



FORUM

Testing ideas about the function of scent marks in territories from spatial patterns

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Strictly speaking, it is difficult to ascribe function to a signal without some direct indication of the benefits that accrue to the signaller. In this ideal world, the signal and the consequent responses of the receiver would be detected and measured and the way in which the responses benefit the signaller would be clarified. This sort of investigation has rarely been achieved in any signalling modality and is particularly difficult in studies of olfactory signals. But, in the case of scent marks, the long-term nature of the signals allows some inference about this signal–response sequence (review in Gosling & Roberts 2001). Scent marks are placed in the environment, often in the absence of a potential receiver and only detected some time later, often when the signaller is no longer present. When signallers are relatively sedentary, scent marks accumulate and their spatial pattern may reveal something about the intended receiver and thus something about function. For example, when a territorial male antelope places more marks at a boundary where the threat of intrusion by competitors is greatest (e.g. oribi, *Ourebia ourebi*, Brashares & Arcese 1999a) then we may conclude that the function of the marks is linked to intrasexual competition and, in this case, to territory defence.

However, this sort of inference about the function of scent marks can be made only under limited circumstances. Other important factors can affect the pattern of marks and may need to be considered for more general explanations. Most important is that the production and maintenance of scent marks involves costs such as the cost of producing the marking substances, and the considerable time taken to establish and replenish marks. These costs introduce economic constraints to the range of spatial patterns that are possible when scent marking territories (Gosling 1981; Roberts & Lowen 1997;

Brashares & Arcese 1999b). Thus owners may not be able to mark the whole territory, or even its entire periphery, and may be forced to make strategic decisions about where to put a limited number of marks. Second, territories are rarely homogeneous and we might expect that owners would mark in relation to variation in resource value within their territories (Gosling 1985). Patterns of scent marks that represent the outcome of economic constraints and variable patterns of resource value may often be complex and thus difficult to interpret without detailed information about these factors. We consider these effects in more detail below.

These remarks were stimulated by a recent paper (Heymann 2000) that presented data on the spatial distribution of scent marks in the ranges of moustached tamarin, *Saguinus mystax*, groups and rejected the hypothesis that scent marking has a territorial function. We believe that this conclusion was not justified and aim to make two points in response. First, we show that the rejection of a territorial function was premature in this species even if one accepts the argument that peripheral marking is definitive of this sort of marking. Second, we expand the point introduced above that particular patterns of marking, such as peripheral marking, will indicate a territorial function only under limited circumstances (which need to be carefully defined). It should also be pointed out that while we believe that scent marks in territories are best understood in terms of providing information for assessment by potential competitors (Gosling 1982, 1990), the term ‘territorial function’ is sufficient for the purposes of this paper and we have retained it for consistency with Heymann’s paper.

The Spatial Distribution of Tamarin Scent Marks

In the paper under discussion, Heymann mapped the number of observed scent-marking events in the ranges of four tamarin groups (EBQB-1, -2 and -3 and EBPI ranges

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in his Figure 1). Each map was divided into quadrats of 50×50 m and frequencies of marks were calculated for each quadrat. Quadrats were also subdivided into whether or not tamarins other than the social group under observation were seen there. Those in which other tamarins were seen were called overlap squares and these all occurred around the periphery of the range. Some fights were observed in the overlap zones, thus raising the possibility of territoriality. Heymann (page 724) then predicted that if scent marks have a territorial function, there should be more scent marks placed in overlap quadrats than nonoverlap quadrats. His analysis was restricted to the three social groups mentioned above because no other tamarins were seen around the range of group EBPI. No significant difference was detected between the two types of quadrat and, on this basis, Heymann concluded that scent marks were randomly distributed and rejected the territorial function hypothesis. We agree that the tested prediction was reasonable and it could have proved correct under some circumstances (see below). However, the failure of the prediction does not mean that scent marking is not concerned with territoriality.

For example, if marks help to keep out intruders, they might instead be concentrated around the periphery of the exclusive area rather than in the overlap zone. Such patterns of marks could be established either because the exclusive area is the most valuable part of the range or because it is the maximum area that it is economically possible to mark on a sustainable basis. We tested this idea by calculating a geometric centre for each of the three ranges that had overlap zones, then calculated the distance from this point to the centre of each scent-marked or overlap quadrat. Values for each scent mark position were obtained using the median of the mark range given to each type of symbol, with 0.5 marks for the smallest symbol and 5.5 for the largest. Pooling the distribution of these values from the three territories and reducing the radii to a common 10% interval scale, we found that the spatial distribution of marking events was nonrandom (one-way ANOVA with number of marking events as the dependent variable and distance to the centre as the factor: $F_{9,483}=2.21, P=0.021$). The number of observations from each range was very variable ($N=283, 177$ and 58 scent-marking events, respectively) and, since this might affect the reliability of the data, we repeated the analysis using appropriately weighted values. This procedure yielded a similar result ($F_{9,483}=3.14, P=0.001$). Inspection of the distribution of these data (Fig. 1) showed high values within the exclusive part of the range with values falling away quickly in the overlap zone. However, the marks did not appear to be uniform within the exclusive area (either in this bar graph or in the maps in Heymann's Figure 1): rather, it appeared that there was a peak of marks immediately within the overlap zone and another area of high frequency further inside the range. Whether or not this last point can be sustained, the overall pattern is consistent with the idea that marks are placed where they could help to defend the exclusive part of the range but that the tamarins do not attempt to defend the overlap zone. Using conventional

