

On the Relationship between Scent-Marking and Territoriality in Callitrichid Primates

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Abstract Across a diverse range of animal groups, scent-marking is integrally related to the defense of territories and maintenance of social status. However, using data from a field study of wild saddleback tamarins (*Saguinus fuscicollis*), the authors of a recent paper claimed to find no evidence to support a relationship between scent-marking and territorial defense. Here I review the same evidence and argue that the data are consistent with the idea that scent-marking plays a critical role in territorial defense. This argument includes an attempt to clarify some misconceptions about the scent-marking mechanism that exist in the literature. I then reexamine the evidence in light of a proposed alternative function for scent-marking (that scent marks are used to explore reproductive opportunity and achieve extragroup copulations), and highlight some critical tests that could serve to distinguish between the two functional interpretations. Scent-marking could serve both in territorial signaling and in signaling to mates, but current evidence suggests that territorial defense is more, or at least equally, likely to be the primary function of scent-marking in callitrichids.

Keywords Animal communication · Olfaction · Scent marking · Signal · Territorial

The Relationship between Scent-Marking and Intrasexual Competition

Scent-marking using feces, urine, or glandular secretions, or a combination of these, is a common form of animal communication. Although scent marks can provide cues relating to fertility and mate quality, an extensive body of studies presents considerable evidence to suggest that scent marks are primarily status signals involved in intrasexual competition in general, and in territorial defense in particular (Brown and Macdonald 1985; Gosling and Roberts 2001a; Ralls 1971). Territory owners, or

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dominant animals in social hierarchies, signal to receivers the potential fitness costs of escalated aggressive encounters (Gosling 1990; Gosling and Roberts 2001a; Gosling *et al.* 2000). Scent-marking may be a uniquely reliable form of status signaling (Gosling 1982; Gosling and Roberts 2001a) because scent marks of territory owners or dominant individuals provide to receivers a continuous record of presence and maintained status. Both signalers and receivers benefit from this communication because they avoid unnecessarily frequent and costly fights. As I discuss later, this does not imply that costly fights never occur, or that the frequency of intergroup encounters should always be markedly reduced. Rather, scent-marking decreases the costs of aggression by reducing the proportion of such encounters that escalate to full-scale conflict. Indeed, Gosling and Roberts (2001a), in noting the apparently obligate link between territoriality and scent-marking, go so far as to suggest that mammalian territoriality might not be viable were it not for the reduction in defense cost afforded by scent marks.

Studies drawing a link between scent-marking and aggression are not restricted to one or a few species, but come from a diverse array of taxa, including arthropods, reptiles, amphibians, and, especially, mammals. Neither is this link restricted to species inhabiting specific habitats, being observed in deserts and semidesert, savannah, tropical forest, and temperate tundra. The link exists across a range of mating systems (from lek breeding to monogamy), in solitary and group-living species, in predators and prey, and in species characterized as diurnal, crepuscular, or nocturnal (Brown and Macdonald 1985; Wyatt 2003).

In primates, too, scent marks are integrally involved in intrasexual aggression. Researchers have shown a link between scent-marking and aggression in strepsirrhines (Lewis 2005; Palagi and Norscia 2009; Pochron *et al.* 2005; Scordato and Drea 2007) and monkeys (Hirano *et al.* 2008; Setchell *et al.* 2010). Some of these examples come from nocturnal species or those existing in tropical forest habitats where visibility is poor (Delbarco-Trillo *et al.* 2011; Lazaro-Perea 2001; Lazaro-Perea *et al.* 1999; Setchell *et al.* 2010; Wolovich and Evans 2007) and the olfactory (or auditory) channel of communication may be relatively advantageous (Setchell *et al.* 2010).

In view of this literature, the argument that scent-marking is not involved in intrasexual aggression in a territorial species is worthy of some interest. The same can be said for the argument that this suggested disconnect between scent-marking and territoriality is due to the particular ecological constraints imposed on scent-mark transmission in a forest habitat. However, these arguments have been proposed recently for saddleback tamarins (*Saguinus fuscicollis*), based on an interesting data set collected from wild groups in the Amazonian rain forest of Peru (Lledo-Ferrer *et al.* 2011). Specifically, these authors conclude that scent-marking is unlikely to be related to territorial defense. They go on to suggest that scent marks function instead to facilitate intergroup information exchange for reproductive opportunities.

