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Scent-deposition Behaviour in Alpine Marmots (*Marmota marmota* L.): its Role in Territorial Defence and Social Communication

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Abstract

Scent-deposition was investigated in *Marmota marmota* L. at Gran Paradiso National Park. 448 h of focal and scan sampling were performed on 22 marmots in four subsequent years. Results show that: (1) 97.4 % of the scent-deposition is done within 25 m of the edge of the territories or of the main burrows ($\chi^2 = 100.4$, df 9, $p < 0.001$); (2) being a reproducing adult is the most prominent factor in scent-deposition ($\chi^2 = 32.4$, df = 18, $p < 0.002$). The role of factors affecting scent-deposition in territorial defence and social communication is discussed.

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Introduction

Olfaction is an important communication channel in both solitary and social mammalian species (JOHNSON 1973; THIESSEN & RICE 1976; SHOREY 1977). Due to its low fading (WILSON 1968), individual characteristics and motivational states of the senders can be detected immediately during the olfactory inspection (RALLS 1971; EBLING 1981) or later, in absence of the emitter of the signal. This fact makes olfactory communication an economical channel for marking limited resources such as territories, sexual partners or food (JOLLY 1966; PETERS & MECH 1975, 1978; EISENBERG & KLEIMAN 1977; MACDONALD 1979; CLAPPERTON et al. 1988; CLAPPERTON 1989). It has been pointed out that deferred communication allows matching across time of the individual and the scent-marked resource, in particular territory, thus reducing the frequency of escalated agonistic encounters among high-quality animals (GOSLING 1982).

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Scent-deposition also serves social olfactory communication in many species of rodents (BUGLASS et al. 1994; EVSIKOV et al. 1994; WERNER 1994). Among the ground-dwelling sciurids, scent glands, in particular oral, cheek and anal glands, are ubiquitous, and it has been reported that odour exchange carries information about sexual, individual, and group identity, motivational state and environmental parameters (STEINER 1974; HARRIS & MURIE 1982; HALPIN 1984). In the yellow-bellied marmot (*M. flaviventris*) (ARMITAGE 1962, 1976), and in the Olympic marmot (*M. olympus*) (BARASH 1973, 1989), scent-deposition and the related displays seem to convey information about social dominance, aggression, and/or social excitement; the Vancouver marmot (*M. vancouvrensis*) is the only North American species where scent-deposition was reported to mark territories, with the adult males being the most prominent scent markers (BARASH 1989). In the alpine marmot, scent-deposition, in particular by means of cheek or anal glands, was hypothesized to serve the purpose of territorialism by many authors. (BOPP 1954, 1956, 1958; MÜLLER-USING 1956; KOENIG 1957; MÜNCH 1958; LATTMAN 1973; LENTI BOERO 1991a,b; but see BARASH 1976), particularly during the mating season in springtime (ZELENKA 1965). However, few quantitative data were presented to support this hypothesis. In this paper the role of scent-deposition of the alpine marmot in resource defence and social communication is investigated.

Methods

The Species

The alpine marmot is a high-altitude hibernator that lives in social groups consisting of a monogamous pair and offspring (BOPP 1954, 1956, 1958; ZELENKA 1965; LATTMAN 1973; LENTI BOERO 1987, 1989, 1991a; MANN & JANEAU 1988; ARNOLD 1990a,b, 1993; PERRIN et al. 1993; but see BARASH 1976). The limiting resource is the hibernating burrow (LENTI BOERO 1988) and social hibernation is a prominent behavioural trait (ARNOLD 1990a,b, 1992). Daily activities mainly consist in foraging and spotting and/or sunning at main burrows or specific spotting points widespread on the territories, with a main function of territory control (ZELENKA 1965; LENTI 1983; LENTI BOERO 1987, 1994a). Three different behaviours related to scent-deposition were discriminated. (1) Cheek rubbing: an animal approaches a log or a rock and rubs its cheeks once or twice alternatively against it, starting from the anterior part of the muzzle (MÜLLER-USING 1956; KOENIG 1957; MÜNCH 1958; ZELENKA 1965). (2) Paw rubbing: the animal rapidly rubs its foreleg on the ground for a few seconds, without removing grass or soil. ZELENKA (1965) hypothesized that this pattern was involved in the removal of conspecifics' scent traces, because it frequently precedes cheek rubbing. In the present study paw rubbing was considered as a scent-deposition pattern for itself because: (a) it was exhibited separately from or *after* cheek rubbing on the same olfactory spots; (b) during trapping and sedation procedures, sweaty paws were frequently observed (LENTI BOERO, pers. obs.), suggesting the existence of exocrine sweat glands in the alpine marmots. Pedal exocrine glands have been described in Mongolian marmot (*Marmota sibirica*) (AD'IA 1993) and in Columbian ground squirrel (*Spermophilus columbianus*) (KIVETT 1978), and in many other rodents (COLLINS et al. 1994; PETRULIS & JOHNSTON 1994; VASILIEVA 1994). (3) Stiff tail posture: while walking, the marmot abruptly stops and sits on the grass on its hind legs, while forelegs are completely extended. The tail is stiff and parallel to the back of the animal and gently waved forward and backward or from left to right, or the anal region is rubbed (BOPP 1954; MÜNCH 1958; COUTURIER 1964). This behaviour is conspicuous and may last for more than 1 min. Three glands, located in the distal portion of the anus, may be involved (LATTMAN 1973; GRIMOND et al. 1991). Those glands are easily extruded by holding the tail up in the anaesthetized animal (LENTI BOERO unpubl. data). In the woodchuk the secretions of anal glands were found to inhibit the activity of conspecifics (BARASH 1989). In the alpine marmot, BOPP (1954) found anal gland secretions near logs in different study colonies. Observing at a distance, I could not see the deposition of secretions, but frequently saw the deposition of other odorous substances, composed of both high- and low-volatility chemicals, such as faeces on the ground. In alpine marmots the possibility of urine scent deposition associated with chemosignalling, as happens in mice, rats and humans (EGGERT et al. 1994; LUSZYC et al. 1994; MUCIGNAT CARETTA et al. 1994), needs further exploration.

