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## **A Reassessment of the Function of Scent Marking in Territories**

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*With 4 figures*

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### **Abstract**

The energetic costs and the risk of injury in agonistic encounters can be reduced by prior assessment of opponents: it will generally pay low quality animals to avoid combat with one of high quality. Following this principle it is suggested that territory owners scent mark their territories to provide intruders with a means of assessment. When the odour of a competitor, or of a mark it is seen to have made, *matches* that of scent marks encountered in the vicinity, then the competitor is probably the territory owner. Since owners are generally high quality animals, and assuming they have more to gain by retaining a territory than an intruder has in taking it over, it will pay the owner to escalate and the intruder to give up early. The advantage to owners in marking may thus be that by allowing themselves to be identified they reduce the costs of territory defence. Published information on the behaviour of territory owners and intruders is consistent with predictions from this hypothesis. The hypothesis offers an explanation for a number of poorly understood behaviours including 'self-anointing' and scent marking during agonistic encounters.

### **Introduction**

The meanings of social odours are probably no less diverse than those of visual or auditory signals and, not surprisingly, have become progressively inaccessible to generalization. Exceptionally, those olfactory signals involved in territory demarkation appear remarkably homogeneous but they have similarly evaded any consensus about function. In this paper I suggest a new functional interpretation of scent marking in territories which emphasises the advantages to the owner in agonistic encounters with intruders that have previously detected scent marks.

Existing hypotheses are critically reviewed in the first part of the paper. Some apply only to particular contexts, for example, pair-bonding (ROTHMAN and MECH 1979), while others are concerned with area defence. The earliest hypothesis (UEXKÜLL and KRISZAT 1934; HEDIGER 1949, 1950) that scent marks help keep away potential rivals has been refuted by observations of undeterred intruders in a wide array of species. Here, the alternative is suggested that territory residents provide marks so that intruders can assess their status in any subsequent encounter. The costs of territory defence are sometimes purely energetic but sometimes owners risk injury or death (GOSLING and PETRIE 1981). These costs can be reduced by prior assessment of the likely outcome of any interaction (MAYNARD SMITH and PRICE 1973; PARKER 1974; MAYNARD SMITH and PARKER 1976; ZAHAVI 1975, 1977). The hypothesis that owners reduce the costs of agonistic behaviour by providing an accurate means of assessment yields a number of predictions that can be tested using the extensive literature on territory marking.

Most examples will be drawn from the behaviour of polygynous artiodactyls, partly because I am most familiar with this group and partly because their behaviour has been observed in some detail under natural conditions. In particular I will deal with the definitive case of single male territories which are marked and defended either seasonally, as in the case of many temperate cervids, or year-round as in many of the plains antelopes of East Africa.

'Territory' will be used in the sense of a spatial reference for dominance and will include both territories with clearly defined boundaries, such as those of Thomson's gazelle, *Gazella thomsoni* (WALTHER 1964, 1978) and more loosely defined areas such as those around female groups which are defended by rutting red deer stags, *Cervus elaphus* (FRASER-DARLING 1937). This definition accords with that of 'dominance fixed in space' (MARLER and HAMILTON 1966) but is intended to imply some degree of exclusive occupancy as envisaged in the views of territory advanced by BURT (1943). I will often refer to the territories of Coke's hartebeest, *Alcelaphus buselaphus cokei*, which I studied (GOSLING 1974). These territories average 0.31 km<sup>2</sup>, contain a year-round food supply, and, collectively, cover most available habitat. Non-territorial animals comprise 62% of all adult males and spend most of their time within territory boundaries. Territorial males chase non-territorial males away and maintain an exclusive area around themselves which varies in size according to what part of the territory they can see and their motivation. This exclusive area does not extend beyond the territory boundaries which are marked with faeces and glandular secretion.

The term 'owner' will be used for the individual or group that actively defends the territory; examples are individual territorial male hartebeest, pairs of dik-dik, *Rhynchotragus kirki* and packs of wolves. 'Intruders' are animals within the territory that can potentially replace an owner.

The figures are intended to illustrate main stages of the argument; all are drawn from photographs.

### Existing Hypotheses

The hypotheses dealt with are those that attempt to answer the question: Why do animals mark their territories?

1. Marking deters potential intruders. By marking their territories animals stop intruders from entering the area or cause their withdrawal (UEXKÜLL and KRISZAT 1934; HEDIGER 1949, 1950). Marks are thus functionally equivalent

to aggressive behaviour by the territory owner, but with the advantage that they can simultaneously protect the entire territory.

This hypothesis receives little support from observations of wild animals. Many observers (MYKYTOWYCZ 1965; GOSLING 1975; GRAU 1976; WALTHER 1979; FRANKLIN 1980, and others) have seen intruders pass undeterred through territories that are known to be marked. A few observers have seen limited adverse responses to marked objects (e.g. cowering and "signs of anxiety" by intruding wolves; JORDAN et al. 1967) but such observations are rare and might be due to a behaviourally established association between an owner and the scent mark. JONES and NOWELL (1974) found that both dominant and subordinate captive mice spent less time in parts of a cage treated with dominant male urine; if repeatable with wild mice, in a setting that is consistent with territory defence, these experiments would support the UEXKÜLL-HEDIGER hypothesis.

2. (a) Marking intimidates intruders. By marking, a resident threatens intruders which are intimidated and thus more likely to lose subsequent agonistic encounters. GEIST (1965) states this idea most explicitly and, like BILZ (1940), regards marks as an extension of the territorial animal. MYKYTOWYCZ (1965) describes the altered behaviour, and readiness to flee, of rabbits, *Oryctolagus cuniculus*, intruding into the territory of others and believes this to be a response to the scent marks of resident animals. An objection to the specific role of odour is that such responses might be due to entering an unfamiliar area (JOHNSON 1973).

2. (b) Marking enhances the confidence of residents. This hypothesis is a partial corollary of 2. (a) and gains intuitive support from the reversal of dominance as a pair of residents in adjoining territories are experimentally shifted back and forth across a common boundary (TINBERGEN 1953: sticklebacks). MYKYTOWYCZ and his co-workers have emphasised the role of confidence enhancement and have shown experimentally that a male rabbit will prove dominant over another when its own odour is present in an otherwise neutral arena (MYKYTOWYCZ et al. 1976). A number of field workers have come to similar conclusions when it became clear that intruders were not excluded as predicted by the UEXKÜLL-HEDIGER hypothesis: VON RICHTER (1972) suggests that territorial male black wildebeest, *Conochaetes gnou*, gain "self-assurance" by being in an area marked by themselves, and JOUBERT (1972) that tsessebe, *Damaliscus lunatus*, gain "a sense of ownership or possession".

The idea that marks give residents 'confidence' and 'intimidate' intruders seems plausible and receives circumstantial support from field and experimental evidence. However, these concepts are subjective and cannot be directly tested. This is not in itself critical because a number of important corollaries, such as the outcome of subsequent encounters between resident and intruder, are testable. However, there are alternative views of such contests that may prove more useful in answering evolutionary questions. For example, territory owners may usually win encounters because they have more to gain

from retaining a familiar area than challengers have in taking it over; it might thus pay a resident to escalate an agonistic encounter and a challenger to avoid the risk of injury by giving up at an early stage. This approach emphasises the costs and benefits of an encounter to both owner and intruder and, in contrast to explanations that depend on intuited psychological states, yields predictions that are testable and that could provide real functional insight.

3. Marks provide intruders with information about the status of the resident. The ability to distinguish subtle properties of scents has been shown in a wide range of animals (EISENBERG and KLEIMAN 1972; JOHNSON 1973; THIESSEN and RICE 1976, and others). MYKYTOWYCZ (1970) argues that, since marking activity is often correlated with social rank, "it is not difficult to imagine that the presence of odour will show not only an animal's presence but also its level of influence and readiness to defend the marked area". MYKYTOWYCZ suggests that such information might influence the outcome of subsequent encounters through the psychological effects on both resident and intruder that were discussed above. However, an experimental demonstration that animals are capable of distinguishing the scents of animals of varying social status is not a demonstration of a functional role for such discrimination in a particular context. I would suggest that a more economical mechanism is available to an intruder into a territory (see next section) and that, being more economical, it is more likely to be favoured by natural selection.

