



---

Female Mate Choice in Mammals

Author(s): By Tim Clutton-Brock and and Katherine McAuliffe

Reviewed work(s):

Source: *The Quarterly Review of Biology*, Vol. 84, No. 1 (March 2009), pp. 3-27

Published by: [The University of Chicago Press](http://www.press.uchicago.edu)

Stable URL: <http://www.jstor.org/stable/10.1086/596461>

Accessed: 07/09/2012 01:00

---

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



The University of Chicago Press is collaborating with JSTOR to digitize, preserve and extend access to *The Quarterly Review of Biology*.

# THE QUARTERLY REVIEW of BIOLOGY



## FEMALE MATE CHOICE IN MAMMALS

TIM CLUTTON-BROCK

*Department of Zoology, University of Cambridge,  
Cambridge CB2 3EJ, United Kingdom*

E-MAIL: THCB@CAM.AC.UK

KATHERINE MCAULIFFE

*Department of Anthropology, Harvard University,  
Cambridge, Massachusetts 02138, USA*

E-MAIL: MCAULIFF@FAS.HARVARD.EDU

### KEYWORDS

sexual selection, mate choice, mammals, mating systems, genetic benefits

### ABSTRACT

*Studies of mate choice in vertebrates have focused principally on birds, in which male ornaments are often highly developed, and have shown that females commonly select mates on the basis of particular phenotypic characteristics that may reflect their genetic quality. Studies of female mate choice in mammals are less highly developed, and they have commonly focused on female mating preferences that are likely to be maintained by benefits to the female's own survival or breeding success. However, recent experimental studies of mate choice in mammals—especially rodents—provide increasing evidence of consistent female preferences that appear likely to generate benefits to the fitness of offspring. As yet, there is no compelling evidence that female mating preferences are less highly developed in female mammals than in female birds, although these preferences may more often be masked by the effects of male competition or of attempts by males to constrain female choice.*

### INTRODUCTION

**I**N THE *DESCENT OF MAN*, Darwin (1871) describes two principal modes of

sexual selection, the first operating through competition between individuals of one sex—usually males—for access to breeding

*The Quarterly Review of Biology*, March 2009, Vol. 84, No. 1

Copyright © 2009 by The University of Chicago. All rights reserved.

0033-5770/2009/8401-0001\$15.00

partners of the opposite sex, leading to the evolution of different forms of weaponry and other characteristics that affect fighting ability, and the second operating through female mating preferences combined with competition between males to attract females, leading to the evolution of various forms of ornamentation in males. Sex differences in weaponry among mammals provided Darwin with many examples of his first mode of sexual selection, while sex differences in avian ornaments provided many of the examples that he used to illustrate the consequences of his second mode of sexual selection. A similar reliance on mammalian examples to illustrate the evolution of male weaponry through intrasexual competition, and on avian examples to illustrate the evolution of male ornamentation through intersexual mate choice, persists to this day (see Huxley 1938; Alexander et al. 1979; Bradbury and Andersson 1987; Andersson 1994; Clutton-Brock 2004; Kraaijeveld et al. 2007).

The reliance on mammalian examples to illustrate the evolution of male weaponry, as well as the widespread evidence of intrasexual competition between males, has resulted in a common perception that intrasexual competition is the predominant form of sexual selection in mammals and that, where female choice does occur, females commonly favor mating with partners that are able to provide protection, access to resources, or paternal care rather than genetic benefits to their offspring (Clutton-Brock 1988; Clutton-Brock et al. 1989). Moreover, there are some reasons to expect that intrasexual competition for access to females is more intense in male mammals than in male birds and that intersexual mate choice is more highly developed in female birds than in female mammals. Most mammals are polygynous, and social monogamy and paternal care are both relatively rare (Eisenberg 1966; Kleiman 1977; Eisenberg 1981). As a consequence of intrasexual competition for access to mates, males are commonly larger than females (Clutton-Brock and Harvey 1977; Alexander et al. 1979) and often use their greater strength to constrain female mate choice (Smuts and Smuts 1993; Clutton-Brock and Parker 1995). Female mam-

mals are often philopatric (Greenwood 1980; Clutton-Brock 1989), and males frequently compete to monopolize access to pre-existing female groups, thus restricting opportunities for mate choice in females. Female mammals are usually less mobile than female birds, and the costs of extra-group forays to monitor mating opportunities or to select alternative mating partners can be very high, especially when relationships between neighboring groups are hostile (Clutton-Brock and Parket 1995; Holekamp and Smale 2000; Clutton-Brock et al. 2006). Since biases in the Operational Sex Ratio are often large and generate intense competition between males for access to females, only males of high quality are likely to obtain access to female groups. The benefits of female choice may, therefore, be relatively small, and selection may favor females that acquiesce to mating with males that win access to their range or group (Pierce and Dewsbury 1991).

Although intense intrasexual competition between males is a conspicuous feature of many mammalian breeding systems, it is likely that the extent to which female mating preferences influence male success has been underestimated (Small 1988, 1989). Compared to birds, a relatively high proportion of mammals are active at dusk or after dark and rely on olfactory or auditory cues rather than visual ones, so that the complexity of male displays and the extent of female preferences are commonly hard to assess (Roberts and Gosling 2003; Clutton-Brock 2004). In addition, the effects of female mating preferences are often difficult to distinguish from those of intrasexual competition between males and male coercive tactics (Clutton-Brock et al. 1993). A growing number of studies on mammals have produced evidence that females show consistent mating preferences for particular categories of males that appear likely to generate fitness benefits to the females themselves or to their offspring (Keddy-Hector 1992; Penn and Potts 1998a; Jennions and Petrie 2000; Roberts and Gosling 2003; Manson 2006). In this review, we assess recent studies of female mate choice in mammals and attempt to dis-

tinguish the cases in which there is credible evidence that female preferences have an important influence on male mating success from those in which variation in male success may be a consequence of intrasexual competition. In the final section, we return to the question of whether there is any indication that patterns of mate choice in mammals differ from those in birds.

Before describing the evidence for female choice, it is worth clarifying exactly what we mean when we say that females choose or show a preference for particular mating partners. We use "female choice" to mean cases where females show an active preference for mating with particular categories of males, whether or not matings lead to conception. Unlike some others, our definition of female choice carries the implication that not all forms of female behavior that affect the distribution of mating success in males should necessarily be regarded as mating preferences. For example, in many animals, females show preferences for particular habitat types because they offer greater protection from predators or improved access to resources, and female habitat preferences often affect the mating success of males holding territories in different areas. The effects of female habitat preferences on male mating success are well-illustrated by recent studies of ungulates. For example, in the desert-adapted Grevy's zebra *Equus grevyi*, females in the later stages of pregnancy restrict their usually large ranges and move to areas where water is available and where they can drink on a daily basis during the period of lactation (Rubenstein 1986). Females have a postpartum estrus, as do other equids, and males establish large territories in the vicinity of water sources in order to mate with receptive females visiting these water sources. Although female movements affect the distribution of male mating success in Grevy's zebra, differences in mating success between males may simply be a consequence of female habitat preferences rather than of preferences for mating with particular categories of partners. Similarly, in puku *Kobus vardonii*, mature males hold

resource-based territories in areas of grassland favored by grazing females (Rosser 1987; 1992). Females (including receptive and nonreceptive individuals) spend more time grazing in territories where annual herbs are abundant, and males defending these territories get more matings than those defending less-favored territories. In such cases, variation in male mating success may be caused principally by intrasexual competition among males for resource-based territories, and this, combined with female preferences for particular habitats, may mask the consequences of any preferences that persist in females for particular categories of mating partners. We refer to examples of this kind as "coincidental" mate choice in order to emphasize that such choices do not involve adaptations that have evolved through a process of sexual selection.

In natural populations, female preferences for mating with particular categories of males are often difficult to distinguish from female preferences for particular areas or habitats, or from other forms of coincidental mate choice. Studies of Uganda kob *Kobus kob thomasi*, a lek-breeding African antelope, provide a good example. In this species, females leave grazing herds as they approach estrus and begin to attract courting males and move to leks, where male territory holders defending small territories that do not contain significant resources keep nonterritorial males away (Clutton-Brock et al. 1993; Deutsch 1994; Nefdt and Thirgood 1997). Once on the lek, females collect on particular territories, and the males that defend these territories often show high mating success (Leuthold 1966). Larger or older males typically defend the most popular territories and commonly show higher mating success than smaller or younger territory holders (Balmford 1992). Although data of this kind are sometimes interpreted as evidence of female mating preferences in lek breeders (Carbone and Taborsky 1996), female kob appear to prefer particular territories rather than the particular males that occupy them (Balmford 1990, 1991), and experiments show that preferred territories are ones that have recently been heavily used

by females, are distant from thickets or other places where predators can hide, and are often close to the centre of the lek (Deutsch and Nefdt 1992). Since the most popular territories tend to be held by the most competitive males, preferences for particular territories are likely to lead to correlations between mating success and male phenotype so that these relationships do not provide reliable evidence of female preferences for mating with particular categories of males (Clutton-Brock et al. 1993, 1996), and similar problems are widespread in other systems. To overcome this problem, it is often necessary to manipulate the size or quality of male traits and to demonstrate that doing so affects female preferences and male success—but, in natural populations, experiments of this kind usually face serious logistical problems, and, consequently, conclusive evidence that female mating preferences are responsible for variation in male mating success is rare.

#### FEMALE MATING PREFERENCES IN MAMMALS

A substantial number of studies have suggested that female mammals mate preferentially with particular categories of males. In order to organize the available evidence of female mate choice in mammals, we have focused on evidence of female preferences for different attributes of males, including their maturity, dominance status, fertility, capacity for investment, relative development of weaponry, symmetry, coloration, vocal displays, olfactory displays, (un)relatedness, genetic similarity or compatibility, and previous mating success. Subsequently, we have examined evidence of variation in female preferences and of the frequency with which females mate with multiple partners. Very few studies have yet been able to measure either the direct or the indirect consequences of mate choice and, although direct benefits appear more likely to maintain some preferences while indirect ones maintain others, in most cases, benefits of both kinds are possible.

#### MATURITY

Where younger or less powerful males are likely to lose mating opportunities to older or stronger individuals unless they copulate quickly, selection often favors coercive strategies in males (Clutton-Brock and Parker 1992). The costs of male coercion to females may be high, especially in systems where multiple males compete simultaneously for the same female (Smuts and Smuts 1993), and, in many of these systems, females avoid mating with immature males that are unable to provide effective defense against rivals (Fox 2002). For example, in elephant seals *Mirounga angustirostris*, females are commonly courted by multiple males, and both females and their pups can be injured or killed unless one mate can control access to them (Reiter et al. 1981; Le Boeuf and Mesnick 1991). Mature males are usually able to monopolize access to females, providing effective protection against harassment by other males, while younger males are unable to do so. Females show a preference for joining larger harems where they—and their pups—are likely to be safer from male harassment (Pistorius et al. 2001; McMahon and Bradshaw 2004), and females that are being courted by younger males give calls that attract the attention of dominant males, who commonly displace the younger suitors (Cox and Le Boeuf 1977). Similarly, in ungulates that form unstable herds, estrous females risk being killed by competing males unless they join males capable of protecting them against rivals (Clutton-Brock et al. 1993; Réale et al. 1996). These species commonly show a preference for joining larger groups (Carranza and Valencia 1999). Also, in some social primates, females often avoid mating with immature partners, which may reduce the risk of dangerous harassment or punishment by older males (Manson 1994a,b; Fox 2002), and, like female elephant seals, females in some species incite competition between males and may gain direct benefits by doing so (Kuester and Paul 1992). An additional reason why females avoid

mating with younger partners may be that immature males are less likely to be fertile (Cox and Le Boeuf 1977; Clutton-Brock et al. 1982; Small 1988; Byers et al. 1994).

#### DOMINANCE

In a number of mammals, females show a consistent preference for mating with dominant males. For example, in some rodents, females offered a choice of dominant or subordinate partners preferentially mate with dominant males (Huck and Banks 1982; Shapiro and Dewsbury 1986; Drickamer 1992; Solomon and Keane 2007). In natural populations of social primates and carnivores, females also appear to favor dominant partners (Seyfarth 1978a,b; Robinson 1982; Silk and Boyd 1983; Janson 1984; West and Packer 2002), although this is not always the case, and, especially in larger groups, dominant males commonly obtain a smaller share of matings than priority of access models would predict (Fedigan 1983; Manson 1992, 1994a,b; Soltis and McElreath 2001; Fox 2002; Alberts et al. 2003; Manson 2006). However, in natural populations, it is usually difficult to exclude the possibility that an increase in female matings with dominant males is not a consequence of competition between males or of their coercive tactics.

