

THE ECONOMIC CONSEQUENCES OF ADVERTISING SCENT MARK LOCATION ON TERRITORIES

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INTRODUCTION

The role of scent-marking in the maintenance of mammalian territories is well-documented (eg. Ralls, 1971; Brown and Macdonald, 1985; Gosling, 1982; Gosling and Roberts, in press). Scent marks are a form of status signal, advertising territory ownership, and recent evidence suggests they may also be condition-dependent signals of quality and competitive ability (Gosling *et al.*, in press). In common with animal signals in other sensory modalities, scent marks thus provide a means of assessment which informs signal receivers about the signaller's quality. Information about the location, density, freshness and chemical properties of scent marks are all likely to contribute to the appraisal of the signaller by the receiver before the participants meet. In a territorial context, the product of this appraisal may be a decision to avoid the risk of meeting the signaller by withdrawing from the territory, for example, if the signaller appears to be of far higher competitive ability. Alternatively, a receiver may defer a decision until it has more information, or until an opportunity arises to check this information in a face-to-face situation. Since scent mark detection often occurs in the signaller's absence, receivers may need to confirm the identity of any opponent as the resource-holder before deciding on their next move. This can be achieved by comparing the odour of the marks with that of their opponent, a process known as scent-matching (Gosling, 1982, 1990; Gosling and McKay, 1990). A positive match, which unambiguously confirms the owner's status, may be sufficient to settle the contest conventionally and scent-marking thus helps to reduce the costs of territory defence (Gosling, 1986; Stenstrom 1998).

While the benefits to owners of scent-marking a territory are clear, a major constraint is the limited spatial range over which marks are typically detectable. This is at least partly due to the need for marks to persist for extended periods, especially in species where territories are large and intervals between successive visits to marking sites are long (Alberts, 1992). Mark detection is therefore frequently probabilistic and signallers benefit if

they deploy their marks in such a way that maximises the likelihood of receivers finding them, while at the same time minimising the distance that intruders travel before detection (Gosling, 1981; Roberts and Lowen, 1997). Field studies which have mapped patterns of scent marks show that marks are often clustered around or within territorial boundaries, sometimes forming characteristic rings or "bowls" (eg Peters and Mech, 1975; Walther, 1978; Gosling, 1981; Roberts and Lowen, 1997; see also Brashares and Arcese 1999). In very large territories, however, the chance of intruders missing widely interspersed boundary marks selects for centrally clustered marking patterns (Gorman, 1990).

If intruders also benefit by detecting scent marks, for example by avoiding costly encounters with opponents of higher competitive ability, it will be in their interest to actively seek out marks when they enter a territory. Detection of marks will not then simply depend on the gradient of airborne volatiles emanating from marks and the probabilistic (at least with respect to scent mark location) movements of intruders, but also on the receiver's motivation and psychology (Guilford and Dawkins, 1991). Intruders would be expected to seek marks provided that the costs of searching are outweighed by the benefits associated with additional information obtained. Observational evidence confirms that receivers seek out marks. For example, Müller-Schwarze (1974) observed that black-tailed deer search for marks after entering a new area, while a study of ring-tailed lemurs, *Lemur catta*, found that 62% of scent marks were investigated within 10 min, with a median latency of only 30s (Kappeler, 1998). This aspect of communication through scent marks is perhaps undervalued, but if intruders do search for marks, it would have profound implications for the economics of scent-marking. In particular, owners should not only deposit scent marks to intercept intruders, but should also advertise the presence of their marks in order to facilitate their detection and maximise the resulting benefits.

Here, we review briefly ways in which signallers might advertise the presence of their scent marks. We then use a simple spatial model to explore the effects of variable mark detectability as a result of receiver searching on the economics of scent-marking and resource-defence territoriality. Finally, we discuss this signalling system in terms of the debate about the evolution of honest signalling.

