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Scent-Marking by Male Mammals: Cheat-Proof Signals to Competitors and Mates

L. M. GOSLING AND S. C. ROBERTS

EVOLUTION AND BEHAVIOUR RESEARCH GROUP
DEPARTMENT OF PSYCHOLOGY
UNIVERSITY OF NEWCASTLE
NEWCASTLE UPON TYNE NE1 7RU
UNITED KINGDOM

I. INTRODUCTION

Uniquely among social signals, scent marks are placed on objects in the environment, often in the absence of any receiver, and may only be detected much later, often in the absence of the signaler. This is curious because social odors in mammals can be transmitted directly from signaler to receiver in a way that is closely analogous to the mode of action in other sensory modalities. Examples include the rapid airborne transmission of volatiles from the dorsal gland of springbok, *Antidorcas marsupialis* (Bigalke, 1972), or the rump gland of pronghorn antelopes, *Antilocapra americana* (Moy, 1970), in antipredator contexts. Although animals clearly do not have time to make scent marks when trying to evade predators, examples of this kind show that direct transmission is possible. If so, why is scent-marking, the most ubiquitous form of chemical signaling in the mammals, so curiously indirect? Why is information transmitted in a fashion which, in many ways, appears to be highly inefficient? Signalers are often not present to reinforce their scent signals in the way that is possible for visual or auditory signals and often they cannot know whether a mark will be detected or who the receiver will be. Scent marks may often be degraded before they can be detected, for example by rain (Alberts, 1992). Despite these apparently severe limitations, scent marks are a very common form of signaling by male mammals. They occur in complex patterns, often involving hundreds of marks that are regularly replenished in active marking and remarking sessions. Most male mammals scent-mark and most, perhaps all, resource defense territories are scent-marked. What information is transmitted by patterns of scent marks

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and what are the benefits of sending signals in this way that outweigh its inefficiencies and account for its widespread role in mammalian intrasexual competition?

Here, we review the development of one idea that addresses this problem, namely that scent-marking by resource holders provides a means of competitor assessment. This idea takes advantage of the theoretical advances made in understanding competitive interactions between individuals, particularly in terms of game theory and competitor assessment (Parker, 1974; Parker and Rubenstein, 1981; Maynard Smith, 1982, 1996). It has been developed explicitly over the past 20 years (Gosling, 1982, 1990; Richardson, 1993) and was implicit in earlier treatments of scent-marking (Uexküll and Kriszat, 1934; Hediger, 1949; Geist, 1965; Mykytowycz, 1965, 1970, 1973, 1975; Ralls, 1971; Richter, 1972). The empirical basis for this development is a large body of observational and experimental work that links scent-marking and male intrasexual competition, and, in the following section, we review this evidence. The notion that scent marks allow assessment by potential opponents is an interpretation rooted in evolutionary theory rather than a new idea. It also has the advantage of providing a unified theoretical basis for what appears to be a unitary phenomenon. Alternative explanations have been reviewed elsewhere (Gosling, 1982; Brown and Macdonald, 1985) and will not be considered here.

The link between scent-marking and territoriality has been helpful in drawing attention to the association between scent-marking and male intrasexual competition, but it is not an obligate one (although the converse, an obligate link between territoriality and scent-marking, may be true). Ralls (1971) noted that scent-marking occurs in a similar form in both territorial and dominance mating systems and argued against a simple link with area defense. Her more general alternative, that in both cases, scent marks function as threats, is reminiscent of the earlier idea that scent marks in territories function as extensions of the owner's body, even in its absence (Hediger, 1949; Geist, 1965). The problem with such ideas is that many intruders appear to be undeterred by scent marks. They smell the marks but then move on through the territory or stay to use its resources. This difficulty can be removed by using a more fundamental view of a threat, namely that it signals fitness costs to a receiver (Gosling, 1990). Scent marks can thus be regarded as signaling fitness costs to an animal that detects them (in the absence of the signaler), where these costs are a product of the probability that the signaler will return and its relative competitive ability. The receiver's decision will be influenced by these costs but it should also take into account other factors such as the relative value of the marked resources to both individuals.

Given the indirect nature of signaling by scent marks, how do signalers ensure that marks are detected by their competitors? We review the evidence

that males place marks to intercept their intended receivers and we also pose the question of whether receivers seek out marks. This is a possibility because receivers may benefit if they can more accurately assess their chances of success in future contests and thus adjust the risks they take. Such decisions could in turn affect the economics of territory defense in a way that depends on the proportion of competitors that opt to avoid contests with the signaler. Next we consider how receivers assess the competitive ability of signalers from scent marks. Reflecting the current literature, we subdivide this treatment into mechanisms appropriate for decisions made without ever meeting the signaler and decisions deferred until after meeting the signaler. In the latter case we again ask what information receivers can get from scent marks that they cannot get directly from the signaler.

These questions have implications for general ideas about signal honesty and we review the evidence for the views that scent marks are signals of status or condition-dependent signals. Whereas this review leads us to think that patterns of marks could provide a cheat-proof record of social status, recent information suggests that scent-marking may also have large intrinsic costs and that signal costs may trade-off against life-history traits including growth and reproductive tenure. Paradoxically, scent-marking could also reduce the costs of area defense if many receivers decide to avoid escalated contests (Gosling, 1986a). We discuss the implications of these reduced costs of area defense for the evolution of resource-defense mating systems.

Recent developments in social signaling have focused attention on the possibility that individuals may intercept signals that are being sent between two other animals, to their own advantage (McGregor, 1993; Johnstone, 1998). This behavior is called eavesdropping. For example, predators such as frog-eating bats may use the mating calls of frogs to locate their prey (Tuttle and Ryan, 1981). Scent marks are very persistent signals and the interval between placing a mark and its reception is often long. Because of this, scent-marking provides exceptional opportunities for eavesdropping by animals who are not the principal target of the signal. Eavesdropping by predators and parasites may place important constraints on status advertisement by scent-marking. Eavesdropping by male competitors could be a significant selective force in the evolution of scent-marking but it has not been investigated.

It could also be argued that eavesdropping by female mammals on scent marks is an important mechanism for assessing the quality of potential mates. Although the strong association between scent-marking and male intrasexual competition suggests that the primary targets for the information carried in scent marks are male competitors, female mammals are the higher investing sex and should be more choosy than males about mate quality (Trivers, 1972). Thus, if scent marks are signals of quality, it might be expected that

females would use this information to assess mate quality, even if they also use odors directly from the body of the signaler at a later stage. The alternative is that scent marks signal directly to females. This is not a trivial distinction because it deals with the extent to which female receiver psychology has shaped the design of scent marks.

But, regardless of which of these alternatives is correct, there is a large body of information showing that females respond to the information in scent marks. Females show physiological (priming) responses and behavioral preferences in relation to the familiarity and status of the male odor donor. Most recently, females have been shown to use odor mediated by the major histocompatibility complex of genes (MHC) to choose mates in relation to their genetic relatedness (Yamazaki *et al.,* 1976; Jordan and Bruford, 1998; Penn and Potts, 1999) and to use odor to distinguish healthy and diseased mates (Penn and Potts, 1998). Most of these studies have been on mice and most use male urine or soiled bedding, but how does this relate to scent-marking? The only studies that explicitly use scent marks are those showing that females compare the odor of a potential mate with marks previously found in the environment to select mates (Reece-Engel, 1990; Johnston *et al.,* 1997a,b; Rich and Hurst, 1998, 1999; Ferkin *et al.,* 1999). Do females obtain information about mate quality using such mechanisms and, if so, how do they trade-off quality against information about genetic relatedness or disease status?

II. Scent-Marking and Competition between Males

The link between male scent-marking behavior and intrasexual competition is well established and is seen most directly in the common occurrence of marking during contests. The aptly named "stink fights" between groups of sifakas, *Propithecus verreauxi,* a territorial lemur, are a well-known example (Jolly, 1966). Many of the boundary encounters between male antelopes in neighboring territories consist mainly of ritualized exchanges in which males alternately scent-mark and attempt to remove the marks of their opponent (e.g., wildebeest, *Connochaetes taurinus;* Estes, 1969). In view of this link it is not surprising that scent-marking and the glands that contribute specialized products to marks are androgen-dependent. This dependence, which has been demonstrated by castration and androgen restoration (Bronson and Whitten, 1968; Mugford and Nowell, 1970; Jones and Nowell, 1973, 1974), extends to the chemical constituents of marks that are known to function in agonistic contexts (Novotny *et al.,* 1984; Harvey *et al.,* 1989).

While there is a clear and well-documented association between scent-marking and the defense of territories, Ralls (1971) noted that marking is

also common by males in dominance mating systems. She suggested that, in both cases, scent marks may act as a kind of threat. If this is the case, then marks perhaps signal potential fitness costs to opponents in general rather than just to intruders into territories (Gosling, 1990). If the signaler is absent when the receiver detects a mark, these costs will depend on the probability that the signaler will return, its relative competitive ability, and the relative value of any marked resources to the two individuals (see Section IV.A). The involvement of these various factors may explain why the responses of intruders to scent marks is so variable. Some intruders into territories appear to be undeterred by scent marks. They smell the marks but then move on through the territory or stay to use its resources. In other cases, best known from studies of mice, males avoid scent-marked substrates, especially when they are of low competitive ability (Gosling *et al.*, 1996a,b) or when the scent is from dominant males (Jones and Nowell, 1989; Hurst, 1993), and are more reluctant to risk or prolong fights with males whose scent suggests that they are territory owners (Gosling and McKay, 1990; Hurst *et al.*, 1994).

Further, there is generally a correlation between marking frequency and social status. Resource holders, both territorial males and dominant males in dominance mating systems, in general mark more than nonresource holders (Miller *et al.*, 1987; Rozenfeld *et al.*, 1987; Hurst, 1990; Allen *et al.*, 1999). This distinction is not always simple, perhaps because there is expected to be greater variance in scent-marking rates (and any form of status signaling) within nonresource holders than within resource holders: the latter have passed through a competitive filter and should be relatively homogeneous. In addition, the scent-marking rates of young males have been found to be the best predictor of intrasexual dominance in later life (Collins *et al.*, 1997).

Further evidence for a link between scent-marking and competition is that investment in marking appears to be regulated by the level of threat from potential opponents. Thus, marks in territories are more dense where the threat of intrusion is greatest (e.g., Thomson's gazelle, *Gazella thomsoni:* Walther, 1978; klipspringer, *Oreotragus oreotragus:* Roberts and Lowen, 1997). Intrusion from competitors may sometimes be confounded by visits by potential mates but a recent study of oribi, *Ourebia ourebia,* avoids this complication. Brashares and Arcese (1999a) found that territorial males marked at common boundaries in relation to the number of male helpers in neighboring territories but not in relation to numbers of females. Investment in marking may also reflect the overall level of competition in a population: in coypus, *Myocastor coypus,* the mean size of the anal gland used for territorial marking is predicted by estimates of the number of male competitors entering the population but not by that of potential mates (Gosling and Wright, 1984). Similarly, male mice housed adjacent to other males were found to develop

larger preputial glands (which are known to be important in scent-marking and maintaining dominance relationships: Bronson and Marsden, 1973; Yamashita *et al.,* 1989; Novotny *et al.,* 1990; Collins *et al.,* 1997), whereas the glands of those housed next to females became smaller (Hayashi, 1986). Investment in marking also appears to be adjusted in relation to the resource-holding potential (*RHP*) of individual opponents. Dominant male mice that are smaller than their subordinate partners have higher marking rates and larger preputial glands than dominant males that are larger than their partners, suggesting that a higher rate of scent-marking can compensate for relatively low *RHP* (Gosling *et al.,* 2000).

Lastly, males appear to use scent-marking when trying to take over territories. Male hartebeest that find vacant territories intensively mark the dung piles in the territory, often giving this high priority even when involved in contests with invasion by neighboring males (Gosling, 1974). Male hartebeest also try to take over territories by daily intrusion in a target territory from small temporary territories nearby. During such intrusions they systematically mark at dung piles rather than confronting the resident male. The resident male follows, paws away the new marks, and replaces them with its own before chasing after the intruder. Again, marking appears to receive higher priority than aggression. Over a period of days or weeks the invading male sometimes takes over ownership of the territory having apparently succeeded in a process of attrition. In similar fashion, scent-marking on territories by intruding aardwolves, *Proteles cristatus,* prior to the mating season, may be a prelude to challenge for ownership or mating opportunities (Richardson, 1987, 1991).

III. How Do Signalers Ensure That Their Scent Marks Are Detected?

Most of this review deals with the kinds of information signalers transmit to intended receivers through their scent marks, and on how receivers respond to this information. In this section, however, we outline some of the specific problems associated with the process of signal transmission and detection through the use of scent marks. How do signalers ensure that their scent marks are detected by their intended receivers and how does this elicit an appropriate response? In an influential paper, Guilford and Dawkins (1991) coined the phrase "receiver psychology" to describe ways in which the environment and sensory capabilities of receivers act as important agents of selection on signal design (Endler, 1993; Guilford and Dawkins, 1993; Endler and Basolo, 1998; Rowe, 1999). As this section illustrates, scent marks as signals impose several particular constraints that are quite distinct from those

relevant to acoustic or visual signals: signalers that use scent marks must be exceptionally good receiver psychologists.

A. Temporal Variation in Efficacy

The crucial parameter of temporal variation for scent-marking signalers is the mark's persistence time, the interval between deposition and the time when the mark can no longer be detected (Bossert and Wilson, 1963; Alberts, 1992). The most widespread solution to the problem of scent-mark decay is the inclusion of relatively larger molecules than in other types of chemical signal and Alberts (1992) found that territorial scent marks were of larger molecular mass than, for example, alarm signals. In most socially functioning mammalian integumental glands there are both apocrine and sebaceous components (see reviews in Grau, 1976; Adams, 1980; Albone, 1984), the latter mainly contributing large lipids (Dryden and Conaway, 1967; Gorman *et al.*, 1974). Other secretions contain lipocalin protein molecules (Singer and Macrides, 1992). Whereas large molecular mass will in itself result in lower volatility and increased persistence (Bossert and Wilson, 1963), large molecules are thought to act as vehicles for volatile constituents in scent secretion (Bacchini and Gaetani, 1992; Bacchini *et al.*, 1992; Ryg *et al.*, 1992; Robertson *et al.*, 1993) and may act as a controlled release system to regulate their emission (Regnier and Goodwin, 1977; Hurst *et al.*, 1998). Recent evidence has, however, suggested that the major urinary proteins (MUPs) in mouse scent marks are an integral part of the signal itself, stimulating countermarking by receivers, whereas the volatiles they release do not, perhaps serving instead to attract receivers to the marks (Humphries *et al.*, 1999).

A small number of studies have estimated persistence times by observing responses of receivers to scent marks of known age. As it is difficult to prove that marks are no longer detectable, these studies use the interval between deposition and the time when the mark fails to elicit a response as a reasonable estimate of effective persistence. Urine of dominant male mice is avoided by subordinates for up to 48 h but its aversive properties had disappeared after 72 h (Jones and Nowell, 1977). However, scent marks appeared to remain active for as long as 7 days in klipspringer antelope (Roberts, 1998), 10 days in dwarf mongooses, *Helogale parvula* (Rasa, 1973), and 100 days in hamsters, *Mesocricetus auratus* (Johnston and Schmidt, 1979), whereas odor from anal gland marks of hyenids can be detected even by humans after 1 to 6 months (Gorman and Mills, 1984; Apps *et al.*, 1989). In female house mice, *Mus domesticus,* two urinary pheromones elicit ultrasonic vocalizations from males, one of which loses efficacy within 18 h, whereas the other lasts up to 30 days (Sipos *et al.*, 1993, 1995). Persistence times of meadow vole, *Microtus pennsylvanicus,* posterolateral and anogenital scents similarly vary, and

there also appear to be sex differences, with anogenital scent from females and males producing responses up to 10 and 25 days, respectively (Ferkin *et al.*, 1995).

The extent to which receivers can accurately discriminate information conveyed by aged, yet detectable, scent marks, remains unclear. Signal degradation appears to at least permit receivers to estimate the age of the mark. Indeed brown hyena, *Hyaena brunnea*, scent marks may explicitly offer this information to receivers. Hyenas deposit two discrete scent secretions each time they mark: a sebaceous portion and a volatile apocrine one. Mills *et al.* (1980) interpreted this as a possible bifunctional mechanism, where the more persistent sebaceous portion provides information about identity and status, while the apocrine secretion mainly allows receivers to estimate the age of the mark and, thus, how recently the owner had left. Differential responses to the age of scent marks by receivers have been shown in recent studies to influence the perceived threat of encounter with competitors (Roberts, 1998) and the attractiveness of potential mates to females, where individuals depositing more recent scent were preferred (Ferkin *et al.*, 1995; Rich and Hurst, 1999), perhaps because this provides the most up to date, or least corrupted, information.

When receivers approach scent marks, they often sniff and lick the scent deposit (Brown and Macdonald, 1985; Idris, 1994; Roberts, 1998). Alberts (1992) has suggested that by introducing moisture in this way, receivers elicit a release of chemicals from the mark and that a series of investigations may thus cause repeated rise and fade-out cycles from a single mark.

