous mates in favour of seeking matings with novel partners. This behaviour
16 is indeed widespread. In males, discrimination against previous partners underlies
17 the well known Coolidge effect, in which sexually exhausted males are able to
18 resume copulation upon introduction to a novel receptive female (Wilson, Kuehn
19 and Beach 1963). The decline in male sexual performance during repeated copu-
20 lation with the same female may allow sperm to be conserved for when additional
21 females are encountered (Wedell, Gage and Parker 2002). There is now evidence
22 for male discrimination against familiar or previously mated females in a num-
23 ber of species (e.g. Olsson and Shine 1998; Kelley et al. 1999; Tokarz 2006). As
24 predicted from the putative benefits of polyandry, females of many species also
25 discriminate against previous partners. In pseudoscorpions (*Cordylochernes scor-*
26 *pioides*) females are nonreceptive towards males from which they have already
27 received sperm in the first few hours after mating (Zeh, Newcomer and Zeh 1998).
28 Female guppies, which use visual signals to choose mates, tend to prefer novel
29 males (Zajitschek et al. 2006) and discriminate against previous mates and those
30 that look like previous mates (Eakley and Houde 2004). Odour cues may play an
31 important role in male avoidance of previous mates through mechanisms such as
32 the Coolidge effect (Johnston and Rasmussen 1984), but there is currently little
33 definitive evidence for any involvement of odour cues in the equivalent female
34 behaviour.

35 Females may avoid males that are familiar because they are previous mates,
36 but they may also prefer novel males because of the genetic benefits of mating
37 with locally rare genotypes (negative frequency dependent selection). In guppies
38 (*Poecilia reticulata*), females familiarized (but not mated) with males of a particular
39 colour morph are significantly more likely to mate subsequently with a male
40 bearing a novel colour pattern than with a familiar colour-type male (Hughes, Du,
41 Rodd and Reznick 1999). Similarly polyandrous female house wrens (*Troglodytes*
42 *aedon*) are more likely to accept extra-pair copulations from males carrying locally
43 rare alleles (Masters, Hicks, Johnson and Erb 2003). Negative frequency dependent
44 selection, which might be based on preference for unfamiliar MHC odours, is widely
45 thought to be a key mechanism underlying the maintenance of MHC heterozygosity

01 in vertebrates (Jordan and Bruford 1998), although evidence for this remains
02 controversial (Thom et al. this volume).

03 Pregnancy block, or the Bruce effect, is a phenomenon whereby recently mated
04 females exposed to the odours of an unfamiliar non-sire male experience pregnancy
05 failure and return to oestrus (Bruce 1959). Exposure to the sire male's scent fails to
06 disrupt pregnancy and, if this coincides with exposure to unfamiliar male odour,
07 has a protective effect and reduces the likelihood of pregnancy block occurring
08 (Parkes and Bruce 1961; Thomas and Dominic 1987). This mechanism relies on a
09 female memorising the odours of the mating male (Kaba, Rosser and Keverne 1989),
10 and distinguishing these from the unfamiliar odours of novel males. A number of
11 hypotheses have been put forward to explain why females may abort their current
12 litter in order to remate with the unfamiliar male, for example, to increase paternal
13 investment from the unfamiliar male, or because of the threat of infanticide from
14 an unfamiliar male towards another male's offspring (see review by Becker and
15 Hurst this volume). Assuming that the female remates with the unfamiliar male
16 that induces pregnancy block, the Bruce effect would result in preference for the
17 unfamiliar male as a mate over the familiar stud male. However, so far the effect
18 has only been observed in artificial laboratory situations and, as yet, there is no
19 evidence that the unfamiliar blocking male goes on to successfully mate with the
20 female. An alternative explanation for the Bruce effect is that unfamiliar male scent
21 in the nest signifies a situation where the likelihood of offspring survival is low and
22 females use this to abort a pregnancy and avoid wasted investment in gestation and
23 lactation without choosing to re-mate with the unfamiliar male (Becker and Hurst
24 this volume). It thus remains to be proven whether the Bruce effect represents a form
25 of post-copulatory mate choice where unfamiliar males gain an advantage.