Study Area and Turnover of Social Groups

Data were collected from 1985 to 1988 during the months of Jul., Aug. and early Sep. The study area was located at 2300 m, above the timberline in a small valley branching from the main Cogne Valley at the Gran Paradiso National Park, Valle d'Aosta, Italy. The area was crossed by a stream and ended on one side in a projecting rock. A small talus was present and vegetation consisted mostly of alpine meadow and rhododendron (*Rhododendron ferrugineum*). For further details see LENTI (1985) and LENTI BOERO (1992a,c). To determine space use and scent-deposition sites, the entire area was subdivided in a grid of 114 squares of 25 m on each side. Each square was denoted by a letter and a number and the whole matrix was superimposed on a photograph of the study area as suggested by BARASH (1973). The surface covered by the grid measured 7.6 ha. During the study the area supported three distinct home ranges, covering 9 ha: Tanab, FamGia and FamGenz (LENTI BOERO 1991c). In 1988 the social groups inhabiting the Tanab and FamGia home ranges were completely replaced by two pairs immigrating from outside the colony. Individual data for animals living in FamGenz home range were available only from 1987, because animals were successfully trapped only from that year. However, some animals in the group were recognized by their natural markings since 1986, thus showing that FamGenz was inhabited by the same family group since 1986. A total of five different social groups was observed during the entire study (further details, LENTI BOERO 1991c, 1994b).

Subjects and Collection of Data

A total of 22 adult and subadult marmots and 13 newborns were live trapped and marked for individual recognition. Adopting a conservative view, as suggested by ARNOLD (1993), nine of these adults were probably related to their offspring, 12 adults and subadults were of unknown relatedness because they were trapped within a social group after reaching adult body size, and only one satellite male was certainly unrelated because he was born and trapped in a distant area 3 yr before his arrival in the study colony (LENTI BOERO 1991c). In addition, 12 unmarked animals of unknown relatedness and age and 5 newborns were observed. Observational data were collected by means of focal animal sampling (ALTMANN 1974) lasting 15 min for each animal sampled at random. The observer noted the presence of conspecifics in the surroundings. In all, 221 h of direct observation, concentrated in the early morning (0600–1100 h) and late afternoon (1700–2000 h) were performed. The observer sat in an inconspicuous place with 10 × 40 binoculars or a 30 × 60 telescope. Observations were recorded on a portable tape recorder and later transcribed. When a scent-deposition episode was performed by an animal, the specific square of its occurrence was verbally recorded on the tape and mapped on the photograph of the area. Additional information on scent-deposition patterns and about space use of each family group was gathered on selected days by means of 1302 scan samples, lasting 10 min each. During this time the colony was thoroughly scanned and the position and activity of any identified animal was marked on the photograph map; consequently foraging ranges and preferred spotting points were determined. The total amount of time spent in scanning was 217 h (LENTI BOERO 1991b, 1994a).

Data Analysis

Data were analysed with the GLIM 3.77 package designed for fitting generalized linear models. The object of statistical modelling is to present a simplified or smoothed representation of the underlying population. This is done by separating random variation from systematic features of the data, represented by a regression function involving parameters which can be simply related to the structure of the sample. Systematic features can be variates (numerical values) or factors, having two or more levels, and the package interactively calculates the scaled deviances and residual sum of squares for each variate, factor, or interaction among them, requested by the experimenter. Scaled deviances asymptotically approach a χ^2 distribution, which is utilized in probability testing (GILCHRIST 1984;

AITKIN et al. 1989). A further advantage of the GLIM 3.77 package is that it is possible to choose the distribution most suitable for representing the data.