B. Spatial Range

The trade-off between odor persistence (which as we have seen results in scent marks of low or controlled volatility) and detectable range (which is directly related to volatility) means that in most scent marks, detection is frequently probabilistic and depends largely on the interaction between movements of intended receivers and the spatial deployment of scent marks. The economic theory of scent-marking (Gosling, 1981, 1986a) was developed in recognition of this fact and the time and energy constraints under which signalers operate. Measuring the distance over which scent marks are detected is problematic, especially outside of the laboratory, as a number of factors will influence detectability (see following section). However Müller-Schwarze (1974) estimated a detection distance of about 2–5 m in black-tailed deer, *Odocoileus hemionus columbianus*, and it seems likely that, at least in larger mammals, distances will be measured in meters, rather than tens of meters. This is in stark contrast to other forms of olfactory signal, notably the insect mate attractant pheromones, which often function over

ranges of hundreds of meters (Caro, 1982; Boake *et al.*, 1996; Zhang and Schlyter, 1996).

C. Spatial Deployment and Receiver Interception

As spatial range of scent marks is typically low, Gosling (1981) stressed the importance of optimal spatial deployment of a limited number of marks across territories, so that they were positioned where they were most likely to intercept intruders (see Fig. 1). Studies that have examined the distribution of scent marks within a territory have usually found that they are either clustered at the territory boundary or toward its center. Perimeter marking has been described in several taxa, including hyenids (Kruuk, 1972; Richardson, 1991), viverrids (Bearder and Randall, 1978), canids (Macdonald, 1979; White *et al.*, 1989; Allen *et al.*, 1999), mustelids (Roper *et al.*, 1986, 1993; Pigozzi, 1990), felids (Smith *et al.*, 1989), rodents (Bel *et al.*, 1995; Boero, 1995; Rosell *et al.*, 1998), and artiodactyls (Gilbert, 1973; Franklin, 1974; Gosling, 1981, 1987; Sun *et al.*, 1994). Dung middens in particular are often placed at the perimeter (Hendrichs and Hendrichs, 1971; Dunbar and Dunbar, 1974; Walther, 1978; Ono *et al.*, 1988; Brashares and Arcese, 1999b). Marking toward the core, or hinterland (Mills *et al.*, 1980), is perhaps less striking and is reported less frequently than perimeter marking. It occurs in preorbital gland marking of small antelopes (Hendrichs and Hendrichs, 1971; Norton, 1980; Ono *et al.*, 1988) and under some circumstances in badgers (*Meles meles:* Roper *et al.*, 1993), but is best documented in studies of

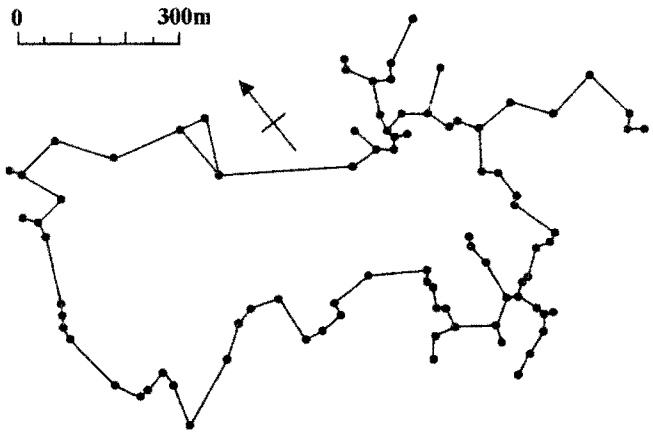

Fig. 1. Map of the scent marks in the territory of a gerenuk, *Litocranius walleri.* The oval of marks and radiating arms may be designed to intercept the movements of competitors moving into the territory. The pattern is shown using a nearest-neighbor mapping technique. Redrawn from Gosling (1981).

hyenids (Mills *et al.*, 1980; Mills, 1983; Gorman and Mills, 1984; Mills and Gorman, 1987; Gorman, 1990; Richardson, 1991).

The shift from predominantly peripheral to predominantly core marking appears to be dependent on the increasing size of the scent-marked area. For example, hyenas living in large clans with small territories mark along the perimeter, but ecologically stressed populations, living in small clans and very large territories, mark toward the territory center. Scent-mark density is also correlated with smaller territory sizes (Richardson, 1991). These trends occur both within and across species and indicate that the marking strategy is not species-specific but dependent on ecological factors that dictate the optimal distribution of scent (Gorman and Mills, 1984; Gorman, 1990). The trends are also consistent with predictions from scent-marking economics; owners of smaller territories can scent-mark at the boundary because the distances between marks are small and the chance of intruders (or potential mates) missing them as they encroach are small. As territory size expands, intermark distances and thus the number of missed detections also increase and, in consequence, a greater proportion of marks are placed toward the core (Gorman, 1990). An attempt to formalize this trend was made by Roberts and Lowen (1997) using an analytical model that examined a territory owner's trade-off between minimizing the cost of an intrusion (estimated by calculating the average area available to intruders before detecting a scent mark) and maximizing the probability of mark detection by the intruder. They found a surprisingly robust relationship between the two variables such that intrusion costs were minimized when a ring of scent marks was positioned at approximately 0.8 of the territory radius. This appears to be because, although positioning the ring closer to the territory center would reduce the likelihood of intruders missing a mark as it passed through the ring, the chances of an intruder missing the ring altogether were increased if it traveled at an oblique angle to the center (cf. Gosling, 1981). Roberts and Lowen (1997) suggest that marks surplus to those required for the optimally positioned ring are therefore added toward the periphery in small territories and toward the core with increasing territory size.

This kind of approach assumes for simplicity that movements of receivers are probabilistic and random across spatially homogeneous territories. In reality, marks are positioned in ways that are more sensitive to intruder movements. The most notable example is the obvious tendency for marks to be placed along trails and pathways (e.g., Peters and Mech, 1975; Gosling, 1981, 1985; Smith *et al.*, 1989; Sun *et al.*, 1994). The strength of this tendency is likely to be correlated with habitat heterogeneity, particularly in relation to topographical features, which effectively channel animal movements. Nonetheless, the probabilistic approach is useful in understanding the kinds of constraints operating on signalers, particularly if a proportion

of intrusions occurs away from trails (e.g., while feeding), where habitats are relatively homogeneous or where a large number of trails intersect the territory; indeed, when trail density is sufficiently high, intruder movements will approximate randomness.

In addition to marking along trails, marks are more likely to intercept intruders if they are clustered along particular boundary areas frequented or contested by receivers (e.g., Walther, 1978; Roberts and Lowen, 1997) or if they adjoin territories whose residents pose a greater threat than elsewhere (Brashares and Arcese, 1999a). Such deployment can be flexible to adapt to changing social circumstances, as illustrated by switching of latrine location in response to experimental manipulation of intruder pressure in the solitary and territorial blind mole-rat, *Spalax ehrenbergi* (Zuri *et al.*, 1997). Lastly, scent marks may be concentrated around especially clumped and contested resources, such as near the burrows of alpine marmots, *Marmota marmota* (Bel *et al.*, 1995; Boero, 1995) and badgers (Roper *et al.*, 1986). Although it could be argued that these patterns simply reflect where animals spend most of their time, several observations suggest that animals frequently travel to certain areas specifically to scent-mark them before returning or moving elsewhere. Boundary scent-marking patrols are one example (e.g., Gilbert, 1973; Tilson and Tilson, 1986), especially if there is evidence of a recent intrusion from a particular boundary (Sliwa and Richardson, 1998).

D. Do Receivers Seek Out Scent Marks?

The economics of scent-marking would be transformed if instead of having to place scent marks where receivers might pass, the receivers could be relied on to seek out the marks. Theoretically, such behavior should only evolve if there is a fitness benefit for receivers that outweighs any costs of searching. A benefit of this kind seems likely because, if marks signal *RHP*, then receivers should benefit from being able to assess the competitive ability of the signaler and use this information to reduce the costs of contests. Thus, it would be expected that receivers should actively seek out marks. Empirical evidence shows that this is often the case. For example, Müller-Schwarze (1974) observed that both captive and wild black-tailed deer search for scent marks after entering a new area. In ring-tailed lemurs, *Lemur catta*, which were free-ranging within a large enclosure, 62% of scent marks were investigated within 10 min, with a median latency of only 30 s (Kappeler, 1998).

If signalers can rely on receivers to seek out marks, then it might be expected that signalers would advertise their presence (Roberts and Gosling, in press). Two sorts of behavior are consistent with this expectation. First, marks

are placed in locally conspicuous places and may be multimodal (Rowe, 1999), with a strong visual component contributing to the detectability of the olfactory signal (Alberts, 1992; Roberts, 1997). For example, klipspringer antelopes prefer to scent-mark on dead trees or branches (mainly of preferred food species) where there are few leaves, most commonly in an area slightly elevated above its surroundings and immediately above a significant break in slope: receivers may thus form a visual search image of likely scent-marked sites (Roberts, 1997). Signalers may also manufacture suitable marking sites where there are none locally available (Gosling, 1972), go to strenuous lengths to place marks as far from the ground as possible to maximize active range (Rasa, 1973; Peters and Mech, 1975; Roberts, 1997), or contribute to signaling sites used by other species (Gosling, 1980; Paquet, 1991), thus gaining in detectability without compromising associated benefits.

Second, many signalers actively create visual anomalies, for example by disturbing vegetation by antler thrashing near scent marks, or marking the ground by pawing and scraping with claws or hooves (Gilbert, 1973; Johansson and Liberg, 1996). In some felids and ungulates (Graf, 1956; Barette, 1977; Bowyer *et al.*, 1994; Feldman, 1994), signalers damage or tear off strips of bark before marking, creating visible wounds to trees at scent-marking sites. Although such wounds might, in some cases, serve to prolong mark persistence, they are generally separate from the secretion and thus appear to be unrelated to the olfactory function of the marks. There is no evidence that receivers are attracted to such visual features, but it would be difficult to explain their widespread existence if receivers did not respond to them.

These behaviors could increase the detectability of marks, in the first case by providing a conventional site at which a receiver is more likely to find a mark than elsewhere, and in the second by reinforcing the visual element of scent-mark location, further drawing the attention of receivers to the marks. They might also make the mark more memorable by providing a component of the signal in an additional sensory modality. If these visual features function wholly or partly as advertisements, then signalers may be subverting the advantage of assessment to opponents. Because competitors are prepared to incur the costs of seeking out marks, signalers should be able to mark at lower density (Roberts and Gosling, in press).

An alternative to the idea that such behavior advertises scent marks is that costly, perhaps condition-dependent signals reinforce the status signal in the scent mark. Behaviors such as pawing or antler thrashing would be more likely to function in this way than placing marks at conspicuous and/or conventional sites. However, there could also be indirect costs of putting marks at conventional sites such as energetic costs of reaching them.

IV. How Do Receivers Use Scent Marks to Assess Signalers?

A. Background to the Receiver's Response to Scent Marks

A unique characteristic of scent marks as a social signal is that receivers often encounter the signal in the absence of the signaler. Because responses to social signals may be influenced by the chance of reinforcement (for example, the chance that a threat will be followed up by attack), the question arises, why do receivers respond to scent marks at all? The answer must be that there is a probability that the signaler will return or that the receiver will encounter it if it proceeds. The difference from a nonolfactory signal is thus one of degree not of kind, although the lack of any immediate reinforcement gives the receiver an option for delaying its response. The second factor that should influence the receiver's decision is the cost of a contest with the signaler. This will depend principally on relative competitive ability (*RHP*) and resource value. In general, the *RHP* of resource holders is greater than that of nonresource holders but the degree of the difference will affect the costs of the contest. For example, some animals of very low quality may opt to avoid all signalers—they would be unlikely to be able to take over ownership of a resource and so any costs of contests would outweigh the benefits. Alternatively, some high quality individuals might be prepared to incur high costs in assessing an opponent because the benefits are potentially high.

In general, receivers should withdraw from a scent-marked area when:

$$p(C * RHP_S \cdot V_S / RHP_R \cdot V_R) > (1 - p)V_R, \tag{1}$$

where p = probability of meeting the signaler; C = costs of an average contest; $RHP_S = RHP$ of signaler; V_S = value of the resource to the signaler; $RHP_R = RHP$ of receiver; and V_R = value of the resource to the receiver.

In reality, the value of the resource to the receiver is complex. For example, it is important to distinguish situations where the receiver only intends to use the defended resources in the absence of the signaler (for example, to feed) and those where it intends to try to take over ownership of the resources. The second alternative will usually involve costly escalated contests because resource value is high.

Thus, while the receiver's decision depends on a complex of factors, crucially it needs to assess the competitive ability of the signaler. However, receivers will vary in the accuracy of the information that they need, depending on the likely net benefits or costs. Some decisions can be made in the absence of the signaler and some can be deferred until after meeting it. But how could scent marks provide information that allows receivers to assess signalers in these two contexts? We will review the evidence for the

mechanisms that have been identified and then evaluate the benefits and costs of these mechanisms.

B. Decisions in the Absence of the Signaler

1. Intrinsic Meaning

Scent marks can potentially give information to receivers in the absence of any knowledge about the signalers themselves and without any further encounter with the signaler. The simplest information is that a signaler has been present in the area. But although there is evidence that animals avoid scent-marked areas even when they have had no contact with the signalers, it is difficult to exclude the possibility that they have used additional information. However, it is possible to imagine that where the receiver's *RHP* is low and the value of the defended resource is low, then any potential costs will outweigh the benefits and the receiver should move to a different area. Additional characteristics on a scale of increasing complexity of information are those of mark abundance, freshness, and the regularity with which marking sites are remarked. Marks also contain chemical information and here the best data are from mice. The scent marks of dominant male mice have stronger aversive properties than those of subordinate males and castrates (Jones and Nowell, 1973, 1989). A number of androgen-dependent volatile compounds, particularly terpenes, thiazole, and brevicomin, have been identified that appear to be responsible for this response (Novotny *et al.*, 1990b; Bacchini *et al.*, 1992; Robertson *et al.*, 1993; Hurst *et al.*, 1998). There is, thus, some evidence that receivers use intrinsic properties of marks to make decisions about use of space. However, real-world observations show that many, perhaps most, animals that detect marks do not leave the marked area (Gosling, 1982; Simons *et al.*, 1997). Indeed this may often be impossible because marks are so widespread.

Intrinsic information in scent marks is not sufficient to make a decision about whether or not to leave a scent-marked area. Receivers also need to compare their own competitive ability with that of the individual who made the scent mark, a process analogous to estimating relatedness through self-referent phenotype matching (Heth *et al.*, 1998; Mateo and Johnston, 2000a). Experiments on mice provide the best empirical evidence, albeit indirect, for the existence of this mechanism. The finding that subordinate mice are more likely to avoid scent-marked areas than dominant mice (Jones and Nowell, 1989) at first appears to support such a mechanism, but the subjects could have been negatively conditioned to the odors (general, not individual) that were present when they became subordinate. However, on the assumption that body size reflected competitive ability, Gosling *et al.* (1996a,b) showed that small adult male mice were more likely to avoid scent-marked areas

than large ones. The males in these experiments were raised in isolation, suggesting that they may recognize their own competitive ability innately.

Extensive studies, conducted mainly on mice, have shown recently that receivers can infer the genetic relatedness of the signaler from odors mediated by the MHC part of the genome (reviewed by Jordan and Bruford, 1998; Penn and Potts, 1999) and also its disease status (reviewed by Penn and Potts, 1998). Such investigations usually focus on a mate choice paradigm but intrinsic information about disease status and relatedness could also be selected for as signals of quality to same-sex competitors. For example, social odors could honestly signal quality if it was too costly for a sick animal to fake a healthy odor. Males should also modify their status signals and thus their competitive behavior in relation to their genetic relatedness (Johnstone, 1998). Information about relatedness and disease status is conveyed by volatile chemicals carried in urine and is thus potentially placed in scent marks. However, no studies have tried to integrate the information available to receivers from patterns of marks and their androgen-dependent volatiles with the chemical information available about disease status (potentially redundant) and that about genetic relatedness (potentially additive).

2. Learned Association

Receivers could also assess the potential costs of meeting the signaler from a learned association between the smell of the mark and the memory of previous contests with the individuals that made the marks. The outcome of these contests could allow predictions about the costs of future meetings with the same individual and receivers could opt to leave the marked area when these costs outweigh the benefits of using the marked resource.

There are a number of prerequisites for the existence of this mechanism. First, subjects must be able to distinguish between the odors of individual conspecifics. This ability has been demonstrated in numerous species in several taxa (reviewed by Halpin, 1980, 1986, and by Voznessenskaya *et al.*, 1992; see also Johnston *et al.*, 1993; Wilcox and Johnston, 1995). Individual odors may also be recognized across species (e.g., Beauchamp *et al.*, 1985; Johnston and Robinson, 1993; Settle *et al.*, 1994). Individual variation in mouse odors has been linked to genetic variation and in particular to variation in the MHC region of the genome. Mice can be trained to discriminate nearly identical mice that differ only at the MHC, whereas they cannot distinguish between genetically identical mice (Brown *et al.*, 1987, 1990; see also Nevison *et al.*, 2000). The chemicals responsible for these distinctive odors are carried in urine and appear to be a mixture of volatile carboxylic acids, which vary in their relative proportions in each individual (Singer *et al.*, 1997). However, it should be emphasized that demonstrations of sensory capacity cannot be used directly to infer how information about individuality is used. For

example, the capacity to discriminate at the level of the individual is also needed for scent-matching (see Section IV. C. 2) a mechanism that does not require past knowledge of individual behavior.