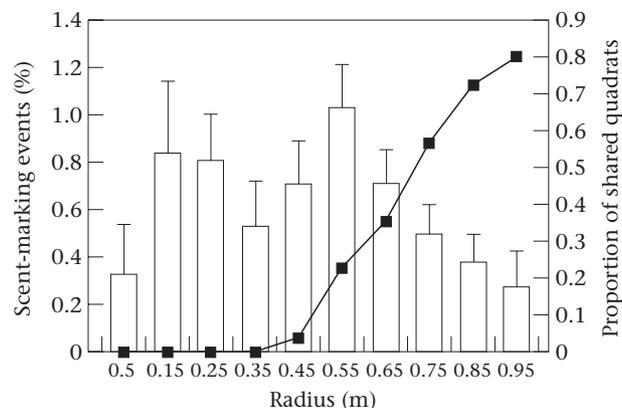


Figure 1. The relationship between the intensity of scent marking and degree of overlap of tamarin ranges with increasing distance from the centre. Data are mean+SE marking events in each of 484 quadrats of 50×50 m in three tamarin ranges as a percentage of the total, and the proportion of quadrats that overlap the ranges of other tamarin groups.

terminology, this may reflect the distinction between the home range of the social group (that is, the total area occupied by the group over a defined period) and its territory.

If this interim suggestion is true, then we would expect the effect demonstrated to be stronger where the threat of intrusion was greatest, that is, where the overlap with potential intruders was greatest. Fortunately, there was considerable variation in this respect within the three territories in which overlap was recorded: some sectors of the ranges mapped had no overlap quadrats at all. We tested this idea by dividing the three territories into quarters (defined by two lines drawn north-south and east-west which intersect at the geometric centre) with the prediction that the proportion of overlap cells per quarter should be positively correlated with the proportion of scent-marking events per quarter. The resulting correlation (weighted least-squares regression: $r_{10}=0.83, P=0.001$; Fig. 2) suggests that marking intensity was directly related to variation in intrusion pressure.

Taken together, these results suggest that tamarin scent marks were not randomly distributed, that they may be placed to intercept the movements of potential intruders and that they could be involved in the maintenance of an exclusive, central part of the range. In this they appeared to have some similarities to the saddleback tamarin, *Saguinus fuscicollis weddelli* (Yoneda 1984), in which scent marking was confined to a small central exclusive area and was absent from large peripheral overlap zones. Mack & Kleiman (1978) also suggested that captive golden lion tamarins, *Leontopithecus rosalia*, scent-mark areas of their cages that corresponded to territory boundaries. Whether or not the exclusive area of moustached tamarins is a territory cannot be determined by scent marks alone and depends on observations of defence. However, the author mentions fights with neighbours in the overlap zone (page 725) and so this must be a strong possibility. Thus a territorial function cannot be rejected for the scent marks

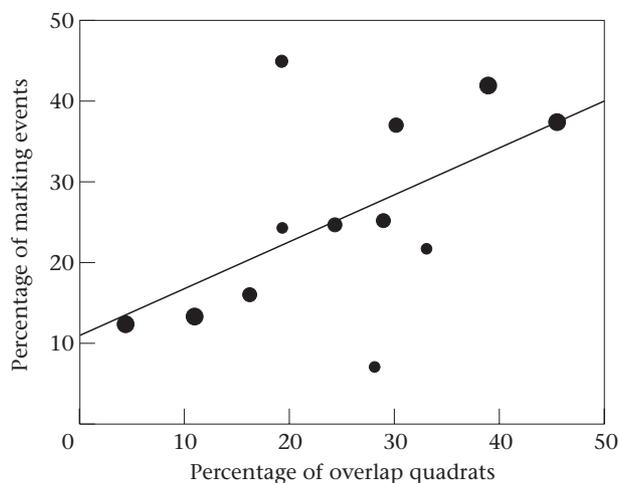


Figure 2. Relationship between intruder pressure (percentage of overlap quadrats) and scent-marking events in tamarin ranges. Data points represent values for ranges (subdivided into quarters) of three tamarin groups described in Heymann (2000). Symbol sizes indicate weighting in analyses according to the number of marking events observed in each range. The relationship is highly significant ($P=0.001$).

of moustached tamarins; indeed, we believe it to be the most likely explanation of the data presented.