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29 **3 Preference for Familiar Individuals as Mates**

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31 While mate choice for unfamiliar partners might be explained by the fitness benefits
32 of multiple mating, inbreeding avoidance, and favouring rare genotypes, preference
33 for familiar males is also sometimes observed. Why would females choose relatively
34 familiar males as mates, given the benefits outlined above of avoiding such males?

35 In many species, males defend territories, with relatively more competitive or
36 dominant males holding higher quality territories. Territory holders may be pre-
37 ferred by females, either because of the better physical resources they can offer
38 females, or because their ability to acquire and defend a territory is associated with
39 positive genetic traits which will be inherited by the choosing female's offspring,
40 particularly their sons. This system is usually mediated through deposition of scent
41 marks in the environment by territorial males, while non-territory holders typically
42 do not mark or have qualitatively different scents. Intruders into a territory may leave
43 competing scent marks, but these are rapidly countermarked by the resident male,
44 which either directly overmarks the intruder's scent (hamsters: Johnston, Chiang
45 and Tung 1994; meadow voles: Johnston, Sorokin and Ferkin 1997b) or deposits

01 a fresher scent nearby (Rich and Hurst 1999). Scent marks and countermarks pro-
02 vide a continuous record of competitive challenges between conspecifics providing
03 a reliable advertisement of an individual's ability to dominate or defend an area to
04 other competitors and potential mates (Hurst, Beynon, Humphries, Malone, Nevi-
05 son, Payne, Robertson and Veggerby 2001). Females use these marks to assess male
06 quality: for example, female house mice prefer males owning exclusively marked
07 territories over males whose territories also contain a few fresh countermarks from
08 another unfamiliar competitor male (Rich and Hurst 1998). The continued presence
09 of one individual's marks in a specific area indicates that the owner is a success-
10 ful territory owner because it has not been displaced. Females will thus tend to
11 become more familiar with the odours of locally dominant territory holders, and
12 because such males are usually preferred mating partners, familiarity could act as
13 a surrogate measure of male quality in mate choice. This preference for familiarity
14 may also apply for non-territorial species where male dominance is associated with
15 higher levels of general scent marking of the environment. Like territoriality, male
16 dominance is associated with higher mating and reproductive success across a range
17 of species (see reviews in: Dewsbury 1982; Ellis 1995), and dominant males are
18 often (though not always) preferred by females (Wong and Candolin 2005).

19 In house mice, we have shown that females are consistently more attracted
20 to a male after brief investigation of his scent marks than to an equivalent male
21 whose scent is unfamiliar (Cheetham 2006). However, if prevented from mating
22 with a familiar male over an extended period of association (reflecting lack of mat-
23 ing attempts by the familiar male), unmated female house mice show increased
24 interest in unfamiliar males (Patris and Baudoin 1998). Nonetheless, the prefer-
25 ence for familiar males is so strong in the closely related mound-builder mouse
26 *Mus spicilegus* that they continue to prefer familiar males even when prevented
27 from mating over an extended period of association, perhaps reflecting monog-
28 amous traits in this species (Patris and Baudoin 1998). Female mice (Rich and
29 Hurst 1999), hamsters (Johnston, Sorokin and Ferkin 1997a), and voles (Johnston
30 et al. 1997a) are also more attracted to the owner of scent countermarks or over-
31 marks than to a male whose scent has been countermarked, consistent with the
32 idea that they use scent marks to assess the relative dominance of males. Prefer-
33 ence for the odours of familiar males has also been shown in a number of other
34 scent-marking rodents, including prairie voles (*Microtus ochrogaster*: Newman and
35 Halpin 1988) and lemmings *Dicrostonyx groenlandicus* (Huck and Banks 1979),
36 as well as non-rodents such as the pygmy loris (*Nycticebus pygmaeus*: Fisher
37 et al. 2003). In the golden hamster (*Mesocricetus auratus*) female sexual recep-
38 tivity increases and aggression reduces toward familiar males, and females mated
39 with familiar males produce larger litters (Tang-Martinez, Mueller and Taylor 1993)
40 suggesting that females may even adjust their reproductive investment in rela-
41 tion to male quality. Preference for familiarity may not be a trivial effect, as it
42 can produce powerful—if sometimes maladaptive—responses: for example, pre-
43 exposure to the odours of parasitized male mice reverses females' usual preference
44 for healthy males, causing them to prefer the parasitized, but now familiar, male
45 (Kavaliers, Colwell, Braun and Choleris 2003).

