

SURVIVORSHIP AMONG YOUNG ALPINE MARMOTS AND THEIR PERMANENCE IN THEIR NATAL TERRITORY IN A HIGH ALTITUDE COLONY

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Abstract - During an eight year study on the ethology and ecology of the alpine marmot (*Marmota marmota* L.), carried out in the Gran Paradiso National Park, Aosta, Italy, 41 young marmots were individually recognized and data on birth rate, litter size, permanence beyond maturity, and productivity were recorded. Litter size had a median of four (range 4-5). No female had a litter in the first year of settling and all females but one had a one year interval in reproduction. 36.6%; 34.1%; 21.5% and 0 animals born in the colony were found in the natal territory when one, two, three and four years old, respectively. The differences found in comparison to other geographical areas might be related to the high turnover rate of social groups and indirectly to the harshness of the habitat where the study area is located.

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1. Introduction.

The permanence of young marmots in the natal group after reaching the reproductive age, that is delayed dispersal, is influenced by many interrelated contingent factors such as the age structure, the group size, the frequency and quality of social interactions, the harshness of the habitat, the quality of burrows, the availability of food during the growing season, and by life-history factors, specifically, social thermoregulation and help from young animals (Barash, 1974; Armitage, 1975, 1991; Downhower & Armitage, 1981; Berger, 1988; Lenti Boero, 1988; Mann & Janeau, 1988; Arnold, 1988, 1990a, 1993; Van Vuren & Armitage, 1990). Large social groups in marmots are generated by delayed dispersal and in North American marmots a cline can be observed, with low elevations and plain dwelling woodchucks (*M. monax*) dispersing as young of the year, Olympic (*M. olympus*), hoary (*M. caligata*) and Vancouver marmots (*M. vancouverensis*) dispersing as two year olds (Barash, 1989; Bryant, 1994), and yellow bellied marmots (*M. flaviventris*) being highly flexible and dispersing as young of the year, yearlings, or two years old, according to ecological conditions such as elevation and vegetational characteristics, social environment such as population density and parental behavior, and individual characteristics such as weight, body mass and sex of the dispersers (Armitage, 1975; Barash, 1989; Webb, 1980). This is in accordance with general theory (Krebs & Davies, 1978).

Alpine marmots (*M. marmota* L.) gain their full adult body size and reproductive maturity (Psenner, 1957; Lattman, 1973; Arnold, 1992) when two years old; that is, after their second hibernation. However, in a study conducted in Berchtesgarden in the Bavarian Alps, Germany, only 20% of the animals dispersed after the second hibernation; in the same study a maximum age of dispersal of four or five years was reported (Arnold, 1990a, 1992).

The distribution of alpine marmots in the Alps includes many different environments, which presumably induce specific behavioural adaptations; hence the relevance of gathering long-term data from many different habitats or microhabitats in order to have a comparative understanding of the role of specific factors influencing dispersal and their possible interactions.

In this paper data on survivorship and permanence in the natal territory in alpine marmots are given from a long-term study carried at the Gran Paradiso National Park, Italy.

2. Methods

Habitat. Data were collected from 1985 to 1992 during July, August and early September in the "vallone del Gran Nomenon", a small valley branching from the main Cogne Valley, Aosta, Italy. The area faces North, and is dominated by the glacier of Mount Grivola, 3969 m, timber consists mostly of firs and pine-trees (*Abies alba*, *Picea abies*, *Pinus cembra*) and timberline reaches 2200 m. The area above the

timberline measures 375 ha, the substrate is moraine and detritus, partially covered by soil, and guarantees about 60 ha (16%) of suitable habitat for marmots. Vegetation consists mostly of Alpine meadow and rhododendron (*Rhododendron ferrugineum*). About 100 head of cattle grazed at Gran Nomenon during the month of August. Mean density of marmots estimated from 1985 to 1987 was 1.01 animal/hectare (Lenti Boero, 1988), lower than the one reported for the whole Park (Peracino & Bassano, 1992). From 9 to 17 active hibernating burrows were found from 1985 to 1992 in the entire valley (Lenti Boero, 1988, 1991a and unpublished data). Valleys contiguous to Gran Nomenon were less adapted to marmot settlements, thus the Gran Nomenon population was at least partially isolated from other populations in the surroundings, having few suitable corridors for marmot dispersal (Lenti Boero, 1988). No one floating animal living alone, as described by Arnold (1993), was identified during the whole study, in particular inside the pinewood.

Study area and collection of data. This study took place in a smaller portion of the valley located at 2300 m and undisturbed by tourism. The area measured 9 ha, was crossed by a stream, and ended on one side in a projecting rock, a small talus was present and vegetation was the same as in the rest of the valley. Snow cover lasted from November to the end of May. Due to its high altitude location emergence from hibernation was observed in the first week of May (Lenti Boero & Boero, 1989) and immergence was observed by the second week of October. Summer activity lasted one month less than in low elevation colonies (Lenti Boero, 1991a, and unpublished) and in other areas of the Aosta Valley (Grimod *et al.*, 1991). During the study 84 animals of all ages and sex classes were observed: 74 of them were trapped and marked for individual recognition, 10 marmots were individually recognized by natural marking. From 1985 until 1992 it was possible to gather data on permanence for 41 subjects born in the colony. Demographic and spatial data were collected on selected days by scanning every 10 minutes a portion of the whole area previously divided in a grid of 114 squares with 25 meters on each side (7 ha) (Lenti Boero, 1991b, 1994). Biometrical measurements of the head, trunk, tail, and paws, as indicated by Lattmann (1973), were taken by means of callipers. Adults and subadults individual weights were measured by means of a

platform scale rounded to one hectogram, and young of the year's weight was measured by means of a spring balance rounded to one gram.