Factors Affecting the Spatial Distribution of Scent Marks in Territories

However, as mentioned above, this debate raises the more fundamental issue that patterns of marks that serve a territorial function may take a variety of forms. If the defended resources in a territory are homogeneous and if marking has no cost, then marks should simply be deposited on all parts of the resource everywhere in the territory. In this way the owner would ensure that an intruder would always detect a scent mark whenever it tried to steal part of the resource. However, this situation never occurs because resources are never homogeneous and marking is never without cost. Costs are not just those in producing the marking substance but also the time involved and the risk of predation when engaged in marking sessions (Viitala et al. 1995; Roberts et al., in press). Thus, a limited number of marks must generally be placed in such a way that they maximize the chance of intercepting the movements of intruders when intruders seek to reach the part of the territory that is most valuable to the owner (Gosling 1981; Roberts & Lowen 1997). While Heymann (2000) calculated an index of economic defensibility of the tamarin ranges that he studied, the index used (Mitani & Rodman 1979) measures only the ability of the residents to reach all parts of the range using usual daily travel paths. Such calculations do not take account of the specific costs of scent marking and so cannot predict where the resident can afford to mark.

In some territories, such as those of antelopes on grassland or scrubland plains, the distribution of resources is moderately homogeneous and owners often try to defend the whole territory. As argued above, the

pattern of marks that they use may vary in relation to economic constraints. When marks are reasonably abundant in relation to the area to be defended the owner may mark the boundary (e.g. Thomson's gazelle, *Gazella thomsoni*: Walther 1978; topi, *Damaliscus lunatus*: Gosling 1987; oribi: Brasheres & Arcese 1999a). However, this provides only one line of marks and an intruder could miss them as it walked into the territory. The chance of intercepting intruders could be increased by adding further lines of marks within the territory; sometimes, as in the case of Thomson's gazelle, these take the form of a number of 'enclosures' within the territory. These patterns can be revealed using a nearest-neighbour mapping technique (Gosling 1981, 1985). When the supply of marks is small in relation to the area to be defended, the owner may place a circle of marks at some distance within the boundary, sometimes with radiating arms of marks to help intercept intruders walking obliquely through the territory. This system was first observed in genenuk, *Litocranius walleri* (Gosling 1981), and has since been modelled by Roberts & Lowen (1997). When territories are very large, owners may mark a core area at the centre of the territory. This pattern, which is a variant of the internal ring pattern mentioned above, is sometimes known as 'hinterland' marking (Gorman & Mills 1984). Like the inner ring pattern it may be adopted when the boundary of a very large territory is too long to be marked economically.

The evidence available suggests that the patterns of marking that have been observed in relatively homogeneous habitats are various ways to intercept intruders. They represent a continuum that can be explained from simple economic considerations. Because the defended resource is moderately homogeneous, the patterns of marks are relatively simple and relatively easy to interpret as being designed to intercept intruders. However, many resources are distributed heterogeneously. Some trees in the territories of browsing ungulates or arboreal primates may have far greater value than others. For example, *Souroubea guianensis* trees are highly favoured by moustached and saddle-back tamarins as food when in fruit (Peres 1993). If such trees are more valuable, it could be predicted that they would be marked more intensively than others (e.g. Roberts 1997). A high level of marking on a valued resource might be adaptive even where there was also boundary marking because the probability of intrusion into a territory is rarely, or never, zero. Patterns of marking in the territory would then be the net outcome of marking particularly valuable resources and, possibly, some attempt to exclude competitors from the area containing one or more of these resources. For example, boundary marking could be combined with marking favourite food trees or even mates.

The interacting factors of economic constraints and resource value must also be affected by variation in the threat of intrusion. The fourth moustached tamarin range (EBPI) mapped by Heymann appeared to have no neighbours and in this case, marking events might have been confined to patches of a favoured resource, perhaps because the boundary marking observed in the other three territories was uneconomic. Variation in

competitive ability of neighbours or neighbouring groups might also give rise to different amounts of marking between different overlap zones within the same territory (e.g. Brashares & Arcese 1999a). In summary, these patterns of marking are likely to reflect variation in the probability or intensity of defending different parts of the territory, and must be more common than the simpler case in which territories are defended uniformly.