Here, I argue that the theoretical basis for the conclusion to reject the link between scent-marking and territoriality, as outlined by Lledo-Ferrer *et al.* is inconsistent with current views of scent-marking mechanisms. Further, on the basis of the evidence they present, the conclusion to reject the link between scent-marking and territoriality is unwarranted.

Testing the Role of Scent-Marking in Territorial Defense

To test the role of scent-marking in territorial defense, Lledo-Ferrer *et al.* (2011) make six predictions. Four are described in the abstract; two of these are reiterated in the introduction, where two further predictions are added (on p. 976; although the authors may have intended predictions 5 and 6 to be fuller accounts of hypotheses 1 and 2 described in the abstract, they are qualitatively different and so here I treat them separately). I list them and then comment on each in turn. Thus, according to Lledo-Ferrer *et al.*, to fulfill a territorial function, scent marks should:

1. Prevent intrusions.
2. Ensure access to feeding resources.
3. Enable avoidance of intergroup encounters.
4. Play an important role in the aggressive encounters between groups.
5. Be concentrated in peripheral areas (border-marking strategy).
6. Be concentrated at the boundary if resources are homogeneously distributed, or, if resources are heterogeneously distributed, they should be associated with the resource and related to their size and importance.

Scent Marks Should Prevent Intrusions

Lledo-Ferrer *et al.* argued that “the large overlap between territories shows that scent marks are not effective in maintaining spatial exclusivity and preventing intrusions” (p. 985), and that this provides evidence against a link between scent-marking and territorial defense.

The first point to make here is that, by focusing on overlap in space use between neighboring territorial groups, Lledo-Ferrer *et al.* appear to disregard the fact that most of the range is nonoverlapping. By subtracting the size of the overlap area from the total range size reported in Table 3 of Lledo-Ferrer *et al.*, one can see that between 50 % and 79 % of the area of the three tamarin ranges were used exclusively by the territorial group. Presumably there are desirable resources here that could be used by other conspecifics if they had the opportunity. By definition, then, this means that in most of their range, intruders appear to have been prevented access to these areas. In other words, for approximately two-thirds of the territory (on average), this prediction is upheld.

The second point is that, perhaps more importantly, the prediction itself is made on shaky theoretical ground. The idea that scent marks should ensure absolute territorial exclusivity (on which this prediction is based) is a long-standing misconception about scent-marking. It arises from early proposals about the function of scent-marking (Hediger 1949). Thirty years ago, Gosling (1982) pointed out that this proposal is not supported by observations and instead presented a more realistic paradigm for understanding scent-marking mechanism and function based on evolutionary game theory. As he recognized, scent marks do not always (or even often) ensure exclusivity, and neighbors/intruders may continue to intrude after detecting a scent mark. This is not because scent-marking has failed in its territorial function, nor does it imply that scent-marking is not involved in territorial defense. Rather, this can occur because the benefits of intruding, e.g., seeking food, mates, outweigh the costs of

retreating, at least until the owner is encountered. Scent-matching, proposed by Gosling (1982), enables an informed decision by intruders about the relative costs and benefits of escalating or withdrawing from an encounter with a territory owner or territorial group; e.g., if the odor of a competitor matches the odor contained in a recently detected scent mark, the competitor is likely to be the territory owner and will probably escalate and defend the territory vigorously. A detailed description of the possible decisions that face territorial intruders on encountering scent marks and putative territory holders, based on this cost–benefit analysis, can be found in Gosling and Roberts (2001a). On the other side, territory owners benefit by reducing the frequency of escalated encounters, as a result of scent-matching, thereby reducing costs of territorial defense. With regard to this prediction, the critical point is that the way these costs and benefits play out means that intrusions do not always have to be prevented for scent-marking to function in territorial defense.