Selective mating with dominant males can provide direct as well as indirect benefits to the fitness of females. In some cercopithecine primates that live in multimale groups, fathers are more likely to protect or support their own progeny than those of other males (Stein and Stacey 1981; Keddy-Hector et al. 1989; Borries et al. 1999; Soltis and McElreath 2001; Buchan et al. 2003). As high-ranking males can provide more effective care for infants than low-ranking males (Alexander 1970; Stein 1984; Agrell et al. 1998), female preferences for dominant males may affect the survival of their offspring while also generating genetic benefits, since the traits that affect dominance are often heritable (Drickamer 1992; Horne and Ylönen 1998).

Studies of a number of lek-breeding mammals also suggest that females may show a preference for dominant males. In

several species of antelope, females leave their usual herds as estrus approaches and move to leks where they commonly show a preference for joining the larger harems that often form at the centre of such leks (Clutton-Brock et al. 1988b, 1993; Nefdt and Thirgood 1997; Bro-Jørgensen 2002). Territories that attract females are usually defended by larger and more dominant males who obtain a high proportion of matings, but, on natural leks, it is usually difficult to separate female preferences for particular territories—or for joining larger groups of females—from preferences for mating with particular males. In an attempt to distinguish between female preferences for particular territories and female preferences for particular males, Clutton-Brock (1989) forced male fallow deer *Dama dama* defending territories on a lek to move to new territories and showed that their relative success on their initial territory was correlated with their success on their new territory. However, correlations of this kind may still be generated by individual differences in the capacity of males to retain females or to acquire popular territories, and, therefore, do not provide conclusive evidence of mating preferences (Clutton-Brock et al. 1993). Subsequent experiments with female fallow deer that had been induced into full estrus showed that these females exhibited a strong tendency to join other females, but that the characteristics of associated males apparently had little effect on their movements (Clutton-Brock and McComb 1993; McComb 1994). Recent studies of topi *Damaliscus lunatus*, where males defending central territories on leks obtain a high proportion of matings, show that females mate more rapidly after arrival on a central territory than on a peripheral one and that they sometimes compete with others for the attentions of males (Bro-Jørgensen 2002; Bro-Jørgensen and Durant 2003). Although this has been interpreted as evidence that female mating preferences are responsible for variation in male success, it is also possible that females in full estrus collect in the centre of leks either as a consequence of random move-



ments between territories (Stillman et al. 1993) or as a result of improvements in the ability of males on central territories to retain females (Clutton-Brock et al. 1993, 1996).

#### FERTILITY

Although males of some polygynous species are capable of fertilizing substantial numbers of females (Clutton-Brock 1982), the ejaculates of males that mate repeatedly over a short period often show reduced sperm counts as well as reduced fertility (Austin and Dewsbury 1986; Huck et al. 1986; Preston et al. 2001), and the capacity of these males to impregnate females may be temporarily limited (Dewsbury 1982a,b,c). Several studies of rodents show that females mate preferentially with unmated males (Krames and Mastromatteo 1973, Huck et al. 1986; Pierce and Dewsbury 1991). Some studies suggest that this tendency is more pronounced in monogamous species, where males commonly care for their offspring and the costs of pairing with an infertile partner may be particularly high, than in polygamous species (Pierce and Dewsbury 1991; Salo and Dewsbury 1995; though see Solomon and Keane 2007). In addition, studies of some polygynous mammals provide evidence of female competition for access to males (Bro-Jørgensen 2002; Bebie and McElligot 2006), and one interpretation of these observations is that the sperm supplies of "popular" partners are limited (see Preston et al. 2001).

#### MALE INVESTMENT

Where males contribute to rearing or protecting their mates or their offspring, females might be expected to favor partners that are prepared to invest heavily in their offspring. In several baboons and macaques that live in multi-male groups, females develop close affiliative relationships or "friendships" with particular males (Smuts 1985; Silk 2002). "Friends" are often males that previously held high status in the group, although they seldom include the current alpha male, and females are often more

likely to mate with male friends than with other males (Seyfarth 1978a,b; Takahata 1982; Rasmussen 1983; Smuts 1985), but this is not always the case (Manson 1994a,b; Hemelrijk et al. 1999; Manson 2006).

In species where females mate preferentially with friends, males might be expected to signal their capacity or readiness to provide care or protection to prospective mates. Some studies of tamarins, where multiple males often help to carry young produced by a single female, have suggested that infant carrying by males may represent a form of courtship (Price 1990; Ferrari 1992). However, direct evidence that females are more likely to mate with males that contributed heavily to previous litters is lacking (Baker et al. 1993; Tardif and Bales 1997), and it seems more likely that carrying is an example of parental care or of kin-related cooperation.

#### WEAPONRY

Several studies of ungulates have shown that variation in horn or antler size in males is correlated with phenotypic quality or mating success, thus suggesting that female choice may play an important role in the evolution of horns and antlers (Espmark 1964; Geist 1971; Ditchkoff et al. 2001; Vanpé et al. 2007). As with virtually all other sexually dimorphic traits, horn size and antler size are correlated with age and body size, which are, in turn, associated with fighting ability, social rank and mating success (Clutton-Brock 1982; Barrette and Vandal 1986; Alvarez 1990; Prichard et al. 1999; Coltman et al. 2002; Mysterud et al. 2005). As a result, evidence of associations between male horn size and male reproductive success provides no firm indication that horn size affects mating success directly, or that relative horn size is used as a signal either in the assessment of competitors by males or of potential mating partners by females. In order to demonstrate that horn size affects mating preferences, it would be necessary to manipulate horn size and to show that this affected female preferences. As yet, all attempts to manipulate relative horn or antler size have been unsuccessful (Lincoln

1994). In experiments where female fallow deer were induced into estrus and then offered a choice of males with antlers or males that had had their antlers removed, no evidence of a preference for antlered males was found (Clutton-Brock and McComb 1993). Despite this, studies of the evolution of horns and antlers continue to suggest that females prefer mating with males with large antlers and that, consequently, female mating preferences have played an important role in the evolution of antlers and horns, even though there is no direct evidence that this is the case (see Vanpé et al. 2007). Male horns and antlers are effective defensive and offensive weapons, and, as yet, there is no firm evidence that mate choice has played an important role in their evolution (Clutton-Brock 1982). In a number of ungulates, females also carry horns or antlers that vary widely in size and that they commonly use in competitive interactions with other females or with males (Packer 1983; Robinson and Kruuk 2007).

#### SYMMETRY

Low levels of fluctuating asymmetry are thought to be an indicator of developmental stability and genetic quality, and several studies of birds suggest that females prefer males with symmetrical plumage (Møller and Pomiankowski 1993; Møller and Swaddle 1997). Some studies of ungulates have also suggested that there may be an association between the mating success of males and the symmetry of their horns (Møller et al. 1996), although detailed studies of red deer provided no evidence that symmetry is related to mating success, and the heritability of this trait appears to be low (Kruuk et al. 2003). In humans, women are more attracted to men with symmetrical faces (Rikowski and Grammer 1999; Thornhill and Gangestad 1999; Johnston et al. 2001), and it is thought that facial symmetry may be related to testosterone levels in men (Thornhill and Gangestad 1999). In addition, male body odor in humans is associated with facial symmetry. Women asked to rate the odor of T-shirts worn by different male subjects rated those

worn by symmetrical males as sexier than those of asymmetrical males (Rikowski and Grammer 1999). Dancing ability, too, is associated with bodily symmetry, and when other aspects of visual appearance are controlled for, women show a preference for "good dancers" (Brown et al. 2005). However, although these studies suggest that symmetry increases female interest, it has yet to be shown that it affects mating decisions.

#### AGGRESSION, COLORATION, AND TESTOSTERONE

In a substantial number of mammals, males with relatively high testosterone levels are both more frequently aggressive and more distinctively colored or patterned than females, as well as males with lower testosterone levels, and are commonly preferred as mating partners (Vandenbergh 1965; Setchell and Dixon 2001; Gerald 2001; Gerald 2003), although it is often difficult to identify which of the correlates of high testosterone levels are used in mate choice. For example, in African lions *Panthera leo*, males with dark manes have higher testosterone levels than light maned individuals and are more likely to take the lead in encounters with other prides (West and Packer 2002), and receptive lionesses commonly mate with the darkest maned male in their group. Experiments in which lionesses were presented with life-sized models of light and dark maned lions showed that lionesses were more likely to approach lions with darker manes, whereas lions presented with the same models were more likely to approach those with light manes (West and Packer 2002). Dark manes retain heat more than light ones, so mane color could be a handicap, providing females with a reliable indication of male quality (Zahavi 1975), but an alternative explanation is that females gain direct benefits from choosing males with dark manes since they have longer breeding tenures (Packer et al. 1988). Territorial males are darker than females or nonterritorial males in a number of lek-breeding antelopes (including Kafue lechwe *Kobus leche kafuensis* and white-eared



kob *Kobus kob leucotis*) (Clutton-Brock et al. 1993), which may indicate that females favor darker males here as well.

In some primates, such as vervet monkeys *Cercopithecus aethiops* (Gartlan and Brain 1968; Gerald 2001), gelada baboons *Theropithecus gelada* (Dunbar 1984), rhesus macaques *Macaca mulatta* (Vandenbergh 1965), and mandrills *Mandrillus sphinx* (Setchell and Dixson 2001), males of high status have more brightly colored faces, perineal regions, or testes than subordinates, and females are attracted to the brightest males (Gerald 2001). For example, in mandrill groups, which include large numbers of individuals, one male is typically brighter than all the others, and females interact, groom, and mate more frequently with the brightest male than with other mature males (Setchell 2005). Although brightly colored males tend to have high status within their groups (Setchell and Dixson 2001), the effects of male coloration are stronger than those of rank and remain when the influence of male rank is allowed for. Experiments with rhesus macaques also suggest that females are strongly attracted to brighter males; captive females presented with redder versus paler versions of male faces spent more time gazing at the redder versions of male faces (Waite et al. 2003).

One possible explanation for female preferences for brightly colored males is that they increase the chance that a female's daughters will inherit genes that provide effective resistance to parasites (Folstad and Karter 1992). This argument is based on the fact that bright skin coloring is commonly associated with testosterone levels (Vandenbergh 1965) and testosterone suppresses immune function, so that male brightness may signal an individual's resistance to infection. While this may be the case, there are several other possible reasons why females pay more attention to brightly colored males. For example, if bright males are likely to have low parasite levels, mating with them may reduce the female's own chances of becoming infected (Loehle 1997). Also, females may pay greater attention to brighter males because they are more likely to have higher

testosterone levels, thus making them more likely to be aggressive and pose greater risks than duller males to females who ignore their advances.

#### VOCAL DISPLAYS

In many mammals, male displays may play an important role in the mating decisions of females and can have direct effects on hormonal levels in females, even influencing the timing of ovulation. For example, in red deer, exposure to the roaring displays of males advances the timing of estrus in females (McComb 1987). In addition, male displays may be used by female mammals in the selection of mating partners. In red deer *Cervus elaphus* and fallow deer *Dama dama*, the repeated roars of harem-holding stags attract the attention of receptive females, who are more likely to join the harems of males with high roaring rates (McComb 1991; McElligott and Hayden 2001). Similar preferences for males with high calling rates have been demonstrated in other mammals, including the grey mouse lemur *Microcebus murinus* (Craul et al. 2004).

Specific acoustic properties of male calls may also be important in attracting females (Davidson and Wilkinson 2004). For example, the formant frequencies of red deer roars decrease with increasing body size, and females preferentially approach speakers producing roars with lower formant values (Charlton et al. 2007). In white-lined bats *Saccopteryx bilineata*, males that defend mating territories in tree buttresses produce complex vocalizations that attract females (Catchpole 1980; Hiebert et al. 1989), and males with more complex "songs" have more females on their territories (Davidson and Wilkinson 2004). It has yet to be shown if the complexity of male songs has a direct effect on female mating preferences or male success. Although these studies support the suggestion that male displays are important to female mate choice, the same displays commonly discourage potential challengers (Clutton-Brock and Albon 1979), so that it is always difficult to assess the extent

to which female preferences are responsible for variation in male success.