4. Marks orientate the resident within its territory. LYALL-WATSON (1964) believes that scent marking "serves to maintain the animal's familiarity with its environment . . . odour is added to specific visual landmarks both to familiarize the animal with new territory and to refamiliarize it with old terrain". KLEIMAN (1966) also considers familiarization to be important and suggests that marks would reassure an animal in an unknown situation. In a careful study of demarkation in a Thomson's gazelle territory, WALTHER (1978) concludes that marking seems mainly "to be significant for the owner himself and for his orientation". HEDIGER (1949) also raised this possibility when speculating on additional functions for scent marks to that of area defence.

The main problem that arises with this hypothesis is that since animals visit marking sites regularly it is impossible to say whether they do so in order to mark (or inspect the mark for contributions by conspecifics) or in order to orientate or familiarize themselves. Most conclusions about self-orientation or familiarization appear to be reached by exclusion of competing hypotheses rather than through direct evidence.

5. Marks attract or stimulate mates. NOBLE (1939) suggested that marks might make an animal's territory stimulating to the opposite sex. Certainly a number of priming effects of male rodent odour have been demonstrated including induction and suppression of oestrus and ovulation, acceleration of female sexual maturity and blocking of implantation in a variety of rodents (reviewed by BRUCE 1966; WHITTEN 1966; BRONSON 1971, and others); various odours, including that of urine, produce these effects and so territorial male mice, for example, could influence the reproductive state of females

through the priming effect of the urine that they use to mark their territories. A number of female canids show an increased frequency of urine marking behaviour while in oestrus (KLEIMAN 1966), and some that mark in this way may also be territorial. The attractiveness of female urine to males has been documented in a wide array of species (JOHNSON 1973; BROWN 1979). These effects of male and female odours do not, of course, provide a universal explanation of territory marking because many species mark outside their breeding season (JOHNSON 1973).

6. Marks assist in pair-bond formation. ROTHMAN and MECH (1979) describe a high frequency of marking when wolves form pairs for the first time and suggest that marking might help establish a social bond. However, pair formation in wolves coincides with establishment of a territory and the high frequency of marking may be necessary to scent mark the territory for a defence function. PETERS and MECH (1975) argue elsewhere that scent marks in wolf territories also deter intruders.

7. Marks assist in population regulation. It has been suggested that the intensity of territory boundary marking might be related to population density and that the responses to these marks might form part of a population density regulatory system (WYNNE-EDWARDS 1962; ALEKSIUK 1968; ROGERS and BEAUCHAMP 1976). If considered at a functional level this suggestion suffers from the general problem that there is an implicit assumption of group selection. It may be that marking is more intensive when intruders are more common but this is more easily explained by an advantage to the owner in influencing the behaviour of intruders than by its population consequences.

8. Marks assist owners to forage optimally. HENRY (1977) has shown that foxes mark depleted food caches with urine and suggests that this allows them to avoid wasting time in reinvestigation. Fresh caches are not marked. An alternative explanation is that excavated caches are visually conspicuous and are used to advertise the scent mark. There is widespread use of such visual reinforcement in other forms of canid demarkation (MACDONALD 1980).

Marks on excavated caches might also provide a means for owners to advertize their identity in a part of the territory that contains a valuable food supply, without drawing attention to an individual food item. CORBETT (in MACDONALD 1980) also found a significant increase in faecal marking in preferred hunting areas of wild cats, *Felis silvestris*.

Other hypotheses exist and the eight listed are selected either because they are frequently cited or because they seem credible. Hypotheses 1 to 3 suggest an area defence role for marking, but all fail to predict important aspects of the behaviour of territory owners. In particular, why do owners in a wide range of species exhibit 'self-anointing', using the same substances that are used to mark territories? The assessment hypothesis, outlined in the following section, provides a theoretical framework for this and other previously unexplained behaviour. It seems probable that some scent marks have a reproductive function, as suggested in hypothesis 5 and it remains to be seen how far this is related to the patterns of marks seen in the wild. It may prove

possible to distinguish marking strategies that function to intercept competitors from those adapted to signal to mates. In the absence of such a distinction in existing descriptions of marking I have assumed that all observed patterns of marks in territories can be used to test the hypothesis proposed in the following section. It may be that marks in territories have multiple functions and that mate selection depends on recognition of an intrinsic property of the secretion. Regardless of this possibility the following review demonstrates that many facets of territory demarkation are predictable from an alternative formulation of the area defence hypothesis.

### The Alternative Hypothesis

The hypothesis presented here as an alternative to those listed, is as follows:

The function of territory marking is to provide an olfactory association between the resident and the defended area which allows intruders to identify the resident when they meet and thus reduce the frequency of escalated agonistic encounters. An animal that can defend an area long enough to mark it comprehensively is likely to win most encounters with intruders because of its physical quality (intruders will vary in quality). It is also more likely to escalate to overt fighting since, with a more detailed knowledge than an intruder of the territory's resources, it has more to gain by retaining ownership (DAWKINS and KREBS 1978). It will thus pay low status intruders to withdraw from encounters with an identified resident. Only a minority of high status intruders might choose to escalate an encounter with a resident in an attempt to displace it. Marks thus provide a way for an intruder to assess the quality of a potential competitor so that they can avoid escalation in encounters that have a high risk of injury, except when the potential benefits of an escalated encounter are also high. The advantage to the resident is that by providing these means of assessment it avoids the costs of establishing dominance by threat or overt aggression towards *every* intruder.

The suggested mechanism of assessment is that intruders *compare* the scent of any animals they meet with the memorized scent of marks that they have encountered in the vicinity. When these scents *match* then the resident is identified and the intruder responds appropriately, usually by withdrawal. This simple physiological mechanism provides a precise means of competitor assessment in the territorial context and is central to the hypothesis.

The number of marks encountered by an intruder is probably important since this could indicate the duration and/or frequency of residence. The number of marks might also be influenced by the well established link between high dominance status and marking frequency, both of which are believed to be androgen dependent (RALLS 1971). However, to minimize the complexity of the present hypothesis I suggest that this effect would operate simply through the increased number of marks that an intruder would encounter

(or a correlated increase in the intensity of odour) rather than any qualitative difference in the odour.

A number of models of the way that intruders respond to marks are possible, depending on assumptions about the way that an animal memorizes scents and the duration of such memory; perhaps intruders simply retain the smell of the majority of marks detected over a particular time. In any event the only property that is essential for the present hypothesis is that intruders can distinguish scents at the resolution of the individual animal (but not necessarily *of individuals*) and that they have an approximate knowledge of the frequency of this scent in marks in the immediate environment when they encounter, and smell, a competitor.

A final aspect of the hypothesis needs emphasis because of the important assumption by DAWKINS and KREBS (1978) that animal signals may sometimes manipulate one participant in an interaction, to its cost, rather than always be of mutual advantage. In the present hypothesis I propose an advantage for an intruder in being able to identify the territory owner; selection should favour behaviour by the owner that allows this assessment because of the advantage to it in the subsequent withdrawal of most intruders. Thus I suggest a mutual advantage both in marking and in detecting marks but that this exists because owners subvert the intruder's response to their own advantage.

### Predictions of the Hypothesis

The hypothesis that marks in territories allow their owners to be assessed by scent matching yields a number of specific predictions about the behaviour of both owners and intruders that are testable by experiment or critical field observation. As in all tests that seek to clarify functional issues of this kind such observations should ideally involve the predicted responses of individuals to defined stimuli. However, the summarized descriptions available in the literature (including those of behaviour in experiments designed for other purposes) can be used to test whether the hypothesis is broadly credible. In the following sections each prediction is stated and then evaluated using documented behaviour.

#### Behaviour of the Territory Owner

1. *The owner should mark the territory in a way that maximizes the chance that marks will be detected by an intruder.* Since marks and time available for marking are a limited resource, marking should be done economically, for example, by placing marks where the chance of intrusion is high and avoiding areas where intrusion is unlikely. Since there is also an advantage for intruders in visiting marks (see above) owners could increase the chance of inspection by making the marks conspicuous, either by placing them on prominent objects or by advertising their presence.