Scent Marks Should Ensure Access to Feeding Resources

Lledo-Ferrer *et al.* suggested that, because feeding trees (which are often scent marked, particularly in overlap areas) were shared in 7/53 intergroup encounters, a resource-defense strategy appears not to be effective (p. 985).

As previously, the data used to support this argument can be inverted to paint a very different picture. Although feeding trees in overlap areas were sometimes shared during encounters, food-sharing did not occur in *ca.* 87 % of encounters. Because the trees in which these encounters occur are scent marked more frequently and intensively than trees elsewhere, the weight of presented evidence is in favor of the suggestion that scent-marking has helped to defend resources in the overlap area rather than the suggestion that it has failed to do so. Further, although trees in overlap areas are sometimes used by non-owners, these trees are, by definition, not in the exclusive area (which forms the majority of the territory; see prediction 1), where scent marks may well have played a further role in ensuring exclusive access.

Territorial species often scent-mark preferentially on food trees or plants (for discussion of possible reasons, see Roberts 1997). Even if scent marks are placed randomly across time spent within a particular part of the territory, this could arise simply as a direct function of the amount of time spent in or near particular tree species. Alternatively, it could arise from investment in defense of specific resources or as a means of maximizing the probability of detection by intruders (Gosling 1981; Roberts and Lowen 1997) if intruders spend time feeding on the territory. The observations, recorded by Lledo-Ferrer *et al.*, of tamarins marking fruits of *Wettinia* without consuming them, is consistent with these latter two suggestions.

Scent Marks Should Enable Avoidance of Intergroup Encounters

Lledo-Ferrer *et al.* suggested that, because intergroup encounters occur more often than predicted by a random-walk model, groups do not avoid confrontation and therefore scent-marking does not reduce the frequency of these encounters.

As for prediction 1, the theoretical basis for this prediction is on shaky ground. There may indeed be circumstances in which intruders do withdraw on meeting a scent mark, e.g., if they are of low quality, if the freshness of the mark indicates the

owner is nearby, if costs of escalated encounters are very high, thus reducing the rate of encounters. However, as described previously (see prediction 1), the prevailing view of scent-marking over the previous 30 yr or more is that scent marks provide a means of assessment that is complete only after both detecting a scent mark and comparing this scent with putative signalers (Gosling 1990; Gosling and Roberts 2001a). There is thus no reason to expect that scent marks should necessarily reduce the rate of intergroup encounters, and the comparison of expected and observed rates of intergroup encounters is thus a weak test with which to refute a territorial function for scent-marking.

In any case, the authors excluded and disregarded encounters with single individuals. They did so “because these interactions were extremely brief and aggressive, with the intruder fleeing immediately” (p. 978). This is exactly the kind of response to be expected in encounters in which a clear asymmetry has been established by prior detection of scent marks by the intruder (see the cost–benefit analysis referred to in prediction 1). By analyzing only encounters with neighboring groups, which they describe elsewhere as dear enemies and whose interests lie not in threatening territory ownership but, at best, by extending their boundary by a few meters, a key reduction in territorial defense costs has been overlooked.

Scent Marks Should Play an Important Role in the Aggressive Encounters between Groups

Lledo-Ferrer *et al.* tested the scent-marking frequency and frequency of olfactory inspections during encounters against two comparators: the same frequencies for the same group (a) 24 h after an intergroup encounter and (b) in the same area in the absence of another group. Further, they also compared the frequencies of scent-marking behaviors (c) in overlap areas compared to exclusive areas and (d) in overlap areas where encounters occurred vs. overlap areas where encounters did not occur.

Their conclusion that prediction 4 is not supported is based purely on the absence of a significant difference in comparison (b). However, they appear to disregard comparison (a), even though they find that both frequencies of scent-marking and olfactory inspections are significantly higher during an intergroup encounter than 24 h later, which upholds the prediction. Perhaps this is partly because they have confused their own Fig. 4 with Fig. 5 (because on p. 984 they refer the reader to Fig. 4b when discussing results shown in Fig. 5). In so doing, they appear to have missed the critical result actually shown in Fig. 4b that shows the significantly higher inspection frequency of scent marks during encounters compared with 24 h later. This is unfortunate because it provides evidence to uphold the prediction that they then refute. Instead, they focus on a result that is not statistically significant, which shows a lower proportion of inspection of own-group marks during encounters (their Fig. 5); even if there was a difference here, it would be unsurprising for any hypothesis involving intergroup communication.