#### OLFACTORY DISPLAYS

Olfactory cues may play an important role in female mating preferences in many mammals (Gosling and Roberts 2001a,b). Females commonly investigate male scent marks, which may reflect male condition and other male characteristics (Moore and Marchinton 1974; Sawyer et al. 1989; Gosling and Roberts 2001a,b). In several rodents, females are less attracted to odors from males infected with parasites than to those of uninfected males (Clayton 1991; Kavaliers and Colwell 1995a,b; Penn and Potts 1998b; Klein et al. 1999; Willis and Poulin 2000; Ehman and Scott 2001), and females given a choice between infected and uninfected males are less likely to mate with infected ones, but, if they do indeed mate with infected males, fewer male offspring will be produced as a result (Hillgarth and Wingfield 1997; Barnard et al. 1998; Ehman and Scott 2002). Since resistance to parasites can be heritable (Enriquez et al. 1988) and parasite load can affect male status (Hausfater and Watson 1976; Freeland 1981; Gosling and Roberts 2001a,b), female preferences for uninfected males are likely to have indirect benefits for their offspring.

Female preferences for mating with dominant partners may often be caused by olfactory cues. Dominant individuals commonly scent mark more frequently than subordinates, often over-marking the scent marks of rivals (Gosling and Roberts 2001a,b). In some species, females appear to use the frequency of scent marking by males, or the frequency with which they over-mark the scents of rivals, as a basis for assessing potential mates (Desjardins et al. 1973; Johnston et al. 1997; Rich and Hurst 1998, 1999; Gosling et al. 2000; Roberts and Gosling 2003). Analysis shows that the odors produced by dominant males differ qualitatively from those produced by subordinates and reflect their higher androgen levels (Novotny et al. 1990). The compounds present in scent marks may also play a more impor-

tant role in attracting females (Yamaguchi et al. 1981; Hayashi 1990; Mossman and Drickamer 1996; Rich and Hurst 1998; Humphries et al. 1999; Thomas 2002). The size of male scent glands, the frequency of scent marking, and the chemical structure of scent marks are all heritable (Horne and Ylönen 1998; Roberts and Gosling 2003), and, in some rodents, females not only show a consistent preference for mating with dominant males but for mating with the sons of these males as well (Drickamer 1992).

#### RELATEDNESS

Breeding with close relatives commonly depresses the number and fitness of offspring (Keller and Waller 2002; Solomon and Keane 2007), and outbreeding is one of the most common forms of mate choice (Solomon and Keane 2007). Females often avoid inbreeding by a combination of dispersal, delaying sexual maturity if their father is still resident in the group (Pusey 1987; Krackow and Matuschak 1991; Pusey and Wolf 1996; Hoogland 2001), and avoiding mating with closely related males or with males that have not immigrated into their group during their lifetime (Packer 1979; Pusey and Wolf 1996; Cooney and Bennett 2000; Constable et al. 2001; Manson 2006). For example, cross-fostering experiments with rodents show that unrelated individuals reared together subsequently avoid breeding with each other whereas relatives reared apart breed with one another readily, thus indicating that inbreeding avoidance is based on the avoidance of mating with familiar individuals (Dewsbury 1988; Pusey and Wolf 1996). Humans may use similar cues in selecting mates, for individuals commonly show a strong aversion to breeding with childhood associates, whether or not they are related (Wolf 1995).

In some mammals, dispersing females continue to avoid breeding with close relatives encountered outside their natal group or territory (Pusey and Wolf 1996), while, in others, females that have dispersed from their natal group will breed with related males if they subsequently encounter them. For example, in reindeer *Rangifer tarandus*,

females will breed with related males that dispersed from their natal herd if they encounter them, although the chance of such encounters is low (Holand et al. 2007). Studies of rodents suggest that differences in the basis of female discrimination may be related to variation in the chance that dispersing individuals will encounter close relatives. For example, in rodents where both sexes are relatively sedentary and females mature at an early age, females typically avoid mating with close relatives, whether or not they are familiar with them (Dewsbury 1988; Ferkin 1990). In such cases, discrimination may be based on odors. In house mice *Mus musculus*, as well as some voles, females are able to discriminate between odors from siblings and odors from unrelated individuals, and avoid mating with siblings (Gilder and Slater 1978; Gavish et al. 1984; Winn and Vestal 1986; Bolhuis et al. 1988; Krackow and Matuschak 1991). Individuals commonly use cues derived either from their own phenotype or from the phenotype of parents or littermates to form a template that is subsequently used in comparisons with other individuals (Beauchamp et al. 1988).

While outbreeding generally increases the fecundity of females and the fitness of their offspring, it can also have costs if it disrupts co-adapted gene complexes, in which case some studies suggest that individuals avoid breeding both with close relatives and with entirely unrelated partners (Bateson 1983). It is not yet clear how common trends of this kind are. Studies of captive white-footed mice *Peromyscus leucopus* have shown that females mate preferentially with cousins, but studies of several other rodents have found no effects of this kind (Solomon and Keane 2007).

#### HETEROZYGOSITY, GENETIC DISSIMILARITY, AND COMPATIBILITY

In many organisms, including several mammals, there is evidence that female mating preferences are related to genetic parameters in males. The degree of male ornamentation in several birds and some mammals is correlated with levels of heterozygosity at particular loci, and, in several species, females show a preference for more

heterozygous partners over more homozygous ones (Potts et al. 1991; von Schantz et al. 1997; Penn and Potts 1998a,b; Foerster et al. 2003). When heterozygous males have higher fitness, females may increase the fitness of their progeny by selectively choosing to mate with partners whose genotypes are dissimilar to their own, and some studies suggest that they do so, although the way in which individuals are able to recognize their own genotype is still uncertain. For example, house mice living in semi-natural enclosures produce offspring that are more heterozygous at the MHC locus than would be expected by chance (Carroll and Potts 2007). Much of this excess appears to be a consequence of extra-territorial matings by females, thus suggesting that females favor matings with genetically dissimilar partners. Similarly, in grey seals *Halichoerus grypus*, the genotypes of maternal half-siblings also are more diverse than would be expected by chance (Amos et al. 2001).

Some of the best evidence of disassortative mating is provided by studies of the effects of the MHC genotype on mate choice in rodents (Carroll and Potts 2007; Solomon and Keane 2007). Individuals that are heterozygous at the MHC locus commonly show higher fitness than homozygotes, and MHC homozygous genotypes are rarer and heterozygous ones more common than would be expected by chance in several vertebrates, thus suggesting that females mate selectively with males that have different MHC genotypes from their own (Potts et al. 1991; Hedrick and Black 1997; Ober et al. 1997; Paterson and Pemberton 1997; Jordan and Bruford 1998; Penn and Potts 1999). Experiments with fish, mice, and humans show that females can detect MHC-related odors and are attracted to individuals with genotypes dissimilar from their own (Potts et al. 1991; Milinski and Wedekind 2001; Carroll et al. 2002; Penn 2002; Milinski 2003; Roberts and Gosling 2003), in some cases favoring partners carrying specific MHC alleles that complement their own genotype (Egid and Brown 1989; Wedekind and Fürri 1997). MHC-based odor preferences may also be involved in kin recognition and in the avoidance of close in-

breeding (Yamazaki et al. 1988; Penn and Potts 1999). For example, cross-fostering experiments show that female mice avoid mating with individuals carrying the MHC genes of the family in which they are reared rather than with individuals carrying their own MHC genes (Penn and Potts 1998a).

MHC-based preferences may be most highly developed in species in which females choose between males using olfactory cues. For example, MHC-related mate choice may be highly developed in fish and mammals because of their advanced olfactory capabilities (Mays and Hill 2004). Another possibility is that MHC-based mate choice initially evolved as a mechanism to allow individuals to identify and avoid mating with close kin. If so, MHC-related preferences might be expected to be weak or absent in species where one sex habitually disperses at adolescence and the chance that dispersers will encounter close relatives is low (Penn and Potts 1999). This could explain why there is no evidence of disassociative mating for the MHC genotype in Soay sheep *Ovis aries*, where male competition appears to determine the identity of mating partners (Paterson and Pemberton 1997; Pemberton 2004).

Evidence that individuals favor genetically dissimilar mates raises the question of how these preferences interact with selection for good genes (Colegrave et al. 2002; Mays and Hill 2004). One possibility is that there is a hierarchy of cues used in mating preferences. For example, individuals may make an initial choice on the basis of "good genes" and then use compatibility criteria to select a mate from among acceptable males. Experiments with mice provide some evidence for hierarchies of this kind (Roberts and Gosling 2003): females prefer males who scent mark frequently—a trait that is associated both with androgen levels and dominance and may be an indicator of genetic quality—but, when there is little variation in the scent marking rate, they show a preference for males with MHC genotypes unlike their own (Roberts and Gosling 2003). Some studies have suggested that the relative importance of selection for good genes ver-

sus compatibility in mates may also vary between individuals. For instance, in species where pair-bonds are enforced by female aggression, dominant females may choose (and monopolize) highly ornamented males, while subordinate females may be forced to choose among less highly ornamented males on the basis of compatibility (Mays and Hill 2004).

#### PREVIOUS MATING SUCCESS

One tactic that females might use in selecting mates is to copy the mating choices of other females. Studies of several social animals suggest that breeding females commonly copy each other's choice of mates and may gain indirect benefits by doing so (Dugatkin 1992). However, a recurrent problem is that female mammals commonly copy each other's movements for reasons unconnected to mating preferences, and so evidence that females follow each other does not necessarily indicate that they are copying each other's choice of mating partners (Clutton-Brock and McComb 1993). For example, in several ungulate species in which males defend mating territories, females commonly follow each other between territories, collecting with particular males (Clutton-Brock et al. 1993). Although this could occur as a result of estrous females copying each other's mating preferences, an alternative possibility is that females are safer from predators or harassing males when they are in larger groups (McComb and Clutton-Brock 1994; Nefdt and Thirgood 1997). In red deer, estrous females suffer less harassment from males when they gather together in larger groups (Carranza and Valencia 1999), while, in elephant seals, dependent pups are less likely to be injured or killed if their mothers join larger harems (McMahon and Bradshaw 2004). If females are indeed copying each other's mating preferences, their tendency to join males with larger harems should be specific to females in estrus. Also, individuals in larger harems might be more likely to mate with harem holders per unit time of spent in their harems than females with less popular males. As predicted, experiments with captive fallow deer that compared the responses of estrous and anestrus



females to mature males with and without females found that the attraction of females to males associated with other females only occurred in estrous females (McComb and Clutton-Brock 1994). However, estrous females showed no preference for males that they had seen mating over those that had not mated, and, in free-ranging populations of fallow deer, females in large harems are no more likely to mate per unit of time than those in small harems (Clutton-Brock and McComb 1993; Clutton-Brock et al. 1993, 1996). While this suggests that estrous females tend to aggregate, it does not support the suggestion that they copy each other's choice of mates.

In a number of mammals where females live in matrilineal groups, related females commonly breed with the same male (Clutton-Brock 1982; Pemberton et al. 1992). For example, in greater horseshoe bats *Rhinolophus ferrumequinum*, related females often visit the same mating partners (Rossiter et al. 2005). It is sometimes suggested that these trends are a consequence of female preferences to mate with the same male as their relatives in order to increase coefficients of relatedness within social groups, thereby reducing competition and increasing the potential for kin-selected cooperation (Rossiter et al. 2005). However, a more likely explanation is that related females copy each other's movements and gain direct benefits by doing so.

Some studies of humans also suggest that women may copy each other's choice of partners. For example, a recent experiment has shown that women give higher ratings to photographs of men paired with smiling female profiles than to photographs of these same men paired with the profiles of the same women who, rather than smiling, are instead wearing neutral expressions (Jones et al. 2007). These pairings have the opposite effect on male subjects, suggesting that female approval affects the attraction of males to other women. Whether this reflects a mating preference is not yet known, and other studies indicate that women do not find "attached" men more attractive than "unattached" ones (Uller and Johansson 2003).

Most studies of mate-choice copying assume that females monitor and copy each other's movements, but another possibility is that males signal the fact that they have mated recently and females respond to these signals. Experiments with rats show that females offered a choice between a male that had copulated recently and one that had not done so consistently preferred the male that had recently copulated (Galef et al. 2008). In contrast, when trials were repeated using females that had no sense of smell, females showed no preference for either male.