MARK ADVERTISEMENT AND DETECTABILITY

Two main kinds of scent-marking behaviour are consistent with the expectation that signallers advertise the location of their marks. The first is that signallers frequently deposit marks in sites that are locally conspicuous or which have characteristic topographical features. For example, klipspringer antelopes prefer to scent-mark on dead trees or branches (mainly of preferred food species), in an area slightly elevated above its surroundings and immediately above a significant break in slope (Roberts, 1997). Marks are often placed within a narrow vertical distribution, in spite of the fact that they are physically able to mark above or below the preferred height and that alternative sites may be available (Gosling, 1981; Roberts, 1997). Where suitable sites are not locally available, signallers may be able to manufacture them (Gosling, 1972). As a final example, signallers may occasionally place their scent marks at signalling sites used by other species (Gosling, 1980; Paquet, 1991), thus gaining in detectability at no additional cost to themselves.

Secondly, signalers actively create visual anomalies near their scent marks. For example, some ungulates disturb nearby vegetation by antler thrashing (Kile and Marchinton, 1977; Johansson and Liberg, 1996). In some felids and ungulates, signallers paw or scrape the ground with claws or hooves (Gilbert, 1973; Feldman, 1994; Johansson and Liberg, 1996). A more striking example is where signallers damage or tear off strips of bark before marking, creating visible wounds to trees at scent-marking sites (Graf, 1956;

Barette, 1977; Bowyer *et al.*, 1994). These wounds are generally separate from the secretion and thus appear to be unrelated to the olfactory function of the marks. There remains no direct 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.

Both kinds of marking-associated behaviour could increase detectability. In the first, marks are placed in conventional sites where receivers are more likely to find them; receivers may thus be able to form a visual search image of likely scent-marked sites (Gosling, 1981; Roberts, 1997). In the second, this visual element is actively reinforced. If receivers use these cues, scent marks become a multimodal signal (Rowe, 1999), having a visual alerting component which draws the attention of receivers to the presence of the olfactory, semantic component. Such behaviours will have the effect of enlarging the distance over which marks are detectable, beyond that attributable solely to the mark's chemical properties. In the following section, we explore the implications of this for scent-marking economics.

DETECTABILITY AND MARKING ECONOMICS

Our model incorporates movements of a single owner and intruder within a territory and variations in the amount of information about the opponent's identity. It plots the probabilities of (a) detection by intruders of owner's scent marks within the territory and (b) the frequency with which owners and intruders will meet while intruders cross the territory. The model distinguishes between territorial encounters occurring in the presence of absence of previous mark detection by the intruder. In the former case, the intruder is able to correctly identify its opponent as the owner, while in the latter, it has relatively little information about its opponent or its competitive ability.

Following Roberts and Lowen (1997), the model assumes the owner defends a circular territory of radius R_0 , within which it positions and maintains n scent marks of equal volume and efficacy. These are non-overlapping and evenly distributed along the circumference of a circle, which is concentric with the territory boundary and with a radius R , such that $R \leq R_0$. The area within the ring of scent marks is termed the defended area. Mark detection is taken to be a function of the distance between the intruder and the mark, such that detection always occurs at a distance of less than or equal to a_0 and never occurs at distances greater than a_0 . Thus, the probability of detecting a scent mark as an intruder crosses into the defended area is $(2na_0/2\pi R)$, and the probability of entering the defended area without detecting a mark is $[1-(2na_0/2\pi R)]$.

The probability of encounters between owner and intruder (P_E) are calculated using a modification of Waser's (1977) gas model (see also Barrett and Lowen, 1998), in which

$$P_E = (4 \cdot p \cdot kv / \pi) d \quad (1).$$

where v is travel speed, d is the distance at which intruders are detected by the owner and k is a constant. Since we are only concerned with pairwise encounters between individuals, p , the population density, is given by $2/\text{territory area (m}^2\text{)}$ and we omit s , the term for group dispersion in the original model. Term (1) actually calculates the expected frequency of encounters given random movement. However, as expected frequencies are usually less than 1 with our parameter values and as we are solely concerned with the first encounter, we can treat these as probabilities and convert to $P_E = 1$ any frequencies greater than 1. For simplicity, we assume animals travel at a speed of 1ms^{-1} and we substitute v for t , the time taken to cross a defined distance. The intruder's travel time between the boundary and the

defended area, following a straight-line trajectory, is then t^{R_0-R} and that for crossing the remainder of the territory is t^{R_0+R} . Note that this produces an approximation of the