Further, they also appear to disregard both predictions (c) and (d), which shows that marking effort is concentrated in areas where encounters occur. Thus, contrary to Lledo-Ferrer *et al.*, an objective conclusion from these four analyses is one of general support for the prediction, or at worst, that the evidence is mixed.

With regard to prediction (b), which was not supported, it is difficult to assess the utility of this analysis in the absence of information about how the sampling period for comparison was selected (other than controlling for time of day). The data could have been collected a significant period before or after the encounter, introducing the possibility of a number of confounds such as seasonal differences, current food abundance in the vicinity, and so on.

Although I agree that the prediction was a reasonable and potentially instructive one, it is perhaps premature to refute it even if comparison (b) was considered to be critical, because these tests are insufficient on their own. First, during an encounter, it is likely that vigilance, monitoring of the other group, vocalizing, and chasing or being chased will often be prioritized over scent-marking. Second, a more illuminating comparison involving rates of scent-marking would be in the periods immediately before and after an encounter. Territory owners often vigorously reassert their scent marks in the immediate aftermath of an encounter (Brashares and Arcese 1999). Third, the rate of scent-marking and olfactory inspections during a given encounter will vary according to whether the observed individuals are in the role of residents or intruders, i.e., it will depend on where they are in the overlap zone and how far they are from their exclusive area. Finally, one should remember that the outcome of an aggressive encounter, i.e., the decision about whether to escalate or withdraw, may well be based on previous experience with scent marks, but these are not accounted for or tested in this analysis.

Scent Marks Should Be Concentrated in Peripheral Areas (Border-Marking Strategy)

Lledo-Ferrer *et al.* predicted that marks should be concentrated in peripheral areas, in other words, pursuing a border-marking strategy. This is in fact what they found. Although this evidence is thus in support of their prediction, they instead attribute this as evidence in favor of their alternative functional interpretation (which I discuss later).

It is perhaps worth noting here, however, that the absence of this pattern alone would not have been sufficient evidence to reject the link between scent-marking and territoriality. Although they may reflect likely fitness benefits accruing to the signaler, spatial patterns of scent marks are dependent on many influences, both social and environmental, and should not be considered in isolation when attributing territorial function (for a discussion on this issue, see Gosling and Roberts 2001b).

Scent Marks Should Be Concentrated at the Boundary if Resources Are Homogeneously Distributed, Or, if Resources Are Heterogeneously Distributed, They Should Be Associated with the Resource and Related to Their Size and Importance

Lledo-Ferrer *et al.* based this prediction on Gosling and Roberts (2001b). They paraphrased the argument proposed by Gosling and Roberts in this way (p. 976): “the spatial pattern of scent marking should be determined by the distribution of resources in the territory.” Unfortunately, this is a misrepresentation of what Gosling and Roberts argued. Gosling and Roberts did indeed suggest that, *all other things being equal*, perimeter marking will tend to occur more frequently where resources are homogeneous, but their main point was that spatial patterns do *not* necessarily

point to any specific function and that more important considerations include the distribution of competitors and where aggressive encounters take place.

Nonetheless, Lledo-Ferrer *et al.* concluded that resources are roughly equally abundant in overlap and exclusive areas, which they take to mean homogeneously distributed. They also showed that scent marks are concentrated at the boundary. Thus, according to the data presented, the prediction is upheld.

Despite this, they argued against it. They stated (p. 985) that because resources are homogeneously distributed, the boundary marking strategy should be sufficient for territorial defense "...with no need for direct, additional marking close to the resource" (the resource being feeding trees). This seems a curious conclusion because a pattern of marking that maximizes the probability of detection by receivers by exploiting *both* spatial positioning and the particular defended resource is exactly what one would predict for any functional interpretation of scent-marking communication. Indeed, the argument of Lledo-Ferrer *et al.* here is internally inconsistent with discussion of their alternative hypothesis, in which they state (p. 987) that "tamarins might then be optimizing signal transmission by marking where the probability of perception by other groups is higher."

