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Long-term dynamics of space and summer resource use in the alpine marmot (*Marmota marmota* L.)

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An alpine marmot's home range is a structured portion of soil, vegetation and rocky outcrops. The dynamics of home range and resource use were investigated in *Marmota marmota* L. at Gran Paradiso National Park, south-west Alps, Italy. Data were collected during 8 years from 73 individually known marmots, occupying three adjacent locations, in 264 hr of scanning and 551 hr of focal animal sampling. Three different locations did not differ in the total dimension of the home range but they differed in the total dimension of pasture. The home range inherited by immigrant monogamous couples supplanting the unrelated previous groups did not contract, and the dimension were not dictated by immediate feeding necessities, thus suggesting that in some way alpine marmots may envisage future needs. The main burrow systems and hibernacula were inherited by the new couples as well, while the spotting/resting points and other burrows varied across years and groups. The capability of the alpine marmots to maintain stable home ranges across years is unique in the marmot genus, and should be ascribed to common use of space and common defence in kin social groups.

KEY WORDS: ground squirrel, *Marmota marmota*, home range dynamics, territoriality, resource inheritance.

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INTRODUCTION

The home range is defined as the area traversed by an animal in its normal activities of food gathering, mating and caring for young (Burt 1943), when it is defended it becomes a territory (Maher & Lott 1995). In terms of cognitive ethology a home range could be defined as "the area memorized and recalled by an animal in which normal activities are performed as safely as possible, due to representation of territorial knowledge" (Gould & Gould 1994), and where social knowledge and recognition of the group members allows selective defence against unwanted intruding conspecifics (Lenti Boero 2002). The alpine marmot (*Marmota marmota* L.) is a monogamous species widespread in the Pyrenees, Alps and Carpathians. A social groups is exclusive towards neighbours (Lenti Boero 1995, 1999, 2002), but its members share a common home range that can be defended throughout year or only during springtime by all but the young of the year (Bopp 1954, 1956; Couturier 1964; Zelenka 1965; Lattman 1973; Lenti Boero & Boero 1989; Mann & Janeau 1988, 1990; Arnold 1990a, 1990b; Lenti Boero 1991, 1994, 1995, 1996, 1999; Sala et al. 1992, 1996; Perrin et al. 1993; Bel et al. 1995).

In addition to food, an alpine marmot territory includes hibernacula, summer burrows and scent-marking/resting points (Bopp 1954, 1956; Couturier 1964; Zelenka 1965; Perrin et al. 1993; Lenti Boero 1996; Sala et al. 1996). Field studies report territory dimensions in different geographical areas (Bopp 1954, 1956; Zelenka 1965; Mann & Janeau 1988, 1990; Perrin et al. 1993; Bassano et al. 1996; Lenti Boero 1996); but few studies deal with size variation across years in this species (Zelenka 1965; Mann & Janeau 1988, 1990; Sala et al. 1996).

Resource inheritance is defined as the transmissibility of durable possessions across generations (Myles 1988). Ground dwelling sciurids, including the alpine marmot, have at least two valuable durable possessions to be inherited: feeding areas and burrows, especially hibernacula (Lenti Boero 1996, 2001). Generally, resources are inherited by the genetic descendants of territory owners, for instance daughters in the case of yellow bellied marmot (Armitage 1984). In the alpine marmot, however, descendants seldom inherit parental resources: generally both sexes migrate and must obtain a territory in order to reproduce; their descendants succeed in staying on the natal territory only if they are strong enough to evict the same sex parent (Arnold 1990a, 1990b; Lenti Boero 1994, 1996, 1999; Hacklaender et al. 2003). If one parent die because of predation, it is almost impossible, or at least very difficult, for orphaned subadults to defend their territory against immigrant mature males and/or females (Lenti Boero 1999). Consequently durable possessions are taken over by non-kin groups and changes in dimension and resource use should be expected in this case.

Because long term studies on the alpine marmot are lacking, in the present paper the dynamics of home range use, and of resource inheritance are investigated.

METHODS

Behaviours

Marmots occupy a space common to the family group and distribute their activity budget in different parts of their home area according to the behaviour performed and to the

hour of the day (PERRIN et al. 1993). They exhibit two readily distinguishable behavioural states (sense LEHNER 1996): foraging and sitting or lying (LENTI BOERO 1996; SALA et al. 1996).

The following behaviours were considered for understanding space use and delimiting the home range areas:

1. Wary-sitting or wary-lying; the animal is quiescent in a specific place, may have the belly in contact with the substrate (stone, ground or log) in a relaxed posture, or may extend the forelegs. I adopt this term in the present paper, instead of the general term of "wariness" used by ARMITAGE & CHIESURA CORONA (1994), because I did not consider the vigilance patterns exhibited by foraging or otherwise moving animals, as those authors did. When performing sitting or lying, marmots are undoubtfully wary, because they are ready to move the head in consequence of alarm signals, or move toward intruders (LENTI BOERO 1992, 2002). This behaviour might be related to territory defence against intruders or predators.

2. Foraging; two foraging patterns were observed (LENTI BOERO 1996): (a) the animal walks in a straight direction and eats the forage from the area that it can reach with the muzzle; (b) when walking, the animal clearly displaces itself some metres away from the previous path in order to select a specific flower or plant, which frequently is grasped with one or both forepaws. As in other marmot species, foraging is alternated with alert postures, mainly head raising (ARMITAGE et al. 1996). Typically, adults and subadults marmots of both sex foraged alone, less frequently at a distance of less than 5 m from each other and seldom exhibited social interactions while foraging, each animal following her/his own path.

3. Locomotion; walking, trotting slowly, running, stopping.

4. Marking; three different patterns were considered: cheek rubbing, paw rubbing, stiff tail posture, while the "tail flagging walk" performed by males was discarded because of too few observations (BEL et al. 1995, LENTI BOERO 1992). Marking was most frequently observed at the external boundaries of the home range where potential intruders were present (LENTI BOERO 1995).

5. Excavating or refurbishing burrows; the head of the marmot is introduced in the tunnel, ground is excavated with forelegs, successively the animal enters the burrow and digs out the detritus with the hind legs, thus creating the characteristic porch.