The major problem in analysing the data from this sample was the disparity of time of observation for each individual, due to different time of permanence in the colony. Consequently, when individuals were included in age and sex class for data analysis, the total number of scent-deposition events observed was considered as primarily related to time of observation and successively to all other factors of interest, following the procedures suggested by AITKIN et al. (1989). In this way it was possible to disentangle the differences that had to be ascribed to time of observation, from the significant differences that had to be ascribed to all other factors or to interactions between them. A Poisson distribution was chosen when time of observation was considered and a binomial distribution was chosen for the analysis of binary data. For further details see LENTI BOERO (1993).

In addition, Friedman two-way ANOVA on behavioural patterns was performed with SYSTAT.

Results

Scent-deposition Patterns and Substratum

Postures related to scent-deposition were abruptly exhibited by walking or foraging marmots. No scent-deposition event was ever observed during sunning or spotting on the burrow, but scent traces might remain after digging or simply after staying for hours in the same place.

Territorial males patrolled the borders by walking along conspicuously and flagging the tail. During such visual display either paw or cheek rubbing was repeatedly exhibited many times. Patrolling the territory borders typically lasted more than 15 min, sometimes up to 1 hr, and was very informative about the boundaries of the area that the animals aimed to delimit. This display should be differentiated from common scent-deposition events because it was never interrupted by feeding.

Scent deposition was exhibited on horizontal substrata (meadow, ground) and/or vertical substrata (rocks, logs, bushes). Patterns seemed to be adopted according to the substratum (Table 1). Stiff tail posture (STP) and paw rubbing were the only patterns exclusively adopted on horizontal substrata; cheek rubbing was exhibited either on horizontal substrata or on vertical substrata, where it was always the chosen pattern. Cheek and paw rubbing were equally frequent ($\chi^2 = 3.7734$, df = 1, $0.10 > p > 0.05$), however, paw rubbing was preferred in scent-deposition on horizontal substrata ($\chi^2 = 39.054$, df = 1, $p < 0.001$). STP was the least common behaviour (8.5 % of all patterns observed). Adult reproducers preferably exhibited cheek rubbing ($F = 10.21$, df = 1, $p = 0.001$) or cheek and paw rubbing in combination ($F = 3.8$, df = 1, $p = 0.05$). No differences in pattern choice were found in non-reproducers.

Scent-deposition Behaviour in Time and Space

The same scent-deposition places, like a particular rock or log or specific areas on the meadow, were utilized by different individuals of a social group. Some stones and rocks polished by frequent use over years were identified in the colony (LENTI BOERO pers. obs.). The individuals recruited to the colony in 1988 deposited scent traces at almost the same spots as the previous residents. Of all scent-deposition, 97.35 % was spatially distributed within 25 m of the main

Table 1: Scent-deposition patterns and substrates (total no. of patterns observed = 283)

Substrates	Cheek and paw rubbing (% on different substrates)	Cheek rubbing (% on different substrates)	Paw rubbing (% on different substrates)	Stiff tail pattern (% on different substrates)
Horizontal[1]	91 (75.8)	34 (56.7)	79 (100)	24 (100)
Vertical[2]	0	26 (43.3)	0	0
Both	29 (24.2)	0	0	0

[1] Meadow, ground
[2] Rocks, logs, bushes

Table 2: Spatial distribution of scent-deposition by social group

Territory	Social group[1]	Total obs. h	No. and (%) of scent-depos. at burrows[2]	No. and (%) of scent depos. at boundaries[3]	No. and (%) of scent depos. at other sites
Tanab	Elioel	117	20 (18.7)	86 (80.3)	1 (1)
	Palli	11	11 (35.5)	19 (61.3)	1 (3.2)
Fam. Gia	Giacomo	41	1 (3.8)	26 (96.2)	0
	Fiorenzo	2	0	28 (100)	0
	Elidue	4	2 (14.3)	11 (78.6)	1 (7.1)
Fam. Genz	Michel	46	5 (25)	12 (60)	3 (15)
Total		221	39 (17.2)	182 (80.2)	6 (2.6)

[1] Each social group is named after the resident male
[2] Within 25 m of the main burrows
[3] Within 25 m of the boundary of the home range of the group

burrows or within 25 m of the boundaries of each family home range or on the overlapping zones (Table 2). Notwithstanding the fact that the periphery of each home range was the least utilized area (LENTI BOERO 1991b, 1994a), scent-deposition was more frequent on the squares of the grid near the boundaries ($\chi^2 = 100.4$, df = 9, $p < 0.001$) than in any other place, including burrows. No scent-deposition was ever observed at those boundaries abutting empty areas. Also, a difference among various social groups in different colonies was found ($\chi^2 = 22.69$, df = 9, $p < 0.0002$), due to a higher rate of scent-deposition among the new resident pairs (new resident adults without offspring vs. old resident adults with offspring: $\chi^2 = 26.05$, df = 11, $p < 0.006$).