Summary of Tests

As I have outlined, Lledo-Ferrer *et al.* reject the hypothesis that scent-marking functions in territorial defense in saddleback tamarins. This is despite two predictions being upheld (predictions 5 and 6), one being mostly upheld (prediction 4) and two that are at least arguably upheld (predictions 1 and 2), while the final prediction (3) is inconsistent with the prevailing view of scent-marking function and mechanism, and in any case might have been upheld if Lledo-Ferrer *et al.* had not discarded an entire class of aggressive encounter.

On the basis of these arguments, I suggest that the decision to discard a link between scent-marking and territorial defense is premature at best, and probably incorrect. Tamarins are territorial and defend their territories aggressively. Scent marks are positioned more in the overlap zones, where these aggressive encounters occur, compared with in the exclusive areas of the territory where they do not. Within overlap areas, marking occurs more frequently where aggressive encounters occur than where they do not. Scent-marking frequency and frequency of olfactory inspections are both significantly higher during intergroup encounters than in the same group at the same time the next day. Further, the facts that there is an exclusive area and that single intruders immediately withdraw are indicative that these strategies appear to be successful in ensuring exclusive use of territorial resources.

However, we should of course consider alternative possibilities in light of new evidence, so let us turn now to their alternative interpretation of the data.

Scent-Marking to Advertise Reproductive Opportunity

Lledo-Ferrer *et al.* argued (p. 974) that "...instead of defending a territory in the classic sense, the tamarins are optimizing signal transmission by depositing their scents where the probability of detection by neighbours is higher. Saddleback

tamarins may use shared areas of their home ranges to exchange information with neighbouring groups, perhaps regarding reproductive opportunities.”

The first thing to say about this statement is that, until the last phrase, this is in no sense incompatible with a territorial defense function. As we have already seen, including in two of the authors' own predictions, scent-marking for effective territorial defense would also involve positioning scents so as to maximize the chance of detection. Further, scent-marking as territorial defense involves information exchange, as does any signal, by definition. Thus the single distinction that is being proposed is that scent marks may be functioning to advertise reproductive opportunity. The authors do not present evidence about this, but they refer to unpublished data on the high frequency of extrapair copulations. The question that is relevant here is whether or not scent-marking behavior is involved in providing opportunities for extrapair copulations and whether it is better explained by this interpretation than with a role in resource-defense territoriality.

Undoubtedly much of the evidence is consistent with this interpretation. Scent marks are placed predominantly in peripheral areas, in those areas where intergroup encounters occur at higher frequency, on food trees where they are more likely to be detected, and on fruits that are then not consumed. Scent marks are placed more frequently during encounters than 24 h later, and more in overlap areas in which encounters occur than in those where they do not. Further, the existence of sex-specific, spatially dependent scent-marking strategies suggests that scent-marking behavior may reflect different interests of males and females, perhaps with regard to reproductive opportunities. Males scent-mark more frequently in the overlap areas, and females more frequently in the exclusive areas (the reverse is true for scent-marking intensity). Unfortunately, the biological importance of the distinction between frequency of scent-marking events and scent-marking intensity (the latter relates to the number of scent-marking acts per event: p. 978) is not fully understood, but the authors suggest that copulation frequency may be related to the former in males and the latter in females.

Thus, this could be an interesting proposal and it raises some further questions that would be worthy of further investigation. Before I discuss these, however, I think it is worth making two general points. First, the idea that scent marks might signal reproductive condition, and be used by potential mates as a means of assessment, certainly features in the recent scent-marking literature (Rich and Hurst 1998, 1999; Roberts and Gosling 2003, 2004). However, in view of the apparently obligate link between territoriality and scent-marking, Gosling and Roberts (2001a) argue that it is likely that the use of scent marks to assess mate quality is a secondarily derived benefit of the use of scent marks. Thus, they describe this as eavesdropping on the preexisting competitive interactions between scent-marking individuals; indeed, this is the theoretical basis of several experiments in this area (Rich and Hurst 1998, 1999; Roberts and Gosling 2003, 2004).