The second prerequisite for individual learning is that receivers can remember the smell of individuals they have encountered in the past. This has been shown in experiments by Roeder (1983), in which two female genets, *Genetta genetta,* were found to be able to remember scent marks of males for between 9 and 12 weeks. With larger sample sizes. Johnston (1993) has shown that the length of time over which individual flank gland odors can be remembered (assessed using habituation methods) is at least 10 days in hamsters, whereas there are indications of memory for up to 4 weeks in guinea pigs (Beauchamp and Wellington, 1984). It has been shown that Belding's ground squirrels. *Spermophilus beldingi,* can even remember familiar versus unfamiliar social odors (from the oral gland) after overwinter hibernation (Mateo and Johnston. 2000b). Subordinate male mice are more likely to avoid the urine odor of a dominant male that defeated them than an unfamiliar odor (Carr *et al.,* 1970). Memorizing individual odors seems most likely, at least in theory, in the case of animals that meet frequently (as with those that live in closed social groups or in neighboring territories). However, there must be limits imposed by the number of potential opponents and the dynamics of changing status within groups. No studies appear to have been carried out on these constraints on adaptive patterns of individual recognition.

C. Decisions Deferred until after Meeting the Signaler

1. Intimidation

A number of authors have suggested that scent marks may alter the psychological state of the signaler and/or receiver such that the confidence of the signaler is enhanced and the receiver is intimidated (Geist, 1965; Mykytowycz, 1965; Richardson, 1993; Sliwa and Richardson, 1998). Although the identification of subjective states cannot be tested directly, they can theoretically be linked to behavioral consequences that can then be tested. However, unfortunately there are no cases where predictions of this hypothesis can be separated from those made from the other candidate mechanisms. Rather it seems to be adopted as an explanation when alternatives have been either excluded or, more commonly, not considered. It may be best to regard ideas about intimidation as suggestions about the mental state of animals that make adaptive decisions based on intrinsic information, learned association, and/or scent-matching, rather than as a separate mechanism.

2. Scent-Matching

The receiver could memorize the smell of the scent marks as it enters a new area and compare this odor with that of any potential opponent that it meets. When the scents matched, the male would know that the opponent was of high status and, depending on its own relative competitive ability and the value of the marked resource, it could withdraw from the encounter at an appropriate stage (Gosling, 1982). Resource holders would benefit from the reduced costs due to these decisions (see the following).

There are a number of prerequisites for the existence of scent-matching and these have interesting parallels to, and crucial distinctions from, some of those outlined above. Scent-matching requires animals to be able to discriminate odors at the level of the individual. It does not require long-term memory of the odor of individuals or a learned association of their smell with past behavior. Scent-matching requires the ability to remember the odor of scent marks that the animal encountered in the recent past and the ability to compare these odors with the smell of potential opponents. The most remarkable demonstration of such sensory capacity comes from tests of the ability of domesticated dogs, *Canis familiaris,* to remember the human odor associated with forensic objects and to later match these either with additional objects that have been impregnated with these smells (Settle *et al.,* 1994; Schoon, 1997) or with their ultimate source, a crime suspect (Schoon and DeBruin, 1994; Schoon, 1996). Less obviously, scent-matching also requires a sequential and spatial memory that allows the receiver to interpret the pattern of scent marks it encounters as a marked area. For example, the majority of the marks that an animal has encountered in the recent past may be from male A, but the most important ones may be the small number it encountered as it walked from the territory of male A into that of male B.

The idea of scent-matching was initially advanced to explain a wide range of observations of scent-marking and linked behavior in wild animals that had previously been difficult to explain (Gosling, 1982). In particular, scent-matching is consistent with the widespread observations that territory owners and other high-status males anoint their own bodies with the substances used for scent-marking and make themselves available for olfactory inspection at the start of many encounters (Fig. 2); many males evert their scent glands as they approach opponents (e.g., hyaenas: Kruuk, 1972). Males also remove marks made by other males and overmark the site with their own odor. It was realized that many early observations that had been interpreted using other mechanisms might be explained more simply by scent-matching. An example is the classic observation that when two male rabbits, *Oryctolagus cuniculus,* are placed in an arena with the scent marks of one of them, that individual is more likely to win any contest (Mykytowycz, 1973, 1975).

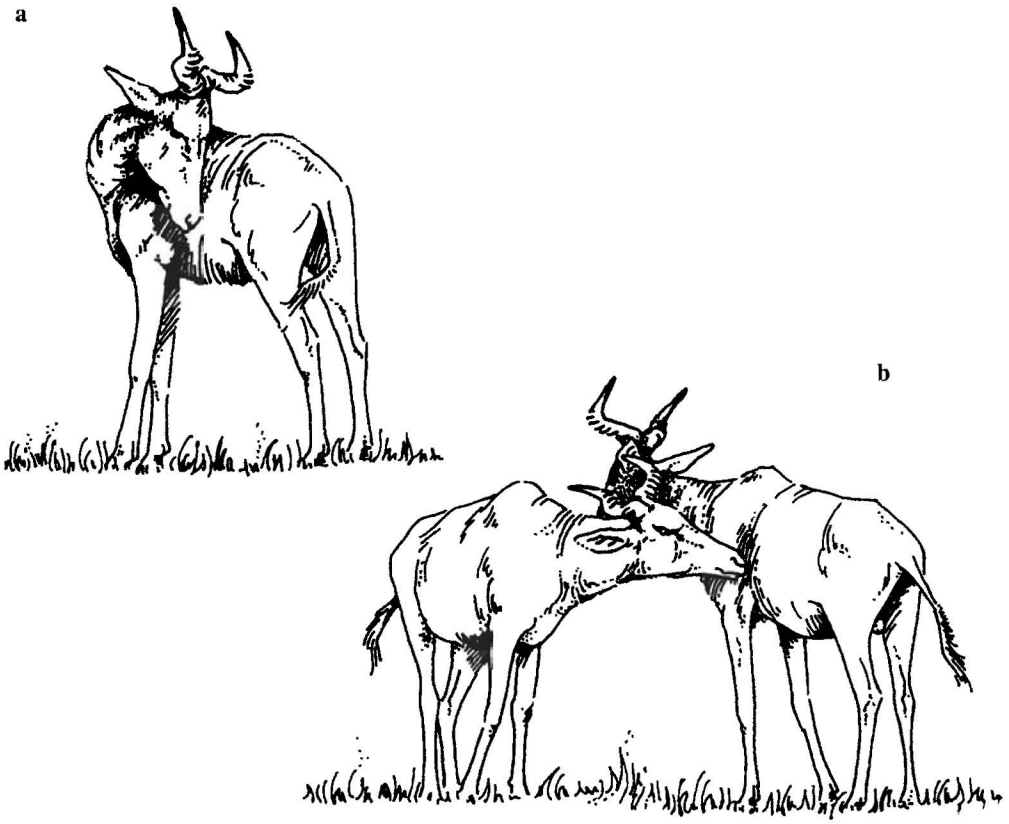

FIG. 2. Territorial male hartebeest, *Alcelaphus buselaphus*, (a) rubbing substances used in scent-marking onto its side and (b) allowing a nonterritorial intruder to sniff the same area. The intruder may thus identify the owner by matching the smell of the owner with the smell of scent marks previously encountered in the territory. The marking substances are secretions from an antorbital gland and feces. Males often lie in their own feces ("dung piles") and rub their head and neck on the ground to further transfer the smell to their body ("self-anointing"). Redrawn from Gosling (1982).

The use of scent-matching by intruders into mouse territories has been confirmed experimentally (Gosling and McKay, 1990). Males that approached a resident male fought at lower intensity when they approached on a substrate that matched the resident than when they approached on substrate marked by a third, unknown male. The use of scent-matching has also been demonstrated in the context of mate choice (discussed later) in hamsters and rabbits (Steel, 1984; Reece-Engel, 1988, 1990).

One of the predictions of the scent-matching hypothesis is that resource holders should remove (e.g., Sun and Müller-Schwarze, 1998) or replace scent marks that do not match their own odor (Gosling, 1982). Replacing scent marks is especially common and is known as overmarking or

countermarking (Johnston *et al.,* 1994; Wilcox and Johnston, 1995; Roberts, 1998; Sliwa and Richardson, 1998; Ferkin, 1999; Roberts and Dunbar, 2000). Debate has included the idea that marks are placed next to the competitor's scent mark rather than on top of it in order to signal an asymmetry between the two males (Ferkin, 1999; Rich and Hurst, 1999).

The circumstances in which scent-matching is a possible mechanism depends, by definition, on the detection of scent marks prior to an encounter between signaler and receiver (Gosling, 1982). We have recently shown (Roberts and Gosling, unpublished), using an analytical model, that the likelihood of this requirement being fulfilled is crucially dependent on the interaction between the efficacy of the network of scent marks within the defended area and its size. The opportunity for scent-matching generally declines with increasing territory size if mark detection is purely probabilistic. However, in reality, increasing the number, effective range, and detectability of marks (Section III; particularly marking on trails along which intruders enter the territory) will substantially enhance the range of territory sizes over which matching is possible.

D. Intraspecific Variation in Mechanisms of Assessment

There has been a tendency in the literature to associate particular mechanisms of assessment using scent marks with particular species. However, it would be surprising if this were the case because selection should favor flexibility in mechanisms where selection pressures, including ecological and social factors, show equal or greater variation within than between species. The available evidence supports this expectation, particularly in the best studied species, the house mouse and its laboratory descendants. Thus, mice are known to respond to intrinsic properties of scent marks and in particular to androgen-dependent chemicals that reflect social dominance. Some mice, but not all, avoid marked areas (Jones and Nowell, 1989; Hurst, 1993). Mice also learn to associate a record of past encounters with their odor and use this information in avoidance decisions (Gosling *et al.,* 1996a,b). However, they also use scent-matching to decide whether or not to escalate contests with novel opponents (Gosling and McKay, 1990; Hurst *et al.,* 1994) and take into account the relative proportions of an opponent's marks and that of its competitors (competitive countermarking: Rich and Hurst, 1998, 1999).

Individual receivers thus appear to use a number of different forms of assessment, the prevalent mechanism probably being determined by the balance of costs and benefits in particular ecological and social contexts. This may mean that particular species tend to use the same mechanism but does not necessarily imply that mechanisms are species-specific.

We have recently explored the circumstances that dictate the switch between mechanisms involved in competitor assessment via scent marks (Roberts and Gosling, unpubl. data), using a game theoretical approach. Game theory seeks to understand how individual behavior varies in relation to the behavior of others (Parker, 1974; Parker and Rubenstein, 1981; Maynard Smith, 1982, 1996); in this case, we were interested in how the strategies of the scent-marking signaler and receiver vary within an owner–intruder paradigm, and how these are dependent on the degree of knowledge about owners that intruders are likely to have gleaned from scent marks before encounters occur. We specifically compared the likely expression of the two most commonly cited mechanisms from the literature, using intrinsic properties of scent marks (cf. Hediger, 1949; Richardson, 1993) and scent-matching (cf. Gosling, 1982). The model examined the circumstances under which it is beneficial for intruders to attempt to assess their opponent further by scent-matching, and those in which owners should either present themselves for scent-matching by intruders or escalate immediately. The stable strategy for intruders (providing benefits of escalation outweigh potential costs of injury) is to attempt to scent-match over most parameter values, especially if there is a moderate degree of owner advantage, but in some circumstances the best option may be immediate escalation or withdrawal (Fig. 3).

On the other hand, it pays owners to allow assessment where mark detection probability is high (usually in small territories), but where it is low they do best by escalating immediately. Thus, although intruders do best when they can maximize their information-gathering about owners, the opportunity to match is effectively denied if owners escalate immediately. The model's predictions are consistent with observed variation in behavior and demonstrate that different mechanisms may result from the balance of costs and benefits along a continuum of information acquisition by intruders.

E. The Accuracy of RHP Assessment Using Scent-Marking

We have seen that when receivers detect a pattern of marks, they can infer that they are in an area occupied by a male of high competitive ability and, moreover, one that has "owner advantage" (Davies, 1978; Alcock and Bailey, 1997). But how should they use this information? Different receivers must vary in the accuracy of the information that they need to make an adaptive decision. For example, individuals of very low competitive ability simply need to know that an area is defended before deciding to withdraw. They do not need to have detailed information about the competitive ability of the signaler because such information is redundant when all resource holders must be of relatively high *RHP*. This decision is based on the cost:benefit analysis in Eq. 1 (Section IV.A), and, in particular, the assessment of relative

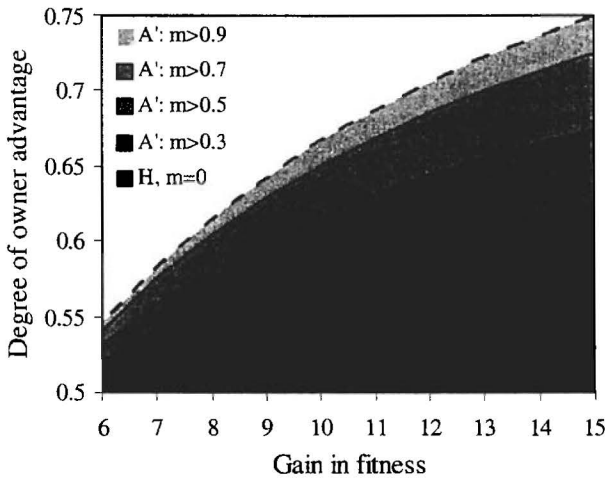

FIG. 3. Variation in evolutionarily stable strategies of intruders. Where both the degree of owner advantage (x; here, $x = 0.5$ indicates no advantage) and probability of scent mark detection prior to an encounter (m) are low, it pays intruders to escalate contests without assessment (that is, play Hawk, H). In this example, H (shaded black) is the ESS for all $m < 3$. Successive curves represent the critical value of x, for a given m (here 0.9, 0.7, 0.5, 0.3), above which H is supplanted by the strategy A′. Where x is high (above the dashed line), intruders should adopt the strategy A. The strategies A and A′ are scent-matching assessment strategies defined by playing Dove (D) if the matching process identifies an opponent as the territory owner, and H if not; they differ in their response to immediate escalation by owners (A plays D, A′ plays H). The results illustrate the potential for flexibility in assessment mechanisms in different socioecological circumstances (Roberts, S. C. and Gosling, L. M., unpublished).

competitive ability. Bearing this procedure in mind, how accurate is the information available in each of the mechanisms of assessment outlined above and under what circumstances would it be useful or not?

We know that animals can obtain information about the status of a signaler directly from intrinsic properties of its scent marks. However, intrinsic information may be too general to give precise information to a male about the likely costs of remaining in a scent-marked area. For example, the concentration of androgen-dependent volatiles could indicate that an opponent was in a generally dangerous category, but it could not indicate which one of a range of potential opponents had made the marks. There could thus be advantages in using intrinsic information, but probably only where the differences in *RHP* between the signaler and receiver are large and therefore easily perceived and assessed. This difference may often be compounded by resource value, particularly where reproductive tenure is dependent on the resources in a territory and where the benefits to an intruder are limited to a short bout of feeding.

Where a receiver meets its competitors frequently and remembers their odors, their identities, and the outcome of these encounters (wins:losses),

the detection of scent marks made by these individuals could provide a precise indication of the costs and outcome of future encounters. However, this information should become progressively less accurate as the frequency of such meetings declines and as the rate of status change in the group increases. It will also generally be less effective in large groups than in small groups because of the effect of group size on the first two variables. Where resource holders meet competitors rarely and there is a good chance that their status will have changed in the meantime, memorized information could be actively misleading. This transition may reflect the fundamental transition from an individual reference for dominance in the multimale groups of dominance mating systems to a spatial reference for dominance in resource-defense polygyny and monogamy (Gosling, 1986b). As noted by Ralls (1971), it is particularly interesting that scent-marking is maintained in dominance mating systems when intrinsic information from odor could be directly transmitted and received.

Where resource holders contend with large numbers of potential competitors, and where they meet individual competitors infrequently, spatial references for dominance must be unambiguous and verifiable. In these circumstances, verification may only be achieved reliably by comparing the odor of the territory's scent marks with that of the owner. In many systems, the number of competitors, and hence the need for such a mechanism, are frequently underestimated. Where a network of resource holders defends contiguous territories, as in the aardwolf (Richardson, 1991) or the monogamous antelopes (Brotherton and Manser, 1997; Roberts and Lowen, 1997), the majority of the population appears to be resource holders. However, offspring are continually produced and become transient "floaters"; these are cryptic in their behavior to avoid detection by resource holders and are consequently also rarely detected by observers. Nonetheless, they are a continual threat to resource holders and indeed eventually replace them.