Sex, Reproductive Status and Social Contexts in Scent Deposition

Scent-deposition behaviour was not sex biased across the summer ($\chi^2 = 3.75$, df = 18, ns) and was exhibited by animals in all age classes, except that no young-of-the-year was ever observed displaying a scent-deposition pattern during the whole study (Table 3). Reproducing adults of both sexes deposited scent traces more than any other age classes ($\chi^2 = 32.4$, df = 18, $p < 0.02$). Scent-deposition was exhibited with greater frequency in Jul. than in Aug. and early Sep. only by reproducing males (reproducing males vs. reproducing females, $\chi^2 = 133.77$, df = 9, $p < 0.0001$). No significant effect was found in seasonal trend when animals of all age and sex classes were considered ($\chi^2 = 49.43$, df = 39, ns). Scent deposition of both adult reproducers was not specifically affected by the presence or absence of a litter ($\chi^2 = 1$, df = 39, ns) and was not affected by the number of group components among related non-reproducers ($\chi^2 = 1.2$, df = 13, ns).

Scent-deposition Displays and Social Interactions

Reproducers and non-reproducers deposited scent traces more often when alone than when a conspecific was foraging in the same or an adjacent square of the grid ($\chi^2 = 26.7$, df = 1, $p < 0.0005$). Scent-deposition in connection with social interactions was equally distributed among animals belonging to the same or different groups ($\chi^2 = 4.16$, df = 1, ns).

Much scent-deposition in the presence of conspecifics was performed in front and in sight of other marmots watching the display or together with social interactions. Of the scent-deposition episodes performed in the presence of marmots from the same social group, 64 % were preceded or followed by close-contact amicable interactions such as sniffing different parts of the partner's body (LENTI BOERO 1987, 1992a) (Table 4). No scent-deposition was ever observed together with social grooming. Individuals belonging to different groups never engaged in amicable interactions related to scent-deposition. However, it must be considered that in the entire study inter-group amicable interactions were very rare (LENTI BOERO 1987, 1992a, unpubl. data). Of the scent-deposition episodes exhibited in the presence of marmots from different social groups, 29 % were performed together with agonistic interactions, such as chasing or biting. Scent deposition was more frequently preceded or followed by amicable interactions

Table 3: Scent-deposition episodes by sex and reproductive status

Subjects	No. of scent-deposition events per h Jul.	Aug.	All summer
Reproductive males (n = 3)	5.1	1.1	2.9
Reproductive females (n = 4)	1.9	1	1.4
Non-reproductive males (n = 10)	1	0.7	0.8
Non-reproductive females (n = 4)	0.7	0.3	0.5
Young-of-the-year (n = 13)	0	0	0
All subjects (n = 34)	1.8	0.7	0.9

than by agonistic ones ($\chi^2 = 58.01$, df = 6, $p < 0.0001$). In the latter case, marmots showed signs of excitement or distress such as pilo-erection and tail-flagging.

Discussion

Role of Scent-deposition in Territorial Defence against Intruders

The classic hypothesis of delayed chemical communication in resource defence (i.e. scent marking) was that by marking animals would inhibit intruders from entering a territory: GOSLING (1982) named this the Uexküll–Hediger hypothesis, after its first proponents. This hypothesis predicts that the deposition of scent marks on a territory would maximize the possibility of being detected by intruders. Indeed this is the case in alpine marmots; as for other territorial mammals (PETERS & MECH 1975, 1978), their scent-deposition always occurred along borders with inhabited territories and no scent mark was ever performed at boundaries with empty areas. Animals seemed to walk along invisible olfactory barriers and actively avoided intruding into neighbours' territories even when residents were temporarily absent; intrusions were rare and were always detected, both by individuals foraging and by those 'spotting at burrows' (LENTI BOERO 1983, 1987, 1991a). Any scent mark from any individual seemed to be effective, suggesting that scent traces from a social group were all efficacious, possibly because they were perceived as having a similar scent.

In the present study, a seasonally declining trend of scent-deposition was observed from Jul. to Aug. and Sep. Additional data testifying to a very high rate of scent-deposition behaviour collected in the last week of Jun. in 1985 and 1986 (LENTI BOERO, unpubl. data) seem to confirm this trend.