Second, in a similar vein, it is worth considering the distinction between signals and cues (Maynard Smith and Harper 2003). It is well known that different kinds of information can occur in the same signal, particularly in olfactory signals, which are usually extremely complex chemical signatures containing both fixed, i.e., likely to

be genetically determined, and variable elements, i.e., likely to be environmentally influenced. For example, scent marks of mice contain information about several aspects of social or reproductive status (Novotny *et al.* 1990; Schwende and Novotny 1982), as well as of genetic quality and of genetic compatibility, and the importance of these in mate choice decision making varies according to social context (Roberts and Gosling 2003). Similar variation in olfactorily transmitted information is used in mate choice by ring-tailed lemurs (*Lemur catta*: Charpentier *et al.* 2010), and in mandrills (*Mandrillus sphinx*: Setchell *et al.* 2011). However, it is likely that at least some of this information may be a cue rather than a signal. To take a clear example, the presence of pathogen infection is detectable in odor and can lead to reduced attraction in mate choice contexts (Kavaliers and Colwell 1995). Although it is detectable in a signal (mouse urine marks), this information is a cue, because it is not part of the signal shaped by selection. In a similar way, and although here the cue would provide supplementary benefits rather than a cost, it is possible that cues of reproductive condition are present and informative to receivers, but are not part of the underlying territorial signal.

Thus, neither theory nor empirical findings are inconsistent with scent marks carrying multiple forms of information that may be used in assessment. In rejecting a territorial function, Lledo-Ferrer *et al.* appear to miss this possibility. However, if we allow for the possibility that the main function of scent-marking in tamarins lies in exploring reproductive opportunities and achieving extragroup copulations, as Lledo-Ferrer *et al.* argue, questions for further research would include the following.

1) Is mate advertisement less subject to signaling constraints than territorial defense?

In arguing against a territorial role, Lledo-Ferrer *et al.* argue that “scent marking is not a very effective communication channel owing to its poor directionality and slow transmission speed. It is thus not well suited for intergroup encounters in callitrichids...” (p. 987). Despite this, their alternative hypothesis is also centered on intergroup communication. Thus, if these properties are less important for communication of mating opportunity, it would be interesting to know how and why this is the case.

2) Do sex differences in scent-marking exclude a territorial function?

This is an interesting question, because if they cannot, this would be a critical observation that would distinguish between the two hypotheses. In tamarins, males overmark female scent marks and vice versa, and Lledo-Ferrer *et al.* argue that this might conceal information from potential competitors instead of ensuring predominance for scent matching (citing Roberts and Dunbar 2000; although in fact these authors argued the opposite). However, regardless of whether overmarking masks underlying scent marks or not, sex-specific variability in scent-marking behavior has been observed in monogamous and territorial species in which doubt has not been raised as to a fundamental link between scent-marking and territoriality (Brotherton and Manser 1997; Roberts and Dunbar 2000; Rosell and Thomsen 2006). Rather, these differences in marking behavior arise from the specific constraints on reproductive success experienced by either sex, even where it has heavily overlapping interest in the reproductive success of the other. Thus female dispersion and territorial behavior may place constraints on male

behavior, leading to the evolution of monogamy in these species, even though they both defend a shared territory.

There are some similarities between the constraints among monogamous antelopes or beavers and polyandrous callitrichids, so it seems possible that similar adaptive explanations for territorial signaling could be made. To test this, it would be necessary to investigate further the differences between patterns of scent-marking behavior of dominant breeders and nonreproductive helpers of either sex.

3) Why do tamarins scent-mark in exclusive areas?

If the function of scent-marking is solely to exchange information about reproductive condition with nongroup members, it could be argued that all scent marks should be placed at the boundaries and that there is no reason to expect marks to be placed in exclusive areas at all. In contrast, marking in the exclusive area is consistent with the resource-defense argument for two reasons. First, resources are spread across the whole territory, not just at the boundary. Second, intruders (perhaps especially single, nonterritorial intruders) do not always withdraw on meeting a scent mark, but usually delay this decision until after encountering the owner, by which time they could be a significant distance onto the territory.