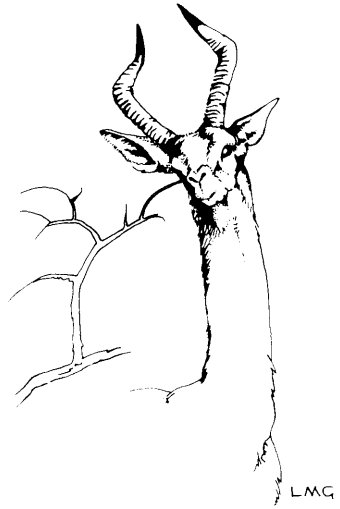
Territory owners should place marks around the territory boundary and along routes usually taken by intruders to raise the chance that they will be detected. A number of studies show this to be the case. WALTHER (1978) showed a line of marks (antorbital gland marks on herb stems and dung piles) along the boundary of a Thomson's gazelle territory and also that this line was best defined where intrusions were most common. A large oval of antorbital gland marks was also found in a gerenuk, *Litocranius walleri*, territory although this may have been an inner concentric ring within the territory boundary (GOSLING 1981). Such lines of marks are made and reinforced during apparently deliberate marking excursions when owners walk along boundaries marking at a high frequency; marking excursions have been seen in a number of territorial male antelopes including Thomson's gazelle (WALTHER 1978), pronghorn antelope, *Antilocapra americana*, (KITCHEN 1974) and impala, *Aepyceros melampus*, (JARMAN 1979), and by territorial carnivores including hyena, *Crocuta crocuta* (KRUUK 1972). Within this broad pattern, marks are placed along trails (e.g. gerenuk: GOSLING 1981; wolves: PETERS and MECH 1975). In closed habitat, boundary marks are less important because intruders are more restricted to trails and, in such cases, for example, in dik-dik, *Rhynchotragus kirki*, in dense East African scrub, marks occur at high density along trails (HENDRICHS and HENDRICHS 1971).

Some scent and particularly that from the interdigital glands might be deposited passively. The anterior opening of glands, such as those in the forefeet of hartebeest and wildebeest (POCOCK 1910), suggest that secretion would be left on herbage as it is pulled between the hooves during walking. The scent would thus accumulate at a frequency related to the intensity of use by the territory owner and be available for detection by intruders. The scattering of marks found within all territories might serve a similar function: the lines of marks found within territories (e.g. gerenuk, GOSLING 1981) could be arranged to maximize the number of times marks will be encountered by intruders rather than the chance of detecting a mark at all.

Marks are generally placed in conspicuous places such as the extreme tips of herbs or projecting twigs on bushes (Fig. 1). Such positions combine a degree of advertisement with an optimal position for passive detection: gerenuk antorbital gland marks are placed on the most prominent twigs of bushes, overhanging trails, and at head height, in spite of the fact that it would be possible to mark much higher and down to ground level (GOSLING 1981). Sometimes the characteristic marking site is deliberately created by the animal. Thus territorial male oribi, *Ourebia ourebia*, bite off tall grass culms at an optimum height for marking (GOSLING 1972) and pronghorn antelope similarly prepare a site for marking with the subauricular gland (KITCHEN 1974). Territorial male hartebeest thrash the dwarf tree *Acacia drepanolobium* with their horns until only a bare upright stump remains which is marked with the antorbital gland (GOSLING 1975). Unequivocal advertisement of marking sites by some disturbance of the nearby environment is common. Roe deer, *Capreolus capreolus*, males fray saplings and produce a visually conspicuous white stem which



Fig. 1: Scent marks in territories are generally placed in conspicuous locations. Territorial male gerenuk mark the ends of projecting twigs that are mostly on bushes next to trails (GOSLING 1981). Such positioning may be an adaptation to intercept the movements of intruders



is marked with the forehead gland (SCHUMACHER 1936; KURT 1968); beavers, *Castor canadensis*, build mounds near to their lodges and mark them with anal gland secretion and urine (ALEKSUIK 1968; SVENDSEN 1978, and others), and pumas, *Felis concolor*, urinate and defaecate on scratch marks made with the feet (HORNOCKER 1969); many artiodactyls break branches or disturb herbage with their horns or antlers before marking with forehead glands (e.g. impala; JARMAN 1979), antorbital glands (e.g. hartebeest; GOSLING 1975); elk, *Cervus canadensis*, dig with the antlers in the ground before urinating or ejaculating on the disturbed area (GRAF 1956; STRUHSAKER 1967). Many artiodactyls paw vigorously with the forefeet before defaecation at dung piles in territories (WALTHER 1979): the conspicuous marks left might function as an advertisement, but, as discussed later, pawing might sometimes remove previous marks.

2. *The owner should mark itself with the substances used to mark the territory except sometimes when the odour is available to an intruder at its site of production or in another available substance.* Intruders would thus be given the opportunity to identify the owner by matching its odour with that of marks in the vicinity.

'Self-anointing' is very common in a wide array of species. It occurs in non-territorial, as well as territorial species, but, as will be discussed in a later section, the scent matching hypothesis may have wider application. The present account is restricted to territorial animals.

Animals mark themselves using all the substances employed in object marking: Lichtenstein's hartebeest, *Alcelaphus lichtensteini*, mark their own shoulders with the secretion of the antorbital gland so that a persistent dark stain is produced on each side of the body (DOWSETT 1966) (Fig. 2). Many artiodactyls scratch the glands of the head with the hind feet and would presumably transfer the secretion to other parts of the body as they scratch.

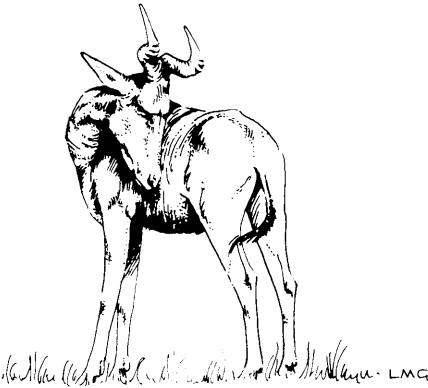


Fig. 2: Territory owners often mark their own bodies with the substances used to scent mark their territories. A territorial male hartebeest rubs the secretion of an antorbital gland onto its shoulder

Reindeer, *Rangifer tarandus*, mark their own antlers by inserting the tips into the interdigital glands and then rub the antlers on other parts of the body (ESPMARK 1977).

Saliva is sometimes used in marking; foxes, *Vulpes vulpes*, draw branches through their mouth, visibly trailing saliva (MACDONALD 1979), and muntjac leave saliva on trees as they bark them (DUBOST 1971). This contribution to marking behaviour might seem insignificant except that the odour of saliva is comprehensively transferred to the pelage during grooming. The function of grooming is primarily for body care and, in this case, selection would favour the use of saliva in marking, rather than the use of a specialised marking substance in self-anointing.

A number of ungulates which mark their territories with dung piles impregnate their pelage with the smell of faeces. Territorial male hartebeest kneel and rub their foreheads in faeces while defaecating at dung piles; they also lie on dung piles during resting periods more often than non-territorial males (GOSLING 1974, 1975). Wildebeest, *Connochaetes taurinus* and *C. gnou*, behave in the same way and, additionally, they roll on their backs in dung concentrations (ESTES 1969).

Self-anointing by urine is uncommon in African antelopes, possibly because urine may often be limited in arid environments. However, male eland, *Taurotragus oryx*, rub their forehead on the ground after urination and then rub the soil and urine mixture onto trees (WALTHER 1966; HILLMAN 1976). Amongst cervids in temperate regions, self-impregnation with urine is common. Some deer spray urine onto their own pelage and sometimes onto specific glands. Reindeer males spray urine over their hind legs and tarsal glands during the rut (ESPMARK 1964); black-tailed deer, *Odocoileus hemionus*, similarly urinate on the tarsal glands while they rub the hocks together ('rub-urination') (MÜLLER-SCHWARZE 1971). Domestic cats, *Felis catus*, spray their urine against trees, walls, etc. then rub their faces first in the urine and then against other objects (LEYHAUSEN 1965). Wallowing in muddy pools impregnated with urine and possibly ejaculate is common in territorial male deer

during the rut. MÜLLER-USING and SCHLOETH (1967) review such behaviour in red deer. Wallows, sometimes known as "rutting-pits" are wet areas that are further excavated by pawing. The composition of the various substances added to the mud would be difficult to determine but the smell is often strong and the pelage of the wallowing animals is thoroughly impregnated. Elk, which lie in wallows for hours, also rub the antorbital gland onto the rim of the pit (STRUHSAKER 1967).