#### PARTNER NUMBER AND POST-COPULATORY MATE CHOICE

In mammals where males and females are closely bonded, including both socially monogamous and polygynous species, females rarely mate with more than one male per season (Brotherton et al. 1997; Clutton-Brock and Isvaran 2006). For example, in both red deer, which form harems, and fallow deer, which mate on resource territories or leks, females have short estrus periods and usually copulate only once or twice per season, usually with a single partner (Clutton-Brock et al. 1982, 1988a,b). In contrast, in other mammalian groups, including monotocous species, such as topi (Bro-Jørgensen 2002), and polytocous ones, such as North American red squirrels *Tamiasciurus hudsonicus* (Berteaux and Boutin 2000), females commonly mate with multiple partners, often in rapid succession (see Jolly 1966; Birdsall and Nash 1973; Bertram 1976; Tutin 1979; Cords et al. 1986; Packer et al. 1991; Pereira and Weiss 1991; East et al. 2003; Wilson et al. 2004). In some species, up to 90% of litters show multiple paternity, as in the yellow-toothed cavy *Galea flavidens* (Hohoff et al. 2003). Intraspecific variation in partner number is also common: in one population of thirteen-lined ground squirrels *Spermophilus tridecemlineatus*, the frequency of multiple paternity within litters ranged from 0–50% between years (Schwagmeyer and Brown 1983; Schwagmeyer and Parker 1987).

In some species, females make no obvious attempt to instigate multiple mating; rather, it appears to be a consequence of

competition between males. In Soay sheep, for example, estrous females commonly mate with large numbers of males, but they show little evidence of active mate choice and often attempt to avoid pursuing males (Wilson et al. 2004). Similarly, female thirteen-lined ground squirrels show little evidence of active female preferences for mating with particular males (Schwagmeyer 1984), and most females copulate with all males that locate and attempt to mate with them (Schwagmeyer 1984, 1986; Schwagmeyer and Wootner 1985). In some groups of mammals, interspecific differences in the number of males that females usually mate with is thought to be a consequence of contrasts in the capacity of males to defend females. For instance, in many sea lions, males are territorial, mating is rarely interrupted, and, as in red deer, females typically mate with a single male (Gentry and Kooyman 1986; Cassini 1999). In contrast, in seal species, such as elephant seals, males vary in dominance but do not defend territories, copulations are frequently interrupted, and females commonly mate with several partners.

In other mammals, females appear to go out of their way to invite or pursue matings with more than one partner. For example, in ring-tailed lemurs *Lemur catta* and blue monkeys *Cercopithecus mitis*, estrous females often solicit mating from several partners from outside their group in the course of a single day (Jolly 1966; Cords et al. 1986). Similarly, female brown capuchin monkeys *Cebus apella*, as well as females in several baboon and macaque species that live in multi-male groups, commonly make active attempts to mate with several different males (Taub 1980; Janson 1984). Even in these situations, it can be difficult to be sure that females are not coerced into mating with multiple partners, but some studies are able to exclude this possibility. For example, in yellow-toothed caviars, estrous females race between males, making it difficult for single males to monopolize them (Rood and Weir 1970; Rood 1972; Schwarz-Weig and Sachser 1996). Experiments in which receptive females were allowed to choose between different males in

an apparatus that prevented harassment or monopolization of females showed that 90% of mating females actively solicited copulations with more than one male, and that females preferred heavier males and those that courted more frequently (Hohoff et al. 2003).

Mating with multiple partners often has substantial costs, including the energy costs of locating suitable partners, the risk of harassment or punishment by dominant males, the risks of acquiring sexually transmissible diseases, reduced control of paternity, and increased competition between offspring born either in the same or successive litters, yet it presumably has substantial benefits as well (Schwagmeyer 1984; Ridley 1988; Wolff and Macdonald 2004). One common suggestion is that mating with multiple partners may reduce the risk of mating with a temporarily or permanently infertile partner. Studies of artificial insemination in domestic mammals show that the use of sperm from more than one male can increase the probability of conception (Hess et al. 1954; Beatty 1960), and, in some natural populations of birds and mammals, mating with multiple males appears to be a response to previous breeding failure (Ens et al. 1993). For example, in rock wallabies *Petrogale assimilis*, which form monogamous pairs, some females breed both with resident males and with extra-group males (Spencer et al. 1998). These females are more likely to breed with males other than their mate if their previous offspring failed to survive to emergence from the pouch. However, not all studies show that multiple mating increases fecundity, and, in some rodents, females that mate with multiple partners show reduced rates of conception (Schwagmeyer 1986). For example, female deer mice *Peromyscus maniculatus* and Djungarian hamsters *Phodopus sungorus sungorus* that mate with multiple partners are less likely to become pregnant than those that mate with a single partner (Dewsbury and Baumgardner 1981; Dewsbury 1982a; Wynne-Edwards and Lisk 1984), perhaps because the risk of male infanticide increases when multiple males have access to a female's territory and because it is beneficial to



females to avoid conception (Dewsbury 1982a).

In other cases, mating with multiple partners may increase the survival of foetuses to term or the survival of young. For example, in captive yellow-toothed caviar, females that are allowed to mate with multiple partners have fewer still-births and successfully wean significantly more of their pups (Keil and Sachser 1998). Since the same males were used to fertilize single versus multiple mating females in this experiment, and young were suckled by multiple females (Künkele and Hoeck 1995), this effect was unlikely to be a consequence of differences in male quality or of differences in parental care, and the most likely explanation is that sperm competition weeded out qualitatively inferior gametes (Sivinski 1984; Keil and Sachser 1998). In other cases, mating with multiple males may increase the survival of juveniles by increasing the amount of care and protection they receive from males (Goldizen 1987) and reducing the risks of infanticide (Hrdy 1981). In Japanese macaques *Macaca fuscata*, males are eight times more likely to attack infants if they have not previously mated with their mothers, and infants born to females that mate with multiple males attract less aggression (Soltis et al. 2000). Similarly, among some rodents in which male infanticide is common, controlled experiments show that resident males are less likely to attack neonates if they have previously had sexual experience with the mother (vom Saal 1984; Ebersperger 1998a,b). A final possibility is that mating with multiple males contributes to the genetic quality of offspring, either by increasing the chance that a female will breed with a higher quality male (trading-up) or by increasing competition between sperm in the female reproductive tract (Schwagmeyer 1984; Eberhard 1996). However, empirical evidence that mating with multiple partners improves the quality of a female's offspring is not yet available for mammals.

#### VARIATION IN FEMALE MATE CHOICE AND PARTNER NUMBER

Although most studies of female mate choice have investigated whether there are consistent female preferences for particular characteristics in males, the benefits and costs of particular choices are likely to vary in space and time. This might be expected to lead to variation in sampling tactics, mating preferences, and degree of choosiness, and there is increasing evidence that this is indeed the case (Zeh and Zeh 1996; Widemo and Saether 1999; Fawcett and Johnstone 2003). Studies of birds show that the strength and, in some cases, the direction of female mating preferences can vary widely (Chaine and Lyon 2008), and several studies indicate that the strength of female mating preferences varies in mammals as well. For example, in mice, preferences for MHC-dissimilar males that can be detected in estrous females disappear when females are not in estrus (Egid and Brown 1989). Several studies of humans also suggest that MHC-related odor preferences as well as female preferences for masculinity in males vary with the stage of the reproductive cycle or the hormonal status of subjects (Jordan and Bruford 1998; Penton-Voak et al. 1999).

The probability that females will mate with multiple partners also changes throughout the reproductive cycle in some species. In several monkey species, for example, females initiate copulation more frequently around the time of ovulation than they do during other times of the cycle, and sexual behavior declines considerably during the luteal phase (Manson 2006). In female chimpanzees *Pan troglodytes*, individuals commonly copulate with multiple males during the early stages of the estrus cycle but are more likely to copulate repeatedly with high-ranking males during the later stages, when conception is most likely (Matsumoto-Oda 1999). However, changes in the probability that females will conceive are also likely to affect the behavior of males, and it is often

difficult to be sure that changes in the number of partners are a consequence of female decisions rather than male coercion.

#### DISCUSSION

As Darwin described, intrasexual competition is widespread in mammals, and it is commonly associated with strong selection favoring the development of traits that enhance competitive success in males, who commonly use their greater size and strength to constrain female mate choice or to coerce females into mating with them (Clutton-Brock and Parker 1995). The prevalence of intrasexual competition and coercive tactics in males and the structure of mammalian breeding systems complicate attempts to demonstrate that female mating preferences have an important influence on male mating success. In particular, the common tendency for females to be attracted to particular sites, combined with male competition for preferred mating territories, means that neither variation in male mating success nor correlations between male mating success and male phenotype provide reliable indications of the importance of female choice. These problems are well-illustrated by recent studies of lek-breeding mammals that were initially thought to offer opportunities to assess female mating preferences uncontaminated by the effects of male competition. However, detailed studies of mammalian leks suggest that male competition for particular territories, as well as individual differences in the capacity of males to exclude marauders and retain females in their territory, probably has an important influence on male success, and even evidence that females are more likely to mate with particular males per unit time spent on their territories is not necessarily an indication of strong mating preferences. The most convincing evidence for female mate choice in mammals comes from studies of captive mammals—mostly rodents—carried out under controlled conditions where the effects of male competition can be excluded and where it is possible to demonstrate that females are attracted to particular categories of males (Gosling et al. 2000; Gosling and Roberts 2001a,b). However, even experiments of this kind have their limitations. As

several studies have demonstrated, the chance that particular males will attract the attention of females does not necessarily reflect the probability that they will indeed mate with them, and mating frequency is not always closely related to the probability of successful fertilization (Dewsbury 1982a). Moreover, as the costs and benefits of mate choice in captive animals may differ from those that are important in natural populations, there is a danger that the extent of mate choice and the basis of female preferences in captive animals under controlled conditions differ from the usual situation in natural populations.

The limitations of existing studies on female mate choice in mammals have implications for future research. In birds, controlled experiments involving the modification of male signals in natural populations have played an important role in studies of mate choice (Andersson 1982, 1994), and male signals have been successfully manipulated under natural conditions in a number of mammals (Brotherton 1994; West and Packer 2002; Brotherton and Komers 2003; Charlton et al. 2007). Since modifying visual signals often presents major logistic problems in mammals, experiments involving the manipulation of olfactory and auditory signals used by males to attract females are now a priority. Future studies might sensibly focus on species, such as some diurnal rodents (Huck et al. 1986; Schradin and Pillay 2004; Schradin 2005a,b; Solomon and Keane 2007), in which individuals can both be easily maintained in captivity and observed in the wild, allowing controlled experiments on female choices under captive conditions to be integrated with experimental and observational approaches in natural populations.

As yet, there is no clear indication that female mate choice is either less important or is less likely to be maintained by indirect benefits in mammals than in birds. Empirical research suggests that the male characteristics favored by female mammals cover much the same range as in birds. These include female preferences for males likely to be successful in competitive interactions, individuals with condition-related displays or secondary sexual characters, unrelated or

genetically compatible partners, and, in some species, the preference for mating with multiple partners. Some female preferences, such as those for mating with dominant partners, appear likely to be maintained by direct fitness benefits. Others, such as preferences for genetically dissimilar partners, appear likely to be maintained by heritable benefits to their offspring. In many cases, benefits of both kinds are likely to be involved. However, it seems likely that there may be qualitative differences between birds and mammals in the basis upon which females select mating partners. As a result of the prevalence of coercive tactics in male mammals and their potentially high costs to females (Smuts and Smuts 1993; Clutton-Brock and Parker 1995), female mammals may show stronger preferences than female birds for mating partners capable of providing adequate protection against other males, which may help to explain why they commonly select for more competitive partners or individuals with high testosterone levels. Conversely, since male contributions to rearing offspring are typically larger in birds than mammals, female birds may more commonly favor partners that are likely to invest heavily in parental care and may be less likely to select competitive partners if they are likely to contribute less to parental care. Whether female mammals, like female birds, commonly adjust their level of parental investment in relation to the quality of their

partner has yet to be investigated, but trends of this kind might be expected (Sheldon 2000).