V. Costs and Benefits

A. Honesty and Signal Costs

Some olfactory information can be simply passed between individuals and does not involve the use of scent marks. For example, the subauricular glands of oribi and rump glands of pronghorn antelopes, *Antilocapra americana,* are designed for direct, airborne transmission of volatile chemicals to conspecifics. Why are scent marks so commonly used as an intermediate vehicle for chemical signals? The answer may be that patterns of scent marks leave a cheat-proof record of individual behavior. The historical element of this record is impossible to fake because the signaler has to be present over the time that it takes to make the pattern of marks. Because it has to be

dominant in space (territoriality) or over competing individuals (in dominance systems) while this is done, the scent marks are cheat-proof. Scent marks are thus a record that is not only of status but that has been probed by competitors and shown to reflect honestly the *RHP* of the signaler. If intruders or subordinates deposit scent marks the resource holder quickly overmarks them; indeed, overmarking may have higher priority than aggression in such circumstances (e.g., hartebeest: Gosling, 1974; aardwolf: Sliwa and Richardson, 1998).

Although it might be expected that scent-marking is a costly trait, there has been little investigation of the costs of this or any other olfactory signal. However, data suggest that scent-marking in mice may have important life-history costs and that these may ultimately affect reproductive success. This has additional significance because scent-marking rates in mice are highly variable between litters (Collins *et al.*, 1997), although it is not yet known whether this variation has a genetic or developmental origin. Data have shown that scent-marking rates are inversely correlated with growth rate and asymptotic body size in male mice housed singly (Fig. 4; Gosling and Roberts, unpubl. data). Although at first sight surprising, major urinary proteins that play a key role in mouse scent-mark function (Section III.A) are produced at urine concentrations of between 10 and 20 mg ml^{-1} (Nevison *et al.*, 2000) and this rate of protein synthesis could account for the observed growth reductions. In male mice housed in pairs, the dominant individual generally marks at a

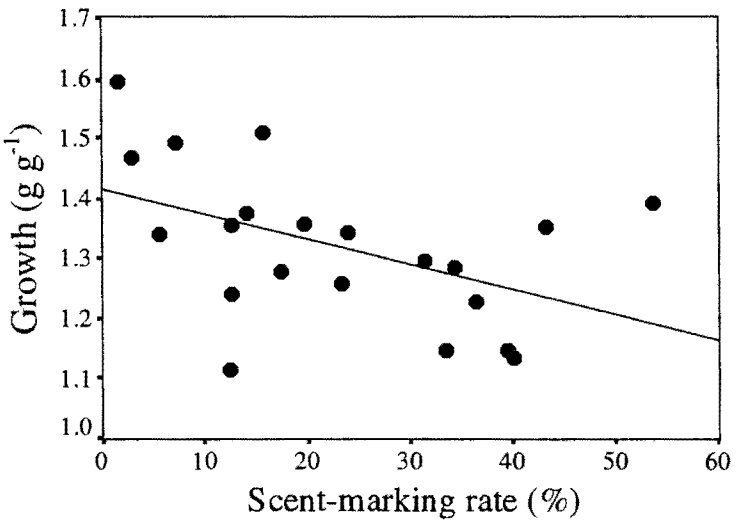

FIG. 4. Relationship between scent-marking rates and growth in singly housed male mice. The inverse relationship suggests that scent-marking has an energetic cost and that, as marking levels increase, resources are progressively diverted from growth. There was also an inverse relationship between marking rate and asymptotic weight (mean of weeks 20–25) in this sample of mice (Gosling, L. M. and Roberts, S. C., unpublished data).

higher rate. But, if the dominant male is smaller than its subordinate partner, it scent-marks at a higher rate than if it is larger than its subordinate partner. Smaller dominants also have larger preputial glands, the site of most mouse pheromone production, than larger dominants, even though their body sizes are smaller. As a result of greater costs of scent-marking and associated gland development, poor competitors grow even more slowly and, as a result, experience a higher rate of dominance reversals (Gosling *et al.*, 2000).

These findings suggest a life-history trade-off between the costs of scent-marking, to help establish and maintain social status, and the time over which dominance can be maintained. Relatively poor competitors may have to invest more heavily in status signaling to maintain dominance, and consequently they incur relatively high costs. But although small dominant males only maintain their dominance for short periods, this period could provide critical fitness benefits particularly when the probability of survival is low, as in *r*-selected species including the wild progenitors of the laboratory mouse, or if small males are relatively vulnerable to some other source of mortality such as predation (Dickman *et al.*, 1991; Koivunen *et al.*, 1998). Males that invest heavily in signaling to maintain dominance may thus be opting for a strategy of breeding early. But why do some larger mice appear to accept a subordinate role early in life? The strategic options appear to be principally some form of sneak-breeding or waiting strategies (Kozlowski, 1992; Maynard Smith, 1996; Pilastro *et al.*, 1997; Kokko and Sutherland, 1998) with low associated costs of scent-marking. There is no direct evidence for the former, although subordinate male mice do occasionally obtain some matings (Wolff, 1985; Franks and Lenington, 1986). Life-history benefits from delaying reproduction are consistent with the dominance reversals observed in our experiments, but the consequences for lifetime reproductive success have not yet been tested.

These data about the costs of scent-marking in mice are consistent with the theoretical notion that selection should favor the evolution of costly status signals because they provide reliable, cheat-proof information about the quality of the signaler (Zahavi, 1975; Grafen, 1990).

B. The Economics of Scent-Marking in Territory Defense

Scent marks provide an opportunity for intruders to identify resource holders and then to modify their behavior in a way that takes account of the benefits of utilizing the defended resource and the costs of meeting the resource holder. Because, on average, animals excluded from resource-holding status will have lower *RHP* than resource holders, many receivers will opt to avoid contests. Others will delay and meet the resource holder to maximize use of the defended resource but, perhaps subject to confirmation of the

resource holder's identity, will withdraw at an early stage of an escalated contest. Resource holders thus avoid or reduce the costs of contests with a large proportion of potential opponents. However, they cannot avoid contests with high-status animals that are seeking to achieve resource-holding status. Scent marks could actually incur additional costs from these contests because they may inadvertently advertise a resource that is worth trying to take over. However, this effect will be offset by owner advantage and, in any case, such individuals are relatively rare. The net costs of these encounters must be low in relation to the costs saved from large numbers of contests with lower status individuals.

The extent of the savings can be envisaged as the sum of the difference in the costs of contests resolved by prior assessment and the comparable costs of escalated contests. These two sets of costs can be expressed as two cost functions that increase linearly at different rates with the value of the defended resource (Fig. 5). Comparison with an asymptotic benefit function show that

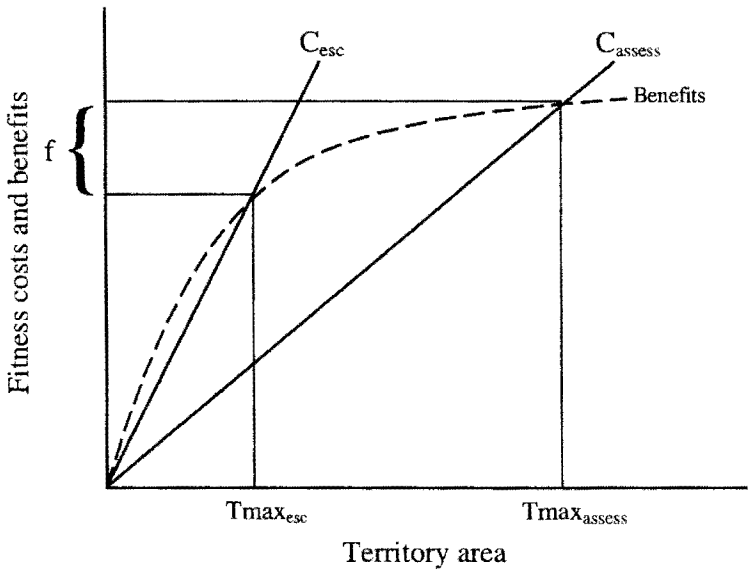

FIG. 5. The economic consequences of scent-marking in territory defense. The steep cost function (C_{esc}) shows the cost of defending a territory of increasing size (or value) when competitors are expelled in contests without prior assessment by scent-marking. The shallow cost function (C_{assess}) shows the cost of defending a territory of increasing size (or value) when competitors assess the owner using its scent marks. Costs are lower because most intruders are of lower *RHP* than resource holders and so most withdraw without escalation. The broken line shows the increasing fitness benefits of monopolizing an area of increasing size. Intercepts between the benefit and cost functions show the increase in territory area that can be defended with scent-marking. The fitness benefit of scent-marking is the difference between the intercepts of the cost and benefit functions on the ordinate. From Gosling (1986).

the value of the defended resource is higher with scent-marking than with escalated contests. The fact that most, perhaps all, resource-defense territorial systems in mammals are characterized by scent-marking suggests an obligate relationship. Scent-marking occurs in some but not all dominance systems. For example, it is absent in a number of tragelaphine antelopes and in the bovines (Gosling, 1985). Perhaps resource-defense mating systems would not be economically viable without the reduction in costs from prior assessment using scent marks. Evidence to support this comes from a spatially explicit mathematical model of territoriality in wolves, *Canis lupus*, which suggests that territory formation cannot occur in the absence of scent-marking (Lewis and Murray, 1993; Lewis *et al.*, 1997). In an important empirical demonstration, Stenström (1998) showed that in fallow deer, *Dama dama*, resource-holding stags scent-marked more when their defended resources were challenged, but that those that scent-marked at high frequencies were subjected to fewer agonistic encounters than those marking at lower rates (Fig. 6). These findings suggest that the evolution of scent-marking may have been necessary before resource-defense systems could replace more primitive systems based on an individual rather than a spatial reference for dominance.

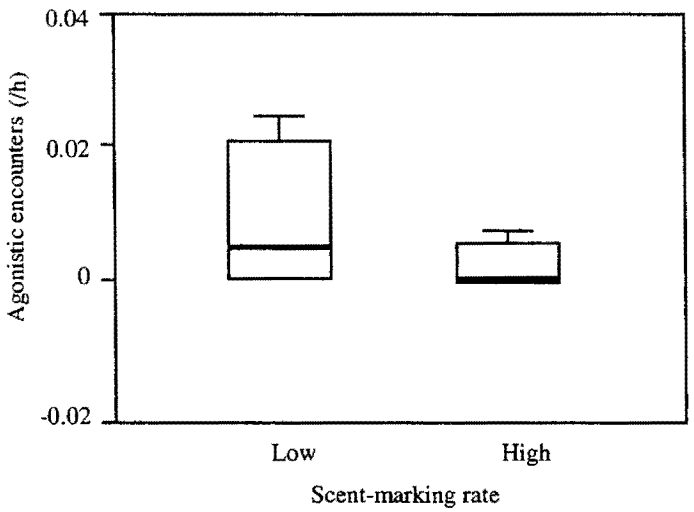

FIG. 6. Relationship between the frequency of scent-marking by fallow deer stags, *Dama dama*, and the number of agonistic challenges in which they are involved. Stags that scent-mark at high rates are involved in fewer encounters. The results lend support to the idea that investment in scent-marking reduces the costs of directly defending territories. Thick lines indicate median values. From Stenström (1998).

VI. Eavesdropping

A. Competitors and Mates

Whenever signals are sent, there is potential for individuals other than the intended receiver to detect and use the information transmitted. This sort of interception is termed eavesdropping (McGregor, 1993). Eavesdropping may have substantial benefits for receivers, and may be cost-neutral, or even disadvantageous, for signalers. For example, it could allow males that observe competitive interactions between other males to assess them as potential opponents at lower cost than by direct assessment. McGregor (1993) was among the first to recognize the potential for eavesdropping, particularly of wide-ranging, conspicuous signals emitted within networks of territorial animals. There is substantial evidence for eavesdropping by receivers of acoustic signals, particularly of territorial birdsong (e.g., Dabelsteen *et al.*, 1997; Naguib *et al.*, 1999; Otter *et al.*, 1999). In contrast, the incidence of eavesdropping in olfactory signals, and scent marks in particular, has rarely been explicitly described. This is surprising, because scent marks are of central importance in mammalian territorial signaling networks (see Section III.C) and their persistence over time offers ample opportunity for many competitors to gather information from them before they become redundant. It may be that difficulties in distinguishing intended receivers and eavesdroppers in scent-marking studies (in view of the often large intervals between signal emission and reception) are responsible for the neglect of this intriguing aspect of scent-marking.

If, as seems likely, scent marks are honest signals of competitive ability to male competitors, it would be surprising if females did not eavesdrop on these signals for mate choice. However, males could also signal their quality and genetic relatedness directly to females. This is not a purely semantic debate because the role of females as intended receivers or as eavesdroppers could affect signal design. Because of the possibility that males signal directly to females, we will treat scent-marking and mate choice separately in the following section.

Because of the long-lasting nature of scent marks, eavesdroppers also have a unique opportunity to remove, conceal, or amend marks to their own advantage. Scent marks may attract a number of receivers in succession and early receivers may remove the marks, for example by pawing, or add their own marks to amend the information in the mark for subsequent receivers. Thus, in some rodents, males may scent-mark next to, or partially overlapping, the earlier scent mark; this has been termed countermarking. Receivers use the region of overlap and the age difference between the marks to discriminate between the scent marks (Johnston and Bhorade, 1998;

Ferkin *et al.*, 1999; Rich and Hurst, 1999). Alternatively, overmarking of one scent mark by another is often interpreted as an attempt to mask the underlying scent, thus denying later arrivals an opportunity to detect the signal (Woodward *et al.*, 1999). In this way, males might overmark female scent to withhold information about mate receptivity from competitors (Tyler, 1972; Moodie and Byers, 1989; Komers, 1996; Brotherton and Manser, 1997). A number of experiments examining the ability of receivers to discriminate the underlying scent mark indicate that overmarking may be successful in masking scent (Johnston *et al.*, 1994; Woodward *et al.*, 1999). However, this is not always the case, for example in the overmarks of male ring-tailed lemurs, where at least some information in the original scent is conserved after overmarking (Kappeler, 1998). The extent to which overmarking actually masks underlying scent in other taxa, as opposed to being in essence a subcategory of countermarking, remains to be shown (Roberts and Dunbar, 2000).

B. Predators, Prey, and Parasites

Just as vocalizations (Cade, 1975; Tuttle and Ryan, 1981; Belwood and Morris, 1997) and insect airborne pheromones (Stowe *et al.*, 1995; Haynes and Yeargan, 1999) may attract and direct the attention of parasitoids and predators, scent marks also enable such unintended receivers to reliably predict the location and movements of signalers.

The best documented example concerns the ability of avian predators to eavesdrop on the scent marks of small rodents, notably voles. Captive kestrels, *Falco tinnunculus*, are able to detect vole (*Microtus, Clethrionomys*) scent marks in ultraviolet light, due to the reflectant properties of protein constituents of the marks (Viitala *et al.*, 1995). Field experiments have also demonstrated the ability of the diurnal kestrel (Viitala *et al.*, 1995) and rough-legged buzzard, *Buteo lagopus* (Koivula and Viitala, 1999; but not nocturnal Tengmalm's owls, *Aegolius funereus:* Koivula *et al.*, 1997), to discriminate and preferentially hunt above areas that contained artificially enhanced levels of scent marks. The use of information about scent mark density by raptors is thus an important potential cost of scent marking. Koivula *et al.* (1999b) have additionally shown that kestrels are even able to discriminate between sex and age of vole prey, apparently on the basis of variable levels of ultraviolet reflectance that exist between classes (Koivula *et al.*, 1999a). This highlights the particular risks to territorial males that may arise from their scent marks. A recent experiment (our unpublished data) has examined the degree to which male mice varying in their signaling investment are prepared to investigate scent marks of an unfamiliar individual in the presence of the odor of a predator (ferret urine). Males that scent-mark at high frequencies are quicker to approach but spend less time investigating the marks, than

males signaling at low rates. These results indicate that there are individual differences in sensitivity to potential eavesdropping by predators, which are related to the individual's own signaling strategy.

Whereas mammalian predators, like their avian counterparts, may eavesdrop on scent marks of their prey in order to hunt more effectively, prey animals might use the same strategy to reduce the risk of predation. White-tailed deer, *Odocoileus virginianus*, densities are highest in buffer zones between wolf territories (Mech, 1977), the location of which are demarcated by wolf scent-mark patterns (Peters and Mech, 1975), although whether this results from eavesdropping is unknown. The aversive effects of predator scent on their prey are especially well known in rodents and include reduced foraging and travel times (Kotler *et al.*, 1992; Epple *et al.*, 1993; Jedrzejewski *et al.*, 1993; Perrot Sinal *et al.*, 1999) and the induction of avoidance behavior (e.g., Stoddart, 1976; Gorman, 1984; Robinson, 1990; Baretto and Macdonald, 1999). How much increased hunting costs resulting from these responses impinge on the intraspecific benefits of scent-marking by predators is unknown, but they could be considerable where prey density is low.

Lastly, a striking example of eavesdropping by parasites is that of a southern African tick and the klipspringer, its small antelope host. The tick, *Ixodes matopi*, aggregates on the preorbital gland scent marks of klipspringers, which are deposited on the ends of low branches (Roberts, 1997; Roberts and Lowen, 1997), in order to gain access to the host on subsequent visits to the marks (Rechav *et al.*, 1978; Spickett *et al.*, 1980). Adult ticks are predominantly active in the rainy season (Colborne *et al.*, 1981) and locate scent marks by following the trail of an aqueous active component of the secretion as it is washed by rainwater down the branches of the shrub (Rechav *et al.*, 1978). Klipspringers tolerate preorbital gland gleaning by passerine birds in an attempt to reduce their parasite load, but this may also lead to direct ingestion of glandular secretion by the birds, thus introducing an (albeit probably small) additional cost (Roberts, 1995).