If, as advanced in the present hypothesis, *matching* is the critical process, rather than recognition of an intrinsic property of the secretion, then it is possible that animals might anoint themselves with *any* odour available in the territory, particularly if the odour was area specific and likely to be detected by an intruder. A group of behaviours that may be explained in this way is the rolling in decaying faeces, carrion or on strongly smelling plants, that is practised by a wide range of carnivores (RIEGER 1979). Another possibility is rubbing the face, horns and antlers against broken or barked plants by bovids and cervids. In some species glandular activity has been confirmed in the area involved but not in all; an example is the careful bark stripping using the incisors by muntjac, *Muntiacus muntjak*, before rubbing the pedicles of the antlers on the exposed bare wood (DUBOST 1971); perhaps the resultant odour on both tree and muntjac is a combination of any glandular secretion from the pedicles and saliva, and the sap odour. Male wapiti, *Cervus elaphus*, strip bark with their teeth then rub their muzzle and lower jaw first on the exposed wood and afterwards on their own flank (GRAF 1956). Wallowing by territorial male deer might similarly combine the smell of urine and ejaculate with the soil odour at a particular site. This idea is attractive because the odour is potentially characteristic of the marked area, or, more generally, it is resource specific.

3. *The owner should make itself available for scent matching by the intruder.* Such behaviour might consist only of approaching to a distance at which odour (or taste) is detectable or it might consist of a posture or movement that makes a particular gland, or scent impregnated area, available to the intruder.

The approach of territory owners to intruders varies according to the motivation of the owner, the type of intruder and its behaviour. Sometimes approaches are clearly aggressive but in many cases the behaviour seems appropriate to making the owner available for inspection by the intruder. Territorial male hartebeest often allow an intruder to make the final approach and stand in an erect posture with the head high and deflected away. Sometimes intruding males simply withdraw with a lowered head, but often they approach and initiate contact behaviour. A conspicuous feature of the behaviour that follows is that the intruder touches the upper neck of the territorial male with its nose, then slides the nose down the neck, with nibbling movements of the lips, often as far as the shoulder of the owner which, meanwhile, remains immobile (GOSLING 1974, 1975). It seems certain that the intruder smells and, possibly, tastes, pelage which is impregnated with faeces, antor-

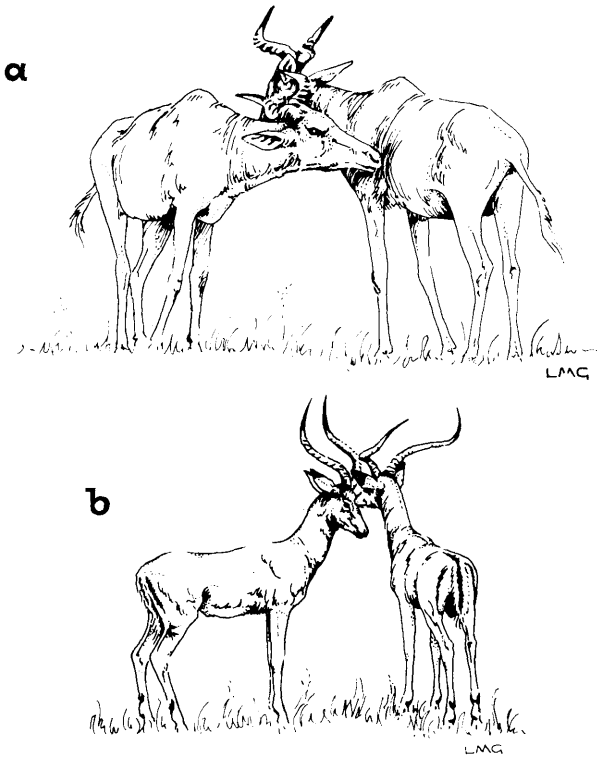


Fig. 3: In encounters with intruders, owners make the odours used to mark the territory available for olfactory inspection. This behaviour may allow intruders to identify the owner by matching the odour they detect with that of scent marks in the territory. (a) A territorial male hartebeest stands immobile while an intruding male smells and nibbles the scent impregnated pelage of its neck and shoulder ('neck-sliding') (GOSLING 1974). (b) A dominant male impala presents the glandular area of its forehead to a subordinate (JARMAN 1979)

bital gland secretion (on the shoulder) as well as any local sebaceous secretion (Fig. 3 a).

The visual aspects of the owner's behaviour are of course also important in such contexts. The hartebeest posture described and similar postures in other ungulates are often termed 'dominance displays' or 'Imponierverhalten' (WALTHER 1974) and emphasise features such as horns or the enlarged broadside view of the displaying animal. In spite of this some features of this behaviour may be primarily concerned with allowing the transmission of olfactory information and some visual features secondary: head deflection, for example, may prevent escalation to overt aggression given the need to remain at close quarters. In some cases there are less ambiguous indicators that displaying animals produce olfactory stimuli. Many deer (MÜLLER-SCHWARZE 1975) and a number of antelopes (WALTHER 1977) dilate the antorbital pouch when threatening other individuals and the opponent thus has the opportunity to smell secretion that is also used to mark objects in the territory.

The diffuse glandular area on the forehead of many ungulates is presumably readily available for olfactory inspection during encounters when the heads of interacting individuals are close together. JARMAN (1979) illustrates a dominant male impala presenting the forehead for inspection by a subordinate (Fig. 3 b); there is some ambiguity in the interpretation of this move-

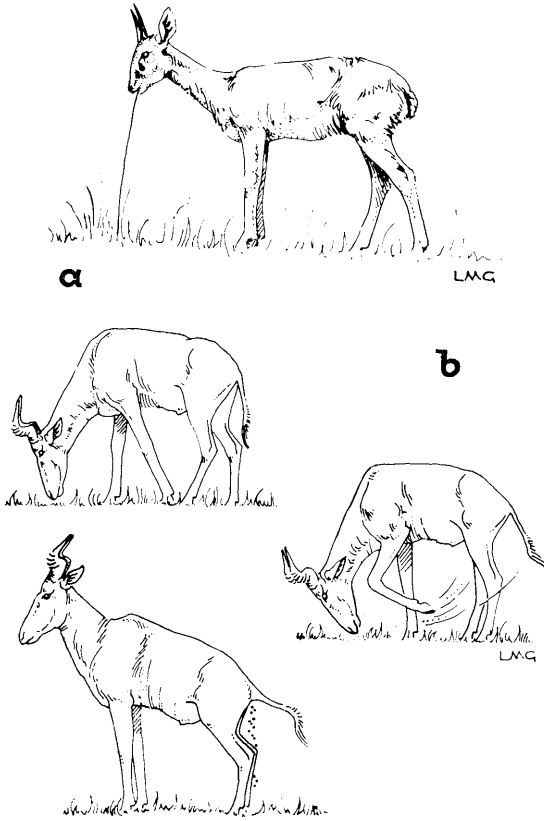
ment because many animals with horns or antlers tilt them forwards as a threat (e.g. Thomson's gazelle, WALTHER 1964). The large forehead gland of the muntjac which is extensively used in marking (DUBOST 1971; BARRETTE 1977) must similarly be easily smelled in agonistic encounters.

The frequency of marking by dominant individuals typically increases during agonistic interactions (JOHNSON 1973). Such marking by territory owners can be interpreted as a way of making odour available for matching while avoiding the danger of escalation in approaching close enough to smell a possible owner. This is not strictly predictable from the hypothesis but it can immediately be explained from its assumptions. By marking in the close vicinity of an intruder the owner provides a particularly unambiguous link between its own odour and that of a mark in the immediate vicinity. This link might have particular significance in this context because of the association with aggressive behaviour. Marking in this type of agonistic encounter is almost universal. Examples are forehead rubbing, antorbital gland marking and defaecation during encounters between territorial male hartebeest and intruders (GOSLING 1974, 1975) and rub-urination by black-tailed deer and reindeer during agonistic encounters in the rut (MÜLLER-SCHWARZE 1971; MOSSING and DAMBER 1981); dominant male muntjac mark most frequently in the presence of subordinate males using the secretion of the forehead gland, urine and faeces (BARRETTE 1977). Other cases are reviewed by RALLS (1971).