4) What is the relationship between scent-marking and extragroup copulations?

Lledo-Ferrer *et al.* find that aspects of scent-marking correlate with the frequency of copulations in both sexes. This is to be expected if scent-marking correlates with social status, as it is in many species (Gosling and Roberts 2001a). What is critical to their hypothesis is whether scent-marking behavior leads directly to coordination of extragroup copulations, although they present no direct evidence for this.

Lledo-Ferrer *et al.* refute their second prediction concerning the function of scent-marking in territoriality because in 13 % of cases the observations were not consistent with the prediction. If one was to apply the same degree of stringency in determining whether a prediction was upheld, we might insist that more than 87 % of encounters must result in an extragroup copulation for a link between scent-marking and reproductive advertisement to be supported. However, such stringency would I think miss much of the subtlety and nuances of animal behavior to which we are not privy as observers.

Perhaps a better approach would be to examine associations between inter-individual variability in scent-marking behavior and the relative costs and benefits of seeking extragroup copulations. Lledo-Ferrer *et al.* imply that lower-ranking individuals within groups might be most motivated to seek extragroup copulations, as reproductive constraints imposed upon them are so high. If so, this would predict a negative relationship between scent-marking frequencies and dominance rank, as, indeed, has been found in common marmosets (*Callithrix jacchus*) during intergroup encounters (Lazaro-Perea *et al.* 1999). This would be a particularly interesting prediction to test, although it would still remain possible that increased marking by subordinates could be one way in which they help contribute to defense of the group territory, relieving the burden placed on reproductively dominant group members (Desjardins *et al.* 2008; Hoogland 1981; Lazaro-Perea 2001).

Conclusions

Lledo-Ferrer *et al.* present very interesting data on scent-marking behavior in wild tamarins. Although they conclude that the evidence does not support a link between scent-marking and territorial defense, I believe this conclusion to be unwarranted. None of the data they present are inconsistent with such a function. On the contrary, five of their six predictions arising from this function are fully or partially confirmed, and where the data appear not to support a prediction based on this function (prediction 3), the prediction itself does not reflect current views of scent-marking mechanisms and might be upheld if a key class of encounter was not discarded.

Further, one has to remember that tamarins are territorial, irrespective of the debate about the function of scent-marking, and most of the encounters observed by Lledo-Ferrer *et al.* were aggressive. Given the link between aggression and scent-marking across a diverse range of taxa, including other arboreal primates, a similar link in tamarins would be phylogenetically parsimonious.

I do agree that the alternative proposal of Lledo-Ferrer, that scent-marking serves to signal reproductive potential and availability, is also consistent with much of the data presented. It might therefore be the case that scent marks inform receivers about both competitive ability and reproductive condition, as has been demonstrated, e.g., in mice. Before we accept this proposal, however, the onus lies with researchers to test specific predictions arising from this idea. I have outlined some possibilities. As is evident from the preceding discussion, the difficulty that arises is that the two ideas often generate similar predictions, so the task is to identify critical tests that can distinguish between them. Ultimately, however, one has to bear in mind that resource-defense territoriality is not simply about defending resources; it is a means to an end, the end being the acquisition of mates or mating opportunities (Emlen and Oring 1977). Thus, even in a territorial species and a system in which scent-marking serves to defend the territory, we should not be surprised to see sensitivity to mating opportunities when they arise.

Finally, future investigation would be particularly likely to benefit from experimental approaches. For example, studies using acoustic playbacks of vocalisations that investigate sex-specific and area-specific responses by animals of known social status are valuable in identifying underlying social structure, particularly where intergroup encounters occur infrequently (Mitani 1987; Raemaekers and Raemaekers 1985). Some researchers have used olfactory “playbacks,” in which scent marks are collected and then repositioned by the experimenter, to test various ideas, commonly in the laboratory (Gosling and McKay 1990; Rich and Hurst 1999; Roberts *et al.* 2001) but also in seminatural or natural conditions (Roberts 1998; Rosell *et al.* 2000; Sliwa and Richardson 1998) with some success.

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