ZELENKA (1965) reports that in his study colonies, scent-deposition was evident at the borders of territories but present only during the mating season in Apr. and May, and never during the summer months. BONESI (1993) reports a seasonal trend in scent deposition at the boundaries of territories, with a higher frequency in Jun. and Jul. LE BERRE (1994) found that marmots marked more near main burrows than at the edges of the territories. BARASH (1976) did not

Table 4: Characteristics of social interactions exhibited together with scent-deposition

Subjects	No. and (%) of scent-deposition events with amicable interactions	No. and (%) of scent-deposition events without interactions	No. and (%) of scent-deposition events with agonistic interactions
Marmots from same group (no. of events = 44)			
Reproducers	22 (50)	12 (27.2)	0
Non-reproducers	6 (13.6)	4 (9)	0
Marmots from different groups (no. of events = 31)			
Reproducers	0	11 (35.4)	6 (19.3)
Non-reproducers	0	11 (35.4)	3 (9.6)

report territorial behaviour after observing two unifamiliar colonies with no neighbouring conspecifics and two contiguous colonies living in the Vanoise National Park; for this reason he argues that there is no evidence in territorial defence in alpine marmots.

The differences encountered in all those studies might suggest that scent-deposition in alpine marmots is adapted to different ecological and social environments and that it cannot be exhibited at all when not socially needed, as at boundaries with empty areas. The differences in seasonal trend encountered might be ascribed to socio-ecological factors such as longer permanence of snow cover and/or greater pressure from intruders involving greater effort in territory defence in the early season. However, further research is needed to clarify this aspect.

Role of Different Age and Sex Classes in Scent-deposition

In discussing this aspect it must be remembered that each olfactory trace conveys information not only for the 'stranger's group', but for the 'home group' as well. In fact, the same scent-deposition places were utilized by different individuals in each social group, and seemed to belong to the whole family as much as burrows, 'spotting points', foraging areas and latrines, as in other ground squirrel species (HALPIN 1984; BARASH 1989). However, two different behavioural profiles related to reproductive status and sex in the second instance emerged in this study: in Jul., male reproducers deposited scent traces more than female reproducers, both adult reproducers deposited more than non-reproducers and young-of-the-year did not deposit scent traces at all. Together with territory patrolling, the seasonal trend was the only sex difference reported in this study, testifying to a temporary and slight sexual dimorphism in territorial defence. Interestingly, scent-deposition rate in reproducers was not related to the presence of a litter, suggesting that the territory itself and/or food and burrows within it are the defended resources of common interest. Scent-deposition rate was lower for reproducers in established groups than for newcomers; this could be ascribed to a 'new residency effect' or, conversely, to the fact that old residents rely on scent marks deposited by other members of the group. Unfortunately it is not possible to disentangle this problem: new residents never had offspring in the first year (LENTI BOERO 1991a,c) and old residents always had offspring, consequently novelty and offspring factors are superimposed. However, the olfactory barrier around each territory inhabited by adults and subadults is provided by the effort of all members of a social group, whether related or unrelated. This cooperative effort in scent marking among subadult classes is probably related to the coincidence of interests: it is important to preserve resources from intruders but, if inheritance of the territory occurs, it is important to know the territory and how to defend it. Too high a rate of scent deposition in subadults, however, might provoke agonistic interactions on the part of reproducing adults (LENTI BOERO, unpubl. data). This might have happened also with the only satellite male which was certainly not related: this animal deposited olfactory scents at the same spots, near boundaries and near the main burrow, as other group members, and those traces were effective in keeping out intruders. However, his scent-deposition frequencies were similar to the frequencies exhibited by male reproducers: 4.1 and 1.4 marks per h in Jul. and Aug., respectively. This animal was continuously chased and disappeared from the colony in Jul. 1987.

Role of Scent-deposition Displays in Social Communication

In the yellow-bellied marmot and in *M. olympus* (ARMITAGE 1976; BARASH 1989), scent deposition was reported as being important mainly in dominance or subordinate relationships, both within a social group and between neighbouring groups, thus acting also as a visual display. BARASH (1989) states that anal glands might excrete an alarm pheromone during tail flipping or during anal social inspection, hence the scent-deposition display might convey two channels of information: visual and olfactorial. Alpine marmots, in particular reproducers, exhibited a high percentage of scent-deposition in front of conspecifics, suggesting a function in communication of hierarchy as well. The detailed anatomy of olfactory investigations that immediately preceded or followed scent deposition in front of subordinates seemed to confirm this observation (LENTI BOERO, unpubl. data).

On the contrary, when displaying in the presence of conspecifics from neighbouring groups, animals gave the impression that 'displaying in front of' prevented escalated fighting. When trespass beyond the olfactory point occurred, an agonistic encounter followed, and the intruder was chased back to the olfactory point or line (LENTI BOERO 1992a). Indeed, nearly all the agonistic interactions among individuals belonging to neighbouring groups were observed along the scent-marked boundaries of territories (LENTI BOERO 1992a). BONESI (1993) reports similar data for a colony studied in the East Alps.