The complete ethogram adopted during this study is fully described in LENTI BOERO & PUNTELLINI (2000).

The study area

The study area was included in a colony of 200 ha, facing North, and was located at 2300 m above the timberline in a small valley branching from the main Cogne Valley in the Gran Paradiso National Park (P.N.G.P.), Valle d'Aosta, Italy (LENTI BOERO 2001). In order to determine space use and scent deposition sites the entire area was subdivided in a grid of 114 squares each with sides of 25 m. Each square was denoted with a letter and a number and the whole matrix was superimposed on a photograph of the study area, to gather finer details of the ecofacies, as suggested by BARASH (1973). Burrows and wariness points utilized at least once were inspected at the end of each season for physical characteristics and number of entrances. Though they were only a subset of all the openings that could be found in the area, no attempt was made to survey all of them. For further details see LENTI BOERO (1992, 1996, 1999). Vegetation, identified from a field book (STEFENELLI 1982), included a few trees (*Larix decidua*, *Pinus cembra*) and shrubs (*Rhododendron ferrugineum*). The feeding areas had two different kinds of vegetation. The flat-sloped quadrates were covered by mixed mono and dicots (*Festuca* spp., *Poa* spp., and other Gramineae among others) and the steep-sloped quadrates were covered by *Festuca ovina*.

Subjects and collection of data

The study was performed from 1985 to 1992 during the months of July, August, and early September. Data were collected from 51 adults, subadults, and infants trapped and individually marked, and from 2 naturally marked adults and 20 recognizable infants (LENTI BOERO 1999). The observer sat in an inconspicuous place with 10 × 40 binoculars or a 30 × 60 telescope. Information about the space use of individuals belonging to each family group was gathered continuously from early morning (5 a.m.) to late evening (20 p.m.) (legal hour) by means of 3 scan samples per hour, lasting 10 min each (ALTMANN 1974). During this time the entire area was thoroughly scanned and the name, activity, and location on the grid and on specific burrows or wary-sitting-lying points was recorded on the photograph map for each individual.

Scan sampling was suspended for 20 min every time a disturbance such as alarm calls that displaced individuals, grazing cattle, tourists or predators altered the normal quiet activity in the colony. The total amount of time spent in scanning was 264 hr Scanning was alternated with 551 hr of focal animal sampling to confirm the quality of space use and the social structure of the groups. Interactions within the group were mostly amicable while those among neighbours were agonistic (LENTI BOERO 1995, 1999, 2002). In addition, from 1986 to 1988, 71 selected days were entirely devoted to scan sampling. In 1990 only qualitative data on burrow use were collected.

Estimation of the home range and data analysis

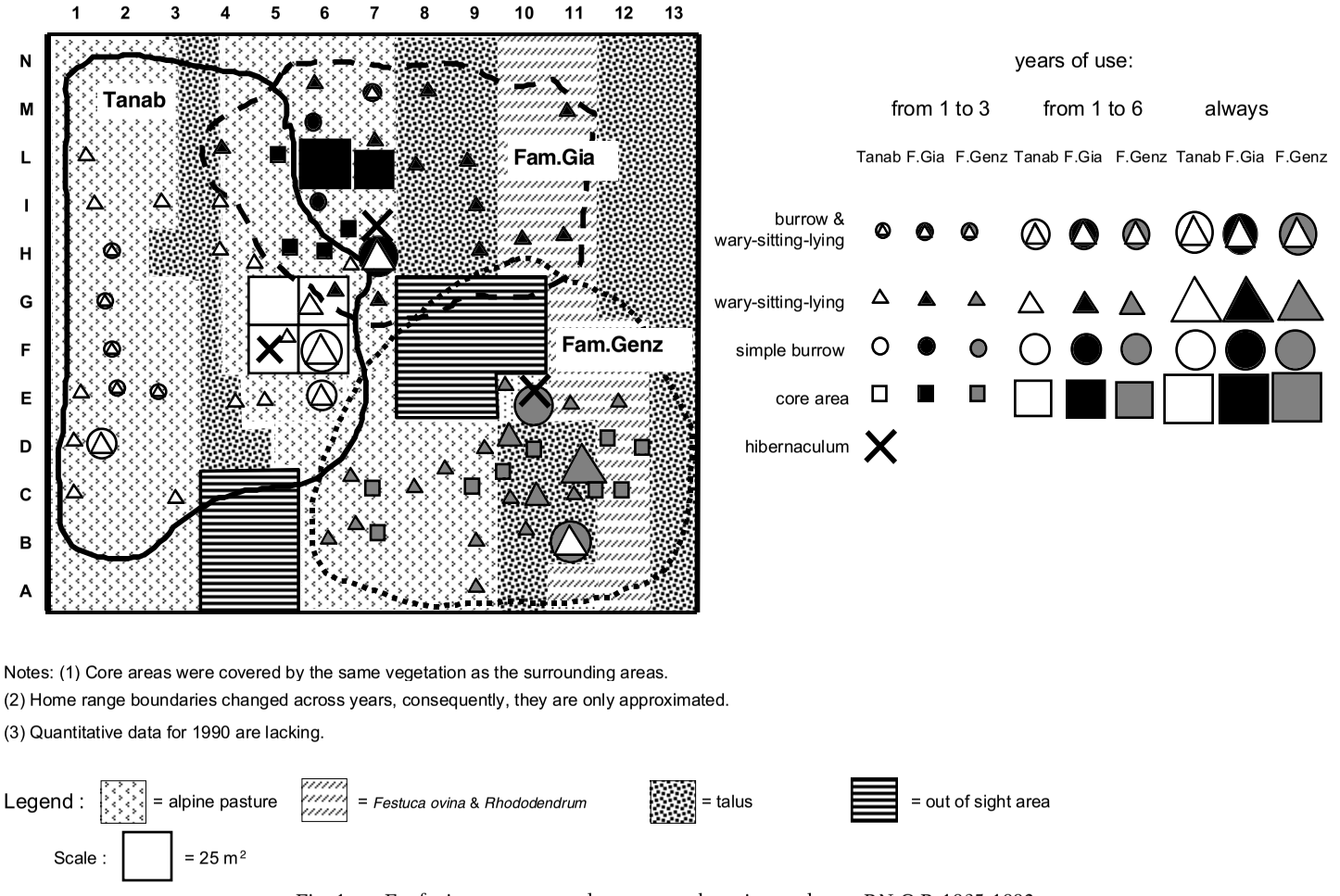
A total of 2342 fixes of wary-sitting-lying animals were collected. Because this behaviour generally lasts for more than 10 min, in order to avoid autocorrelation problems, I discarded for each individual all instances recorded after the first whenever I found the animal in the same behaviour and at the same location of the grid, and reconsidered the fixes when the animal changed its location. Consequently, I discarded 1778 fixes for wary-sitting-lying marmots. In data analysis a total of 3076 fixes (mean ± SD = 439.43 ± 167.31 for each year) was considered, 81% were foraging and locomotion patterns, and 19% wary-sitting-lying.