Aggressive head contact behaviour, from gentle 'horn-tangling' to aggressive 'clashes', are moderately frequent in some encounters between ungulate territory owners and intruders. By definition such behaviours are most common in the escalated encounters which are presumably of greatest importance in territory defence. Thus, the concentration of glands around the horns and antlers (mandibular, antorbital, forehead, post-cornual and sub-auricular) might be a result of selection for availability of the odour during head-to-head contact.

4. *The owner should remove or replace marks in the territory that do not match its own odour.* Strange marks might be the result of qualitative changes over time of the resident's own marks, or they might be made by intruders or by a previous owner. In all cases the hypothesis predicts that the strange odour should be removed and replaced by the smell of the owner. An example of such removal is carried out by territorial male oribi. These small antelopes mark the tip of grass stalks with the copious secretion of an antorbital gland (HEDIGER 1951). Before re-marking they bite off and appear to eat the previous mark (GOSLING 1972) (Fig. 4a). Presumably most of the marks removed in this way are made by the owner itself and it is difficult to explain this behaviour in any way except for the advantage to the male in having completely fresh marks in the territory.

Other antelopes simply add more secretion to existing marks and marks sometimes become very large. Gerenuk antorbital gland secretion marks reach up to 1 cm in diameter even though the secretion from a single marking may dry to a barely discernible size (GOSLING 1981). Additions to existing marks



*Fig. 4:* Territory owners sometimes remove previous scent marks before marking themselves. This behaviour may function to remove odours that do not match those of the owner. (a) A territorial male oribi bites off the antorbital gland secretion from the tip of a grass culm before re-marking (GOSLING 1972). The previous mark was probably made by the same animal and may have deteriorated. (b) A territorial male hartebeest sniffs faeces left by another male, scatters it by pawing and defaecates on the same spot

occur with a variety of marking substances: a male Thomson's gazelle observed by WALTHER (1978) had 18 dung piles in its territory and contributed to these on regular 'marking walks'.

Many ungulates paw with the forefeet before marking with faeces (GRAU 1976; WALTHER 1979). Coke's hartebeest territorial males sniff the most recent faeces on a dung pile then scatter it by pawing before stepping forward to defaecate precisely on the same spot (GOSLING 1975) (Fig. 4 b). This behaviour occurs both when replacing a male's own faeces and when replacing that of an intruder or neighbouring territorial male. Pronghorn antelope respond similarly to the faeces and urine of another male although in this case they perform linked urination and defaecation (MÜLLER-SCHWARZE and MÜLLER-SCHWARZE 1972), a behaviour that is common in the same context in the gazelles (WALTHER 1968). Territorial beavers over-mark experimentally introduced anal gland secretion; males over-mark more frequently and they respond more frequently to male than to female secretion (BUTLER and BUTLER 1979). Dominant male rabbits intensively mark strange dung-hills that are similarly introduced into their territories (MYKYTOWYCZ and HESTERMAN 1970).

### Behaviour of the Intruder

1. *Intruders should seek out or otherwise detect the characteristic scent marks of territory owners.* There is little information about the behaviour of intruders in relation to scent marks although MÜLLER-SCHWARZE (1974) states that black-tailed deer entering a new area sniff many twigs that may carry scent from forehead rubbing, before engaging in any social encounter. Most accounts refer to interest shown by territory owners, or their experimental equivalents, in scent marks, but REIFF (cited in BARAN and GLICKMAN 1970) noticed that wild rat scents had an attractive effect on newcomers to colonies; reviewing these accounts JOHNSON (1973) concludes that "male scent marks probably do not bring about avoidance by other males, but that the converse may be true, i.e. that they have attractive properties".

The response of intruders to a pattern of scent marks may generally prove difficult to investigate because owners should usually place marks in positions where they are most likely to intercept the normal movement of non-territorial animals. For example, territorial otters, *Lutra lutra*, living in lakes, place scent marks where streams and ditches enter, possibly because these are the normal routes for otters entering an area (ERLINGE 1968).

2. *When intruders meet animals that could be the territory owner they should smell, and perhaps taste, any secretion or odour used in marking the territory.* This behaviour might take the form of a response to the presentation of a particular gland or scent impregnated area of the body by the territory owner.

Examples of behaviour consistent with this prediction have been mentioned when discussing the behaviour of owners in making scent available; in most situations these two categories of behaviour will form an action-response sequence. Thus intruding impala and hartebeest respond to the presentation of the forehead gland or the scent impregnated neck and shoulders of the owner by stretching out the nose and sniffing or tasting the scented area (GOSLING 1974, 1975; JARMAN 1979). Subordinate male black buck, *Antilope cervicapra*, sniff the antorbital gland of dominants during agonistic behaviour (SCHMIED 1973). Intruding hartebeest also sniff the rump of owners although this behaviour is common only with high status intruders and in encounters between territorial males (GOSLING 1975). Sniffing the rump or anal region is common in ungulates (SCHLOETH 1956) and might reflect the common use of faeces, often accompanied by the odour of anal glands (reviewed by ORTMANN 1960), in territory demarkation.

Human observers standing within a metre or so of most male ungulates can often detect a characteristic odour. Conspecifics in agonistic encounters can undoubtedly do as well and olfactory information may be obtained simply by inhaling such air-borne odour. This possibility would be difficult to test except perhaps by measuring the timing of an intruder's response in relation to wind direction; do intruders attempt to approach possible owners from down-wind?

3. *Low status intruders should withdraw if the scent of a possible territory owner matches that of marks detected previously.* If the scents do not match, the ensuing interaction should be non-agonistic in character (e.g. gregarious) or, any agonistic encounter should employ other assessment criteria, such as age, size etc.; some encounters should escalate to overt aggression.

Observations of intruders withdrawing from territory owners and remaining, in groups, with non-territorial animals are commonplace. The inference that this response involves scent rests on the smelling and tasting behaviours described in the previous section. MYKYTOWYCZ et al. (1976) have shown experimentally that male rabbits prove subordinate when placed with a male accompanied by the odour of its own anal and chin gland secretion; this situation seems analogous to that of an intruder meeting an animal whose odour matches that of nearby scent marks. Inguinal gland secretion is not used in territory demarcation by male rabbits and does not affect the outcome of agonistic encounters (MYKYTOWYCZ et al. 1976).

4. *High status intruders should usually withdraw when the scent of a possible territory owner matches that of marks detected previously.* Sometimes high status intruders should escalate, and, in this context, escalation can be regarded as competition for ownership of the territory. Competition for ownership should include a high intensity of marking, over-marking and other attempts to remove the marks of the existing owner. Sometimes high status animals will find vacant territories and, if behaviourally and physiologically ready to become territorial, such animals should mark at a very high intensity and over-mark and remove marks of previous occupants. As competitors for ownership and new occupants progressively succeed in establishing their scent in the area they should then conform to the predicted behaviours of owners (see above).

Predictions of the behaviour of high status intruders when the scent of a possible territory owner does not match that of marks in the vicinity are the same as for low status intruders.

As in the previous case there is no direct evidence about whether or not the smell detected by high status intruders on possible owners matches that of surrounding marks. However, most intruders do withdraw from owners after behaviour that includes smelling and tasting (e.g. hartebeest, GOSLING 1975).

Intruders that are likely to take over a territory are usually difficult to identify objectively. However, in the case of Coke's hartebeest, high status males establish very small territories next to the 'activity centres' of large, long-term territories, and use these as a base for intrusions which, over a period of days or weeks, sometimes lead to displacing the owner from the large territory. The intrusions consist essentially of marking behaviour, often at a very high rate, interspersed with flight from the defending owner. Usually intruders walk from one dung pile to another where they paw and defaecate. The resident male approaches, vigorously paws the faeces left by the intruder and defaecates itself, before resuming the pursuit. Meanwhile the intruder has



moved on to another dung pile. Sometimes the owner overtakes the intruder and agonistic encounters of variable length occur. The intruder almost invariably withdraws and eventually returns to its small territory where it remains until the next intrusion (GOSLING 1974, 1975). Such behaviour appears to be a clear attempt to scent mark the large territory as part of a protracted attempt to assume ownership. These tactics have the advantage of not only displacing a male with little risk of injury but also of ensuring a comprehensively marked territory, in advance of assuming ownership, to assist in defence against other intruders in the initial stage of occupancy.