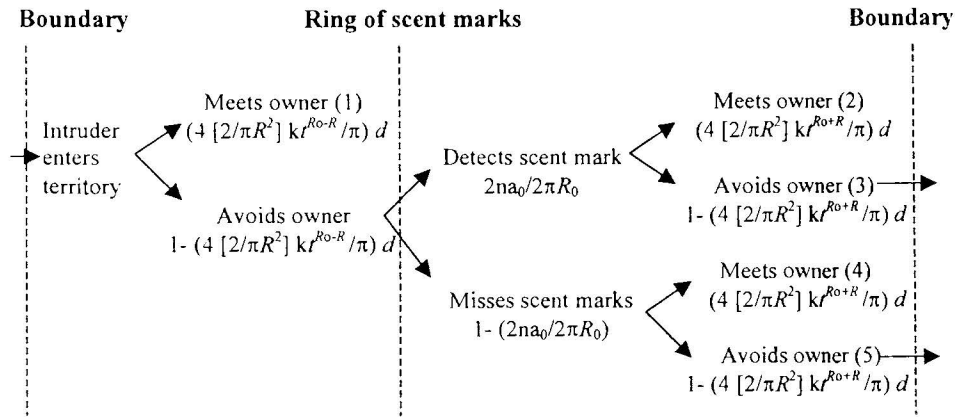


Figure 1. Summary of possible outcomes of a territorial intrusion. Numbers in parentheses relate to the categories of outcomes as outlined in the text. Terms used in functions are explained in the text.

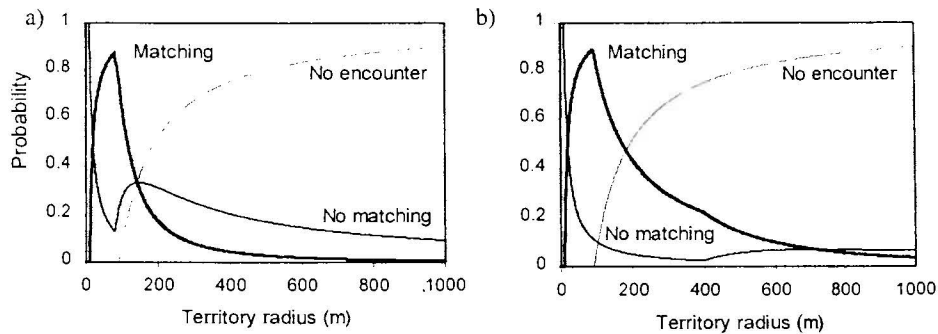


Figure 2. Probability of the three main outcomes of intrusions onto scent-marked territories in relation to mark detectability. Intruders may leave the territory without meeting the owner. Alternatively, they will encounter the owner having either detected or missed its scent marks; in the former case, they are thereby able to correctly identify the owner by scent-matching. Effective radius of marks, a_0 , is (a) 2m and (b) 10m. Here, $R=0.8R_0$, $d=50$ and $n=100$.

duration of an intruder's presence within the territory before and after crossing into the defended area; because intruders do not necessarily move in a straight line, the constant k (set here at 1.25) estimates additional travel time resulting from random deviations. Probabilities of intrusion outcomes can now be calculated. After entering the territory, it takes intruders kt^{R_0-R} seconds to reach the demarcated ring, during which they may meet the owner (outcome 1, see Figure 1). If not, intruders may detect a mark while entering the defended area, and may subsequently meet the owner during the kt^{R_0+R} seconds it takes to cross the territory. We can then find the probability of encounters without opportunity for

scent-matching (outcomes 1+4), where matching can occur (2) or in which intruders are not detected (3+5).

The model demonstrates the relationship between the opportunity for scent-matching and territory size (Figure 2). Since mark detection decreases exponentially with increasing territory size (assuming constant n), there is, on small territories at least, a high probability of encounters in which intruders have already encountered owner's marks. Indeed, this is usually the most probable outcome. The range of territory sizes in which this is true clearly depends on the model's parameters, but given reasonable values (those in Figure 2 are within the ranges found in our field studies on African antelopes: Gosling, 1981; Roberts and Lowen, 1997), the opportunity for matching is inversely related to territory size and eventually becomes less likely than either alternative outcome. The main exception to this trend lies in a narrow range of extremely small territories, where encounters without matching are the predominant outcome. This is because, despite the fact that intruders would be certain to detect marks in the ring, owners intercept intruders before they have the opportunity to do so.