The perception that female mate choice is less highly developed and that it less commonly involves preferences for male characteristics associated with genetic quality in mammals than in birds has probably arisen partly because of differences in the relative importance of visual and olfactory signaling modalities in the two groups. The evolution in many birds of elaborate plumage that is more highly developed in males suggests the importance of mate choice and indicates the cues that females are likely to use in choosing mates, whereas the elaboration of male olfactory signaling in mammals is less obvious to human observers. Both the complexity of olfactory signals and the extent of sexual dimorphism in signal structure have still been rather sparsely explored (Roberts and Gosling 2003), and it is possible that in some mammals, males produce olfactory signals that match the elaboration and complexity of the peacock's tail (Petrie et al. 1991) or the sedge warbler's song (Catchpole 1980).

#### ACKNOWLEDGMENTS

We are grateful to Maurice Gosling, Marc Hauser, Marion Petrie, James Thomson, Richard Wrangham, and two anonymous referees for their comments.

#### REFERENCES

- Agrell J., Wolff J. O., Ylönen H. 1998. Counter-strategies to infanticide in mammals: costs and consequences. *Oikos* 83:507–517.
- Alberts S. C., Watts H. E., Altmann J. 2003. Queuing and queue-jumping: long-term patterns of reproductive skew in male savannah baboons *Papio cynocephalus*. *Animal Behaviour* 65(4):821–840.
- Alexander B. K. 1970. Parental behaviour of adult male Japanese monkeys. *Behaviour* 36:270–285.
- Alexander R. D., Hoogland J. L., Howard R. D., Noonan K. M., Sherman P. W. 1979. Sexual dimorphism and breeding systems in pinnipeds, ungulates, primates and humans. Pages 402–435 in *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective*, edited by N. A. Chagnon and W. Irons. North Scituate (MA): Duxbury Press.
- Alvarez F. 1990. Horns and fighting in male Spanish ibex, *Cara pyrenaica*. *Journal of Mammalogy* 71(4): 608–616.
- Amos W., Wilmer J. W., Kokko H. 2001. Do female grey seals select genetically diverse mates? *Animal Behaviour* 62(1):157–164.
- Andersson M. 1982. Female choice selects for extreme tail length in a widowbird. *Nature* 299:818–820.
- Andersson M. 1994. *Sexual Selection*. Princeton (NJ): Princeton University Press.

- Austin D., Dewsbury D. A. 1986. Reproductive capacity of male laboratory rats. *Physiology and Behavior* 37(4):627–632.
- Baker A. J., Dietz J. M., Kleiman D. G. 1993. Behavioural evidence for monopolization of paternity in multi-male groups of golden lion tamarins. *Animal Behaviour* 46(6):1091–1103.
- Balmford A. P. 1990. Lekking in Uganda kob. Ph.D. diss., University of Cambridge.
- Balmford A. P. 1991. Mate choice on leks. *Trends in Ecology and Evolution* 6:87–92.
- Balmford A. P., Albon S. D., Blakeman S. 1992. Correlates of male mating success and female choice in a lek-breeding antelope. *Behavioral Ecology* 3(2):112–123.
- Barnard C. J., Behnke J. M., Gage A. R., Brown H., Smithurst P. R. 1998. The role of parasite-induced immunodepression, rank and social environment in the modulation of behaviour and hormone concentration in male laboratory mice (*Mus musculus*). *Proceedings of the Royal Society of London, Series B: Biological Sciences* 265(1397):693–701.
- Barrette C., Vandal D. 1986. Social rank, dominance, antler size, and access to food in snow-bound wild woodland caribou. *Behaviour* 97(1–2):118–145.
- Bateson P. P. G. 1983. Optimal outbreeding. Pages 257–277 in *Mate Choice*, edited by P. P. G. Bateson. Cambridge (UK): Cambridge University Press.
- Beatty R. A. 1960. Fertility of mixed semen from different rabbits. *Journal of Reproduction and Fertility* 1:52–60.
- Beauchamp G. K., Yamazaki K., Bard J., Boyse E. A. 1988. Prewaning experience in the control of mating preferences by genes in the major histocompatibility complex of the mouse. *Behavior Genetics* 18(4):537–547.
- Bebie N., McElligott A. G. 2006. Female aggression in red deer: does it indicate competition for mates? *Mammalian Biology* 71(6):347–355.
- Berteaux D., Boutin S. 2000. Breeding dispersal in female North American red squirrels. *Ecology* 81(5):1311–1326.
- Bertram B. C. R. 1976. Kin selection in lions and in evolution. Pages 281–301 in *Growing Points in Ethology*, edited by P. P. G. Bateson and R. A. Hinde. Cambridge (UK): Cambridge University Press.
- Birdsall D. A., Nash D. 1973. Occurrence of successful multiple insemination of females in natural populations of deer mice (*Peromyscus maniculatus*). *Evolution* 27(1):106–110.
- Bolhuis J. J., Strijkstra A. M., Moor E., van der Lende K. 1988. Preferences for odours of conspecific non-siblings in the common vole, *Microtus arvalis*. *Animal Behaviour* 36(5):1551–1553.
- Borries C., Launhardt K., Epplen C., Epplen J. T., Winkler P. 1999. Males as infant protectors in Hanuman langurs (*Presbytis entellus*) living in multilevel groups—defence pattern, paternity and sexual behaviour. *Behavioral Ecology and Sociobiology* 46(5):350–356.
- Bradbury J. W., Gibson R. M., McCarthy C. E., Vehrencamp S. L. 1989. Dispersion of displaying male sage grouse. *Behavioral Ecology and Sociobiology* 24(1):1–14.
- Bro-Jørgensen J. 2002. Overt female mate competition and preference for central males in a lekking antelope. *Proceedings of the National Academy of Sciences USA* 99(14):9290–9293.
- Bro-Jørgensen J., Durant S. M. 2003. Mating strategies of topi bulls: getting in the centre of attention. *Animal Behaviour* 65(3):585–594.
- Brotherton P. N. M. 1994. The evolution of monogamy in the dik-dik. Ph.D. diss., University of Cambridge.
- Brotherton P. N. M., Komers P. E. 2003. Mate guarding and the evolution of social monogamy in mammals. Pages 42–58 in *Monogamy: Mating Strategies and Partnerships in Birds, Humans and Other Mammals*, edited by U. H. Reichard and C. Boesch. Cambridge (UK): Cambridge University Press.
- Brotherton P. N. M., Pemberton J. M., Komers P. E., Malarky G. 1997. Genetic and behavioural evidence of monogamy in a mammal, Kirk's dik-dik (*Madoqua kirkii*). *Proceedings of the Royal Society of London, Series B: Biological Sciences* 264(1382):675–681.
- Brown W. M., Cronk L., Grochow K., Jacobson A., Liu C. K., Popović Z., Trivers R. 2005. Dance reveals symmetry especially in young men. *Nature* 438(7071):1148–1150.
- Buchan J. C., Alberts S. C., Silk J. B., Altmann J. 2003. True paternal care in a multi-male primate society. *Nature* 425(6954):179–181.
- Byers J. A., Moodie J. D., Hall N. 1994. Pronghorn females choose vigorous mates. *Animal Behaviour* 47(1):33–43.
- Carbone C., Taborsky M. 1996. Mate choice or harassment avoidance? A question of female control at the lek. *Behavioral Ecology* 7(3):370–373.
- Carranza J., Valencia J. 1999. Red deer females collect on male clumps at mating areas. *Behavioral Ecology* 10(5):525–532.
- Carroll L. S., Penn D. J., Potts W. K. 2002. Discrimination of MHC-derived odors by untrained mice is consistent with divergence in peptide-binding region residues. *Proceedings of the National Academy of Sciences USA* 99(4):2187–2192.
- Carroll L. S., Potts W. K. 2007. Sexual selection: using social ecology to determine fitness differences. Pages 57–67 in *Rodent Societies: An Ecological and Evolutionary Perspective*, edited by J. O. Wolff and P. W. Sherman. Chicago (IL): University of Chicago Press.
- Cassini M. H. 1999. The evolution of reproductive

- systems in pinnipeds. *Behavioral Ecology* 10(5):612–616.
- Catchpole C. K. 1980. Sexual selection and the evolution of complex songs among European warblers of the genus *Acrocephalus*. *Behaviour* 74(1–2): 149–166.
- Chaine A. S., Lyon B. E. 2008. Adaptive plasticity in female mate choice dampens sexual selection on male ornaments in the lark bunting. *Science* 319(5862):459–463.
- Charlton B. D., Reby D., McComb K. 2007. Female red deer prefer the roars of larger males. *Biology Letters* 3(4):382–385.
- Clayton D. H. 1991. The influence of parasites on host sexual selection. *Parasitology Today* 7(12):329–334.
- Clutton-Brock T. H. 1982. The functions of antlers. *Behaviour* 79(2–4):108–125.
- Clutton-Brock T. H. 1988. Reproductive success. Pages 472–485 in *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems*, edited by T. H. Clutton-Brock. Chicago (IL): University of Chicago Press.
- Clutton-Brock T. H. 1989. Female transfer and inbreeding avoidance in social mammals. *Nature* 337(6202):70–71.
- Clutton-Brock T. H. 2004. What is sexual selection? Pages 24–36 in *Sexual Selection in Primates: New and Comparative Perspectives*, edited by P. M. Kappeler and C. P. van Schaik. Cambridge (UK): Cambridge University Press.
- Clutton-Brock T. H., Albon S. D. 1979. The roaring of red deer and the evolution of honest advertisement. *Behaviour* 69(3–4):145–170.
- Clutton-Brock T. H., Albon S. D., Guinness F. E. 1988a. Reproductive success in male and female red deer. Pages 325–343 in *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems*, edited by T. H. Clutton-Brock. Chicago (IL): University of Chicago Press.
- Clutton-Brock T. H., Deutsch J. C., Nefdt R. J. C. 1993. The evolution of ungulate leks. *Animal Behaviour* 46(6):1121–1138.
- Clutton-Brock T. H., Green D., Hiraiwa-Hasegawa M., Albon S. D. 1988b. Passing the buck: resource defence, lek breeding and mate choice in fallow deer. *Behavioral Ecology and Sociobiology* 23(5):281–296.
- Clutton-Brock T. H., Guinness F. E., Albon S. D. 1982. *Red Deer: Behavior and Ecology of Two Sexes*. Chicago (IL): University of Chicago Press.
- Clutton-Brock T. H., Harvey P. H. 1977. Primate ecology and social organization. *Journal of Zoology* 183(1):1–39.
- Clutton-Brock T. H., Hiraiwa-Hasegawa M., Robertson A. 1989. Mate choice on fallow deer leks. *Nature* 340(6233):463–465.
- Clutton-Brock T. H., Hodge S. J., Spong G., Russell A. F., Jordan N. R., Bennett N. C., Sharpe L. L., Manser M. B. 2006. Intrasexual competition and sexual selection in cooperative mammals. *Nature* 444(7122):1065–1068.
- Clutton-Brock T., Isvaran K. 2006. Paternity loss in contrasting mammalian societies. *Biology Letters* 2(4):513–516.
- Clutton-Brock T. H., McComb K. 1993. Experimental tests of copying and mate choice in fallow deer (*Dama dama*). *Behavioral Ecology* 4(3):191–193.
- Clutton-Brock T. H., McComb K. E., Deutsch J. C. 1996. Multiple factors affect the distribution of females in lek-breeding ungulates: a rejoinder to Carbone and Taborsky. *Behavioral Ecology* 7(3): 373–378.
- Clutton-Brock T. H., Parker G. A. 1992. Potential reproductive rates and the operation of sexual selection. *Quarterly Review of Biology* 67(4):437–456.
- Clutton-Brock T. H., Parker G. A. 1995. Sexual coercion in animal societies. *Animal Behaviour* 49(5): 1345–1365.
- Colegrave N., Kotiaho J. S., Tomkins J. L. 2002. Mate choice or polyandry: reconciling genetic compatibility and good genes sexual selection. *Evolutionary Ecology Research* 4:911–917.
- Coltman D. W., Festa-Bianchet M., Jorgensen J. T., Strobeck C. 2002. Age-dependent sexual selection in bighorn rams. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 269(1487):165–172.
- Constable J. L., Ashley M. V., Goodall J., Pusey A. E. 2001. Noninvasive paternity assessment in Gombe chimpanzees. *Molecular Ecology* 10(5):1279–1300.
- Cooney R., Bennett N. C. 2000. Inbreeding avoidance and reproductive skew in a cooperative mammal. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 267(1445):801–806.
- Cords M., Mitchell B. J., Tsingalia H. M., Rowell T. E. 1986. Promiscuous mating among blue monkeys in the Kakamega Forest, Kenya. *Ethology* 72:214–226.
- Cox C. R., Le Boeuf B. J. 1977. Female incitation of male competition: a mechanism in sexual selection. *American Naturalist* 111(978):317–335.
- Craul M., Zimmermann E., Radespiel U. 2004. First experimental evidence for female mate choice in a nocturnal primate. *Primates* 45(4):271–274.
- Darwin C. 1871. *The Descent of Man, and Selection in Relation to Sex*. London (UK): John Murray.
- Davidson S. M., Wilkinson G. S. 2004. Function of male song in the greater white-lined bat, *Saccopteryx bilineata*. *Animal Behaviour* 67(5):883–891.
- Desjardins C., Maruniak J. A., Bronson F. H. 1973. Social rank in house mice—differentiation revealed by ultraviolet visualization of urinary marking patterns. *Science* 182(4115):939–941.
- Deutsch J. C. 1994. Uganda kob mating success does