VII. Scent-Marking and Mate Choice

As discussed above, it is not yet known whether males signal directly to females or whether females simply eavesdrop on signals aimed at other males. But, regardless of which of these, or both, occur, there is good evidence that females respond to a wide variety of male odors. In research on mice, many of these odors originate in urine or soiled bedding because these are convenient sources of odor in laboratory experiments. Urine is used for scent-marking and so scent marks could be the normal mode of information transmission in nature. Some evidence does exist for responses to

scent marks and to patterns of marks. Female white-tailed deer investigate and scent-mark at male marking sites (Moore and Marchinton, 1974), and make unusual visits outside their normal range (Sawyer *et al.*, 1989) when they are in estrus, leading Sawyer *et al.* to suggest that they use marking sites to assess potential mates. In addition, female rabbits, hamsters, and mice prefer males who match the scent marks, or the predominant scent marks, that they had previously been exposed to (Steel, 1984; Reece-Engel, 1988; Rich and Hurst, 1998, 1999). Females thus appear to discriminate between males on the basis of their ability to maintain territory integrity by scent-marking, preferring males whose territories contain only the owner's marks over those that had been partially marked by intruders (Rich and Hurst, 1998) or the male that most effectively countermarked the scent of intruders onto its territory (Johnston *et al.*, 1997b; Rich and Hurst, 1999; Fig. 7). Females also prefer males with larger scent-marking glands and higher marking rates (Clark *et al.*, 1992), and the scent of their mate to that of unfamiliar individuals (Newman and Halpin, 1988; Tang-Martinez *et al.*, 1993).

Female mice also show a wide range of behavioral and physiological responses to intrinsic properties of male urine. Thus female mice prefer the urine of dominant over subordinate males (Parmigiani *et al.*, 1982; Drickamer, 1989; Hayashi, 1990; other rodents: Carr *et al.*, 1982; Evsikov *et al.*, 1995) and intact over castrate urine (Scott and Pfaff, 1970; Hayashi and Kimura, 1978). The chemical basis of this preference is known to include at least four volatile chemicals, a thiazole, a brevicomin, and α and β farnesenes, all of which are attractive to females (Jemiolo *et al.*, 1985, 1991). The thiazole and brevicomin bind to MUPs (Bacchini *et al.*, 1992) and because of this are lasting components of scent marks (Hurst *et al.*, 1998), but this is less certain in the case of the farnesenes (Novotny *et al.*, 1999). Further indications of mate quality are that female mice can distinguish the odor of parasitized and unparasitized males (Kavaliers and Colwell, 1992) and that the urine odor of parasitized males loses its attractiveness (Kavaliers and Colwell, 1995a,b; Penn *et al.*, 1998). Significantly, the odor of infected males does not become aversive to females suggesting that this response is adapted to avoiding mating with infected males rather than avoiding infection. Such data are consistent with the more general suggestion that females prefer to mate with males that have extravagant sexual displays because they are the healthiest and the most resistant to parasites (Hamilton and Zuk, 1982).

Perhaps linked to these ideas about the role of immunocompetence in sexual selection is the finding that rats, mice, and humans use odors mediated by variation in the MHC for mate choice. The most extensive data are from inbred mouse strains and, in general, these show that mice choose mates disassortatively with respect to MHC variation (e.g., Yamazaki *et al.*, 1976; Egid and Brown, 1989; Jordan and Bruford, 1998). The best data on female

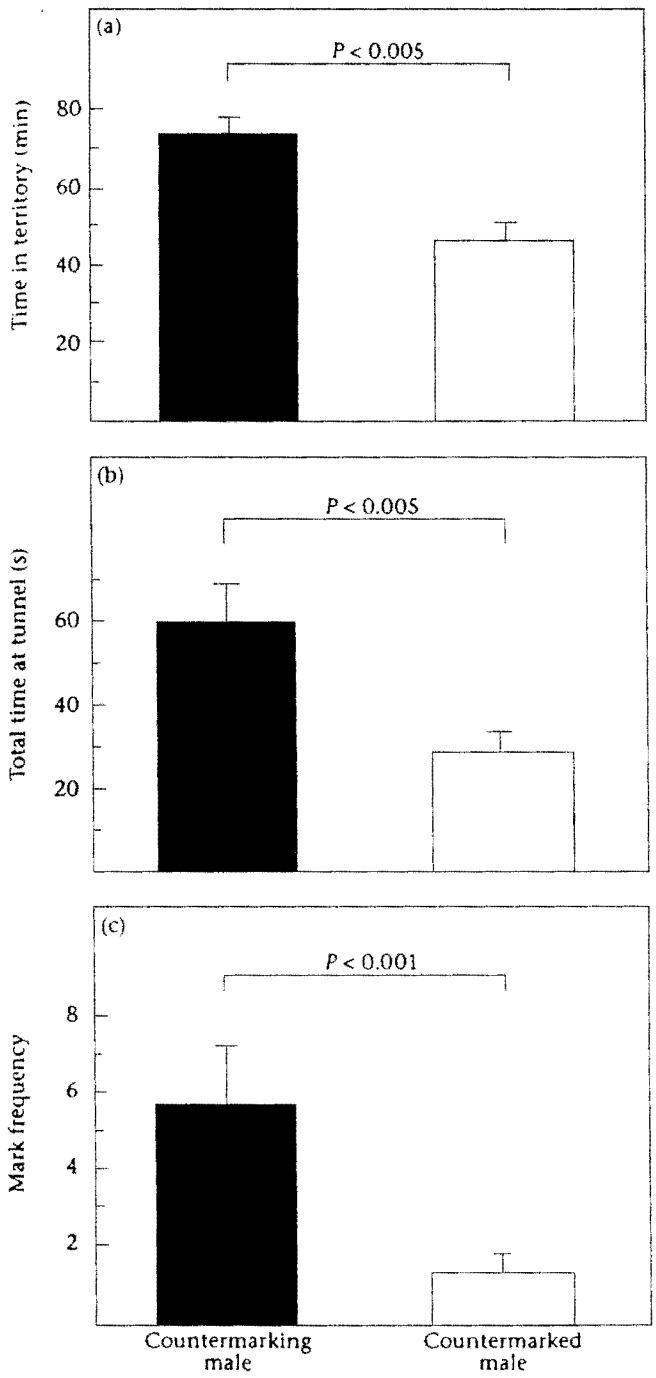

FIG. 7. Female preferences for male mice, *Mus domesticus*, which scent-mark near competitor's marks in response to simulated territorial intrusions. Males that deposit scent marks in response to introduced intruder scent (countermarking males) are preferred over those that fail to do so (countermarked males). (a) Time spent by females in male territories within a 2 h observation period, (b) time spent exploring tubes carrying odors of the territorial males, and (c) number of scent marks deposited by females while exploring the tubes. From Rich and Hurst (1999).

choice are experiments under seminatural conditions that showed that females often mated with males outside their own territory. In these matings, the other males were more MHC-dissimilar than their own territorial males (Potts *et al.*, 1991, 1992). Choice appears to be based on odor and tests involving the responses of trained mice in Y-mazes suggest that variable proportions of volatile carboxylic acids are used to separate nearly identical mice that differ only at the MHC (Singer *et al.*, 1997). MHC-disassortative mating may be a mechanism to increase heterozygosity specifically at the MHC, for example to increase the resistance of their offspring to parasites and diseases, or to prevent inbreeding in general (Jordan and Bruford, 1998; Penn and Potts, 1998).

All of the data reviewed in this section could possibly be linked to signals of quality that reflect immune response genotype and immunocompetence. Differences in approach could account for the differences in emphasis on androgen-dependent features such as marking frequencies and MUP-borne volatiles and odors that signal disease resistance. However, it is too early to arrive at any such conclusions. Further work is necessary to integrate the various approaches and to test if females take into account both mate quality and genetic relatedness when choosing mates.

All of the male odors dealt with so far lead to behavioral responses by females and in particular preferences for males. However, females in a wide range of rodents also show a number of priming or physiological responses. Best known are the effects of the urine odor of males on advancing female puberty (Vandenburgh, 1971; Bronson and Desjardins, 1974; Colby and Vandenbergh, 1974), induction of estrus (Whitten, 1956; Marsden and Bronson, 1964; Bronson and Whitten, 1968; Chipman and Albrecht, 1974), and, when an unfamiliar male is involved, in inducing abortions (Bruce, 1959; Chipman and Fox, 1966; Dewsbury, 1982; Hafer, 1990). Much is also known about the specific chemical components responsible for these effects (Vandenbergh *et al.*, 1975, 1976; Jemiolo *et al.*, 1986, 1989; Novotny *et al.*, 1990a,b). Nearly all of the research on these phenomena has been carried out in captivity and male urine has been presented in a number of ways (soiled bedding, sprayed onto the female, applied directly to the nares). Because females are the higher investing sex (Trivers, 1972), females are expected to respond selectively to males in relation to their mate quality and genetic relatedness. To our knowledge such intrasexual variation in response has not been measured. Similarly, no studies have measured physiological responses to simulated patterns of scent marks and so the potential influence of any signal of *RHP* through this medium is unknown.

We cannot exclude the possibility that the intrinsic information in rodent urine discussed above is designed to be transmitted directly between individuals or that the chemicals emitted are highly volatile and thus transient

components of urine rather than longer-lasting components of scent marks (MUPs and/or the volatiles that bind to them). Self-anointing with scent-marking substances is a common behavior and some glands are designed for direct transmission of odor. Some experiments have shown that the response of females to male odors is greater when the signaler is present than when the odor is presented alone (Milligan, 1975; review in Brown, 1985). However, this could indicate a mechanism that involves information in scent marks with conditional or obligate reinforcement from the signaler (as in scent-matching, Section IV.C).

VIII. Conclusions and Future Directions

A. Signaling to Competitors

A large body of historical and contemporary data supports the consensus that emerged in the 1980s that scent-marking by male mammals provides a means of competitor assessment. However, relatively little of this information has been collected with this hypothesis in mind (exceptions are reviewed in Gosling and McKay, 1990, and Stenström, 1998) and there is a need for further experimental tests, both in the laboratory and in the field. Patterns of scent marks provide a uniquely spatial element that may simply indicate a spatial reference for dominance or, in game theory terms, an owner's signal in a bourgeois strategy. However, asymmetries in *RHP* or resource value are ignored in this conditional strategy and this seems unlikely in the real world. Patterns of scent marks also indicate an animal's ability to defend an area over the time that it takes to mark. This important information seems unlikely to be ignored, although no experiments have addressed this hypothesis explicitly.

The idea that selection should favor signals that honestly reflect the signaler's quality has received surprisingly little attention in studies of scent-marking (Penn and Potts, 1998). However, recent experimental results suggest that scent-marking is costly both in energetic terms and in risks of attracting predators. Thus scent marks could be condition-dependent signals of quality as well as signals of ownership in a bourgeois strategy. The circumstances under which these signaling strategies operate remain to be clarified. Ideas about signals of quality and the economics of scent-marking also need to be integrated with current findings that information about the signaler's genotype and disease status are conveyed in social odors. How does intrinsic information about relatedness and disease status modify information from patterns of marks?

Most, perhaps all, territories of male mammals are scent-marked (although not all males that scent-mark are territorial). This suggests that

resource-defense polygyny might not be economically feasible without the reduction in costs of contest behavior that occurs when territory owners are assessed using scent marks. This proposition has been tested directly only once (Stenström, 1998) but further experiments in a wider range of species are needed. The general conclusion about reduction in costs would also benefit from comparative analysis. Costs of area defense would be further reduced if intruders seek out marks. The benefits of assessment, the widespread existence of visual advertisements, and the small range of marks (most may need water or water vapor from a receiver before volatiles are released) suggest that they do. Perhaps the practice of placing a signal in the environment in a fashion that does not allow rapid reinforcement might not exist if the benefits to receivers from the information in marks did not exceed the costs of seeking them out.

We have reviewed the evidence and theoretical support for the idea that scent marks may be condition-dependent signals of quality. In this they appear to be consistent with the handicap principle, namely that only animals of high quality can afford to use costly signals. We have also outlined the argument that resource holders use scent-marking to manipulate the behavior of nonresource holders to reduce the costs of resource defense. We have even suggested that resource-defense polygyny in mammals might generally not be economically viable without the cost savings that follow from competitor assessment by scent-marking. How can this apparent paradox be resolved? Perhaps only animals that can pay the high costs of scent-marking can also afford the high risk of escalated contests that is involved in acquiring a territory. But having done so, the additional costs of area defense are lower than those of contest behavior in the competing strategy that would involve escalated contests with every competitor. The universal association of resource-defense territoriality and scent-marking suggests that the sum of the costs of scent-marking and a reduced level of escalated contest should be less that those of escalated contests in the absence of assessment by scent-marking. However, this proposition has not been tested empirically, and this remains a priority for understanding the economics of scent-marking in territories.

B. Mechanism

Much of the literature on scent-marking has been divided according to the taxon studied and according to favored mechanisms for information transmission. We find no evidence that this reflects biological reality. In the best known species, the mouse, it is known that receivers make decisions on the basis of all three principal mechanisms: the use of intrinsic information (for example mark density and the concentration of androgen-dependent

volatiles), the use of memorized information about past opponents and their odors, and the scent-matching of new opponents with the smell of scent marks recently encountered. These mechanisms are also known across a range of species and we believe that when more information is collected, it will prove unusual for animals to be restricted to only one mechanism. Game theoretical analysis has defined the circumstances under which it pays intruders to switch between an assessment of a signaler using intrinsic information and scent-matching. Further investigation is required to explore the importance of the accuracy of assessment that is possible using different mechanisms. For example, it might be expected that learning from past encounters will have limits due to changing social relationships and the number of individuals that can be remembered. Scent-matching is theoretically most accurate and should thus be used where the fitness benefits of a decision outweigh the risks of close approach to a potentially dangerous opponent. Future understanding of alternative mechanisms may depend mainly on advances in receiver psychology, including the limits to spatial and sequential memory and interpretation of patterns of marks.

C. Signals to Mates

Although the patterns of scent marks in wild mammals show that they are designed principally as signals to male competitors, selection should also favor choice within the highest investing sex (Trivers, 1972) and so females are expected to use information about male quality in scent marks for mate choice. Empirical studies confirm that females do use information in scent marks although we do not know whether they obtain this information by eavesdropping on signals intended for other males or whether the signals are designed for reception by females. This is a research priority that could be addressed using existing techniques. There is a striking lack of data about the responses of females to male scent marks in natural systems.

If the spatial element of patterns of scent marks provides a cheat-proof signal of competitive ability, we would expect females to use these patterns for mate choice. A small body of experimental data suggests that they do and that they use scent-matching between the predominant odor of scent marks and that of potential mates. However, most information about female preferences comes from responses to intrinsic properties of male social odors, a process that need not involve reference to patterns of marks. Some of the information conveyed by qualitative characteristics of marks is potentially redundant with respect to patterns of marks. For example, dominance status and freedom from parasites, both of which can be detected by females using volatiles in mouse urine, may be correlated with an animal's ability to

establish and maintain patterns of scent marks. We know nothing about the interaction between intrinsic information about quality and that available from patterns of scent marks for mate choice.

Information about genetic relatedness from volatiles mediated by MHC variation may provide additional information to that about quality. If females benefit from disassortative mating either to avoid inbreeding depression or because their progeny benefit by increased disease resistance, then they should take account of this information during mate choice. Once again, we do not know how the signals interact or whether their design is influenced by female psychology.

Nearly all accounts of physiological responses to male odors, such as puberty advancement or abortion, are treated in the literature as successful manipulations by males of female reproductive physiology. But because females are the higher investing sex, selection should favor their ability to resist manipulation by males and to control their own reproduction. The outcome of such sexual conflict may vary in relation to ecological and frequency-dependent factors but little research has been done using this paradigm. For example, is there variation between females in their estrus advancement in relation to male quality or genetic relatedness? If a female aborts and reconceives with a new male, does the female gain because the new male then invests more heavily in the litter? Is a female more likely to abort when there is a chance of mating with an MHC dissimilar male? The questions are legion.

IX. Summary

Scent-marking is a ubiquitous form of olfactory signaling in male mammals and both territorial males in resource-defense mating systems and dominant males in dominance mating systems scent-mark. A large body of evidence suggests a link between scent-marking by male mammals and intrasexual competition. Resource holders appear to mark to help establish and maintain their status. They may do this because scent marks allow potential opponents to assess the status or *RHP* of the signaler. Nonresource holding competitors benefit because they can adjust the level of escalation in relation to potential costs and benefits and avoid risky contests. Resource holders benefit through reduced costs because many nonresource holders withdraw to avoid escalated contests.

Three basic mechanisms allow receivers to make decisions after detecting scent marks. Receivers may (1) detect intrinsic properties of scent marks (e.g., concentrations of androgen-dependent volatiles), (2) remember past contests and the odor of each individual involved and associate these with

the odor of scent marks, and (3) remember the smell of marks recently encountered and match this smell with potential opponents that they meet subsequently. It is now known that all of these mechanisms are used, sometimes within one species (e.g., mice) and we argue that the mechanisms are used conditionally, depending on information available and potential costs and benefits to receivers. Game theoretical analysis has recently shown how territorial intruders may switch from using intrinsic properties of marks to scent-matching when making decision about whether to remain in a territory.