Fixes were clumped, thus suggesting that "sampling saturation" (KENWARD 1987) and a good appraisal of space use was achieved. The few empty cells due to sight obstruction were added by adopting the linked cells method (KENWARD 1987), and the dimensions of the home ranges and their ecofacies were calculated by adding these cells to the area of all squares containing fixes as described by VOIGT & TINLINE (1980). The spatial overlap was calculated as suggested by MACDONALD et al. (1980): they defined the overlap area A as the proportion of an animal's home range, which is overlapped by an other animal's home range. That is: $S_{12} = A/A_1$ and $S_{21} = A/A_2$, where A is the overlap area, A_1 and A_2 the home ranges of animals 1 and 2 respectively, and S_{12} is the overlap of animal 2 on animal 1. It is important to note that this index is not reflexive. Data were analyzed by means of SPSS, SYSTAT.10 and GLIM software (AITKIN et al. 1989, CRAWLEY 1993).

RESULTS

Home range dimension and characteristics

Throughout this study the observed area was partitioned into three different sites, named Tanab, Fam.Gia and Fam.Genz (Fig. 1). In order to determine home range dimension I took into account all the behaviours of the catalogue. Wary-sitting or lying and foraging were the most frequent: together with locomotion and scent marking they were performed by all the marmots in a group in the entire



Notes: (1) Core areas were covered by the same vegetation as the surrounding areas.
(2) Home range boundaries changed across years, consequently, they are only approximated.
(3) Quantitative data for 1990 are lacking.

Legend : = alpine pasture = *Festuca ovina* & *Rhododendrum* = talus = out of sight area

Scale : = 25 m²

Fig. 1. — Ecofacies, core areas, burrows and wariness places, P.N.G.P. 1985-1992.

home range. Consequently foraging areas and marking sites were nearly superimposed for all the individuals reaching a sufficient number of observation points (i.e. did not migrate or disappear early in the season), and the size of a group home range was determined by summing the observations of the activities of each individual member.

The mean ± SD total home range area through the 8 years was 1.92 ha ± 0.49, 1.52 ha ± 0.42, 1.84 ha ± 0.47, respectively for Tanab, Fam.Gia and Fam.Genz. According to the site and to slight variations in the shape through the years, the home ranges included some or all of the ecofacies mentioned above (Table 1). For instance, shrubs were not included in the Fam.Gia and Fam.Genz home ranges in 1986 and 1987. The proportion of talus varied from 14% of Tanab home range in 1986 to 30% of Fam.Gia home range in 1989.

The area of home ranges did not differ significantly across sites during this study (SYSTAT GLM, F = 1.83; df = 2,15; $P = 0.21$), nor it did change across years (SYSTAT, GLM, F = 1.47; df = 5,12; $P = 0.27$). The interaction between sites and years was also not significant (SYSTAT GLM, F = 0.52; df = 7,10; $P = 0.83$), nor was the effect of social groups on home range dimension (F = 3.02; df = 8,5; $P = 0.119$).

All the home ranges hosted different social groups through the years: both adult members were replaced in Tanab in July 1988 and in July 1990, and in Fam.Gia in 1986 and 1988. The replacing pair did not attempt reproduction in the first year, and always succeeded in evicting all the former residents, reducing the inhabitants from 8 and 5 to 2 in Tanab, and from 4 and 3 to 2 in Fam.Gia. Because a home range contraction could be expected due to a lesser number of inhabitants, I ran an ANOVA considering the dimensions for consecutive years of old and new settlements, the ANOVA was not significant (GLIM ANOVA, $\chi^2 = 0.03$; df = 11; $P > 0.10$). The areas of the sites slightly expanded or contracted from one year to another, however, those differences were not significant (SPSS ANOVA, F = 2.11; df = 4,20; $P = 0.127$) (Table 1). Furthermore, immigrants did not expand or contract their newly acquired home range in their second year (SPSS ANOVA, F = 0.05; df = 1,9; $P = 0.836$).

The total dimension of home range areas did not depend on the row number of adults and subadults of the social groups — SYSTAT, F = 1.84; df = 1,18; $P = 0.191$, regression coefficients: 1.605 (constant), 0.048 (slope) — nor on the total animal resident, including infants — SYSTAT, F = 2.78; df 1,18, $P = 0.113$, regression coefficients: 1.556 (constant) and 0.04 (slope) — in fact the total dimension of the home range area explained only 9% of the variance when only adults and subadults were considered, and 13% of the variance when all the animals were taken into account.

Animal density

During this study the three sites supported a significantly different number of animals (mean ± SD: 5.86 ± 2.672, 4.14 ± 1.77, 11.5 ± 1.64, respectively for Tanab, Fam.Gia and Fam.Genz; ANOVA F = 13.63; df = 2,17; $P < 0.001$). Post hoc tests demonstrated that the Fam.Genz territory had a significantly higher mean number of marmots than the other two territories (pairwise mean differences with Bonferroni adjustment: Fam.Gia and Tanab = 1.45; $P = 0.961$; Fam.Genz and Tanab =

Table 1

Home range size (ha), ecofacies characteristics, and density at Grand Nomenon, P.N.G.P. Italy, from 1985 to 1988.