- not increase on larger leks. *Behavioral Ecology and Sociobiology* 34(6):451–459.
- Deutsch J. C., Nefdt R. J. C. 1992. Olfactory cues influence female choice in two lek-breeding antelopes. *Nature* 356(6370):596–598.
- Dewsbury D. A. 1982a. Dominance rank, copulatory behaviour, and differential reproduction. *Quarterly Review of Biology* 57(2):135–159.
- Dewsbury D. A. 1982b. Ejaculate cost and male choice. *American Naturalist* 119(5):601–610.
- Dewsbury D. A. 1982c. Pregnancy blockage following multiple-male copulation or exposure at the time of mating in deer mice, *Peromyscus maniculatus*. *Behavioral Ecology and Sociobiology* 11(1):37–42.
- Dewsbury D. A. 1988. Kin discrimination and reproductive behavior in muroid rodents. *Behavior Genetics* 18(4):525–536.
- Dewsbury D. A., Baumgardner D. J. 1981. Studies of sperm competition in two species of muroid rodents. *Behavioral Ecology and Sociobiology* 9(2):121–133.
- Ditchkoff S. S., Lochmiller R. L., Masters R. E., Hooper S. R., Van Den Bussche R. A. 2001. Major-histocompatibility-complex-associated variation in secondary sexual traits of white-tailed deer (*Odocoileus virginianus*): evidence for good-genes advertisement. *Evolution* 55(3):616–625.
- Drickamer L. C. 1992. Estrous female house mice discriminate dominant from subordinate males and sons of dominant from sons of subordinate males by odor cues. *Animal Behaviour* 43(5):868–870.
- Dugatkin L. A. 1992. Sexual selection and imitation: females copy the mate choice of others. *American Naturalist* 139(6):1384–1389.
- Dunbar R. I. M. 1984. *Reproductive Decisions: An Economic Analysis of Gelada Baboon Social Strategies*. Princeton (NJ): Princeton University Press.
- East M. L., Burke T., Wilhelm K., Greig C., Hofer H. 2003. Sexual conflicts in spotted hyenas: male and female mating tactics and their reproductive outcome with respect to age, social status and tenure. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 270(1521):1247–1254.
- Ebensperger L. A. 1998a. Strategies and counterstrategies to infanticide in mammals. *Biological Reviews* 73(3):321–346.
- Ebensperger L. A. 1998b. Do female rodents use promiscuity to prevent male infanticide? *Ethology Ecology and Evolution* 10(2):129–141.
- Egid K., Brown J. L. 1989. The major histocompatibility complex and female mating preferences in mice. *Animal Behaviour* 38(3):548–549.
- Ehman K. D., Scott M. E. 2001. Urinary odour preferences of MHC congenic female mice, *Mus domesticus*: implications for kin recognition and detection of parasitized males. *Animal Behaviour* 62(4):781–789.
- Ehman K. D., Scott M. E. 2002. Female mice mate preferentially with non-parasitized males. *Parasitology* 125(5):461–466.
- Eisenberg J. F. 1966. The social organisation of mammals. *Handbook of Zoology* 8:1–92.
- Eisenberg J. F. 1981. *The Mammalian Radiations: An Analysis of Trends in Evolution, Adaptation, and Behavior*. Chicago (IL): University of Chicago Press.
- Enriquez F. J., Zidian J. L., Cypess R. H. 1988. *Nematospiroides dubius*—genetic control of immunity to infections of mice. *Experimental Parasitology* 67(1):12–19.
- Ens B. J., Safrieli U. N., Harris M. P. 1993. Divorce in the long-lived and monogamous oystercatcher, *Haematopus ostralegus*: incompatibility or choosing the better option? *Animal Behaviour* 45(6):1199–1217.
- Espmark Y. 1964. Rutting behaviour in reindeer (*Rangifer tarandus L.*). *Animal Behaviour* 12(1):159–163.
- Fawcett T. W., Johnstone R. A. 2003. Mate choice in the face of costly competition. *Behavioral Ecology* 14(6):771–779.
- Fedigan L. M. 1983. Dominance and reproductive success in primates. *Yearbook of Physical Anthropology* 26:91–129.
- Ferkin M. H. 1990. Kin recognition and social behavior in microtine rodents. Pages 11–24 in *Social Systems and Population Cycles in Voles*, edited by R. H. Tamarin et al. Basel (Switzerland): Birkhäuser.
- Ferrari S. F. 1992. The care of infants in a wild marmoset (*Callithrix flaviceps*) group. *American Journal of Primatology* 26(2):109–118.
- Foerster K., Delhey K., Johnsen A., Lifjeld J. T., Kempenaers B. 2003. Females increase offspring heterozygosity and fitness through extra-pair matings. *Nature* 425(6959):714–717.
- Folstad I., Karter A. J. 1992. Parasites, bright males, and the immunocompetence handicap. *American Naturalist* 139(3):603–622.
- Fox E. A. 2002. Female tactics to reduce sexual harassment in the Sumatran orangutan (*Pongo pygmaeus abelii*). *Behavioral Ecology and Sociobiology* 52(2):93–101.
- Freeland W. J. 1981. Parasitism and behavioral dominance among male mice. *Science* 213(4506):461–462.
- Galef B. G., Jr., Lim T. C. W., Gilbert G. S. 2008. Evidence of mate choice copying in Norway rats, *Rattus norvegicus*. *Animal Behaviour* 75(3):1117–1123.
- Gartlan J. S., Brain C. K. 1968. Ecology and social variability in *Cercopithecus aethiops* and *C. mitis*. Pages 253–292 in *Primates: Studies in Adaptation and Variability*, edited by P. C. Jay. New York (NY): Holt, Rinehart and Winston.



- Gavish L., Hofmann J. E., Getz L. L. 1984. Sibling recognition in the prairie vole, *Microtus ochrogaster*. *Animal Behaviour* 32(2):362–366.
- Geist V. 1971. *Mountain Sheep: A Study in Behavior and Evolution*. Chicago (IL): University of Chicago Press.
- Gentry R. L., Kooyman G. L. (editors). 1986. *Fur Seals: Maternal Strategies on Land and at Sea*. Princeton (NJ): Princeton University Press.
- Gerald M. S. 2001. Primate colour predicts social status and aggressive outcome. *Animal Behaviour* 61(3):559–566.
- Gerald M. S. 2003. How color may guide the primate world: possible relationships between sexual selection and sexual dichromatism. Pages 141–171 in *Sexual Selection and Reproductive Competition in Primates: New Perspectives and Directions*, edited by C. B. Jones. Norman (OK): American Society of Primatologists.
- Gilder P. M., Slater P. J. B. 1978. Interest of mice in conspecific male odors is influenced by degree of kinship. *Nature* 274(5669):364–365.
- Goldizen A. W. 1987. Tamarins and marmosets: communal care of offspring. Pages 34–43 in *Primate Societies*, edited by B. B. Smuts et al. Chicago (IL): University of Chicago Press.
- Gosling L. M., Roberts S. C. 2001a. Scent-marking by male mammals: cheat-proof signals to competitors and mates. *Advances in the Study of Behavior* 30:169–217.
- Gosling L. M., Roberts S. C. 2001b. Testing ideas about the function of scent marks in territories from spatial patterns. *Animal Behaviour* 62(3):F7–F10.
- Gosling L. M., Roberts S. C., Thornton E. A., Andrew M. J. 2000. Life history costs of olfactory status signalling in mice. *Behavioral Ecology and Sociobiology* 48(4):328–332.
- Greenwood P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28(4):1140–1162.
- Hausfater G., Watson D. F. 1976. Social and reproductive correlates of parasite ova emissions by baboons. *Nature* 262(5570):688–689.
- Hayashi S. 1990. Social condition influences sexual attractiveness of dominant male mice. *Zoological Science* 7:889–894.
- Hedrick P. W., Black F. L. 1997. HLA and mate selection: no evidence in South Amerindians. *American Journal of Human Genetics* 61(3):505–511.
- Hemelrijk C. K., Meier C., Martin R. D. 1999. 'Friendship' for fitness in chimpanzees? *Animal Behaviour* 58(6):1223–1229.
- Hess E. A., Ludwick T., Rickard H. C., Ely F. 1954. Some of the influences of mixed ejaculates upon bovine fertility. *Journal of Dairy Science* 37(6):649–650.
- Hiebert S. M., Stoddard P. K., Arcese P. 1989. Repertoire size, territory acquisition and reproductive success in the song sparrow. *Animal Behaviour* 37(2):266–273.
- Hillgarth N., Wingfield J. C. 1997. Parasite-mediated sexual selection: endocrine aspects. Pages 78–104 in *Host-Parasite Evolution: General Principles and Avian Models*, edited by D. H. Clayton and J. Moore. Oxford (UK): Oxford University Press.
- Hohoff C., Franzen K., Sachser N. 2003. Female choice in a promiscuous wild guinea pig, the yellow-toothed cavy (*Galea musteloides*). *Behavioral Ecology and Sociobiology* 53(6):341–349.
- Holand Ø., Askim K. R., Røed K. H., Weladji R. B., Gjøstein H., Nieminen M. 2007. No evidence of inbreeding avoidance in a polygynous ungulate: the reindeer (*Rangifer tarandus*). *Biology Letters* 3(1):36–39.
- Holekamp K. E., Smale L. 2000. Feisty females and meek males: reproductive strategies in the spotted hyena. Pages 257–285 in *Reproduction in Context: Social and Environmental Influences on Reproductive Physiology and Behavior*, edited by K. Wallen and J. E. Schneider. Cambridge (MA): MIT Press.
- Hoogland J. L. 2001. Black-tailed, Gunnison's, and Utah prairie dogs reproduce slowly. *Journal of Mammalogy* 82(4):917–927.
- Horne T. J., Ylönen H. 1998. Heritabilities of dominance-related traits in male bank voles (*Clethrionomys glareolus*). *Evolution* 52(3):894–899.
- Hrdy S. B. 1981. *The Woman That Never Evolved*. Cambridge (MA): Harvard University Press.
- Huck U. W., Banks E. M. 1982. Male dominance status, female choice and mating success in the brown lemming, *Lemmus trimucronatus*. *Animal Behaviour* 30(3):665–675.
- Huck U. W., Lisk R. D., Allison A., van Dongen C. G. 1986. Determinants of mating success in the golden hamster (*Mesocricetus auratus*): social dominance and mating tactics under semi-natural conditions. *Animal Behaviour* 34(4):971–989.
- Humphries R. E., Robertson D. H. L., Beynon R. J., Hurst J. L. 1999. Unravelling the chemical basis of competitive scent marking in house mice. *Animal Behaviour* 58(6):1177–1190.
- Huxley J. S. 1938. Darwin's theory of sexual selection and the data subsumed by it, in the light of recent research. *American Naturalist* 72(742):416–433.
- Janson C. H. 1984. Female choice and mating system of the brown capuchin monkey, *Cebus apella* (Primates: Cebidae). *Zeitschrift für Tierpsychologie* 65: 177–200.
- Jennions M. D., Petrie M. 2000. Why do females mate multiply? A review of the genetic benefits. *Biological Reviews* 75(1):21–64.
- Johnston R. E., Sorokin E. S., Ferkin M. H. 1997. Scent counter-marking by male meadow voles: fe-