01 Many examples of females exhibiting a preference for familiar males are linked
02 to the benefits of mating with a dominant animal, but this behaviour would also be
03 expected where the benefits of monogamy outweigh those associated with multiple
04 mating. There is limited evidence in support of the idea that monogamous species
05 prefer to mate with their familiar partner: along with the *Mus* examples discussed
06 above, females of the monogamous common vole (*Microtus arvalis*) prefer their
07 familiar partner to novel males (Rícanková, Sumner and Sedláček 2007), as do
08 monogamous *M. ochrogaster* (Shapiro, Austin, Ward and Dewsbury 1986). Polyga-
09 mous *M. montanus*, in contrast, either show no preference or prefer unfamiliar males
10 (Shapiro et al. 1986).

11 We can identify a number of other hypothetical benefits arising from a preference
12 for familiar males as mates. Assessing quality, health, and social status might require
13 several encounters with a male or his signals, in which case females will tend to have
14 better information about familiar than unfamiliar males. For example, female house
15 mice are more attracted to the owner of a familiar scent than to a completely unfam-
16 ilar one, even when the familiar animal's scent has been countermarked by a com-
17 petitor male (Cheetham 2006). This suggests that prior familiarity has an important
18 impact on recognition and initial attraction to males. Furthermore, females might
19 only be able to assess some aspects of male quality, such as parental ability, either
20 by reproducing with the male or by observing the male's reproductive success. In
21 subsequent mating bouts, sires offering higher levels of paternal care might be pre-
22 ferred over novel partners with unknown abilities. This could explain why in some
23 birds with biparental care, extrapair copulations tend to be with familiar males (the
24 female's initial social mate) rather than completely novel males (Slagsvold, Johnsen,
25 Lampe and Lifjeld 2001; Walsh, Wilhelm, Cameron-Macmillan and Storey 2006).
26 Prior reproductive success certainly appears to influence subsequent mate choice
27 in birds: for example female canaries (*Serinus canaria*) show a preference for a
28 previous mate when reproductive success was good (at least two chicks hatched),
29 but do not prefer their previous mate when only a single chick resulted from the
30 pairing (Beguín, Leboucher, Bruckert and Kreutzer 2006). Where mate assessment
31 is difficult, females may need to copulate with a male to assess its quality (Hunter,
32 Petrie, Otronen, Birkhead and Møller 1993), or they may use males' responses to
33 copulation solicitation as an indication of male condition (e.g. Lens, Van Dongen,
34 VandenBroeck, Van Broeckhoven and Dhondt 1997). This could lead to preference
35 for familiarity since previously-mated males are of known quality while the quality
36 of the unfamiliar male remains unknown until copulation.

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40 **4 Conclusions**

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42 Animals that encounter some individuals more often than others theoretically have
43 the ability to segregate conspecifics into categories of familiar and unfamiliar,
44 although the extent to which they do so is likely to vary according to capacity
45 and necessity. This simple basis of assessment is likely to influence a range of

01 intraspecific interactions, but the effect on mate choice is particularly intriguing
 02 because of the apparently opposite effects of familiarity in different circumstances.
 03 The effects of familiarity during development on mate choice can be explained by
 04 its function as a simple surrogate of relatedness, which may be sufficiently effective
 05 in many species to ensure that inbreeding remains rare. Familiarity through mat-
 06 ing during adulthood may also modulate the mating system, by allowing promiscu-
 07 ous species to increase fitness through avoidance of partners with which they
 08 have already mated, while serving the opposite purpose in monogamous species.
 09 Further, familiarity with an individual's sexual signals during adulthood may play
 10 an essential role in allowing females to assess the quality and compatibility of the
 11 signal owner, resulting in a preference for familiar individuals when the assessment
 12 indicates that they are suitable mates. Thus familiarity acquired during different
 13 life stages, and in differing social contexts, can have quite disparate but generally
 14 predictable effects on subsequent mate choice. Since the ability to distinguish famil-
 15 iarity probably exists in most vertebrates, this potentially widespread factor in mate
 16 choice deserves more extensive exploration to understand its specific effects.

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