Year	Site	Family group	*F. ovina* ha % of tot	Meadow ha % of tot	Total forage ha % of tot	Talus ha % of tot	Shrub† ha % of tot	Total ha	Spatial overlap	Sub/ adults	Infants	Density ad/sub
1985	Tanab	Elioel	0 (0%)	1.56 (71%)	1.56 (71%)	0.28 (13%)	0.34 (16%)	2.18	22% on Giacomo	5	4	2.29
	Fam.Gia	Giacomo	0.31 (15%)	0.88 (44%)	1.19 (60%)	0.28 (14%)	0.53 (27%)	2	20% with Elioel	4	0	2
1986	Tanab	Elioel	0 (0%)	1.81 (74%)	1.81 (74%)	0.28 (12%)	0.34 (14%)	2.43	48% with Giac	6	0	2.46
	Fam.Gia	Fiorenzo	0.31 (20%)	0.81 (52%)	1.12 (72%)	0 (0%)	0.44 (28%)	1.56	18% with Elioel	2	0	1.28
	Fam.Genz	Michel	0.38 (23%)	0.81 (50%)	1.19 (73%)	0 (0%)	0.44 (27%)	1.63	0 (0%)	6	5	3.68
1987	Tanab	Elioel	0 (0%)	1.75 (75%)	1.75 (75%)	0.16 (6%)	0.44 (19%)	2.35	48% with Fior	5	4	2.14
	Fam.Gia	Fiorenzo	0 (0%)	0.66 (73%)	0.66 (73%)	0 (0%)	0.25 (27%)	0.91	19% with Elioel	3	0	3.3
	Fam.Genz	Michel	0.38 (19%)	1.13 (58%)	1.51 (77%)	0 (0%)	0.44 (23%)	1.95	0 (0%)	7	4	3.61
1988	Tanab	Palli	0 (0%)	1.34 (69%)	1.34 (69%)	0.22 (11%)	0.38 (20%)	1.94	14 % with Elid 5% with Michel	3	0	1.55
	Fam.Gia	Elid	0.38 (21%)	0.94 (48%)	1.32 (69%)	0.13 (7%)	0.50 (27%)	1.95	13% with Palli	2	0	1.1
	Fam.Genz	Michel	0.63 (24%)	1.16 (45%)	1.79 (69%)	0.25 (10%)	0.53 (21%)	2.57	6 % with Palli	10	4	3.89
1989	Tanab	Palli	0 (0%)	1.28 (68%)	1.28 (68%)	0.28 (15%)	0.31 (17%)	1.88	24% with Elid	2	4	1.06
	Fam.Gia	Elid	0.25 (16%)	0.69 (44%)	0.94 (60%)	0.16 (10%)	0.47 (30%)	1.56	20% with Palli	2	4	1.28
	Fam.Genz	Michel	0.50 (23%)	0.94 (44%)	1.44 (68%)	0.25 (12%)	0.44 (21%)	2.13	0 (0%)	8	5	3.13
1991	Tanab	Emilio	0 (0%)	0.88 (74%)	0.88 (74%)	0.16 (13%)	0.16 (13%)	1.19	22% with Matteo	2	0	1.68
	Fam.Gia	Matteo§	0 (0%)	0.91 (66%)	0.91 (66%)	0.16 (12%)	0.31 (22%)	1.38	26% with Emilio	4+2	3+4	4.35
	Fam.Genz	Fam.Ren	0.19 (15%)	0.94 (75%)	1.13 (90%)	0 (0%)	0.13 (10%)	1.25	0 (0%)	10	0	8
	Fam.Gia	Noccicuc	0 (0%)	0.44 (88%)	0.44 (88%)	0 (0%)	0.06 (12%)	0.50	36% with Matteo	—	—	—
1992	Tanab	Emilio	0 (0%)	1.50 (78%)	1.50 (78%)	0.22 (11%)	0.22 (11%)	1.94	15% with Matteo	2	4	1.03
	Fam.Gia	Matteo	0.38 (19%)	0.84 (42%)	1.22 (61%)	0.22 (11%)	0.56 (28%)	2	16% with Emilio	3	0	1.5
	Fam.Genz	B.Gialla	0.25 (12%)	1.31 (64%)	1.56 (76%)	0 (0%)	0.50 (24%)	2.06	0 (0%)	8	3	3.88

† *Rhododendron ferrugineum*. § Two groups lived in this home range in 1991.
The overlap among home ranges was asymmetrical across years. *Festuca ovina*, a less preferred food, was not present in Tanab site, and was variable in the other two sites.

5.81; $P = 0.003$, Fam.Gia and Fam.Genz = 7.26, $P < 0.001$). Consequently, there was a significantly different density in the three sites (mean ± SD 2.84 ± 0.99; 3.21 ± 2.46; 6.21 ± 1.01; respectively for Tanab, Fam.Gia and Fam.Genz; SPSS ANOVA, F = 7.67; df = 2,17; $P = 0.004$), with Fam.Genz having an higher density than Tanab (pairwise mean differences with Bonferroni adjustment: = 3.65; $P = 0.006$, and = 3, P = 0.015, respectively for Tanab and Fam.Gia, while Tanab and Fam.Gia had similar density (pairwise mean differences with Bonferroni adjustment: 0.365; $P = 1$).

Dimension of foraging areas

I determined the dimension of foraging areas by taking into account only the data points from foraging animals, and excluding the data points from marking behaviour, locomotion and burrow refurbishing. The mean size of foraging areas was 1.4 ha ± 0.31, 0.97 ha ± 0.24, 1.35 ha ± 0.3, respectively for Tanab, Fam.Gia and Fam.Genz. Contrast analysis showed that it was significantly smaller in the Fam.Gia site with respect to Tanab and Fam.Genz (SYSTAT, F = 9.75; df = 1,15; $P = 0.007$), while the latter sites were similar (SYSTAT, F = 0.004; df = 1,15; $P = 0.95$). The ratio between the foraging area and the total home range was also significantly smaller for the Fam.Gia site with respect to Fam.Genz, and nearly significantly in respect to Tanab (SYSTAT, ANOVA for the three sites: F = 5.781; df = 2,17; $P = 0.012$, Bonferroni post-hoc test, mean difference = – 0.104; $P = 0.01$; and – 0,075; $P = 0.079$; respectively between Fam.Gia and Fam.Genz, and Fam.Genz and Tanab).