- males prefer the top-scent male. *Ethology* 103:443–453.
- Johnston V. S., Hagel R., Franklin M., Fink B., Grammer K. 2001. Male facial attractiveness: evidence for hormone-mediated adaptive design. *Evolution and Human Behavior* 22(4):251–267.
- Jolly A. 1966. *Lemur Behavior: A Madagascar Field Study*. Chicago (IL): University of Chicago Press.
- Jones B. C., DeBruine L. M., Little A. C., Burriss R. P., Feinberg D. R. 2007. Social transmission of face preferences among humans. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 274(1611):899–903.
- Jordan W. C., Bruford M. W. 1998. New perspectives on mate choice and the MHC. *Heredity* 81(2):127–133.
- Kavaliers M., Colwell D. D. 1995a. Discrimination by female mice between the odours of parasitized and non-parasitized males. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 261(1360):31–35.
- Kavaliers M., Colwell D. D. 1995b. Odours of parasitized males induce aversive responses in female mice. *Animal Behaviour* 50(5):1161–1169.
- Keddy-Hector A. C. 1992. Mate choice in non-human primates. *American Zoologist* 32:62–70.
- Keddy-Hector A. C., Wilczynski W., Ryan M. J. 1989. Intraspecific variation in the tuning of female cricket frogs. *American Zoologist* 29:16A.
- Keil A., Sachser N. 1998. Reproductive benefits from female promiscuous mating in a small mammal. *Ethology* 104(11):897–903.
- Keller L. F., Waller D. M. 2002. Inbreeding effects in wild populations. *Trends in Ecology and Evolution* 17(5):230–241.
- Kleiman D. G. 1977. Monogamy in mammals. *Quarterly Review of Biology* 52(1):39–69.
- Klein S. L., Gamble H. R., Nelson R. J. 1999. *Trichinella spiralis* infection in voles alters female odor preference but not partner preference. *Behavioral Ecology and Sociobiology* 45(5):323–329.
- Kraaijeveld K., Kraaijeveld-Smit F. J. L., Komdeur J. 2007. The evolution of mutual ornamentation. *Animal Behaviour* 74(4):657–677.
- Krackow S., Matuschak B. 1991. Mate choice for non-siblings in wild house mice: evidence from a choice test and a reproductive test. *Ethology* 88:99–108.
- Krames L., Mastromatteo L. A. 1973. Role of olfactory stimuli during copulation in male and female rats. *Journal of Comparative and Physiological Psychology* 85(3):528–535.
- Kruuk L. E. B., Slate J., Pemberton J. M., Clutton-Brock T. H. 2003. Fluctuating asymmetry in a secondary sexual trait: no associations with individual fitness, environmental stress or inbreeding, and no heritability. *Journal of Evolutionary Biology* 16(1):101–113.
- Kuester J., Paul A. 1992. Influence of male competition and female mate choice on male mating success in Barbary macaques (*Macaca sylvanus*). *Behaviour* 120:192–217.
- Künkele J., Hoeck H. N. 1995. Communal suckling in the cavy *Galea musteloides*. *Behavioral Ecology and Sociobiology* 37(6):385–391.
- Le Boeuf B. J., Mesnick S. 1991. Sexual behaviour of male northern elephant seals: I. Lethal injuries to adult females. *Behaviour* 116(1–2):143–162.
- Leuthold W. 1966. Variations in territorial behaviour of Uganda kob *Adenota kob thomasi* (Neumann 1896). *Behaviour* 27(1–2):215–256.
- Lincoln G. A. 1994. Teeth, horns and antlers: the weapons of sex. Pages 131–158 in *The Differences Between Sexes*, edited by R. V. Short and E. Balaban. Cambridge (UK): Cambridge University Press.
- Loehle C. 1997. The pathogen transmission avoidance theory of sexual selection. *Ecological Modelling* 103(2–3):231–250.
- Manson J. H. 1992. Measuring female mate choice in Cayo Santiago rhesus macaques. *Animal Behaviour* 44(3):405–416.
- Manson J. H. 1994a. Male aggression: a cost of female mate choice in Cayo Santiago rhesus macaques. *Animal Behaviour* 48(2):473–475.
- Manson J. H. 1994b. Mating patterns, mate choice, and birth season heterosexual relationships in free-ranging rhesus macaques. *Primates* 35(4):417–433.
- Manson J. H. 2006. Mate choice. Pages 447–463 in *Primates in Perspective*, edited by C. J. Campbell et al. Oxford (UK): Oxford University Press.
- Matsumoto-Oda A. 1999. Female choice in the opportunistic mating of wild chimpanzees (*Pan troglodytes schweinfurthii*) at Mahale. *Behavioral Ecology and Sociobiology* 46(4):258–266.
- Mays H. L., Jr., Hill G. E. 2004. Choosing mates: good genes versus genes that are a good fit. *Trends in Ecology and Evolution* 19(10):554–559.
- McComb K. 1987. Roaring by red deer stags advances the date of oestrus in hinds. *Nature* 330(6149):648–649.
- McComb K. 1991. Female choice for high roaring rates in red deer, *Cervus elaphus*. *Animal Behaviour* 41(1):79–88.
- McComb K., Clutton-Brock T. H. 1994. Is mate choice copying or aggregation responsible for skewed distributions of females on leks? *Proceedings of the Royal Society of London, Series B: Biological Sciences* 255(1342):13–19.
- McElligott A. G., Hayden T. J. 2001. Postcopulatory vocalizations of fallow bucks: who is listening? *Behavioral Ecology* 12(1):41–46.
- McMahon C. R., Bradshaw C. J. A. 2004. Harem

- choice and breeding experience of female southern elephant seals influence offspring survival. *Behavioral Ecology and Sociobiology* 55(4):349–362.
- Milinski M. 2003. The function of mate choice in sticklebacks: optimizing *Mhc* genetics. *Journal of Fish Biology* 63(supplement 1):1–16.
- Milinski M., Wedekind C. 2001. Evidence for MHC-correlated perfume preferences in humans. *Behavioral Ecology* 12(2):140–149.
- Møller A. P., Cuervo J. J., Soler J. J., Zamora-Muoz C. 1996. Horn asymmetry and fitness in gemsbok, *Oryx g. gazella*. *Behavioral Ecology* 7(3):247–253.
- Møller A. P., Pomiankowski A. 1993. Fluctuating asymmetry and sexual selection. *Genetica* 89(1–3):267–279.
- Møller A. P., Swaddle J. P. 1997. *Asymmetry, Developmental Stability, and Evolution*. Oxford (UK): Oxford University Press.
- Moore W. G., Marchinton R. L. 1974. Marking behaviour and its social function in white-tailed deer. Pages 447–456 in *The Behaviour of Ungulates and its Relation to Management*, edited by V. Geist and F. Walther. Morges (Switzerland): International Union for the Conservation of Nature Publications.
- Mossman C. A., Drickamer L. C. 1996. Odor preferences of female house mice (*Mus domesticus*) in seminatural enclosures. *Journal of Comparative Psychology* 110:131–138.
- Mysterud A., Meisingset E., Langvatn R., Yoccoz N. G., Stenseth N. C. 2005. Climate-dependent allocation of resources to secondary sexual traits in red deer. *Oikos* 111(2):245–252.
- Nefdt R. J. C., Thirgood S. J. 1997. Lekking, resource defense, and harassment in two subspecies of lechwe antelope. *Behavioural Ecology* 8(1):1–9.
- Novotny M., Harvey S., Jemiolo B. 1990. Chemistry of male dominance in the house mouse, *Mus domesticus*. *Cellular and Molecular Life Sciences* 46(1):109–113.
- Ober C., Weitkamp L. R., Cox N., Dytch H., Kostyu D., Elias S. 1997. HLA and mate choice in humans. *American Journal of Human Genetics* 61(3):497–504.
- Packer C. 1979. Inter-troop transfer and inbreeding avoidance in *Papio anubis*. *Animal Behaviour* 27(1):1–36.
- Packer C. 1983. Sexual dimorphism: the horns of African antelopes. *Science* 221(4616):1191–1193.
- Packer C., Gilbert D. A., Pusey A. E., O'Brien S. J. 1991. A molecular genetic analysis of kinship and cooperation in African lions. *Nature* 351(6327):562–565.
- Packer C., Herbst L., Pusey A. E., Bygott J. D., Hanby J. P., Cairns S. J., Borgerhoff Mulder M. 1988. Reproductive success of lions. Pages 363–383 in *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems*, edited by T. H. Clutton-Brock. Chicago (IL): University of Chicago Press.
- Paterson S., Pemberton J. M. 1997. No evidence for major histocompatibility complex-dependent mating patterns in a free-living ruminant population. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 264(1389):1813–1819.
- Pemberton J. 2004. Measuring inbreeding depression in the wild: the old ways are the best. *Trends in Ecology and Evolution* 19(12):613–615.
- Pemberton J. M., Albon S. D., Guinness F. E., Clutton-Brock T. H., Dover G. A. 1992. Behavioral estimates of male mating success tested by DNA fingerprinting in a polygynous mammal. *Behavioral Ecology* 3(1):66–75.
- Penn D. J. 2002. The scent of genetic compatibility: sexual selection and the major histocompatibility complex. *Ethology* 108(1):1–21.
- Penn D., Potts W. 1998a. MHC-disassortative mating preferences reversed by cross-fostering. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 265(1403):1299–1306.
- Penn D., Potts W. K. 1998b. Chemical signals and parasite-mediated sexual selection. *Trends in Ecology and Evolution* 13(10):391–396.
- Penn D. J., Potts W. K. 1999. The evolution of mating preferences and major histocompatibility complex genes. *American Naturalist* 153(2):145–164.
- Penton-Voak I. S., Perrett D. I., Castles D. L., Kobayashi T., Burt D. M., Murray L. K., Minamisawa R. 1999. Menstrual cycle alters face preference. *Nature* 399(6738):741–742.
- Pereira M. E., Weiss M. L. 1991. Female mate choice, male migration, and the threat of infanticide in ringtailed lemurs. *Behavioral Ecology and Sociobiology* 28(2):141–152.
- Petrie M., Halliday T., Sanders C. 1991. Peahens prefer peacocks with elaborate trains. *Animal Behaviour* 41(2):323–331.
- Pierce J. D., Dewsbury D. A. 1991. Female preferences for unmated versus mated males in two species of voles (*Microtus ochrogaster* and *Microtus montanus*). *Journal of Comparative and Physiological Psychology* 105(2):165–171.
- Pistorius P. A., Bester M. N., Kirkman S. P., Taylor F. E. 2001. Pup mortality in southern elephant seals at Marion Island. *Polar Biology* 24(11):828–831.
- Potts W. K., Manning C. J., Wakeland E. K. 1991. Mating patterns in seminatural populations of mice influenced by MHC genotype. *Nature* 352(6336):619–621.
- Preston B. T., Stevenson I. R., Pemberton J. M., Wilson K. 2001. Dominant rams lose out by sperm depletion. *Nature* 409(6821):681–682.
- Price E. C. 1990. Infant carrying as a courtship strat-