Scent-marking may be a uniquely cheat-proof signal of status because males must be able to defend their territory or dominance status over the time taken to mark it. A pattern of marks is thus a signal of status that has been tested in intrasexual competition. It also seems likely that marks are intrinsically costly both in energetic terms and by increasing predation risk. Mice can detect whether urine is from a parasitized or nonparasitized individual and these odors could potentially signal immunocompetence if mediated by variation at the MHC region of the genome. This remains to be tested. It is known that mice can detect relatedness via urine volatiles mediated by the MHC and it has been predicted that males should modify their competitive behavior in the light of this information. Again this remains to be tested. Information about disease status and genetic relatedness does not explain why males maintain patterns of scent marks.

Most, perhaps all, territories are scent-marked. This may be because most intruders are of lower *RHP* than resource holders and these males should usually withdraw after assessing the resource holder by its scent marks. The costs of defending a territory may thus be substantially reduced. The obligate link between scent-marking and territoriality suggests that resource-defense polygyny in mammals may not be economically viable without this reduction in the costs of area defense.

A little information is available to show that females use information from patterns of scent marks and a great deal of information shows that they use intrinsic information. It is not known whether males signal to females to enable mate choice or if females eavesdrop on signals sent between male competitors. Most known responses are to male urine by female rodents. For example, females show physiological (priming) responses to male odors (e.g., advancing and synchronizing estrus, inducing abortion). Other research has identified factors responsible for female mate preferences in choice tests. For example, the dominance status of the signaling male is a predictor of female interest and such studies have identified androgen-dependent volatiles responsible for the response. More recently, females have been shown to use odor mediated by the MHC locus to choose mates in relation to their genetic relatedness and to use odor to distinguish healthy and diseased mates. Most of these studies have been on mice and most use male urine, but the effect

of patterns of urine scent marks has not been investigated. The only studies that explicitly use scent marks are those showing that females match the odor of potential mates with marks previously found in the environment to select mates. Future research should aim to clarify how information about the quality of potential mates is transmitted and how females trade-off such information against genetic relatedness.

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References

Adams, M. G. (1980). Odour-producing organs of mammals. *Symp. Zool. Soc. London* **45,** 57–86.

Alberts, A. C. (1992). Constraints on the design of chemical communication systems in terrestrial vertebrates. *Am. Nat.* **139,** (Suppl.), S62–S89.

Albone, E. S. (1984). "Mammalian Semiochemistry: The Investigation of Chemical Signals between Mammals." Wiley, New York.

Alcock, J., and Bailey, W. J. (1997). Success in territorial defense by male tarantula hawk wasps *Hemipepsis ustulata:* The role of residency. *Ecol. Entomol.* **22,** 377–383.

Allen, J. J., Bekoff, M., and Crabtree, R. L. (1999). An observational study of coyote (*Canis latrans*) scent-marking and territoriality in Yellowstone National Park. *Ethology* **105,** 289–302.

Apps, P. J., Viljoen, H. W., Richardson, P. R. K., and Pretorius, V. (1989). Volatile components of anal gland secretion of aardwolf (*Proteles cristatus*). *J. Chem. Ecol.* **15,** 1681–1688.

Bacchini, A., and Gaetani, E. (1992). Mouse urinary proteins bind pheromones. *Chem. Senses* **17,** 818.

Bacchini, A., Gaetani, E., and Cavaggioni, A. (1992). Pheromone binding proteins of the mouse, *Mus musculus. Experientia* **48,** 419–421.

Barette, C. (1977). Scent-marking in captive muntjacs, *Muntiacus reevesi. Anim. Behav.* **25,** 536–541.

Baretto, G. R., and Macdonald, D. W. (1999). The response of water voles, *Arvicola terrestris,* to the odours of predators. *Anim. Behav.* **57,** 1107–1112.

Bearder, S. K., and Randall, R. M. (1978). The use of faecal marking sites by spotted hyaenas and civets. *Carnivore* **1,** 32–38.

Beauchamp, G. K., and Wellington, J. L. (1984). Habituation to individual odors occurs in brief, widely-spaced presentations. *Physiol. Behav.* **32,** 511–514.

Beauchamp, G. K., Yamazaki, K., Wysocki, C. J., Slotnick, B. M., Thomas, L., and Boyse, E. A. (1985). Chemosensory recognition of mouse major histocompatibility types by another species. *Proc. Nat. Acad. Sci.* **82,** 4186–4188.

Bel, M. C., Porteret, C., and Coulon, J. (1995). Scent deposition by cheek rubbing in the alpine marmot (*Marmota marmota*) in the French Alps. *Can. J. Zool.* **73,** 2065–2071.

Belwood, J., and Morris, G. K. (1997). Bat predation and its influence on calling behaviour in Neotropical katydids. *Science* **238,** 64–67.

Bigalke, R. C. (1972). Observations on the behaviour and feeding habits of the springbok, *Antidorcas marsupialis*. *Zool. Afr.* **7,** 333–359.

Boake, C. R. B., Shelly, T. E., and Kaneshiro, K. Y. (1996). Sexual selection in relation to pest-management strategies. *Ann. Rev. Entomol.* **41,** 211–229.

Boero, D. L. (1995). Scent-deposition behaviour in alpine marmots (*Marmota marmota* L.): Its role in territorial defence and social communication. *Ethology* **100,** 26–38.

Bossert, W. H., and Wilson, E. O. (1963). The analysis of olfactory communication among animals. *J. Theor. Biol.* **5,** 443–469.

Bowyer, R. T., Vanbellenberghe, V., and Rock, K. R. (1994). Scent marking by Alaskan moose—characteristics and spatial distribution of rubbed trees. *Can. J. Zool.* **72,** 2186–2192.

Brashares, J. S., and Arcese, P. (1999a). Scent marking in a territorial African antelope: I. The maintenance of borders between male oribi. *Anim. Behav.* **57,** 1–10.

Brashares, J. S., and Arcese, P. (1999b). Scent marking in a territorial African antelope: II. The economics of marking with faeces. *Anim. Behav.* **57,** 11–17.

Bronson, F. H., and Desjardins, C. (1974). Circulating concentrations of FSH, LH, estradiol, and progesterone associated with acute, male-induced puberty in female mice. *Endocrinology* **94,** 1658–1668.

Bronson, F. H., and Marsden, H. M. (1973). The preputial gland as an indicator of social dominance in male mice. *Behav. Biol.* **9,** 625–628.

Bronson, F. H., and Whitten, W. K. (1968). Estrus-accelerating pheromone of mice: Assay, androgen-dependency and presence in bladder urine. *J. Reprod. Fert.* **15,** 131–134.

Brotherton, P. N. M., and Manser, M. B. (1997). Female dispersion and the evolution of monogamy in the dikdik. *Anim. Behav.* **54,** 1413–1424.

Brown, R. E. (1985). The rodents: I Effects of odours on reproductive physiology (primer effects). *In* "Social Odours in Mammals" (R. E. Brown and D. W. Macdonald, eds.), Vol. 1, pp. 245–344. Clarendon Press, Oxford.

Brown, R. E., and Macdonald, D. W., eds. (1985). "Social Odours in Mammals." Clarendon Press, Oxford.

Brown, R. E., Singh, P. B., and Roser, B. (1987). The major histocompatibility complex and the chemosensory recognition of individuality in rats. *Physiol. Behav.* **40,** 65–73.

Brown, R. E., Roser, B., and Singh, P. B. (1990). The MHC and individual odours in rats. *In* "Chemical Signals in Vertebrates V" (D. W. Macdonald, D. Müller-Scharze, S. E. Natynczuk, eds.), pp. 230–243. Plenum Press, New York.

Bruce, H. M. (1959). An exteroceptive block to pregnancy in the mouse. *Nature* **184,** 105.

Cade, W. H. (1975). Acoustically orienting parasitoids: Fly phonotaxis to cricket song. *Science* **190,** 1312–1313.

Caro, J. H. (1982). The sensing, dispersion and measurement of pheromone vapors in air. *In* "Insect Suppression with Controlled Release Pheromone Systems" (A. F. Kydonieus and M. Beroza, eds.), Vol. I, pp. 145–158. CRC Press, Boca Raton Fl.

Carr, W. J., Martorano, R. D., and Krames, L. (1970). Responses of mice to odors associated with stress. *J. Comp. Physiol. Psychol.* **2,** 223–228.

Carr, W. J., Kimmel, K. R., Anthony, S. L., and Schlocker, D. E. (1982). Female rats prefer to mate with dominant rather than subordinant males. *Bull. Psychonomic Soc.* **20,** 89–91.

Chipman, R. K., and Albrecht, E. D. (1974). The relationship of the male preputial gland to the acceleration of estrus in the laboratory mouse. *J. Reprod. Fert.* **38,** 91–96.

Chipman, R. K., and Fox, K. A. (1966). Oestrous synchronization and pregnancy blocking in wild house mice (*Mus musculus*). *J. Reprod. Fert.* **12,** 233–236.

Clark, M. M., Tucker, L., and Galef, B. G., Jr. (1992). Stud males and dud males: Intrauterine position effects on the reproductive success of male gerbils. *Anim. Behav.* **43,** 215–221.

Colborne, J., Norval, R. A. I., and Spickett, A. M. (1981). Ecological studies on *Ixodes (Afrixoides) matopi* Spickett, Keirans, Norval and Clifford, 1980 (Acarina: Ixodidae). *Onderstepoort J. Vet. Res.* **48,** 31–35.

Colby, D. R., and Vandenbergh, J. G. (1974). Regulatory effects of urinary pheromones on puberty in the mouse. *Biol. Reprod.* **11,** 268–279.

Collins, S. A., Gosling, L. M., Hudson, J., and Cowan, D. (1997). Does behaviour after weaning affect the dominance status of adult male mice (*Mus musculus*)? *Behaviour* **134,** 989–1002.

Dabelsteen, T., McGregor, P. K., Holland, J., Tobias, J. A., and Pedersen, S. B. (1997). The signal function of overlapping singing in male robins. *Anim. Behav.* **53,** 249–256.

Davies, N. B. (1978). Territorial defence in the speckled wood butterfly (*Pararge aegeria*): The resident always wins. *Anim. Behav.* **26,** 138–147.

Dewsbury, D. A. (1982). Pregnancy blockage following multiple male copulation or exposure at the time of mating in deer mice, *Peromyscus maniculatus*. *Behav. Ecol. Sociobiol.* **11,** 37–42.

Dickman, C. R., Predavec, M., and Lynam, A. J. (1991). Differential predation of size and sex classes of mice by the Barn Owl, *Tyto alba*. *Oikos* **62,** 67–76.

Drickamer, L. C. (1989). Odor preferences of wild stock female house mice (*Mus domesticus*) tested at three ages using urine and other cues from conspecific males and females. *J. Chem. Ecol.* **15,** 1971–1987.

Dryden, G. L., and Conaway, C. H. (1967). The origin and hormonal control of scent production in *Suncus murinus*. *J. Mammal.* **48,** 420–428.

Dunbar, R. I. M., and Dunbar, E. P. (1974). Social organization and ecology of the klipspringer (*Oreotragus oreotragus*) in Ethiopia. *Z. Tierpsychol.* **35,** 481–493.

Egid, K., and Brown, J. L. (1989). The major histocompatibility complex and female mating preferences in mice. *Anim. Behav.* **38,** 548–549.

Endler, J. A. (1993). Some general comments on the evolution and design of animal communication systems. *Philos. Trans. R. Soc. London B* **340,** 215–225.

Endler, J. A., and Basolo, A. L. (1998). Sensory ecology, receiver biases and sexual selection. *Trends. Ecol. Evol.* **13,** 415–420.

Epple, G., Mason, J. R., Nolte, D. L., and Campbell, D. L. (1993). Effects of predator odors on feeding in the mountain beaver (*Aplodontia rufa*). *J. Mammal.* **74,** 715–722.

Estes, R. D. (1969). Territorial behavior of the wildebeest (*Connochaetes taurinus* Burchell, 1823). *Z. Tierpsychol.* **26,** 284–370.

Evsikov, V. I., Nazarova, G. G., and Potapov, M. A. (1995). Female odor choice, male social rank, and sex ratio in the water vole. *Adv. Biosciences* **93,** 303–307.

Feldman, H. N. (1994). Methods of scent marking in the domestic cat. *Can. J. Zool.* **72,** 1093–1099.

Ferkin, M. H. (1999). Meadow voles (*Microtus pennsylvanicus*, Arvicolidae) over-mark and adjacent-mark the scent marks of same-sex conspecifics. *Ethology* **105,** 825–837.

Ferkin, M. H., Burda, J., O'Connor, M. P., and Lee, C. J. (1995). Persistence of the attractiveness of two sex-specific scents in meadow voles, *Microtus pennsylvanicus*. *Ethology* **101,** 228–238.

Ferkin, M. H., Dunsavage, J., and Johnston, R. E. (1999). What kind of information do meadow voles (*Microtus pennsylvanicus*) use to distinguish between the top and bottom scent of an over-mark? *J. Comp. Psychol.* **113,** 43–51.

Franklin, W. L. (1974). The social behaviour of the vicuna. *In* "The Behaviour of Ungulates and Its Relation to Management" (V. Geist and F. R. Walther, eds.), Vol. 2, pp. 477–487. IUCN, Morges.

Franks, P., and Lenington, S. (1986). Dominance and reproductive behavior of wild house mice in a seminatural environment correlated with T-locus genotype. *Behav. Ecol. Sociobiol.* **18,** 395–404.

Geist, V. (1965). On the rutting behaviour of the mountain goat. *J. Mammal.* **45,** 551–568.
Gilbert, B. K. (1973). Scent marking and territoriality in pronghorn (*Antilope americana*) in Yellowstone National Park. *Mammalia* **37,** 25–33.
Gorman, M. L. (1984). The response of prey to stoat (*Mustela erminea*) scent. *J. Zool. (London)* **202,** 419–423.
Gorman, M. L. (1990). Scent marking strategies in mammals. *Rev. Suisse Zool.* **97,** 3–29.
Gorman, M. L., and Mills, M. G. L. (1984). Scent marking strategies in hyaenas (Mammalia). *J. Zool. (London)* **202,** 535–547.
Gorman, M. L., Nedwell, D. B., and Smith, R. M. (1974). An analysis of the contents of the anal scent pockets of *Herpestes auropunctatus* (Carnivora: Viverridae). *J. Zool. (London)* **172,** 389–399.
Gosling, L. M. (1972). The construction of antorbital gland marking sites by male oribi (*Ourebia ourebia,* Zimmerman 1783). *Z. Tierpsychol.* **30,** 271–276.
Gosling, L. M. (1974). The social behaviour of Coke's hartebeest (*Alcelaphus buselaphus cokei*). *In* "The Behaviour of Ungulates and Its Relation to Management." (V. Geist and F. R. Walther, eds.), Vol. 1, pp. 485–511. IUCN, Morges.
Gosling, L. M. (1980). Defence guilds of savannah ungulates as a context for scent communication. *Symp. Zool. Soc. London* **45,** 195–212.
Gosling, L. M. (1981). Demarkation in a gerenuk territory: An economic approach. *Z. Tierpsychol.* **56,** 305–322.
Gosling, L. M. (1982). A reassessment of the function of scent marking in territories. *Z. Tierpsychol.* **60,** 89–118.
Gosling, L. M. (1985). The even-toed ungulates: Order Artiodactyla. *In* "Social Odours in Mammals" (R. E. Brown and D. W. Macdonald, eds.), Vol. 2, pp. 550–618. Oxford University Press, UK.
Gosling, L. M. (1986a). Economic consequences of scent marking in mammalian territoriality. *In* "Chemical Signals in Vertebrates IV" (D. Duvall, D. Müller-Schwarze, and R. M. Silverstein, eds.), pp. 385–395. Plenum Press, New York.
Gosling, L. M. (1986b). The evolution of mating strategies in male antelopes. *In* "Ecological Aspects of Social Evolution" (D. I. Rubenstein and R. W. Wrangham, eds.), Princeton Univ. Press, New Jersey.
Gosling, L. M. (1987). Scent marking in an antelope lek territory. *Anim. Behav.* **35,** 620–622.
Gosling, L. M. (1990). Scent marking by resource holders: Alternative mechanisms for advertising the costs of competition. *In* "Chemical Signals in Vertebrates V" (D. W., Macdonald, S. Natynczuk, and D. Müller-Schwarze, eds.), pp. 315–328. Oxford University Press, UK.
Gosling, L. M., and McKay, H. V. (1990). Competitor assessment by scent matching: An experimental test. *Behav. Ecol. Sociobiol.* **26,** 415–420.
Gosling, L. M., and Wright, K. H. M. (1984). Scent marking and resource defence by male coypus (*Myocastor coypus*). *J. Zool. (London)* **234,** 423–436.
Gosling, L. M., Atkinson, N. W., Collins, S. A., Roberts, R. J., and Walters, R. L. (1996a). Avoidance of scent-marked areas depends on the intruder's body size. *Behaviour* **133,** 491–502.
Gosling, L. M., Atkinson, N. W., Dunn, S., and Collins, S. A. (1996b). The response of subordinate male mice to scent marks varies in relation to their own competitive ability. *Anim. Behav.* **52,** 1185–1191.
Gosling, L. M., Roberts, S. C., Thornton, E. A., and Andrew, M. A. (2000). Life history costs of olfactory status signalling in mice. *Behav. Ecol. Sociobiol.* **48,** 328–332.
Graf, W. (1956). Territorialism in deer. *J. Mammal.* **37,** 165–170.
Grafen, A. (1990). Biological signals as handicaps. *J. Theor. Biol.* **144,** 517–546.
Grau, G. A. (1976). Olfaction and reproduction in ungulates. *In* "Mammalian Olfaction,

Reproductive Processes and Behaviour" (R. L. Doty, ed.), pp. 219–242. Academic Press, New York.