Only for Tanab was the foraging area related to the number of adults and subadults, explaining 64% of the variance — F = 8.87; df = 1,5; $P = 0.031$, regression coefficients = 0.920 (constant), 0.147 (slope). However, the presence of infants at Tanab was not related to the foraging area (F = 0.5; df = 1,5; $P = 0.5$, constant = 1.343, slope = 0.045). In the other two sites, the foraging area was not related to the number of adults and subadults (F = 0.2; df = 1,5; $P = 0.66$; constant = 1.222, slope = – 0.028; F = 0.29; df = 1,4; $P = 0.62$; constant = 1.11, slope = 0.04, respectively for Fam.Gia and Fam.Genz), nor to the presence of infants (F = 0.74; df = 1,5; $P = 0.42$, constant = 1.076, slope = – 0.033; F = 0.655, df = 1,4; $P = 0.46$, constant = 1.265, slope = 0.049, respectively for Fam.Gia and Fam.Genz).

Functional use and permanence of home range features

Core foraging areas. When foraging, marmots generally concentrated in adjacent quadrates that were considered the core foraging areas (Fig. 1). In order to determine their dimension I started from the quadrates with the higher number of fixes and gradually added adjacent quadrates until a value of at least 60% of the fixes was reached. This procedure produced different sized areas (Table 2); permanent and located near the most used burrow during the entire study in Tanab, while interspersed over the whole feeding areas and not permanent in Fam.Gia and Fam.Genz (Fig. 1). Mean core area (± SD) was 0.32 ± 0.07; 0.5 ± 0.113; 0.65 ± 0.15, for Tanab, Fam.Gia and Fam.Genz respectively. The core areas were significantly different among sites (SYSTAT, F = 11.57; df = 2,15; $P = 0.001$). The Fam.Gia and Fam.Genz had greater core areas than Tanab (SYSTAT, pairwise mean differences with Bonferroni adjustment = 0.174; $P = 0.054$; and = 0.332; $P = 0.001$; for Fam.Gia and Tanab, and Fam.Genz and Tanab respectively) while the Fam.Genz core area

Table 2.

Core areas and their size as a ratio of the feeding areas and total home ranges. Grand Nomenon 1985-1992.

Year	Location	Social group	% of all fixes	Core area (ha)	% of total area	Core/feeding ratio	Core/total ratio
1985	Tanab	Elioel	66	0.38	17	0.24	0.17
1986	Tanab	Elioel	75	0.38	16	0.2	0.15
1987	Tanab	Elioel	65	0.38	16	0.2	0.16
1988	Tanab	Palli	63	0.25	13	0.18	0.13
1989	Tanab	Palli	67	0.25	13	0.19	0.13
1991	Tanab	Emilio	81	0.38	32	0.43	0.13
1992	Tanab	Emilio	72	0.25	13	0.16	0.13
1985	Fam.Gia	Giacomo	62	0.5	25	0.42	0.25
1986	Fam.Gia	Fiorenzo	60	0.56	36	0.5	0.34
1987	Fam.Gia	Fiorenzo	72	0.25	27	0.38	0.27
1988	Fam.Gia	Elid	60	0.50	26	0.42	0.27
1989	Fam.Gia	Elid	71	0.56	36	0.6	0.36
1991	Fam.Gia	Matteo	60	0.56	41	0.62	0.4
1992	Fam.Gia	Matteo	64	0.5	25	0.46	0.28
1986	Fam.Genz	Michel	75	0.69	42	0.58	0.43
1987	Fam.Genz	Michel	65	0.38	19	0.25	0.19
1988	Fam.Genz	Michel	65	0.56	22	0.31	0.21
1989	Fam.Genz	Michel	60	0.75	35	0.52	0.35
1991	Fam.Genz	René	64	0.75	60	0.66	0.6
1992	Fam.Genz	B.Gialla	65	0.75	36	0.48	0.36

The permanent core areas in the Tanab site were smaller than the core area in Fam.Gia and Fam.Genz that had a turn over across the years.

was not significantly different from Fam.Gia (mean difference = 0.148; $P = 0.146$). Throughout the years, the core area was not related to the number of residents (SPSS regression, F = 0.85; df = 1,5; $P = 0.394$; F = 0.24; df = 1,5; $P = 0.643$; F = 1.60; df = 1,4; $P = 0.273$, respectively for Tanab, Fam.Gia and Fam.Genz), nor did it vary according to the different social groups that utilized the same quadrates (SPSS ANOVA, F = 4.86; df = 2,6; $P = 0.085$; F = 0.54; df = 3,6; $P = 0.686$; F = 0.6; df = 2,5; $P = 0.605$, respectively for groups in Tanab, Fam.Gia and Fam.Genz).

I determined the ratio of core area to the total feeding area for each site (Table 2), and found those derived measures significantly different (SYSTAT F = 10.11; df = 2,17; $P = 0.001$). Pairwise Bonferroni comparison demonstrated that the Fam.Gia site had significantly the largest ratio (mean difference from Tanab = 0.25; $P = 0.002$, and from Fam.Genz = 0,23; $P = 0.006$), while there was no difference between Tanab and Fam.Genz (mean difference = – 0.016; $P = 1$).

Summer burrows and wary-sitting-lying places. Beyond wary-sitting-lying when the architecture allowed it, the use of burrows was inferred by animals entering and exiting, and by social activities. Wary-sitting-lying was also performed by soli-

tary marmots on spots that had no adjacent burrows. For this reason, the fixes for wary-sitting-lying marmots were widespread on the home ranges, I chose the arbitrary threshold of at least 20 fixes of wary-sitting-lying behaviour, and 10% of fixes on a single burrow or spotting point throughout the years for it to be considered as a permanent feature.

Exploring the area, it was possible to find many more burrows than the ones actually used during this study and short blind tunnels: all were very seldom utilized as emergency burrows, generally marmots rapidly oriented themselves and headed to the main burrows when in danger.

