

TERRITORY MARKING IN GERBILS: VERIFICATION OF GOSLING'S HYPOTHESIS

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Most mammals have a highly developed olfactory sense that they employ in social communication using chemical signals originating in urine, faeces, or scent glands. Many use specific action patterns to deposit the chemical signals on environmental objects. Such behaviour is referred to scent marking or territory marking.

After Hediger, territory marking has been considered as a means to deter potential intruders: by marking their territories, animals stop intruders from entering the area or cause their withdrawal. Marks are thus functionally equivalent to aggressive behaviour. This hypothesis received little support from observations of wild animals. Some researchers suggest territory marking as a means to acquire and maintain the individual or group home range. For description of this function, they use the term "familiarization" meaning that the saturation of the resident territory with its own scent serves to make the area more familiar and, perhaps, to enhance the confidence of territory owners and intimidate intruders. Most importantly, deposition of odoriferous secretions is a part of a system of olfactory communication. Scent marks are thought to identify species, individuals and group members and to communicate social and reproductive status. Thus, the functions of scent marking are still a matter of debate.

Gosling suggested a new functional interpretation of territory marking. In accordance with his hypothesis, the function of territory marking is to provide an olfactory association between the resident and the defended area that allows intruders to identify the resident when they meet and thus reduce the frequency of agonistic encounters. 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 vicinity. When these scents match then the resident is identified, and the intruder responds appropriately. The number of marks encountered by an intruder is probably important since this could indicate the duration of residence. This so called "scent matching" hypothesis predicts the behaviour of a territory owner that should: (1) mark the territory in a way that maximizes the chance that marks will be detected by an intruder (e.g. marks should be placed along trails and boundaries), (2) mark itself with the substances used to mark the territory (so called "self-anointing"), (3) make itself available for scent matching by the intruder, (4) remove or replace marks in the territory that do not match its own odour.

The main goal of this report is to compare predictions of the Gosling's hypothesis with the marking behaviour of three gerbils' species, in that number fat sand rat, *Psammomys obesus*, Midday gerbil, *Meriones meridianus*, and Mongolian gerbil, *Meriones ungiculatus*. These species were observed both in nature and large open enclosures of 400 sq. m. in size. Fat sand rats are known to be essentially solitary: adult individuals occupy separate and partly protected home ranges without distinct boundaries. Midday gerbil is a gregarious species which forms breeding colonies, but all members of the colony live individually occupying overlapped and unprotected home ranges. Mongolian gerbil lives in

family groups: every group consists of one adult male defending a territory that encompasses one or two protected ranges of adult fe-males with their offspring.

To mark home range or territory, gerbils use the secretion of the ventral gland, urine, and feces. Most frequently, gerbils mark objects in their environment by rubbing with the ventral gland. The second and also very common kind of the territory marking is to make small heaps of ground (commonly of sand) with fecal pellets and urine drops inside (so-called "signal heaps"). Marking activity of gerbils is found to be sexually di-morphic: both sexes usually mark but males do so more frequently. Territory marking is characteristic of not only adult but also young individuals which marking activity is much lower than that one of adults. Besides, marking activity shows a distinct seasonal variation with peak in spring and early summer and depression in autumn and winter.

Analysis of the spatial distribution of scent marks revealed that females marked mainly core area of their home ranges but not trails or boundaries. Only females of Mongolian gerbil were found to place some marks near the boundary between neighbouring territories, especially after agonistic encounters, as did males of this species too. Males of fat sand rat and of Mongolian gerbil commonly marked the core areas of fe-males and placed their marks mainly over the female marks. Males of Midday gerbil occupying overlapped and unprotected ranges compete for females in aggressive encounters, so dominance hierarchy exists between them. The dominant and subdominant males were found to mark regularly the female ranges, and often replaced the marks of the opponent. In contrast, the subordinate males rarely marked the female ranges and commonly did not place their marks over marks of the dominant and subdominant males.

Females of any gerbil species and males of the fat sand rat usually avoid entering marked areas of same-sexed conspecifics. Such behaviour seems to be consistent with Gosling's hypothesis. But the spatial distribution of scent marks and the marking behaviour of males in Midday and Mongolian gerbils are not entirely consistent with the predictions of "scent matching" hypothesis. As for specific "self-anointing", it is difficult to find such behaviour in gerbils, except so-called sandbathing. But every sandbathing site accumulates odour of many individuals and thus the resident gains a smell of several conspecifics, so it does not assist scent matching. The only gerbil behaviour that is completely consistent with Gosling's hypothesis is over-marking: by this way, the territory owner replaces the marks that do not match its own odour.

Our study shows that young gerbils begin to mark the area for the first time at the age of 1-1.5 month being not sexually matured, and the first marks were "signal heaps" but not deposition of the ventral gland secretion. Young individuals couldn't be considered resource holders (a term used for males monopolizing resources that limit reproduction, e.g. a territory or a group of females), and thus they can not advertise their status to competitors. Therefore, Gosling's hypothesis does not explain motivation of territory marking of young individuals.

It is well known that scent marking occurs as a response to novelty. Our experiments with Mongolian and Midday gerbils in enclosures showed that a marked rise of the marking activity was observed when new object were placed or some part of the ground was removed in the vicinity of burrows or trails. We also revealed that the marking activity of both young and adult Mongolian gerbils occupying a defended territory was as much as 8-10 times higher than that one of the individuals not possessing own home range or lost it as a result of agonistic encounters. All our findings seem to be more consistent with "familiarization" hypothesis that of cause does not exclude the "scent matching" function of the territory marking.

Thus, I suggest that the main function of scent marking is familiarization of the home range or territory to make the area more familiar and, perhaps, to enhance self-confidence of the territory owners. By this way, every female monopolizes its home range, especially core area, and males in turn monopolize rather females than some areas, in accordance with spacing and reproduction strategies of different sexes. Another, also very important function of territory marking is to provide conspecifics with information about sex, age, reproductive and social status of the resident. As a consequence of this function, the territory marks attract and stimulate mates.

Scent marks originating from different sources may have different effects and thus fulfil different functions. In gerbils, ventral gland secretion seems to be used for individual recognition only and serves as an effective means for marking of burrows, tunnels and some environmental objects. "Signal heaps" with urine are more evident as visual and olfactory landmarks conveying complex information for olfactory communication. Marking activity could be considered a specific feedback response to particular level of external stimulation: lack or insufficient number of own fresh marks stimulates the resident's marking activity, and appearance of an intruder marks within the resident home range has the same effect. Gerbils are usually undeterred by scent marks in an area but can avoid escalation of agonistic encounters by matching the odour of the resident with the odour of its scent marks. Such avoidance is usually characteristic of females but not males of many gerbil species.

In conclusion, I'd like to add that it is new information obtained due to observations of different rodent species both in nature and large open enclosures that allow us to reassess and supplement our knowledge concerning the territory marking.