Newly formed pairs of wolves mark at a very high frequency but while ROTHMAN and MECH (1979) emphasise the role of marking in pair bond formation this behaviour is exactly that expected to establish a comprehensive pattern of marks and thus allow intruders ('lone wolves') to accurately assess the newly territorial pair. ROTHMAN and MECH (1979) and PETERS and MECH (1975) regard 'territory advertisement and enforcement' as a parallel function to that of pair formation and reproductive synchronization.

### Behaviour of Neighbouring Territory Owners

Neighbouring territory owners can be regarded as a particular type of high status potential intruder and the form of the interactions between neighbours can be predicted as in the case of those between owners and non-territorial intruders. Neighbours differ in being continually present. They offer a continual threat through territory expansion as envisaged in HUXLEY'S (1934) "rubber disk" theory of territory size. This idea has empirical support from observations of hartebeest which show that exceptionally vigorous males can sometimes expand their territories at the expense of neighbours (GOSLING 1975). Thus, in the present context, owners should mark their territories where this threat is most frequent, mark themselves and make themselves available for scent matching to the neighbouring males.

The frequent interactions between territorial male hartebeest occur on or near dung piles and have a large scent marking component. Both males, in turn, sniff the dung pile, paw vigorously, kneel and rub the face glands on the ground then stand and defaecate. The males frequently rub their faces onto their shoulders and side. Smelling and nibbling the neck of the opponent ('neck-sliding') while it stands immobile occurs almost invariably. Sniffing the rump of the other male is frequent and usually leads to a circling mutual withdrawal (GOSLING 1974, 1975). Wildebeest have similar boundary encounters at dung piles and employ the additional behaviour of lying down after pawing and rolling in the dung pile (ESTES 1969). Agonistic interactions between neighbouring groups of sifaka, *Propithecus verreauxi*, a territorial lemur, involve "a frenzy of scent marking, urination and defaecation" (JOLLY 1966); sifaka territories are extensively marked, particularly with urine and the secretion of a neck gland. Scent marking behaviour often has a clear visual signal value: for example, territorial male Thomson's gazelle perform defaecation and urination in ritualized and exaggerated postures during boundary

agonistic behaviour (WALTHER 1964, 1968). In spite of this development, which is presumably secondary, many boundary encounters, such as those of hartebeest and wildebeest, seem to consist largely of an exchange of olfactory information with both participants smelling both each other and the marks produced. The encounters differ from those between owner and intruder in their symmetrical nature but are consistent with a hypothesis of assessment by scent matching.

This becomes clearer in a situation when a new owner has not established scent marks in the territory. If a hartebeest territory becomes vacant, usually as a result of predation, there is immediate competition to occupy it. The territory is visited by a number of high status non-territorial males and one male, often a male that has previously occupied the territory, eventually establishes itself as the new owner. The process of establishment involves a very high frequency of marking with face glands and faeces, both as part of agonistic behaviour and while the male is alone. The importance of marking is illustrated by the behaviour of neighbouring territorial males which, atypically, intrude deep into the disputed territory and initiate prolonged encounters with the new resident (GOSLING 1975). This behaviour is consistent with that expected from the matching hypothesis. After a day or two, when the territory is comprehensively marked, the intrusions cease.

### Assessment by Scent Matching in Other Contexts

RALLS (1971) has drawn attention to the link between androgen dependent dominance behaviour and scent marking in a range of non-territorial animals. Many of these species mark objects, over-mark the marks of competitors and mark frequently in agonistic encounters. Territoriality can be regarded as dominance with a spatial reference and so the observations reviewed by RALLS (1971) suggest a link with the functional interpretation and the mechanism of assessment proposed in this paper: animals that win most interactions in hierarchical systems also mark more often; thus the outcome of an interaction is predictable, to each competitor, by matching the scent of the opponent with the majority scent on marked objects in the vicinity. If the majority scent mark is the animal's own then it escalates; if it is the opponent's, then it withdraws. It might seem tempting to suggest an assessment of hierarchical position based on the frequency of scent marks in the vicinity but this is unlikely because the hierarchy is primarily a descriptive system developed by the biologist and the relationships that compose it, as in the case of territoriality, are dyadic rather than continuous phenomena.

The males in species with polygynous mating systems sometimes mark females; these observations suggest that an analogous process to that described for territories could exist where conspecifics are a comparable resource. In polygynous mammals, females are defended against competitors and seem comparable as a spatial reference for dominance. Examples are the marking of the shoulder or rump of female gerenuk by males using the antorbital gland

(BACKHAUS 1958; WALTHER 1958) and urination on female mara, *Dolichotis patagonum*, by males (DUBOST and GENEST 1974), a behaviour that is common amongst hystricomorph rodents (KLEIMAN 1974). Male Gray's waterbuck, *Kobus megaceros*, saturate their own underparts and especially the long hair of the throat region by 'spray-urination'; sometimes they also urinate on the ground and then lie down and rub the throat in the urine. The male then rubs its dripping throat on the head or rump of a female (WALTHER 1966). In essentially monogamous antelopes such as Maxwell's duiker, *Philantomba maxwelli*, males and females mark each other (AESCHLIMANN 1963).

As in the case of territory demarkation, marking conspecifics might simply provide subordinates (= intruder) with an odour on an important resource that can be matched with that of the dominant animal (= owner). Its functional significance might thus lie in the effect that such information has on the outcome of encounters which may determine access to the conspecific, for example, access by males to a receptive female in species with a polygynous mating system. The hypothesis that marking provides a means of assessment to competitors may thus be applicable to contexts involving the defence of any limited resource. Perhaps this principle can be extended to the defence of any conspecifics whose welfare affects the inclusive fitness of the marking animal. If so, then allomarking within social groups of closely related individuals (such as mongooses, *Helogale undulata*: RASA 1973) becomes understandable: all other members of the group are an important 'resource' to each individual member.

The other main class of animals that enter territories are potential mates. As in the case of intruding competitors these may gain an advantage by accurate identification of the territory owner. In male territorial systems, for example, females may enhance their fitness by mating only with males that succeed in occupying territories. Matching the odour of a potential mate with that of the prevalent odour of nearby scent marks would provide a simple way of making such assessment. Females have a prolonged opportunity to make this comparison during precopulatory behaviour and often sniff males, particularly the genital region. As might be predicted males often mark during precopulatory behaviour and in some cases they mark more often during mating seasons (e.g. JOHNSON 1973; PETERS and MECH 1975; BROWN 1979). Female choice in non-territorial mating systems could operate using a similar process to that already suggested for assessment of high status males by subordinates (cf. RALLS 1971). Scent marking might thus have the dual function of providing both intruders and potential mates with a means of assessing the owner.

The extension of the assessment hypothesis to dominance hierarchies, marking conspecifics and mate choice clearly require more extensive documentation than the cursory treatment given here. The objective of the present section is to show that it might be possible to extend the idea to other conceptual areas and that the assessment hypothesis is not invalidated by observations of scent marking by animals that are not territorial. After this brief digression, the following discussion will return to the main objective of the paper, the function of territory demarkation.

### Discussion

Most of the behaviours cited as consistent with the predictions of the scent matching hypothesis have, individually, been explained in other ways. The functional interpretation outlined here differs in providing a comprehensive framework for existing empirical data and a theoretical basis for a number of behaviours that are not predicted by current theory. Examples are self-anointing, marking during agonistic encounters and the systematic removal of previous marks by territorial male oribi.

The hypothesis is designed to be testable and such attempts should take note of its two parts. The first is the functional consideration that a territory owner gains an advantage by allowing intruders to assess its status. This part has theoretical analogies in other areas of competitor assessment and may prove the most durable part of the hypothesis: it could persist if a different mechanism were to replace that advanced here. For example, chemicals that were specific to territory owners might exist. The second part of the hypothesis is concerned with the mechanism that intruders use to recognize territory owners. The reasons for selecting the process of scent matching include its simplicity: not only are there procedural advantages in first testing the simplest hypothesis available but, more important, natural selection might often be expected to favour the most economical mechanism that is available.