According to functional use, burrows were subdivided into main burrows, were at least 10% of observation of animals performing wary-sitting-lying, entering or exiting, and social activities occurred, and other less utilized burrows. A total of 18 burrows were used during this study, but only 4 (22%) were permanent across all years: two were located in Fam.Genz, one in Fam.Gia, one in Tanab, where a second burrow was used for 6 years (Fig. 1). The permanent burrows in Tanab and in Fam.Gia were located under rocks and had wary-sitting-lying places (Fig. 1). In Fam.Gia the main burrow also served as a hibernaculum, while in Tanab, it only served as a summer burrow, and the hibernaculum was nearly always closed and never utilized during the summer. Only one burrow in Fam.Genz, located in the talus, had a wary-sitting-lying place, the second was in the soil, with no observation place and it was always used as a hibernaculum (Fig. 1). Among the other burrows 4 (31%) were excavated in the ground and wary-sitting-lying was performed on the dirt porch at the entrance, 7 (54%) had a stone as an architrave and observation place, and 2 (15%) had a log as an architrave and wary-sitting-lying place.

Contrast analysis demonstrated that the Tanab home range had significantly more wary-sitting-lying burrows than the other two home ranges (SYSTAT, Tanab vs Fam.Gia and Fam.Genz; $F = 30.28$; $df = 1,17$; $P < 0.000$), while the Fam.Gia and Fam.Genz home ranges did not show any difference (SYSTAT, Fam.Gia vs Fam.Genz, $F = 0.27$; $df = 1,17$; $P = 0.61$).

The mean number of entrances was 1.53 (SD 0.91, range 1-4). All the burrows within a home range were exclusively utilized by a family group, except in one case in 1987 when a highly harassed 2-year-old male was accepted by the neighbouring group for awhile.

In order to estimate the potential sight-angle of the burrows with wary-sitting-lying places, during field excursions I visited each burrow, bent down in order to keep my head at about 35 cm from the ground, and noted the quadrates that were in sight. I estimated that all the main burrows were located on slopes allowing observation from 2.06 to 1.06 ha around. In Fam.Gia and Tanab the main burrows were not located at the centre of the home range, as might be expected, but were located 70 m apart from each other and about 35 m from the territory boundary (Fig. 1).

During the study a total of 47 wary-sitting-lying places was identified. They were located at varying distances from the nearest boundaries of the home ranges. The mean ± SD number of used wary-sitting-lying points for each site per year was 3.49 ± 3.552, 2.86 ± 2.544, 6.17 ± 3.544, respectively for Tanab, Fam.Gia and Fam.Genz. The mean number of wary-sitting-lying places did not differ significantly among sites (SPSS ANOVA, $F = 1.9$; $df = 2,17$; $P = 0.181$). Only one wary-sitting-lying place was always used throughout this study, the others were used for less time: from 4 times to only once per year (Fig. 1).

The area that could be surveyed from the wary-sitting-lying places was correlated with the distance from the boundary (r = 0.36; P = 0.012). Wary-sitting-lying points were exclusively utilized by the same group members, but in two cases, when boundaries of the territories changed, two points were utilized by different family groups in 2 different years.

The total number of wary-sitting-lying sites did not depend on the number of animals living in the territories nor on the number of adults and subadults of both sexes living in adjacent territories respectively (SPSS regression, F = 1.62; df = 1,18; P = 0.22; F = 2.23; df = 1,18; P = 0.152). However, they were related to the total foraging area (SPSS regression, F = 6.0; df = 1,18; P = 0.024), and the relationship with total home range area was nearly significant (SPSS regression, F = 3.50; df = 1,18; P = 0.077).

DISCUSSION

Animals compete for a number of resources, such as food, cover, shelter and mates. One way they compete is by excluding potential competitors from the area containing the resources (i.e. by being territorial) (Davies 1980, Maher & Lott 1995). A way to understanding what resources are of interest is if they are protected (by means of scent marking), and actively defended (by chasing intruders) (Maher & Lott 1995). In order to deeply understand alpine marmot territoriality, in the present study I investigated (a) the characteristics and use across time of burrows and wary-sitting-lying places, (b) how home range dimension and use of the space may be inferred by different activities, and (c) whether those features are permanent across years.

Alpine marmots extended family groups share a common home range and hibernate together (Barash 1976, Arnold 1990b, Perrin et al. 1993, this study) and exhibit two kinds of settlements: isolated family, were a single group occupies a large area (from 2 to 5.75 ha) with no adjacent families (Zelenka 1965; Mann & Janeau 1988, 1990) and colonies, where many groups occupy home ranges adjacent to each other (Zelenka 1965; Mann & Janeau 1988, 1990; Perrin et al. 1993, Lenti Boero 1996; Sala et al. 1996; this study). Within colonies, home ranges might be signalled by means of scent marking during springtime (Zelenka 1965), or during the whole summer season at the locations where there is a major risk of intrusion, and they are actively defended from intruding conspecifics by the owners (Bel et al. 1995; Lenti Boero 1995, 2002). All the described alpine marmot home ranges include feeding areas and hibernacula, summer burrows, secondary burrows and emergency burrows, (i.e. a tunnel utilized only when the escaping animals cannot reach the main burrow) (Bopp 1954, 1956; Couturier 1964; Zelenka 1965; Pigozzi 1984; Mann & Janeau 1988; Perrin et al. 1993; Lenti Boero 1996, 2001).