Figure 2 also demonstrates the impact of mark advertisement on the context in which encounters occur. As detectability increases, there is a linear increase in the range of territory sizes over which intruders will be able to scent-match should an encounter occur (for a given probability of matching). In addition, mark advertisement will have knock-on effects for other aspects of marking economics. For example, for any given territory size, the number of marks required to return the same probability of mark detection decreases exponentially (Figure 3). Thus, if competitors are prepared to incur the costs of seeking out marks, signalers are able to mark at lower density.

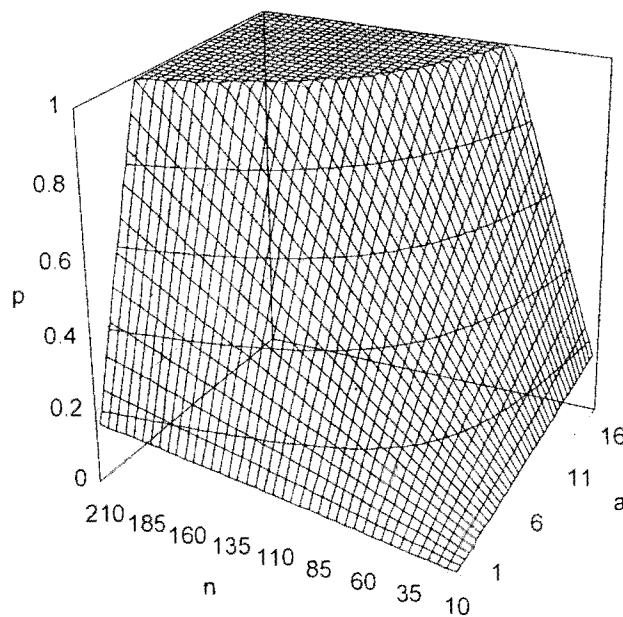


Figure 3. Surface plot of the relationship between the probability of mark detection by intruders (p), the number of marks (n) and the effective radius of each mark (a).

CONCLUSIONS

We have argued that intruders stand to gain by actively seeking out marks, because this helps to avoid costly fights. We have also shown that signallers which advertise scent mark location could benefit by their marks being more likely to be detected, particularly if intruders actively search for them. This will tend to increase the frequency of encounters in which intruders can identify owners' status, which in turn will reduce the frequency and costs of escalated resource defence. In addition, the increased detectability of scent marks conferred by advertisement and receiver searching means that owners can scent-mark at lower densities, hence offsetting to receivers some of the costs of signal transmission. It may also carry consequences for the chemistry of scent marks: selection for volatility and large effective range is reduced since the interest of receivers is gained visually. Information from marks is therefore only gained at close range, often by licking the marks to release soluble scent constituents (Alberts, 1992; Roberts, 1998), while the reduced volatility prolongs mark persistence time.

We have suggested elsewhere, in view of the apparently universal link between mammalian territoriality and scent-marking, that marking may be a prerequisite for viable territoriality (Gosling and Roberts, in press). Furthermore, our model suggests that advertisement of marks and receiver searching, through increasing the range of territory sizes over which scent-matching is possible, would appear to play important roles in the economics of territoriality. However, receivers may differ in the extent to which they are willing to seek out marks. Those of poor quality may stand to gain more by detecting marks than those of higher quality, being more likely to withdraw immediately. Conversely, good competitors may need to maximise information about the owner in preparation for a take-over attempt. Whichever is true in a particular case, such assessment can only be evolutionarily stable if the signals are reliable. Scent-marking can be seen as an honest form of signalling since owners must occupy and defend the territory at least for long enough to demarcate it (Gosling, 1982, 1990). If advertisement of marks helps to increase the likelihood of matching, then it must also reinforce the reliability of scent marks as honest signals.

Finally, advertisement of scent mark location could provide other benefits to signallers beyond that of reducing costs of escalated territory defence. While we have framed our argument in terms of an owner-intruder paradigm, improved detectability and accuracy of assessment would apply to other categories of receiver, notably potential mates. In addition, while we have considered the detection of only a single mark, advertisement of mark location is also likely to increase the chances of receivers detecting multiple marks. This may be necessary for receivers to predict owners' movements, navigate across or between territories, or to reduce the possibility of error during subsequent assessment.

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