In conclusion, deposition of olfactory traces in a social group of alpine marmots is a multipurpose behaviour aiming both at territorial defence and at social communication.

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Literature Cited

AD'IA, Y. 1993: The skin glands of the Mongolian marmot (*Marmota sibirica*). In: Abs. Int. (V) Conf. Marmots CIS-States (BIBIKOV, D. I., NIKOL'SKII, A. A., RUMIANTZEV, V. Y. U. & SUNTZOV, V. V., eds). Ther. Soc. Comm. Marmot Investig. Kharkov State Univ., Moscow. p. 42.

AITKIN, M., ANDERSON, D., FRANCIS, B. & HINDE, J. 1989: Statistical Modelling in GLIM. Oxford Univ. Press, Oxford.

ALTMANN, J. 1974: Observational study of behaviour: sampling methods. Behaviour **49**, 227—265.

ARMITAGE, K. B. 1962: Social behaviour of a colony of the yellow-bellied marmot. Anim. Behav. **10**, 319—331.

— — 1976: Scent marking by yellow-bellied marmots. J. Mammal. **57**, 583—584.

ARNOLD, W. 1990a: The evolution of marmot sociality: 1. Why disperse late? Behav. Ecol. Sociobiol. **27**, 229—237.

— — 1990b: The evolution of marmot sociality: 2. Costs and benefits of joint hibernation and helping. Behav. Ecol. Sociobiol. **27**, 239—246.

— — 1992: Social evolution and obligatory group hibernation in marmots. In: Proc. 1st Int. Symp. Alpine Marmot (*Marmota marmota*) and genus *Marmota* (BASSANO, B., DURIO, P., GALLO ORSI, U. & MACCHI, E., eds). Desk Top Pre-Press ColorTypeSetting, Torino. pp. 41—54.

— — 1993: Social evolution in marmots and the adaptive value of joint hibernation. Verh. Dtsch. Zool. Ges. **86**, 79—93.

BARASH, D. P. 1973: The social biology of the Olympic marmot. Anim. Behav. Monogr. **76**, 171—245.

— — 1976: Social behaviour and individual differences in free-living Alpine marmots (*Marmota marmota* L.). Anim. Behav. **24**, 27—35.

— —1989: Marmots. Social Behaviour and Ecology. Stanford Univ. Press, Stanford.

BONESI, L. 1993: *Marmota m. marmota* (Linnè 1758): Biologia del comportamento e utilizzo dello spazio di una popolazione alloctona delle Prealpi Giulie. Unpubl. Thesis, Univ. of Trieste.

BOPP, P. 1954: Zur Topographie der Murmeltierterritorien. Rev. Suisse Zool. **61**, 374—380.

— — 1956: Zur Topographie eines Kolonialterritoriums bei Murmeltieren. Rev. Suisse Zool. **63**, 255—261.

— — 1958: Fluchtdistanzen und territoriales Verhalten beim Murmeltier. Mitt. Naturforsch. Ges. **26**, 1—6.

BUGLASS, A. J., KHAZANEHDARI, C. & WATERHOUSE, J. S. 1994: The anal gland of the mole: a semiochemically important gland. In: Abs. Chemical Signals in Vertebrates VII (APFELBACH, R., REUTTER, K. & WEILER, E., eds). Univ. Tübingen. p. 34.

CLAPPERTON, B. K. 1989: Scent marking behaviour of the ferret, *Mustela furo*. Anim. Behav. **38**, 436—446.

— —, MINOT, E. O. & CRUMP, D. R. 1988: An olfactory recognition system in the ferret *Mustela furo* L. (Carnivora: Mustelidae). Anim. Behav. **36**, 541—553.

COLLINS, S. A., WATKINS, R. W., HUDSON, J. A., GURNEY, J. E. & COWAN, D. P. 1994: The effect of increased scent marking rate on urogenital glands of *Mus domesticus*. In: Abs. Chemical Signals in Vertebrates VII (APFELBACH, R., REUTTER, K., WEILER, E., eds). Univ. Tübingen. p. 38.

COUTURIER, M. 1964: Le Gibier des Montagnes Francaises. Arthaud, Paris.

EBLING, F. J. G. 1981: The role of odour in mammalian aggression. In: The Biology of Aggression (BRAIN, P. F. & BENTON, D., eds). NATO Adv. Inst. Ser., Sijthoff & Noordhoff, Alpen aan den Rijn. pp. 301—321.

EGGERT, F., HOLLER, C., LUSZYC, D. & FERSTL, R. 1994: MHC-associated urinary chemosignals in mice. In: Abs. Chemical Signals in Vertebrates VII (APFELBACH, R., REUTTER, K. & WEILER, E., eds). Univ. Tübingen. p. 41.