The present study confirms that burrows may serve more than one function: shelter, wary-sitting-lying, that can be disjointed if the architecture of a burrow lacks a wary-sitting-lying point, and hibernation, that also can be disjointed from summer use. When a burrow does not include a wary-sitting-lying point, the latter is linked to the most used burrows by a clearly visible trail. In addition, seldom and never used burrows might exist on a marmot home range (Bopp 1954, 1956; Perrin et al. 1993; Sala et al. 1996; this study). Marmots seem very opportunistic in burrow use: in Tanab the burrow most used for shelter and wary-sitting-lying

was separate from the hibernaculum, which was closed most summers (Lenti Boero 2001), in Fam.Gia the most used summer burrow served also as hibernaculum, in Fam.Genz the hibernaculum was used in the summer for spending the night and for daily shelter, but most wary-sitting-lying was performed on a big boulder that had no nearby burrow. Different functions imply different characteristics; and such diverse burrow utilization is a consequence of the variable architecture of burrows and of intrinsic valuable characteristics that may be appraised by marmots. Only one permanently used main burrow was identified during this study in each home range. This was not so for the wary-sitting-lying places, that changed from one year to another, and may be considered variable features in the home range structures. As in other studies the main burrows were scent marked (Bel et al. 1995, Lenti Boero 1995).

Core areas were the most intensively used feeding areas and were not scent marked at the boundaries. Even if the three studied sites were adjacent, and apparently similar, the pattern of use of the core foraging area was not the same; permanently grazed and located near the main burrow in Tanab, interspersed and not permanent in Fam.Gia and Fam.Genz, the latter areas were significantly larger.

Feeding areas were determined by taking into account only the data points from foraging animals. For the Fam.Gia site the mean size of the foraging area was significantly smaller in respect to the other two sites, and the ratio to the total home range was also significantly smaller. On the contrary, the ratio between the core and the feeding area was significantly greater. It appears that the marmots living in the site seemed to do their best in exploiting the vegetation resources of a relatively small area. It is of interest to parallel this information with indirect indicators that Fam.Gia was a suboptimal location: had the largest animal turnover and the lowest number of litter (Lenti Boero 1991, 1994, 1999). The foraging areas were related to the number of adults and subadults, but not infants, only in Tanab site.

Those results are concordant with the available data that suggest that the pattern of space use is not always the same in *Marmota marmota*: Perrin et al. (1993) found that animals feed at the periphery and distant from the main burrows, while Bassano et al. (1996), and Sala et al. (1996) found that the intensively used feeding areas are near the main burrow system. In addition both the latter groups report that feeding activity increases on the flat slopes. In my study colony the core areas were flat, and covered by many species, the steep parts of the home ranges, covered with *Festuca ovina*, a less preferred food (Bassano et al. 1996), were less utilised for feeding. The key for understanding the pattern of use of feeding areas might be in alimentary choice that still poorly known in the alpine marmot. Massemin & Ramousse (1992), Bassano et al. (1996), and Mori (2001) found that dycots and flowering plants are preferred when available. In the most accurate study on this topic Arnold et al. (2002) demonstrated that alpine marmots that select and can feed on plants with high content of linoleic acid have better performances on subsequent hibernation than marmots feeding on plants rich in alpha-linoleic acid. Other species of the genus like the Olympic, hoary, yellow-bellied Vancouver and golden marmot feed selectively, suggesting that they might depend on specific nutrients such as proteins while avoiding plants with a high alkaloid content (Armitage 1979, Barash 1989, Frase & Armitage 1989, Blumstein & Foggin 1997). An additional aspect to be considered is that marmots might be able to change the floristic and vegetation cover by selective grazing, and trampling (Barash 1989, Semenov et al. 2001), and possibly by seed dispersion that could be one of the possible function of latrines that are found interspersed on the feeding areas.

The home range was determined, for each site, by all the social, marking, locomotion and feeding activities. The home ranges were scent marked at the boundaries where potential intruders could enter (LENTI BOERO 1995) and actively defended by chasing intruders (LENTI BOERO 2002). The dimensions of the home ranges were not significantly different among the three sites, and did not depend on the number of residents, nor it was possible to find a year and/or a social group effect. SALA et al. (1996) report that the home range dimensions are independent of the number of residents in the Apennines.

The home ranges were always larger than the feeding areas, indeed, it is noticeable that some of the square grids covered with pasture and located at the edges were only used for locomotion and not for feeding: apparently marmots avoided feeding at the periphery in absence of confining social groups. Thus, marmots left a "buffer" zone around the feeding areas, where other activities, including scent marking, took place, and the home ranges extended beyond the edges of the feeding areas. It is noticeable that those "buffered" home ranges had permanent sizes across years, and did not shrink, even when the resident group crashed, i.e. when the territories were taken over by a new pair not related to old tenants (LENTI BOERO 1999). Unexpectedly, the newcomers were observed to scent mark at almost the same spots as previous residents, but at higher rates than the older tenants (LENTI BOERO 1995). That means that a new resident couple, postponing the first reproduction to the year following the first settling (LENTI BOERO 1999), defended a territory adapted to an entire social group. Thus, the evidence points to the fact that the dimension of an alpine marmot home range is not dictated by immediate feeding necessity. How did newcomers determine the dimension of the home range? A possible explanation is that the newcomers find the scent barriers of neighbouring groups, and adapt to them, if this is true, however, we must explain why neighbouring individuals do not profit of the vacuum in order to enlarge their home range as other species do (ARMITAGE 1974, HOOGLAND 1995). When I started observations at the end of June, I realized that both male and female newcomers behaved very aggressively towards intruders (LENTI BOERO 1995), and alpine marmot adult males have been reported to have high testosterone levels (ARNOLD & DITTAMI 1997). SWITZER et al. (2001) suggest that individuals may profit from a long-term view of their territory occupation, and that territorial behaviour should be understood as a long-term, dynamic set of interactions between individuals. They developed a model where residents could suffer energy deficits at the beginning of their territorial tenure in order to accrue the benefits of decreasing future intrusions. This might be the case for the alpine marmots: a territorial tenure has to last for at least two to many more years, in order to guarantee efficient reproduction, and the neighbouring conspecifics will be probably the same in future years, thus it might profit the newcomers to invest energetically in territorial defence, as they actually do, in order to dissuade or discourage future intrusions. A "why" explanation to be tested is that future envisioning of necessities has been shaped by natural selection in the marmots' brain by implementing a "protect the maximum sized territory that you can, and defend all the territory that you can protect" rule.

Results from studies of colonial settlements performed on the Western and Northern side of the Western Alps (ZELENKA 1965; MANN & JANEAU 1988, 1990; PERRIN et al. 1993) are reported in Table 3. As can be seen, they seem remarkably stable: only two sites are significantly different in front of six possible comparisons. ZELENKA (1965) does not report any size change for 2 consecutive years, and MANN

Table 3.