- egy of breeding male cotton-top tamarins. *Animal Behaviour* 40(4):784–786.
- Prichard A. K., Finstad G. L., Shain D. H. 1999. Factors affecting velvet antler weights in free-ranging reindeer in Alaska. *Rangifer* 19(2):71–76.
- Pusey A. E. 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends in Ecology and Evolution* 2(10):295–299.
- Pusey A., Wolf M. 1996. Inbreeding avoidance in animals. *Trends in Ecology and Evolution* 11(5):201–206.
- Rasmussen K. L. R. 1983. Influence of affiliative preferences upon the behaviour of male and female baboons during sexual consortships. Pages 116–120 in *Primate Social Relationships: An Integrated Approach*, edited by R. A. Hinde. Oxford (UK): Blackwell Scientific.
- Réale D., Boussès P., Chapuis J. L. 1996. Female-biased mortality induced by male sexual harassment in a feral sheep population. *Canadian Journal of Zoology* 74:1812–1818.
- Reiter J., Panken K. J., Le Boeuf B. J. 1981. Female competition and reproductive success in northern elephant seals. *Animal Behaviour* 29(3):670–687.
- Rich T. J., Hurst J. L. 1998. Scent marks as reliable signals of the competitive ability of mates. *Animal Behaviour* 56(3):727–735.
- Rich T. J., Hurst J. L. 1999. The competing countermarks hypothesis: reliable assessment of competitive ability by potential mates. *Animal Behaviour* 58(5):1027–1037.
- Ridley M. 1988. Mating frequency and fecundity in insects. *Biological Reviews* 63:509–549.
- Rikowski A., Grammer K. 1999. Human body odour, symmetry and attractiveness. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 266(1422): 869–874.
- Roberts S. C., Gosling L. M. 2003. Genetic similarity and quality interact in mate choice decisions by female mice. *Nature Genetics* 35(1):103–106.
- Robinson J. G. 1982. Intrasexual competition and mate choice in primates. *American Journal of Primatology* 3(supplement 1):131–144.
- Robinson M. R., Kruuk L. E. B. 2007. Function of weaponry in females: the use of horns in intrasexual competition for resources in female Soay sheep. *Biology Letters* 3(6):651–654.
- Rood J. P. 1972. Ecological and behavioural comparison of three genera of argentine cavies. *Animal Behaviour Monographs* 5:1–83.
- Rood J. P., Weir B. J. 1970. Reproduction in female wild guinea pigs. *Journal of Reproduction and Fertility* 23:393–409.
- Rosser A. M. 1987. Resource defence in an African antelope, the puku (*Kobus vardonii*). Ph.D. diss., University of Cambridge.
- Rosser A. M. 1992. Resource distribution, density, and determinants of mate access in puku. *Behavioral Ecology* 3(1):13–24.
- Rossiter S. J., Ransome R. D., Faulkes C. G., Le Comber S. C., Jones G. 2005. Mate fidelity and intra-lineage polygyny in greater horseshoe bats. *Nature* 437(7057):408–411.
- Rubenstein D. I. 1986. Ecology and sociality in horses and zebras. Pages 282–302 in *Ecological Aspects of Social Evolution*, edited by D. I. Rubenstein and R. W. Wrangham. Princeton (NJ): Princeton University Press.
- Salo A. L., Dewsbury D. A. 1995. Three experiments on mate choice in meadow voles *Microtus pennsylvanicus*. *Journal of Comparative Psychology* 109(1): 42–46.
- Sawyer T. G., Marchinton R. L., Miller K. V. 1989. Response of female white-tailed deer to scrapes and antler rubs. *Journal of Mammalogy* 70(2):431–433.
- Schradin C., Pillay N. 2004. The striped mouse (*Rhabdomys pumilio*) from the succulent Karoo, South Africa: a territorial group-living solitary forager with communal breeding and helpers at the nest. *Journal of Comparative Psychology* 118(1):37–47.
- Schradin C., Pillay N. 2005a. The influence of the father on offspring development in the striped mouse. *Behavioral Ecology* 16(2):450–455.
- Schradin C., Pillay N. 2005b. Intraspecific variation in the spatial and social organization of the African striped mouse. *Journal of Mammalogy* 86:99–107.
- Schwagmeyer P. L. 1984. Multiple mating and intersexual selection in the thirteen-lined ground squirrels. Pages 275–293 in *The Biology of Ground-Dwelling Squirrels*, edited by J. O. Murie and G. R. Michener. Lincoln (NE): University Press of Nebraska.
- Schwagmeyer P. L. 1986. Effects of multiple mating on reproduction in female thirteen-lined ground squirrels. *Animal Behaviour* 34(1):297–298.
- Schwagmeyer P. L., Brown C. H. 1983. Factors affecting male-male competition in thirteen-lined ground squirrels. *Behavioral Ecology and Sociobiology* 13(1): 1–6.
- Schwagmeyer P. L., Parker G. A. 1987. Queueing for males in thirteen-lined ground squirrels. *Animal Behaviour* 35(4):1015–1025.
- Schwagmeyer P. L., Wootner S. J. 1985. Mating competition in an asocial ground squirrel, *Spermophilus tridecemlineatus*. *Behavioral Ecology and Sociobiology* 17(3):291–296.
- Schwarz-Weig E., Sachser N. 1996. Social behaviour, mating system and testes size in cuis (*Galea musteloides*). *Zeitschrift für Säugetierkunde-International Journal of Mammalian Biology* 61:25–38.
- Setchell J. M. 2005. Do female mandrills (*Mandrillus sphinx*) prefer brightly colored males? *International Journal of Primatology* 26:715–735.



- Setchell J. M., Dixson A. F. 2001. Changes in the secondary sexual adornments of male mandrills (*Mandrillus sphinx*) are associated with gain and loss of alpha status. *Hormones and Behavior* 39(3): 177–184.
- Seyfarth R. M. 1978a. Social relationships among adult male and female baboons. I. Behaviour during sexual consortship. *Behaviour* 64(3–4):204–226.
- Seyfarth R. M. 1978b. Social relationships among adult male and female baboons. II. Behaviour throughout the female reproductive cycle. *Behaviour* 64(3–4):227–247.
- Shapiro L. E., Dewsbury D. A. 1986. Male dominance, female choice and male copulatory behavior in two species of voles (*Microtus ochrogaster* and *Microtus montanus*). *Behavioral Ecology and Sociobiology* 18(4):267–274.
- Sheldon B. C. 2000. Differential allocation: tests, mechanisms and implications. *Trends in Ecology and Evolution* 15(10):397–402.
- Silk J. B. 2002. Using the 'F'-word in primatology. *Behaviour* 139(2–3):421–446.
- Silk J. B., Boyd R. 1983. Female cooperation, competition, and mate choice in matrilineal macaque groups. Pages 315–347 in *Social Behavior of Female Vertebrates*, edited by S. K. Wasser. New York (NY): Academic Press.
- Sivinski J. 1984. Sperm in competition. Pages 86–115 in *Sperm Competition and the Evolution of Animal Mating Systems*, edited by R. L. Smith. London (UK): Academic Press.
- Small M. F. 1988. Female primate sexual behavior and conception: are there really sperm to spare? *Current Anthropology* 29(1):81–100.
- Small M. F. 1989. Female choice in nonhuman primates. *Yearbook of Physical Anthropology* 32:103–127.
- Smuts B. B. 1985. *Sex and Friendship in Baboons*. New York: Aldine.
- Smuts B. B., Smuts R. W. 1993. Male aggression and sexual coercion of females in nonhuman primates and other mammals: evidence and theoretical implications. *Advances in the Study of Animal Behaviour* 22:1–63.
- Solomon N. G., Keane B. 2007. Reproductive strategies in female rodents. Pages 42–56 in *Rodent Societies: An Ecological and Evolutionary Perspective*, edited by J. O. Wolff and P. W. Sherman. Chicago (IL): University of Chicago Press.
- Soltis J., McElreath R. 2001. Can females gain extra paternal investment by mating with multiple males? A game theoretic approach. *American Naturalist* 158(5):519–529.
- Soltis J., Thomsen R., Matsubayashi K., Takenaka O. 2000. Infanticide by resident males and female counter-strategies in wild Japanese macaques (*Macaca fuscata*). *Behavioral Ecology and Sociobiology* 48(3):195–202.
- Spencer P. B. S., Horsup A. B., Marsh H. D. 1998. Enhancement of reproductive success through mate choice in a social rock-wallaby, *Petrogale assimilis* (Macropodidae) as revealed by microsatellite markers. *Behavioral Ecology and Sociobiology* 43(1): 1–9.
- Stein D. M. 1984. Ontogeny of infant-adult male relationships during the first year of life for yellow baboons (*Papio cynocephalus*). Pages 213–243 in *Primate Paternalism*, edited by D. M. Taub. New York: Van Nostrand Reinhold.
- Stein D. M., Stacey P. B. 1981. A comparison of infant-adult male relations in a one-male group with those in a multi-male group for yellow baboons (*Papio cynocephalus*). *Folia Primatologica* 36(3–4): 264–276.
- Stillman R. A., Clutton-Brock T. H., Sutherland W. J. 1993. Black holes, mate retention, and the evolution of ungulate leks. *Behavioral Ecology* 4(1):1–6.
- Takahata Y. 1982. Social relations between adult males and females of Japanese monkeys in Arashiyama B troop. *Primates* 23:1–23.
- Tardif S. D., Bales K. 1997. Is infant-carrying a courtship strategy in callitrichid primates? *Animal Behaviour* 53(5):1001–1007.
- Taub D. M. 1980. Female choice and mating strategies among wild Barbary macaques (*Macaca sylvanus*). Pages 287–344 in *The Macaques: Studies in Ecology, Behavior and Evolution*, edited by D. G. Lindburg. New York: Van Nostrand Reinhold Press.
- Thomas S. A. 2002. Scent marking and mate choice in the prairie vole, *Microtus ochrogaster*. *Animal Behaviour* 63(6):1121–1127.
- Thornhill R., Gangestad S. W. 1999. Facial attractiveness. *Trends in Cognitive Sciences* 3:452–460.
- Tutin C. E. G. 1979. Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioural Ecology and Sociobiology* 6(1):29–38.
- Uller T., Johansson L. C. 2003. Human mate choice and the wedding ring effect. Are married men more attractive? *Human Nature* 14(3):267–276.
- Vandenbergh J. G. 1965. Hormonal basis of sex skin in male rhesus monkeys. *General and Comparative Endocrinology* 5(1):31–34.
- Vanpé C., Gaillard J.-M., Kjellander P., Mysterud A., Magnien P., Delorme D., Van Laere G., Klein F., Liberg O., Hewison A. J. M. 2007. Antler size provides an honest signal of male phenotypic quality in roe deer. *American Naturalist* 169(4):481–493.
- vom Saal F. S. 1984. Proximate and ultimate causes of infanticide and parental behavior in male mice. Pages 401–424 in *Infanticide: Comparative and Evolutionary Perspectives*, edited by G. Hausfater and S. B. Hrdy. New York: Aldine.
- von Schantz T., Wittzell H., Göransson G., Grahn M. 1997. Mate choice, male condition-dependent or-

- namentation and MHC in the pheasant. *Hereditas* 127(1–2):133–140.
- Waitt C., Little A. C., Wolfensohn S., Honess P., Brown A. P., Buchanan-Smith H. M., Perrett D. I. 2003. Evidence from rhesus macaques suggests that male coloration plays a role in female primate mate choice. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 270(supplement 2):S144–S146.
- Wedekind C., Fürti S. 1997. Body odour preferences in men and women: do they aim for specific MHC combinations or simply heterozygosity? *Proceedings of the Royal Society of London, Series B: Biological Sciences* 264(1387):1471–1479.
- West P. M., Packer C. 2002. Sexual selection, temperature, and the lion's mane. *Science* 297(5585):1339–1343.
- Widemo F., Sæther S. A. 1999. Beauty is in the eye of the beholder: causes and consequences of variation in mating preferences. *Trends in Ecology and Evolution* 14(1):26–31.
- Willis C., Poulin R. 2000. Preference of female rats for the odours of non-parasitised males: the smell of good genes? *Folia Parasitologica* 47:6–10.
- Wilson K., Grenfell B. T., Pilkington J. G., Boyd H. E. G., Gulland F. M. D. 2004. Parasites and their impact. Pages 113–165 in *Soay Sheep: Dynamics and Selection in an Island Population*, edited by T. H. Clutton-Brock and J. M. Pemberton. Cambridge (UK): Cambridge University Press.
- Winn B. E., Vestal B. M. 1986. Kin recognition and choice of males by wild female house mice (*Mus musculus*). *Journal of Comparative Psychology* 100:72–75.
- Wolf A. P. 1995. *Sexual Attraction and Childhood Association: A Chinese Brief for Edward Westermarck*. Stanford (CA): Stanford University Press.
- Wolff J. O., Macdonald D. W. 2004. Promiscuous females protect their offspring. *Trends in Ecology and Evolution* 19(3):127–134.
- Wynne-Edwards K. E., Lisk R. D. 1984. Djungarian hamsters fail to conceive in the presence of multiple males. *Animal Behaviour* 32(2):626–628.
- Yamaguchi M., Yamazaki K., Beauchamp G. K., Bard J., Thomas L., Boyse E. A. 1981. Distinctive urinary odors governed by the major histocompatibility locus of the mouse. *Proceedings of the National Academy of Sciences USA* 78(9):5817–5820.
- Yamazaki K., Beauchamp G. K., Kupniewski D., Bard J., Thomas L., Boyse E. A. 1988. Familial imprinting determines H-2 selective mating preferences. *Science* 240(4857):1331–1332.
- Zahavi A. 1975. Mate selection—a selection for a handicap. *Journal of Theoretical Biology* 53(1):205–214.
- Zeh J. A., Zeh D. W. 1996. The evolution of polyandry I: intragenomic conflict and genetic incompatibility. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 263(1377):1711–1717.