EISENBERG, J. F. & KLEIMAN, D. 1977: Communication in lagomorphs and rodents. In: How Animals Communicate (SEBEOK, T. A. ed). Indiana Univ. Press, Bloomington. pp. 634—654.

EVSIKOV, V. I., NAZAROVA, G. G. & POTAPOV, M. A. 1994: Female odour choice, male social rank, and sex ratio manipulation in the water vole. In: Abs. Chemical Signals in Vertebrates VII (APFELBACH, R., REUTTER, K. & WEILER, E., eds). Univ. Tübingen. p. 46.

GILCHRIST, W. 1984: Statistical Modelling. J. Wiley & Sons, New York.

GOSLING, L. M. 1982: A reassessment of a function of scent marking in territories. Z. Tierpsychol. **60**, 89—118.

GRIMOD, I., BASSANO, B. & TARELLO, V. 1991: La marmotta (*Marmota marmota*) in Valle d'Aosta. Ecologia e distribuzione (1988–1989). Regione Auton. Valle d'Aosta, Aosta.

HALPIN, Z. T. 1984: The role of olfactory communication in the social systems of ground sciurids. In: The Biology of Ground Dwelling Squirrels (MURIE, J. O. & MICHENER, G. R., eds). Univ. Nebraska Press, Lincoln. pp. 201—225.

HARRIS, M. A. & MURIE, J. O. 1982: Responses to oral gland scents from different males in Columbian ground squirrels. Anim. Behav. **30**, 140—148.

JOHNSON, R. P. 1973: Scent marking in mammals. Anim. Behav. **21**, 521—535.

JOLLY, A. 1966: Lemur Behaviour: a Madagascar Field Study. Univ. Chicago Press, Chicago.

KIVETT, V. K. 1978: Integumentary glands of Columbian ground squirrels (*Spermophilus columbianus*): Sciuridae. Can. J. Zool. **56,** 374—381.

KOENIG, L. 1957: Beobachtungen über Reviermarkierung sowie Droh- Kampf- und Abwehrverhalten des Murmeltieres (*Marmota marmota* L.). Z. Tierpsychol **14,** 510—521.

LATTMAN, P. 1973: Beiträge zur Ökologie und zum Verhalten des Alpenmurmeltieres. Ergebn. Wiss. Unt. Schw. Nat. Park. **66,** 275—347.

LE BERRE, M. 1994: Some recent results of the French programme of research on marmot. In: Abs. Int. (V) Conf. Marmots CIS-States (BIBIKOV, D. I., NIKOL'SKII, A. A., RUMIANTZEV, V. Y. U. & SUNTZOV, V. V., eds). Ther. Soc. Comm. Marmot Investig. Kharkov State Univ., Moscow. p. 47.

LENTI, D. 1983: Lo stazionamento nella marmotta alpina e il suo significato nella sorveglianza del territorio. Estr. III Conv. Assoc. A. Ghigi Stud. Vert. Bellagio. p. 50.

— — 1985: Ecologia degli insediamenti e utilizzo delle tane nella marmotta alpina (*Marmota marmota* L.). Att. IV Congr. Naz. Div. Ric. Bas. Psicol. Ravello. pp. 35—36.

LENTI BOERO, D. 1987: La difesa del territorio familiare nella marmotta alpina (*Marmota marmota*). Estr. V Conv. Assoc. A. Ghigi Stud. Vert., Pistoia. p. 28.

— — 1988: Distribuzione degli insediamenti e stima della densità di marmotta alpina (*Marmota marmota* L.).: metodi di indagine per zone campione. Suppl. Ric. Biol. Selv. XIV, Modena. pp. 253—264.

— — 1991a: Aspetti della biologia del comportamento della marmotta alpina (*Marmota marmota* L.). In: XIII Camminata Renzo Videsott. Ad memoriam (GABUTTI, A., ed.). Colle Sià, Valle dell'Orco. pp. 28—46.

— — 1991b: Territorialismo e uso dello spazio nella marmotta alpina. Riass. X Congr. Naz. Div. Ric. Bas. Psicol, Padova. pp. 187—188.

— — 1991c: Permanenza sui territori, avvicendamento di gruppi familiari, natalità e sopravvivenza in una colonia di marmotta alpina (*Marmota marmota* L.): dati preliminari. Suppl. Ric. Biol. Selv. XIX, Bologna. pp. 461—474.

— — 1992a: Space use and social interaction in a colony of alpine marmots (*Marmota marmota* L.). 6th Bien. Meet. Int. Soc. Comp. Psych. Brussels. p. 52.

— — 1992b: Building a functional ethogram for alpine marmots (*Marmota marmota* L.): the role of marking patterns. In: Proc. 1st Int. Symp. Alpine Marmot (*Marmota marmota*) and Genus *Marmota* (BASSANO, B., DURIO, P., GALLO ORSI, U. & MACCHI, E., eds). Desk Top Pre-Press ColorTypeSetting, Torino. pp. 95—100.