A number of recent reviews have concentrated on the complexity and variety of signals that might be transmitted by scent marks (e.g. RALLS 1971; EISENBERG and KLEIMAN 1972; JOHNSON 1973; THIESSEN and RICE 1976; MACDONALD 1980). This approach is, in part, a healthy response to early views of the relationship between marking and territoriality but it may obscure the existence of a genuinely analogous group of scent marking behaviours which are directly, and comprehensively, linked to the fundamental concept of a spatial reference for dominance. The process of falsification in hypotheticodeductive science is useful only if the hypothesis under testing is correctly formulated; this was not the case for the idea that marks deter intruders from entering a territory. Consequently, the falsification of this hypothesis does not mean that marking has no role in area defence: the hypothesis presented and developed here suggests that marking gives a distinct advantage to an owner in maintaining preferential access to a particular resource or group of resources. In the case of an exclusively occupied area of land, the classically defined territory, marking objects may help in defence by providing intruders with a means of identifying the owner, rather than by repelling intruders that detect the marks.

The possibility of multiple functions for marks in territories has been discussed in recent reviews (e.g. EWER 1968; JOHNSON 1973; THIESSEN and RICE 1976). However, many of these functions are simply extrapolated from studies of olfactory communication in other contexts and there is little evidence for their existence in territories. An exception is the extensive

documentation of a reproductive function, taking the form either of a 'signal pheromone' or a 'priming pheromone', that is, one that elicits a behavioural response or one that causes a physiological change. Examples are, respectively, the attraction of mates or the induction of oestrus. Both processes have been demonstrated either in the field or under laboratory conditions that approximate to those of natural territoriality. However, there are no detailed observations of the patterns of marks that convey such information, in relation to the movements of possible mates, and it is not known whether marks that attract mates can simultaneously be used by competitors for assessment. In any event, mate attraction and the various priming effects depend on intrinsic properties of the scent rather than on any association between the marking animal and the spatial pattern of the marks and, not surprisingly, very similar processes are seen in non-territorial contexts. Thus a fundamental difference exists between this type of sexual advertisement and the functional role advocated in this paper: the first is concerned with transmitting information that is similar regardless of social context, while the assessment hypothesis aims to explain the universal occurrence of a characteristic pattern of scent marks in association with area defence. This difference is clear in animals that mark and defend territories continuously but are only reproductively active in a short breeding season. An example occurs in resident populations of wildebeest where 90% of all conceptions occur in a 4 week period but where males defend territories for much of the year (ESTES 1966, 1969; ESTES and ESTES 1979).

Previous assumptions of functional complexity in object marking rest partly on the demonstration that animals can distinguish subtle differences in odour. For example, the ability to discriminate between the scent of individuals has been demonstrated in a number of species including mongooses, *Herpestes auro punctatus*, and badgers, *Meles meles* (GORMAN 1980). However, this ability is not a demonstration that these animals do recognize individuals in the wild or that such recognition has any adaptive significance. On the contrary, it seems important for an intruder to identify whether or not an animal is a territory owner but not which individual it is; this information would be misleading if a particular animal has only recently occupied the territory or just lost it. In the context of territory defence, the information obtained from matching scents is precisely appropriate. The odour discrimination needed would be similar to that required for individual recognition but, in the subsequent matching process, the animal would avoid redundant and potentially misleading information. In general, the ability of animals to discriminate odours becomes relevant only in a particular context; functional issues are rarely resolved by experimental demonstrations of sensory capacity.

The mechanism suggested provides a means of assessing a possible owner regardless of whether the individual concerned is known to the intruder. It does not exclude the possibility that intruders will eventually learn the identity of an individual scent. Indeed, the high frequency of marking by owners in interactions with intruders might have the function of providing

information for this learning process. Learning the identity of individuals seems most likely between neighbouring territory owners, a special case of potential intrusion, where two animals meet regularly over an extended period. This process might explain the general observation that territorial male artiodactyls rarely intrude into neighbouring territories except when forced by factors such as a water shortage (OWEN-SMITH 1977). Individual learning may be implicated in the avoidance of neighbouring territories by wolf packs (PETERS and MECH 1975). Marks are more frequent around the boundaries but since lone non-territorial wolves are often chased and killed by resident packs, if detected, there is little opportunity for scent matching. Perhaps in this case the process of associative learning, which may be secondary to scent matching in most territorial species, assumes primary significance.

Given the existence of the scent matching mechanism it would not be surprising if the information that scents did *not* match were used to signal that an animal was *not* the territory owner (or a dominant animal). Such information would have clear relevance in appeasement or submissive behaviours which function to reduce the chance of escalation in encounters with potentially dangerous opponents. Animals that benefit from advertising subordinate status would be expected to mark their environment less frequently than dominants and to make the odour used available for inspection. Subordinate behaviour frequently conforms with these predictions: subordinates mark less frequently (e.g. rabbits: MYKYTOWYCZ 1965; Maxwell's duiker, *Cephalophus maxwelli*: RALLS 1971) and often present the ano-genital area for inspection by dominant animals (e.g. wolves: SCHENKEL 1948). The presentation of brightly coloured and swollen ano-genital areas by both dominant and subordinate male primates (reviewed by WICKLER 1967) might have evolved from the presentation of scents that respectively matched and did not match those of marks in the territory. How frequently this link persists in contemporary primate signalling is not known. The visual component of the signal may usually operate independently, particularly in species where object marking is reduced or absent. If so, it would be interesting to explore how, or if, deceitful signals are avoided in these species; from this viewpoint, selection should favour the retention of object marking and scent matching which, for reasons discussed below, are uniquely cheat-proof.

Odour is clearly not the *only* factor used by intruders in assessing possible owners. Intruding hartebeest, for example, often flee when the owner approaches from a distance that precludes any involvement of odour. Also, the striking visual displays employed in agonistic encounters, vocalizations and contact behaviours, particularly those involving horns or antlers, all clearly indicate the use of other stimuli. In some cases territory owners have a different appearance to non-territorial animals: territorial male hartebeest rub mud on their pelage significantly more often than other males and can often be picked out at a great distance by human observers (GOSLING 1975). Such factors are probably all used in assessment, but to different extents by intruders of different status. Low status intruders, for example young animals

that have not reached full body size, are unlikely to win an encounter with a territorial male and would risk injury in any such encounter. It would thus be advantageous for them to withdraw when an approaching animal is still far away even though identification mistakes are possible using only visual information (speed of approach, posture, etc.). Higher status males are involved in competition for reproductive status which often consists of competition for dominance with non-territorial males and attempts to occupy a territory. Such males have more to lose by early withdrawal and more to gain from an escalated encounter. They should thus attempt to gain more reliable information about an animal that might be an owner before withdrawing. Odours are one class of information that the intruder can obtain in a close agonistic encounter before escalating to overt aggression.

However, the existence of signals that accurately reflect social status poses an evolutionary problem. If high status confers a fitness advantage, why do low status animals not imitate the signals of high status to their own advantage? The answer may be that there are fitness advantages in being subordinate, at least in the short term (ROHWER and EWALD 1981) or that selection favours signals that are difficult to mimic. This property can be because the signal is linked to a characteristic that only high status animals possess or because the signalling process is extremely expensive. Thus the low croaks of high status toads are physically dependent on a large body size (DAVIES and HALLIDAY 1978) and the roaring bouts of rutting red deer stags are potentially exhausting (CLUTTON-BROCK and ALBON 1979). Selection should also favour signals that can be reinforced (these will be successful more often) or, in other words, signals that are cheat-proof. Olfactory signals may be more difficult to fabricate than visual or auditory signals because they may reflect physiological state more directly. However, there is no theoretical reason why selection should not favour the production of a 'high quality pheromone' by a low quality animal. Cases such as the production of a sex attractant pheromone which lures moths to the webs of bolas spiders, *Mastophora* spp. (EBERHARD 1977) demonstrate that subtle and highly specific olfactory deception can occur even between species; presumably the raw material for the selection of such a signalling process would be more easily available intraspecifically. In contrast, the assessment criteria suggested in the scent matching hypothesis are uniquely cheat-proof. Firstly, territory demarkation is very expensive, in the sense that a new owner must invest heavily in time and energy in order to comprehensively mark the area (GOSLING 1975; WALTHER 1978). Secondly, comprehensive marking can only be achieved by an animal that actually has occupied the entire area for a reasonable period of time (about one week in Thomson's gazelle: WALTHER 1972). By matching the scent of a competitor with those of nearby scent marks an intruder employs the unique property of olfactory signalling that it provides both a historical and spatial record of an individual's behaviour. Territory owners can thus signal their status to intruders in a way that cannot be mimicked and that is to their advantage in subsequent encounters.