Complex patterns of marks are thus to be expected when animals place their marks economically in relation to heterogeneous patterns of resource value within territories, varying territory size, varying probabilities of intrusion by competitors and varying costs of intrusions. Without detailed information about these factors it may not be possible to conclude whether an observed pattern of scent marking is linked to territoriality. In the case of moustached tamarins our analysis shows a type of boundary marking and variation in mark frequency in relation to intrusion pressure. However, given the complex interactions outlined here we would not have felt confident in rejecting a territorial function in this case, even if we had failed to find boundary or 'hinterland' patterns of marking. Unfortunately, Heymann (2000) presented no data on the composition of neighbouring groups or the resource value of particular trees. However, with respect to the latter, Lazaro-Perea et al. (1999) found concentrations of marks made by common marmosets, *Callithrix jacchus*, on gum trees in the centre of their ranges. It seems possible in moustached tamarins that the patches of marks deep within the exclusive area of each range are on particularly valuable trees. It would be worth testing whether the distribution of such limiting resources and that of territorial competitors might explain more fully the observed distribution of scent marks.

References

- Brashares, J. S. & Arcese, P. 1999a. Scent marking in a territorial African antelope: I. The maintenance of borders between male oribi. *Animal Behaviour*, **57**, 1–10.
- Brashares, J. S. & Arcese, P. 1999b. Scent marking in a territorial African antelope: II. The economics of marking with faeces. *Animal Behaviour*, **57**, 11–17.
- Gorman, M. L. & Mills, M. G. L. 1984. Scent marking strategies in hyaenas (Mammalia). *Journal of Zoology*, **202**, 535–547.
- Gosling, L. M. 1981. Demarkation in a genenuk territory: an economic approach. *Zeitschrift für Tierpsychologie*, **56**, 305–322.
- Gosling, L. M. 1982. A reassessment of the function of scent marking in territories. *Zeitschrift für Tierpsychologie*, **60**, 89–118.
- Gosling, L. M. 1985. The even-toed ungulates: order Artiodactyla. Sources, behavioural context, and function of chemical signals. In: *Social Odours in Mammals* (Ed. by R. E. Brown & D. W. Macdonald), pp. 550–618. Oxford: Oxford University Press.
- Gosling, L. M. 1987. Scent marking in an antelope lek territory. *Animal Behaviour*, **35**, 620–622.
- Gosling, L. M. 1990. Scent-marking by resource holders: alternative mechanisms for advertising the costs of competition. In: *Chemical Signals in Vertebrates, V* (Ed. by D. W. Macdonald, D. Muller-Schwarze & S. E. Natynczuk), pp. 315–328. Oxford: Oxford University Press.
- Gosling, L. M. & Roberts, S. C. 2001. Scent-marking by male mammals: cheat-proof signals to competitors and mates. *Advances in the Study of Animal Behavior*, **30**, 169–217.
- Heymann, E. W. 2000. Spatial patterns of scent marking in wild moustached tamarins, *Saguinus mystax*: no evidence for a territorial function. *Animal Behaviour*, **60**, 723–730.
- Lazaro-Perea, C., Snowdon, C. T. & Fatima Arruda, M. de. 1999. Scent marking behaviour in wild groups of common marmosets (*Callithrix jacchus*). *Behavioral Ecology and Sociobiology*, **46**, 313–324.
- Mack, D. S. & Kleiman, D. G. 1978. Distribution of scent marks in different contexts in captive lion tamarins *Leontopithecus rosalia* (Primates). In: *Biology and Behaviour of Marmosets* (Ed. By H. Rothe, J. Wolters & J. P. Hearn), pp. 181–188. Göttingen: Eigenverlag Rothe.
- Mitani, J. & Rodman, P. S. 1979. Territoriality: the relation of ranging pattern and home range to defendability, with an analysis of territoriality among primate species. *Behavioral Ecology and Sociobiology*, **5**, 241–251.
- Peres, C. A. 1993. Diet and feeding ecology of saddle-back (*Saguinus fuscicollis*) and moustached (*S. mystax*) tamarins in an Amazonian terra firme forest. *Journal of Zoology*, **230**, 567–592.
- Roberts, S. C. 1997. Selection of scent-marking sites by klipspringers (*Oreotragus oreotragus*). *Journal of Zoology*, **243**, 555–564.
- Roberts, S. C. & Lowen, C. 1997. Optimal patterns of scent marks in klipspringer (*Oreotragus oreotragus*) territories. *Journal of Zoology*, **243**, 565–578.
- Roberts, S. C., Gosling, L. M., Thornton, E. A. & McClung, J. In press. Scent-marking by male mice under the risk of predation. *Behavioral Ecology*.
- Viitala, J., Korpimäki, E., Palokangas, P. & Koivula, M. 1995. Attraction of kestrels to vole scent marks visible in ultra violet light. *Nature*, **373**, 425–427.
- Walther, F. R. 1978. Mapping the structure and the marking system of a territory of the Thompson's gazelle. *East African Wildlife Journal*, **16**, 167–176.
- Yoneda, M. 1984. Ecological study of the saddle backed tamarin (*Saguinus fuscicollis*) in Northern Bolivia. *Primates*, **25**, 1–12.