Mean and SD of home range areas for the reported sites in the Alps, and pairwise Bonferroni comparison.

	Cases	Altitude (m)	Mean ± SD	Range	*P* (a)	*P* (b)	*P* (c)	*P* (d)
Vanoise (France) (1)	4	2350	2.17 ± 0.86	2.8-0.9	—			
Hautes-Alpes (France) (2)	4	2050/2350	1.26 ± 0.26	1.5-0.9	= 0.051 *	—		
Aosta Valley (3)	20	2300	1.83 ± 0.43	2.57-0.91	= 1 NS	= 0.203 NS	—	
Southern Swiss Alps (4)	9	1500/1600	1.5 ± 0.12	1.8-1.4	= 0.134 NS	= 1 NS	= 0.597 NS	—

Bracketed numbers and letters refers to: (1) PERRIN et al. 1993, (2) MANN & JANEAU 1988, (3) this study, (4) ZELENKA (1965); (a) Vanoise, (b) Hautes-Alpes, (c) Aosta Valley, (d) Southern Swiss Alps.

& JANEAU (1990) remarkably found the home range size to be unaltered *10 years after* their first study.

Newcomers are also conservative as regards the use of hibernacula (LENTI BOERO 2001) and the use of the main summer burrow (present study). Future research should be devoted to understanding the cues that newcomers utilize to identify the proper burrows (summer and/or hibernacula) and the boundaries of the territories.

Cross species comparison

In mammals, and specifically in the ground dwelling sciurids, the home range of social groups and individuals may vary in characteristics and dimensions according to ultimate and proximate causes such as the life history of the species, the level of sociality, the mating system, sex, and ecological pressures (ARMITAGE 1974, 1988, 2000; BARASH 1989; HOOGLAND 1995).

Some patterns of resource use and inheritance seem common to the 14 species of the genus *Marmota* and to other ground squirrels as well: underground excavated burrows, serving different functions — spending the night, rearing offspring, escaping from weather and predators, and hibernation — are a constant and fundamental factor in those species, that spend from 50 to 80% of their time below ground (BARASH 1989, HOOGLAND 1995, BIBIKOW 1996). The complex architecture and the plasticity of burrow use have been documented for other marmot species as well (ARMITAGE 1962, SVENDSEN 1976, BARASH 1989, BIBIKOW 1996).

Other aspects, noticeably the way the home range is distributed and utilized by different sex and age classes are remarkably different.

The alpine marmot is the only species where a stability of home range size is described across years and in different areas: in *Marmota caudata* the area of the home range is subject to significant change according to the ecology of the habitat (DAVIDOV et al., quoted in BARASH 1989). The home ranges in this species contract and expand depending on the number of residents, but do not depend on the availability of food resources (BLUMSTEIN & FOGGIN 1997, BLUMSTEIN & ARNOLD 1998). *Marmota bobak* occupy common home ranges, however, the social groups are

unstable, especially in habitats subjected to heavy anthropogenic pressure (Nikol'skii & Savchenko 1999). The widest difference is with *Marmota flaviventris,* a polygynous species were males occupy territories that include one or more females and do not have a constant dimension. Provided the vital minimum food and shelter are available, the dimension of a male home range depend on the male's vigour in defending it from intruding competitors, or by the chance of not having competitors in the surrounding (Armitage 1974). The adult and yearling females of the matrilines occupy separate home ranges, having areas that vary gratly in overlap (from 2.7 to 93.2%). The yearlings with the areas of greatest overlap are the ones with the best chance of being recruited into the maternal natal territory in future years (Armitage 1975, 1984). Prairie dog territories are highly stable, but their dimensions may greatly expand when nearby conspecifics disappear because animals may rapidly profit of the vacuum of a near territory that they know well, better than any newcomer from a distance (Hoogland 1995).

The patterns described above are completely different from those of *Marmota marmota*. This species share and jointly defend a common home range common summer burrows and hibernacula and it exhibits thermoregulatory helping (Bopp 1954, 1956; Couturier 1964; Zelenka 1965; Lattman 1973; Mann & Janeau 1988, 1990; Lenti Boero & Boero 1989; Arnold 1990a 1990b; Lenti Boero 1991, 1994, 1995, 1996, 1999; Sala et al. 1992, 1996; Perrin et al. 1993; Bel et al. 1995; this study). The ability to protect and defend a large and stable home range certainly adds to the fitness of individual members of a family group, that have access to any part of the area, and seems to be related with the high social complexity of the species, the second highest in the genus, according to Blumstein & Armitage (1998). A pivotal cue is that the protection and defence of the common home range is the job of all the members of the family group, even if the greatest part of the task is accomplished by the adult pair (Bel et al. 1995; Lenti Boero 1995, 2002). Males have been observed to come to the aid of sons attacked by conspecific intruders (Lenti Boero pers. obs). Apparently, common group defence works better and stabilizes the resource of interest better than the defence practised by the single, isolated marmots of other species. The evolutionary ground for this is, in my view, due to late dispersal in alpine marmots. The high level of habitat saturation means the young must survive on their parents' territory beyond the stage at which reproductive maturity is reached (Arnold 1990a, 1990b; Lenti Boero 1994, 1999). The adult males reproductively suppress their sons in their own family group and do not allow them to build new hibernacula on their own natal territory (Arnold & Dittami 1997, Lenti Boero 2001). However, it is obviously in the genetic interest of the fathers that their sons should survive and reproduce elsewhere. Genes must propagate across generations, and a descendant that does not propagate is a dead genetic end. These reasons are probably the cause of common defence of territories by all the group members (Lenti Boero 1995).

In conclusion, the most used summer burrows and hibernacula, the core foraging and the feeding area, the dimension of the home range are permanent and stable structural components of alpine marmots' territories, and they can be inherited by different and unrelated social groups. The stability of the home ranges across time and across different social groups might be achieved by common social effort, and by the envisioning of future necessities (Switzer et al. 2001) by newcomer residents.

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