Guilford, T., and Dawkins, M. S. (1991). Receiver psychology and the evolution of animal signals. *Anim. Behav.* **42,** 1–14.

Guilford, T., and Dawkins, M. S. (1993). Receiver psychology and the design of animal signals. *Trends in Neurosci.* **16,** 430–436.

Hafer, A. A. (1990). Dominance status and its influence on the Bruce effect in house mice. *In* "Chemical Signals in Vertebrates V" (D. W. MacDonald, D. Müller-Scharze, and S. E. Natynczuk, eds.), pp. 269–275. Plenum Press, New York.

Halpin, Z. T. (1980). Individual odors and individual recognition: Review and commentary. *Biol. Behav.* **5,** 233–248.

Halpin, Z. T. (1986). Individual odors among mammals: Origins and functions. *Adv. Stud. Behav.* **16,** 39–70.

Hamilton, W. D., and Zuk, M. (1982). Heritable true fitness and bright birds: A role for parasites? *Science* **218,** 384–387.

Harvey, S., Jemiolo, B., and Novotny, M. (1989). Pattern of volatile compounds in dominant and subordinate male mouse urine. *J. Chem. Ecol.* **15,** 2061–2072.

Hayashi, S. (1986). Effects of a cohabitant on preputial gland weight of male mice. *Physiol. Behav.* **38,** 299–300.

Hayashi, S. (1990). Social condition influences sexual attractiveness of dominant male mice. *Zool. Sci.* **7,** 889–894.

Hayashi, S., and Kimura, T. (1978). Effects of exposure to males on sexual preference in female mice. *Anim. Behav.* **26,** 290–295.

Haynes, K. F., and Yeargan, K. V. (1999). Exploitation of intraspecific communication systems: Illicit signalers and receivers. *Annals Entomol. Soc. Am.* **92,** 960–970.

Hediger, H. (1949). Säugetier-Territorien und ihre Markierung. *Bijdr. Dierkd.* **28,** 172–184.

Hendrichs, H., and Hendrichs, U. (1971). "Dikdik und Elefanten: Ökologie und Soziologie zweier Afrikanischer Huftiere." R. Piper, Munich.

Heth, G., Todrank, J., and Johnston, R. E. (1998). Kin recognition in golden hamsters: Evidence for phenotype matching. *Anim. Behav.* **56,** 409–417.

Humphries, R. E., Robertson, D. H. L., Beynon, R. J., and Hurst, J. L. (1999). Unravelling the chemical basis of competitive scent marking in house mice. *Anim. Behav.* **58,** 1177–1190.

Hurst, J. L. (1990). Urine marking in populations of wild house mice *Mus domesticus* Rutty. I. Communication between males. *Anim. Behav.* **40,** 209–222.

Hurst, J. L. (1993). The priming effects of urine substrate marks on interactions between male house mice, *Mus musculus domesticus,* Schwartz and Schwartz. *Anim. Behav.* **45,** 55–81.

Hurst, J. L., Hayden, L., Kingston, M., Luck, R., and Sorensen, K. (1994). Response of the aboriginal house mouse *Mus spretus* Lataste to tunnels bearing the odours of conspecifics. *Anim. Behav.* **48,** 1219–1229.

Hurst, J. L., Robertson, D. H. L., Tolladay, U., and Beynon, R. J. (1998). Proteins in urine scent marks of male house mice extend the longevity of olfactory signals. *Anim. Behav.* **55,** 1289–1297.

Idris, M. (1994). Behavioural responses of the Indian desert gerbil, *Meriones hurriane,* towards conspecific and interspecific sebum odor. *Annals of Arid Zone* **33,** 137–141.

Jedrzejewski, W., Rychlik, L., and Jedrzejewska, B. (1993). Responses of bank voles to seven species of predators: Experimental data and their relevance to natural predator-vole relationships. *Oikos* **68,** 251–257.

Jemiolo, B., Alberts, J., Sochinski-Wiggins, S., Harvey, S., and Novotny, M. (1985). Behavioural and endocrine responses of female mice to synthetic analogues of volatile compounds in male urine. *Anim. Behav.* **33,** 1114–1118.

Jemiolo, B., Harvey, S., and Novotny, M. (1986). Promotion of the Whitten Effect in female mice by synthetic analogs of male urinary constituents. *Proc. Nat. Acad. Sci.* **83,** 4576–4579.

Jemiolo, B., Andreolini, F., Xie, T., Wiesler, D., and Novotny, M. (1989). Puberty-affecting synthetic analogs of urinary chemosignals in the house mouse, *Mus domesticus*. *Physiol. Behav.* **46,** 293–298.

Jemiolo, B., Xie, T. M., and Novotny, M. (1991). Socio-sexual olfactory preference in female mice: Attractiveness of synthetic chemosignals. *Physiol. Behav.* **50,** 1119–1122.

Johansson, A., and Liberg, O. (1996). Functional aspects of marking behaviour by male roe deer (*Capreolus capreolus*). *J. Mammal.* **77,** 558–567.

Johnston, R. E. (1993). Memory for individual scent in hamsters (*Mesocricetus auratus*) as assessed by habituation methods. *J. Comp. Psychol.* **107,** 201–207.

Johnston, R. E., and Bhorade, A. (1998). Perception of scent over-marks by golden hamsters (*Mesocricetus auratus*): Novel mechanisms for determining which individual's mark is on top. *J. Comp. Psychol.* **112,** 230–243.

Johnston, R. E., and Robinson, T. A. (1993). Cross-species discrimination of individual odors by hamsters (Muridae, *Mesocricetus auratus, Phodopus campbelli*). *Ethology* **94,** 317–325.

Johnston, R. E., and Schmidt, T. (1979). Responses of hamsters to scent marks of different ages. *Behav. Neural Biol.* **26,** 64–75.

Johnston, R. E., Derzie, A., Chiang, G., Jernigan, P., and Lee, H. C. (1993). Individual scent signatures in golden hamsters: Evidence for specialisation of function. *Anim. Behav.* **45,** 1061–1070.

Johnston, R. E., Chiang, G., and Tung, C. (1994). The information in scent over-marks of golden hamsters. *Anim. Behav.* **48,** 323–330.

Johnston, R. E., Sorokin, E. S., and Ferkin, M. H. (1997a). Female voles discriminate males' over-marks and prefer top-scent males. *Anim. Behav.* **54,** 679–690.

Johnston, R. E., Sorokin, E. S., and Ferkin, M. H. (1997b). Scent counter-marking by male meadow voles: Females prefer the top-scent male. *Ethology* **103,** 443–453.

Johnstone, R. A. (1998). Conspiratorial whispers and conspicuous displays: Games of signal detection. *Evolution* **52,** 1554–1563.

Jolly, A. (1966). "Lemur Behaviour: A Madagascar Field Study." Univ. of Chicago Press, Illinois.

Jones, R. B., and Nowell, N. W. (1973). The effect of urine on the investigatory behaviour of male albino mice. *Physiol. Behav.* **11,** 35–38.

Jones, R. B., and Nowell, N. W. (1974). Effects of androgen on the aversive properties of male mouse urine. *J. Endocrinol.* **60,** 19–25.

Jones, R. B., and Nowell, N. W. (1977). Aversive potency of male mouse urine: A temporal study. *Behav. Biol.* **19,** 523–526.

Jones, R. B., and Nowell, N. W. (1989). Aversive potency of urine from dominant and subordinate male laboratory mice (*Mus musculus*): Resolution of a conflict. *Aggressive Behav.* **15,** 291–296.

Jordan, W. C., and Bruford, M. W. (1998). New perspectives on mate choice and the MHC. *Heredity* **81,** 127–133.

Kappeler, P. M. (1998). To whom it may concern: The transmission and function of chemical signals in *Lemur catta*. *Behav. Ecol. Sociobiol.* **42,** 411–421.

Kavaliers, M., and Colwell, D. D. (1992). Aversive responses of female mice to the odors of parasitized males: Neuromodulatory mechanisms and implications for mate choice. *Ethology* **95,** 202–212.

Kavaliers, M., and Colwell, D. D. (1995a). Discrimination by female mice between the odors of parasitized males and non-parasitized males. *Proc. R. Soc. London B* **261,** 31–35.

Kavaliers, M., and Colwell, D. D. (1995b). Odors of parasitized males induce aversive responses in female mice. *Anim. Behav.* **50,** 1161–1169.

Koivula, M., and Viitala, J. (1999). Rough-legged buzzards use vole scent marks to assess hunting areas. *J. Avian Biol.* **30,** 329–332.

Koivula, M., Korpimäki, E., and Viitala, J. (1997). Do Tengmalm's owls see vole scent marks visible in ultraviolet light. *Anim. Behav.* **54,** 873–877.

Koivula, M., Koskela, E., and Viitala, J. (1999a). Sex and age-specific differences in ultraviolet reflectance of scent marks of bank voles (*Clethrionomys glareolus*). *J. Comp. Physiol. A* **185,** 561–564.

Koivula, M., Viitala, J., and Korpimäki, E. (1999b). Kestrels prefer scent marks according to species and reproductive status of voles. *Ecoscience* **6,** 415–420.

Koivunen, V., Korpimäki, E., and Hakkarainen, H. (1998). Refuge sites of voles under owl predation risk: Priority of dominant individuals? *Behav. Ecol.* **9,** 261–266.

Kokko, H., and Sutherland, W. J. (1998). Optimal floating and queuing strategies: Consequences for density dependence and habitat loss. *Am. Nat.* **152,** 354–366.

Komers, P. E. (1996). Obligate monogamy without paternal care in Kirk's dikdik. *Anim. Behav.* **51,** 131–140.

Kotler, B. P., Blaustein, L., and Brown, J. S. (1992). Predator facilitation—The combined effects of snakes and owls on the foraging behaviour of gerbils. *Annal. Zool. Fennici* **29,** 199–206.

Kozlowski, J. (1992). Optimal allocation of resources to growth and reproduction: Implications for age and size at maturity. *Trends Ecol. Evol.* **7,** 15–19.

Kruuk, H. (1972). "The Spotted Hyaena, A Study of Predation and Social Behaviour." Univ. of Chicago Press, Illinois.

Lewis, M. A., and Murray, J. D. (1993). Modelling territoriality and wolf-deer interactions. *Nature* **366,** 738–740.

Lewis, M. A., White, K. A. J., and Murray, J. D. (1997). Analysis of a model for wolf territories. *J. Math. Biol.* **35,** 749–774.

Macdonald, D. W. (1979). Some observations and field experiments on the urine marking behaviour of the red fox, *Vulpes vulpes* L. *Z. Tierpsychol.* **51,** 1–22.

Marsden, H. M., and Bronson, F. H. (1964). Estrous synchrony in mice: Alteration by exposure to male urine. *Science* **144,** 1469.

Mateo, J. M., and Johnston, R. E. (2000a). Kin recognition and the "armpit effect": Evidence of self-referent phenotype matching. *Proc. R. Soc. London B* **267,** 695–700.

Mateo, J. M., and Johnston, R. E. (2000b). Retention of social recognition after hibernation in Belding's ground squirrels. *Anim. Behav.* **59,** 491–499.

Maynard Smith, J. (1982). "Evolution and the Theory of Games." Cambridge Univ. Press, UK.

Maynard Smith, J. (1996). The games lizards play. *Nature* **380,** 198–199.

McGregor, P. K. (1993). Signalling in territorial systems: A context for individual identification, ranging and eavesdropping. *Philos. Trans. R. Soc. London B* **340,** 237–244.

Mech, L. D. (1977). Wolf-pack buffer zones as prey reservoirs. *Science* **198,** 320–321.

Miller, K. V., Marchinton, R. L., Forand, K. J., and Johansen, K. L. (1987). Dominance, testosterone levels, and scraping activity in a captive herd of white-tailed deer. *J. Mammal.* **68,** 812–817.

Milligan, S. R. (1975). Further observations on the influence of the social environment on ovulation in the vole, *Microtus agrestis*. *J. Reprod. Fert.* **44,** 543–544.

Mills, M. G. L. (1983). Behavioural mechanisms in territory and group maintenance of the brown hyaena *Hyaena brunnea* in the southern Kalahari. *Anim. Behav.* **31,** 503–510.

Mills, M. G. L., and Gorman, M. L. (1987). The scent marking behaviour of the spotted hyaena (*Crocuta crocuta*) in the southern Kalahari. *J. Zool. (London)* **212,** 483–497.

Mills, M. G. L., Gorman, M. L., and Mills, M. E. J. (1980). The scent marking behaviour of the brown hyaena *Hyaena brunnea*. S. *Afr. J. Zool.* **15,** 240–248.

Moodie, J. D., and Byers, J. A. (1989). The function of scent marking by males on female urine in pronghorns. *J. Mammal.* **70,** 812–814.

Moore, W. G., and Marchinton, R. L. (1974). Marking behaviour and its social function in white-tailed deer. *In* "The Behaviour of Ungulates and Its Relation to Management" (V. Geist and F. Walther, eds.), pp. 447–456. IUCN, Morges.

Moy, R. F. (1970). Histology of the subauricular and rump glands of the pronghorn (*Antilocapra americana* Ord.). *Am. J. Anat.* **129,** 65–88.

Mugford, R. A., and Nowell, N. W. (1970). Pheromones and their effect on aggression in mice. *Nature* **226,** 967–968.

Müller-Schwarze, D. M. (1974). Social functions of various scent glands in certain ungulates and the problems encountered in experimental studies of scent communication. *In* "The Behaviour of Ungulates and Its Relation to Management" (V. Geist F. R. Walther, eds.), pp. 107–113. IUCN, Morges.

Mykytowycz, R. (1965). Further observations on the territorial function and histology of the submandibular cutaneous (chin) glands in the rabbit, *Oryctolagus cuniculus* (L.). *Anim. Behav.* **13,** 400–412.

Mykytowycz, R. (1970). The role of skin glands in mammalian communication. *In* "Advances in Chemoreception. Communication by Chemical Senses" (J. W. Johnston, D. G. Moulton, and A. Turk, eds.), **Vol. 1,** pp. 327–360. Appleton-Century-Crofts, New York.

Mykytowycz, R. (1973). Reproduction of mammals in relation to environmental odours. *J. Reprod. Fert. Suppl.* **19,** 433–446.

Mykytowycz, R. (1975). Activation of territorial behaviour in the rabbit, *Oryctolagus cuniculus,* by stimulation with its own chin gland secretion. *In* "Olfaction and Taste" (D. A. Denton J. P. Coghlan, eds.), **Vol. 5,** pp. 425–432. Academic Press, New York.

Naguib, M., Fichtel, C., and Todt, D. (1999). Nightingales respond more strongly to vocal leaders of simulated dyadic interactions. *Proc. R. Soc. London B* **266,** 537–542.

Nevison, C. M., Barnard, C. J., Beynon, R. J., and Hurst, J. L. (2000). The consequences of inbreeding for recognising competitors. *Proc. R. Soc. London B* **267,** 687–694.

Newman, K. S., and Halpin, Z. T. (1988). Individual odours and mate discrimination in the prairie vole (*Microtus ochrogaster*). *Anim. Behav.* **36,** 1779–1787.

Norton, P. M. (1980). The habitat and feeding ecology of the klipspringer *Oreotragus oreotragus* (Zimmerman 1783) in two areas of the Cape Province. Unpubl. M.S. Thesis. University of Pretoria, South Africa.

Novotny, M., Schwende, F. J., Wiesler, D., Jorgeson, J. W., and Carmack, M. (1984). Identification of a testosterone-dependent unique volatile constituent of male mouse urine: 7-exo-ethyl-5-methyl-6, 8-dioxabicyclo[3.2.1]-3-octene. *Experientia* **40,** 217–219.

Novotny, M., Harvey, S., and Jemiolo, B. (1990a). Chemistry of male dominance in the house mouse, *Mus domesticus*. *Experientia* **46,** 109–113.

Novotny, M., Jemiolo, B., and Harvey, S. (1990b). Chemistry of rodent pheromones: Molecular insights into chemical signalling in mammals. *In* "Chemical Signals in Vertebrates V" (D. W. Macdonald, D. Müller-Schwarze, and S. E. Natynczuk, eds.), pp. 1–22. Oxford University Press, UK.