### Summary

Taking an evolutionary perspective, it is suggested that animals scent mark their territories to provide intruders with a means of identifying the owner during agonistic encounters. The suggested mechanism of identification is scent matching: intruders compare the odour of a possible owner, or of a mark the animal is seen to make, with the odour of the majority of marks detected on objects in the vicinity. When these odours match, the animal is probably the territory owner. The advantage to the owner is that intruders will often withdraw at this point because owners are usually prepared to escalate any encounter that follows. The cost of marking a territory (mainly in time and energy expended) may thus be outweighed by reduction in the cost of active defence (mainly energy expended and risk of injury).

Relevant marking and agonistic behaviour are reviewed for consistency with the predictions of the hypothesis. The predictions are that owners should (1) mark their territory in a way that maximizes the chance that marks will be detected by an intruder, (2) mark themselves with the substances used to mark the territories, (3) make themselves available for scent matching by intruders, and (4) remove or replace marks in the territory that do not match their own odour. These predictions are generally fulfilled by observed behaviour. The predictions of intruder behaviour are that they should (1) seek out or otherwise detect the scent marks of owners, (2) when they meet a possible owner they should smell any odour used in territory marking, (3) when the scents on the opponent and the marks *match*, most intruders should withdraw, and (4) when the scents match, intruders that are competing for territory ownership should escalate. When the scents do not match the following encounter should be non-agonistic (e.g. gregarious) or, if agonistic, should employ other assessment criteria (e.g. body size). There are fewer critical observations of intruder behaviour but those available are consistent with these predictions.

The mechanism suggested provides a means of assessing a possible owner regardless of individual recognition. Such an assessment process has the advantage to the intruder that it would avoid the sort of error that might occur when known individuals have recently gained, or lost, a territory. However, it seems likely that animals will sometimes learn the odour of a particular individual, especially when they meet frequently. A definitive example is that of territorial neighbours: both animals are potential intruders and both meet regularly over long periods. Under these circumstances interactions assume a stereotyped character and individual recognition may be particularly important. However, agonistic interactions, for example in hartebeest, consist essentially of an exchange of olfactory information from habitually used marking sites and from the body of the opponent. These encounters appear to be a more ritualized version of encounters with non-territorial intruders when owners make themselves available for scent matching.

It may be possible to extend the principle of assessment by scent matching to other contexts. Examples are in social systems with individual, rather than



spatial, references for dominance and in any situations where marking, and thus defending, a resource increases the inclusive fitness of the marking animal. Such 'resources' might include mates and genetically related members of social groups.

The existence of signals that accurately reflect social status poses an evolutionary problem. If high status confers a fitness advantage, why do low status animals not imitate the high status signal? It is suggested that the assessment criteria proposed in the scent matching hypothesis are uniquely cheat proof. Territory demarkation is expensive in time and energy and, most important, the owner must be able to occupy, and defend, the area for a reasonable length of time in order to mark it comprehensively. Territory owners can thus signal their status in a way that cannot be mimicked, by providing intruders with the opportunity to employ the unique property of scent marks, that they provide both a historical and a spatial record of individual behaviour.

### Zusammenfassung

Evolutionsbiologische Argumente machen wahrscheinlich, daß Tiere ihre Territorien duftmarkieren, um Eindringlingen die Möglichkeit zu geben, bei Begegnungen den Eigentümer zu identifizieren. Diese Identifikation müßte auf einem Duft-Vergleich beruhen. Eindringlinge vergleichen den Duft eines Individuums mit dem Duft der häufigsten Duftmarken in der Umgebung. Wenn diese Düfte zusammenpassen, ist das Tier wahrscheinlich der Eigentümer des Territoriums. Der Vorteil für den Eigentümer liegt darin, daß sich Eindringlinge dann vermutlich wieder zurückziehen, da Eigentümer gewöhnlich bereit sind, ihr Revier stark zu verteidigen. Der zur Markierung eines Territoriums nötige Aufwand (hauptsächlich Zeit und Energie) könnte so durch die eingesparten Kosten einer aktiven Verteidigung (hauptsächlich Energieaufwand und Verletzungsgefahr) überwogen werden.

Das bekannte Markier- und Kampfverhalten verschiedener Tiere wird mit den Voraussagen der Hypothese verglichen. Voraussagen über den Eigentümer sind: 1. er sollte sein Territorium auf eine Weise markieren, die eine maximale Möglichkeit bietet, daß die Marken von einem Eindringling bemerkt werden; 2. er sollte sich selbst mit den zur Markierung des Territoriums verwendeten Substanzen markieren; 3. er sollte sich zum Zwecke eines Duftvergleichs dem Eindringling stellen; und 4. er sollte andere Marken im Territorium entfernen oder durch eigene ersetzen. Diese Voraussagen werden in der Regel vom beobachteten Verhalten bestätigt. Voraussagen über das Verhalten von Eindringlingen sind: 1. sie sollten die Duftmarken des Eigentümers ausfindig zu machen suchen; 2. sie sollten bei der Begegnung mit einem möglichen Eigentümer dessen zur Reviermarkierung verwendeten Duft prüfen; 3. sie sollten sich meistens zurückziehen, wenn der Duft des Gegners zum Duft der Markierungen paßt; und 4. Eindringlinge, die um den Besitz des Territoriums wetteifern wollen, sollten miteinander kämpfen, wenn die Düfte zusammenpassen. Wenn die Düfte nicht zusammenpassen, sollte die Begegnung

nichtagonistisch (d. h. gesellig) verlaufen, oder, falls doch agonistisch, sollten weitere Beurteilungskriterien (z. B. Körpergröße) herangezogen werden. Die Anzahl kritischer Beobachtungen über das Verhalten von Eindringlingen ist zwar gering, doch stimmen die Befunde mit diesen Voraussagen überein.

Der vermutete Mechanismus erlaubt das Identifizieren eines Eigentümers ohne ein individuelles Wiedererkennen. Für den Eindringling hat das den Vorteil, daß er die Irrtümer vermeidet, die vorkommen könnten, wenn bekannte Individuen ein Revier in jüngster Vergangenheit erworben oder verloren haben. Dennoch werden Tiere auch den Duft eines bestimmten Individuums erlernen, besonders, wenn sie ihm häufig begegnen. Das gilt vor allem für Reviernachbarn: Beide sind potentielle Eindringlinge und begegnen sich regelmäßig.

Vielleicht spielt das Prinzip der Beurteilung durch Duftvergleich auch in anderen Situationen eine Rolle, z. B. in Sozialsystemen, in denen die Dominanz individuen- und nicht raumbezogen ist, oder wenn die Markierung, und folglich die Verteidigung einer Ressource direkt der Fitness des markierenden Tieres dient; so werden auch Paarungspartner und genetisch verwandte Mitglieder in sozialen Gruppen markiert.

Wenn Signale den sozialen Status genau widerspiegeln und wenn ein hoher Rang einen Tauglichkeitsvorteil bringt, warum wird dann das Statussignal nicht von niederrangigen Tieren nachgeahmt? Es scheint, daß die in der Duftvergleichshypothese unterstellten Beurteilungskriterien in besonderer Weise täuschungssicher sind. Das Setzen von Reviermarken ist zeit- und energieaufwendig; außerdem — und dies ist am wichtigsten — muß der Eigentümer das Gebiet lange genug bewohnen und verteidigen, um es durchwegs markieren zu können. Revierbesitzer können daher ihren Status auf eine Weise signalisieren, die nicht nachgeahmt werden kann, weil die Geruchsmarken sowohl zeitlich als auch räumlich das Verhalten des Individuums bezeugen.

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