— — 1992c: Alarm calls in marmots: evidence for semantic communication. Ethol. Ecol. Evol. **4,** 125—138.

— — 1993: La funzione comportamento di marcatura nella marmotta alpina nella comunicazione olfattiva di possesso del territorio. Ric. Psicol. **17,** 75—90.

— — 1994a: Space use in alpine marmot (*Marmota marmota* L.): data from a long term research. Abstr. 2nd Int. Conf. on Marmots, Besancon. pp. 88—89.

— — 1994b: Survivorship among young marmots and their permanence in the natal territory in a high altitude colony. Ibex J.M.E. **2,** 9—16.

— — & BOERO, E. 1989: Dati preliminari sulla dispersione e predazione nella marmotta alpina (*Marmota marmota* L.): uno studio a lungo termine. Att. VIII Congr. Naz. Div. Ric. Bas. Psicol., Padova. pp. 57—59.

LUSZYC, D., WOBST, B., EGGERT, F., ZAVAZAVA, N., MÜLLER-RUCHHOLTZ, W. & FERSTL, R. 1994: MHC-molecules and urine odor formation. In: Abs. Chemical Signals in Vertebrates VII (APFELBACH, R., REUTTER, K. & WEILER, E., eds). Univ. Tübingen. p. 73.

MACDONALD, D. W. 1979: Some observations and field experiments on the urine marking behaviour of the red fox (*Vulpes vulpes* L.). Z. Tierpsychol. **51,** 1—22.

MANN, C. S. & JANEAU, G. 1988: Occupation de l'espace, structure sociale, et dynamic d'une population de marmottes des Alpes. Gib. Faun. Sauv. **5,** 427—445.

MUCIGNAT CARETTA, C., CARETTA, A. & CAVAGGIONI, A. 1994: Murine major urinary proteins are involved in pheromonal communication. In: Abs. Chemical Signals in Vertebrates VII (APFELBACH, R., REUTTER, K. & WEILER, E., eds). Univ. Tübingen. p. 78.

MÜLLER-USING, D. 1956: Zum Verhalten des Murmeltieres. Z. Tierpsychol. **13,** 135—142.

MÜNCH, H. 1958: Zur Ökologie und Psychologie von *Marmota m. marmota*. Z. Säugetier. Ped. **23,** 129—138.

PERRIN, C., ALLAINE, D. & LE BERRE, M. 1993: Socio-spatial organization and activity distribution of the alpine marmot *Marmota marmota*: preliminary results. Ethology **93**, 21—30.

PETERS, R. & MECH, D. 1975: Scent marking in wolves. Am. Scient. **63**, 628—637.

— — & — — 1978: Scent marking in wolves. In: Wolf and Man. Evolution in Parallel (HALL, R. & SHARP, H., eds). Acad. Press, New York. pp. 133—147.

PETRULIS, A. & JOHNSTON, R. 1994: Odor modulation of scent marking. In: Abs. Chemical Signals in Vertebrates VII (APFELBACH, R., REUTTER, K. & WEILER, E., eds). Univ. Tübingen. p. 87.

RALLS, K. 1971: Mammalian scent marking. Science **171**, 443—449.

SHOREY, H. H. 1977: Pheromones. In: How Animals Communicate (SEBEOK, T. A., ed.). Indiana Univ. Press, Bloomington. pp. 137—163.

STEINER, A. L. 1974: Body-rubbing, marking, and other scent-related behaviour in some ground squirrels (Sciuridae): a descriptive study. Can. J. Zool. **52**, 889—906.

THIESSEN, D. & RICE, M. 1976: Mammalian scent gland marking and social behaviour. Psychol. Bull. **83**, 505—539.

VASILIEVA, N. Y. 1994: Social cues influencing sexual maturation in golden hamsters (*Mesocricetus auratus*): the role for males' flank gland secretions, vaginal discharge and litter composition. In: Abs. Chemical Signals in Vertebrates VII (APFELBACH, R., REUTTER, K. & WEILER, E., eds). Univ. Tübingen. p. 122.

WERNER, I. 1994: The smell of male sexual experience affects the sexual maturation in female field voles. In: Abs. Chemical Signals in Vertebrates VII (APFELBACH, R., REUTTER, K. & WEILER, E., eds). Univ. Tübingen. p. 130.

WILSON, E. O. 1968: Chemical systems. In: Animal Communication. Techniques of Study and Results of Research (SEBEOK, T. A., ed.). Indiana Univ. Press, Bloomington. pp. 75—102.

ZELENKA, G. 1965: Observations sur l'écologie de la marmotte des Alpes. Terre et Vie **19**, 238—256.

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