Novotny, M. V., Ma, W., Zidek, L., and Daev, E. (1999). Recent biochemical insights into puberty acceleration, estrus induction and puberty delay in the house mouse. *In* "Advances in Chemical Communication in Vertebrates" (R. E. Johnston, D. Müller-Schwarze, and P. Sorenson, eds.), pp. 99–116. Plenum, New York.

Ono, Y., Doi, T., Ikeda, H., Baba, M., Takeishi, M., Izawa, M., and Iwamoto, T. (1988). Territoriality of Guenther's dikdik in the Omo National Park, Ethiopia. *Afr. J. Ecol.* **26,** 33–49.

Otter, K., McGregor, P. K., Terry, A. M. R., Burford, F. R. L., and Peake, T. M. (1999). Do female great tits (*Parus major*) assess males by eavesdropping? A field study using interactive song playback. *Proc. R. Soc. London B* **266,** 1305–1309.

Paquet, P. C. (1991). Scent marking behaviour of sympatric wolves (*Canis lupus*) and coyotes (*C. latrans*) in Riding Mountain National Park. *Can. J. Zool.* **69,** 1721–1727.

Parker, G. A. (1974). Assessment strategy and the evolution of fighting behaviour. *J. Theor. Biol.* **47,** 223–243.

Parker, G. A., and Rubenstein, D. I. (1981). Role assessment, reserve strategy, and acquisition of information in asymmetric animal conflicts. *Anim. Behav.* **29,** 221–240.

Parmigiani, S., Brunoni, V., and Pasquali, A. (1982). Behavioural influences of dominant, isolated and subordinated male mice on female socio-sexual preferences. *Bollettino di Zoologia* **49,** 31–35.

Penn, D., and Potts, W. K. (1998). Chemical signals and parasite-mediated sexual selection. *Trends Ecol. Evol.* **13,** 391–396.

Penn, D. J., and Potts, W. K. (1999). The evolution of mating preferences and major histocompatibility complex genes. *Am. Nat.* **153,** 145–164.

Penn, D., Schneider, G., White, K., Slev, P., and Potts, W. (1998). Influenza infection neutralizes the attractiveness of male odour to female mice (*Mus musculus*). *Ethology* **104,** 685–694.

Perrot Sinal, T. S., Ossenkopp, K. P., and Kavaliers, M. (1999). Effects of repeated exposure to fox odor on locomotor activity levels and spatial movement patterns in breeding male and female meadow voles (*Microtus pennsylvanicus*). *J. Chem. Ecol.* **25,** 1567–1584.

Peters, R. P., and Mech, L. D. (1975). Scent-marking in wolves. *Am. Sci.* **63,** 628–637.

Pigozzi, G. (1990). Latrine use and the function of territoriality in the European badger, *Meles meles*, in a Mediterranean coastal habitat. *Anim. Behav.* **39,** 1000–1002.

Pilastro, A., Giacomello, E., and Bisazza, A. (1997). Sexual selection for small size in male mosquitofish (*Gambusia holbrooki*). *Proc. R. Soc. London B* **264,** 1125–1129.

Potts, W. K., Manning, C. J., and Wakeland, E. K. (1991). Mating patterns in seminatural populations of mice influenced by MHC genotype. *Nature* **352,** 619–621.

Potts, W. K., Manning, C. J., and Wakeland, E. K. (1992). MHC-based mating preferences in *Mus* operate through both settlement patterns and female controlled extra-territorial matings. *In* "Chemical Signals in Vertebrates VI" (R. L. Doty and D. Müller-Schwarze, eds.), pp. 229–235. Plenum, New York.

Ralls, K. (1971). Mammalian scent marking. *Science* **171,** 443–449.

Rasa, O. A. E. (1973). Marking behaviour and its social significance in the African dwarf mongoose, *Helogale undulata rufula*. *Z. Tierpsychol.* **32,** 293–318.

Rechav, Y., Norval, R. A. I., Tannock, J., and Colborne, J. (1978). Attraction of the tick *Ixodes neitzi* to twigs marked by the klipspringer antelope. *Nature* **275,** 310–311.

Reece-Engel, C. (1988). Female choice of resident male rabbits *Oryctolagus cuniculus*. *Anim. Behav.* **36,** 1241–1242.

Reece-Engel, C. (1990). Scent marking, residency, and female choice in the European rabbit (Oryctolagus cuniculus). *In* "Chemical Signals in Vertebrates V" (D. W. MacDonald, D. Müller-Scharze, and S. E. Natynczuk, eds.), pp. 329–335. Plenum Press, New York.

Regnier, F. E., and Goodwin, M. (1977). On the chemical and environmental modulation of pheromone release from vertebrate scent marks. *In* "Chemical Signals in Vertebrates I" (D. Müller-Schwarze and M. M. Mozell, eds.), pp. 115–133. Plenum Press, New York.

Rich, T. J., and Hurst, J. L. (1998). Scent marks as reliable signals of the competitive ability of mates. *Anim. Behav.* **56,** 727–735.

Rich, T. J., and Hurst, J. L. (1999). The competing countermarks hypothesis: Reliable assessment of competitive ability by potential mates. *Anim. Behav.* **58,** 1027–1037.

Richardson, P. R. K. (1987). Aardwolf mating system: Overt cuckoldry in an apparently monogamous mammal. *S. Afr. J. Sci.* **83,** 405–410.

Richardson, P. R. K. (1991). Territorial significance of scent marking during the nonmating season in the aardwolf *Proteles cristatus* (Carnivora: Protelidae). *Ethology* **87,** 9–27.

Richardson, P. R. K. (1993). The function of scent marking in territories: A resurrection of the intimidation hypothesis. *Trans. R. Soc. S. Afr.* **48,** 195–206.

Richter, W. von (1972). Territorial behaviour of the black wildebeest. *Zool. Africana* **7,** 207–231.

Roberts, S. C. (1995). Gleaning in klipspringer preorbital glands by Redwinged Starlings and Yellowbellied Bulbuls. *Ostrich* **66,** 147–148.

Roberts, S. C. (1997). Selection of scent-marking sites by klipspringers (*Oreotragus oreotragus*). *J. Zool. (London)* **243,** 555–564.

Roberts, S. C. (1998). Behavioural responses to scent marks of increasing age in klipspringer *Oreotagus oreotragus*. *Ethology* **104,** 585–592.

Roberts, S. C., and Dunbar, R. I. M. (2000). Female territoriality and the function of scent-marking in a monogamous antelope (*Oreotragus oreotragus*). *Behav. Ecol. Sociobiol.* **47,** 417–423.

Roberts, S. C., and Gosling, L. M. The economic consequences of advertising scent mark location in territories. *In* "Chemical Signals in Vertebrates IX" (A. Marchlewska-Koy, ed.). Plenum Press. In press.

Roberts, S. C., and Lowen, C. (1997). Optimal patterns of scent marks in klipspringer (*Oreotragus oreotragus*) territories. *J. Zool. (London)* **243,** 565–578.

Robertson, D. H. L., Beynon, R. J., and Evershed, R. P. (1993). Extraction, characterisation, and binding analysis of two pheromonally active ligands associated with major urinary protein of house mouse (*Mus musculus*). *J. Chem. Ecol.* **19,** 1405–1416.

Robinson, I. (1990). The effect of mink odour on rabbits and small mammals. *In* "Chemical Signals in Vertebrates V" (D. W. Macdonald, D. Müller-Schwarze, and S. E. Natynczuk, eds.), pp. 566–572. Oxford Univ. Press, New York.

Roeder, J. J. (1983). Memorisation des marques olfactives chez la genette (*Genetta genetta* L.): Duree de reconaissance par les femelles de marques olfactives de males. *Z. Tierpsychol.* **61,** 311–314.

Roper, T. J., Shepherdson, D. J., and Davies, J. M. (1986). Scent-marking with faeces and anal secretion in the European badger (*Meles meles*): Seasonal and spatial characteristics of latrine use in relation to territoriality. *Behaviour* **97,** 94–117.

Roper, T. J., Contradt, L., Butler, J., Christian, S. E., Ostler, J., and Schmid, T. K. (1993). Territorial marking with faeces in badgers (*Meles meles*): A comparison of boundary and hinterland latrine use. *Behaviour* **127,** 289–307.

Rosell, F., Bergan, P., and Parker, H. (1998). Scent-marking in the Eurasian beaver (*Castor fiber*) as a means of territory defense. *J. Chem. Ecol.* **24,** 207–219.

Rowe, C. (1999). Receiver psychology and the evolution of multicomponent signals. *Anim. Behav.* **58,** 921–931.

Rozenfeld, F. M., Le Boulangé, E., and Rasmont, R. (1987). Urine marking in male bank voles (*Clethrionomys glareolus* Schreber, 1780; Microtidae, Rodentia) in relation to their social rank. *Can. J. Zool.* **65,** 2594–2601.

Ryg, M., Solberg, Y., Lydersen, C., and Smith, T. G. (1992). The scent of rutting male ringed seals (*Phoca hispida*). *J. Zool. (London)* **226,** 681–689.

Sawyer, T. G., Marchinton, R. L., and Miller, K. V. (1989). Response of female white-tailed deer to scrapes and antler rubs. *J. Mammal.* **70,** 431–433.

Schoon, G. A. A. (1996). Scent identification lineups by dogs (*Canis familiaris*): Experimental design and forensic application. *Appl. Anim. Behav. Sci.* **49,** 257–267.

Schoon, G. A. A. (1997). Scent identifications by dogs (*Canis familiaris*): A new experimental design. *Behaviour* **134,** 531–550.

Schoon, G. A. A., and DeBruin, J. C. (1994). The ability of dogs to recognise and cross-match human odors. *Forensic Sci. Intl.* **69,** 111–118.

Scott, J. W., and Pfaff, D. W. (1970). Behavioral and electrophysiological responses of female mice to male urine odors. *Physiol. Behav.* **5,** 407–411.

Settle, R. H., Sommerville, B. A., McCormick, J., and Broom, D. M. (1994). Human scent matching using specially trained dogs. *Anim. Behav.* **48,** 1443–1448.

Simons, R. R., Jaeger, R. G., and Felgenhauer, B. E. (1997). Competitor assessment and area defense by territorial salamanders. *Copeia* **1,** 70–76.

Singer, A. G., and Macrides, F. (1992). Lipocalins associated with mammalian pheromones. *In* "Chemical Signals in Vertebrates VI" (R. L. Doty and D. Müller-Schwarze, eds.), pp. 119–124. Plenum Press, New York.

Singer, A. G., Beauchamp, G. K., and Yamazaki, K. (1997). Volatile signals of the major histocompatibility complex in male mouse urine. *Proc. Nat. Acad. Sci.* **94,** 2210–2214.

Sipos, M. L., Nyby, J. G., and Serran, M. F. (1993). An ephemeral sex pheromone of female house mice (*Mus domesticus*): Pheromone fade-out time. *Physiol. Behav.* **54,** 171–174.

Sipos, M. L., Alterman, L., Perry, B., Nyby, J. G., and Vandenburgh, J. G. (1995). An ephemeral pheromone of female house mice—degradation by oxidation. *Anim. Behav.* **50,** 113–120.

Sliwa, A., and Richardson, P. R. K. (1998). Responses of aardwolves, *Proteles cristatus*, Sparrman 1783, to translocated scent marks. *Anim. Behav.* **56,** 137–146.

Smith, J. L. D., McDougal, C., and Miquelle, D. (1989). Scent marking in free-ranging tigers, *Panthera tigris*. *Anim. Behav.* **37,** 1–10.

Spickett, A. M., Keirans, J. E., Norval, R. A. I., and Clifford, C. M. (1980). *Ixodes (Afrixoides) matopi* n.sp. (Acarina:Ixodidae): A tick found aggregating on preorbital gland scent marks of the klipspringer in Zimbabwe. *Onderstepoort J. Vet. Res.* 48.

Steel, E. (1984). Effect of the odour of vaginal secretion on non-copulatory behaviour of male hamsters (*Mesocricetus auratus*). *Anim. Behav.* **32,** 597–608.

Stenström, D. (1998). Mating behaviour and sexual selection in non-lekking fallow deer (*Dama dama*). Ph.D. Thesis. University of Uppsala, Sweden.

Stoddart, D. M. (1976). Effect of the odour of weasels (*Mustela nivalis* L.) on trapped samples of their prey. *Oecologia* **22,** 439–441.

Stowe, M. K., Turlings, T. C. J., Loughrin, J. H., Lewis, W. J., and Tumlinson, J. H. (1995). The chemistry of eavesdropping, alarm and deceit. *Proc. Nat. Acad. Sci.* **92,** 23–28.

Sun, L., and Müller-Schwarze, D. (1998). Beaver response to recurrent alien scents: Scent fence or scent match? Anim. *Behav.* **55,** 1529–1536.

Sun, L., Xiao, B., and Dai, N. (1994). Scent marking behaviour in the male Chinese water deer. *Acta Theriol.* **39,** 177–184.

Tang-Martinez, Z., Mueller, L. L., and Taylor, G. T. (1993). Individual odours and mating success in the golden hamster, *Mesocricetus auratus*. *Anim. Behav.* **45,** 1141–1151.

Tilson, R. L., and Tilson, J. W. (1986). Population turnover in a monogamous antelope (*Madoqua kirki*) in Namibia. *J. Mammal.* **67,** 610–613.

Trivers, R. L. (1972). Parental investment and sexual selection. *In* "Sexual Selection and the Descent of Man, 1871–1971" (B. Campbell, ed.), pp. 136–179. Heinemann, London.

Tuttle, M. D., and Ryan, M. J. (1981). Bat predation and the evolution of frog vocalisations in the neotropics. *Science* **214,** 677–678.

Tyler, S. (1972). The behaviour and social organisation of the New Forest Ponies. *Anim. Behav. Monogr* **5,** 85–196.

Uexküll, J. V., and Kriszat, G. (1934). Striefzüge durch die Umwelten von Tieren und Menschen. Cited in Hediger (1944).

Vandenburgh, J. G. (1971). The influence of the social environment on sexual maturation in male mice. *J. Reprod. Fert.* **24,** 383–390.

Vandenbergh, J. G., Whitset, J. M., and Lombardi, J. R. (1975). Partial isolation of a pheromone accelerating puberty in female mice. *J. Reprod. Fert.* **43,** 515–523.

Vandenburgh, J. G., Finlayson, J. S., Dobrogosz, W. J., Dills, S. S., and Kost, T. A. (1976). Chromatographic separation of puberty accelerating pheromone from male mouse urine. *Biol. Reprod.* **15,** 260–265.

Viitala, J., Korpimäki, E., Palokangas, P., and Koivula, M. (1995). Attraction of kestrels to vole scent marks visible in ultraviolet light. *Nature* **373,** 425–427.

Voznessenskaya, V. V., Parfyonova, V. M., and Zinkevich, E. (1992). Individual odortypes. *In* "Chemical Signals in Vertebrates VI" (R. L. Doty and D. Müller-Schwarze, ed.), pp. 503–508. Plenum Press, New York.

Walther, F. R. (1978). Mapping the structure and the marking system of a territory of the Thomson's gazelle. *E. Afr. Wildl. J.* **16,** 167–176.

White, P. J., Kreeger, T. J., Tester, J. R., and Seal, U. S. (1989). Anal-sac secretions deposited with faeces by captive red foxes (*Vulpes vulpes*). *J. Mammal.* **70,**

Whitten, W. K. (1956). Modification of the oestrous cycle of the mouse by external stimuli associated with the male. *J. Endocrinol.* **13,** 399–404.

Wilcox, R. M., and Johnston, R. E. (1995). Scent counter marks: Specialised mechanisms of perception and response to individual odours in golden hamsters, *Mesocricetus auratus*. *J. Comp. Psychol.* **109,** 349–356.

Wolff, R. J. (1985). Mating behaviour and female choice: Their relation to social structure in wild caught House mice (*Mus musculus*) housed in a semi-natural environment. *J. Zool. (London)* **207,** 43–51.

Woodward, R. L., Schick, M. K., and Ferkin, M. H. (1999). Response of prairie voles, *Microtus ochrogaster* (Rodentia, Arvicolidae), to scent over-marks of two same-sex conspecifics: A test of the scent-masking hypothesis. *Ethology* **105,** 1009–1017.

Yamashita, J., Hayashi, S.-I., and Hirata, Y. (1989). Reduced size of preputial glands and absence of aggressive behaviour in the genetically obese (ob/ob) mouse. *Zool. Sci.* **6,** 1033–1036.

Yamazaki, K., Boyse, E. A., Mike, V., Thaler, H. T., Mathieson, B. J., Abbott, J., Boyse, J., Zayas, Z. A., and Thomas, L. (1976). Control of mating preferences in mice by genes in the major histocompatibility complex. *J. Exp. Med.* **144,** 1324–1335.

Zahavi, A. (1975). Mate selection: A selection for a handicap. *J. Theor. Biol.* **53,** 205–214.

Zhang, Q. H., and Schlyter, F. (1996). High recaptures and long sampling range of pheromone traps for fall web worm moth *Hyphantria cunea* (Lepidoptera: Arctiidae) males. *J. Chem. Ecol.* **22,** 1783–1796.

Zuri, I., Gazit, I., and Terkel, J. (1997). Effect of scent-marking in delaying territorial invasion in the blind mole-rat *Spalax ehrenbergi*. *Behaviour* **134,** 867–880.