Mean productivity per territory was calculated by dividing the number of young marmots produced in each territory by the years of observation, as suggested by Mann & Janeau (1988). Productivity per female was calculated by including all females that reproduced at least once divided by the number of years of permanence of each female in the colony.

Turnover of social groups. The three hibernating burrows (named B. Tanab, B. FamGia, and B. FamGenz) were included in three distinct but contiguous territories, actively defended from intruders and named Tanab, FamGia and FamGenz (Lenti Boero, 1991c, and unpublished data). The size of the territories varied from 12.500 to 28.125 m² (mean = 18.977,27; S.D. = 4.883,58) and was not related with the number of occupants or the presence of young of the year (Lenti Boero, 1994). The mean number of adult and subadult occupants during the study was 3.5 (range 2-6), 3.3 (range 2-5), and 6.5 (range 4-9) in Tanab, FamGia and FamGenz territory, respectively. Vegetation and geological substrate were similar for all territories. FamGenz territory was the only one inhabited by the same social group throughout nearly the entire study, unfortunately individual data for animals living there were available only from 1987, because trapping was successful only from that year. However, some animals in the group had been recognized by means of natural marking since 1986, thus showing that FamGenz was inhabited by the same family group since 1986. The social group inhabiting Tanab territory was completely substituted in 1988, in consequence of the death of the adult male predated by an eagle, and in 1991. The social group inhabiting FamGia territory was partially substituted in 1986, 1991 and 1992, and totally substituted in 1988 (Lenti Boero, 1991a, and unpublished data). In addition to the eagle, the fox and the goshawk (*Accipiter gentilis*) were documented predators in the area (Lenti Boero, 1991a, 1992).

3. Results

Reproductive activity and litter size. Birth rate and productivity vary greatly in the three territories (Tab. 1). Litter size is almost identical for the five adult females that reproduced in the colony. However, productivity per female

Table 1: Young marmots per litter and productivity in Gran Nomenon, P.N.G.P. Aosta, Italy

	1985	1986	1987	1988	1989	1990	1991	1992	All years	Productivity (per year)
Tanab terr.	4	0	4	0***	4	0	0***	4	16	2
FamGia terr.	0	0*	0	0***	4	0	0*	0	4	0.5
FamGenz terr.	4	4	5	4	4	4	0	0*	25	3.1
Whole colony	8	4	9	4	12	4	0	4	45	5.6
Average prod. per year	2.7	1.3	3	1.3	4	1.3	0	1.3	—	1.9

* = substitution of the resident male

** = substitution of the resident female

*** = substitution of the reproducing pair

highly differed: the least productive was the female living from 1988 to 1991 in FamGia territory: only 1 young per year. The three females successively inhabiting Tanab produced 2.66, 1.33 and 2 young per year. The most productive was the female living in FamGenz territory during the whole study: she produced at least 3 young per year (including years from 1986 to 1992); this female had the same partner for six years, and this pair was the one which lasted longest in the study. Any other pair observed had a litter once every two years. No litter was found when the male or the female partner was substituted in a pair, and when a new pair entered a territory. The entire productivity of the colony was 5.6, whilst the average productivity per year per territory was 1.9.

Survivorship and permanence of young. In Tab. 2 a two year follow up is given for all juveniles born in each territory until 1990. In all territories the greatest loss of animals was observed from the first to the second summer, that is for animals less than one year old. In two cases predation was documented. Only one animal disappeared in the period from the second to the third summer and this disappearance was due to documented predation.

From the cohort of 37 animals born from 1985 to 1989 and eligible for analysis of permanence until the fourth summer, no animal was retained in Tanab territory, 2 animals (50%) were retained in FamGia territory, and 6 animals (28.6%) were retained in FamGenz territory.

From the cohort of 25 animals born from 1985 to 1988 no animal was retained until the fifth summer.

Settling in the colony. Two marmots (one male and one female) born in FamGenz were found in the adjacent FamGia and Tanab territories with a new partner in their fifth summer and the female gave birth to a litter in the following year. Those animals, especially the female, had started intruding in the neighbouring territories in the previous year.

Conversely, four males and three females coming from outside the colony successfully settled and gave birth to viable litters. Two adult males came and lived in the colony for two consecutively years but did not produce any viable offspring: one of the two lived with a pair as a satellite and the other was the only male in a pair in FamGia in 1986 and 1987.

4. Discussion

Reproductive activity and litter size. The three territories in this study area were adjacent and very similar to each other as regards to substrate and vegetation, however a great difference was found as regards to reproduction rates: in two territories all females had a one-year interval in reproduction, as reported for alpine marmots in other areas, and other marmot species as well (Armitage, 1975, 1991; Barash, 1989; Bryant, 1994), in the third territory young marmots were produced by the same female for at least five years consecutively. Above and beyond peculiar characteristics of this individual female, this might be due to two reciprocally interacting factors: the size of the hibernating kin groups and the stability of the pairs. In groups with at least four or five adults closely related to juveniles, overwinter mortality is very low (Arnold,

Tab. 2: Permanence in the natal group in Gran Nomenon, P.N.G.P.

	newborn (1st summer)	1 year (2nd summer)	2 years (3rd summer)
Tanab terr.	12 (100%)	3 (25%)	2 (16.7%)
FamGia terr.	4 (100%)	2 (50%)	2 (50%)
FamGenz terr.	25 (100%)	10 (40%)	10 (40%)
Total	41 (100%)	15 (36.6%)	14 (34.14%)

For all years following birth, percentages are calculated on the total number of animals born in each territory and cumulatively for the whole colony.

1990b, 1993); and it might be argued that social thermoregulation from related subordinates helps energy saving by the female for further reproduction. In fact the FamGenz group, composed by closely related animals, was the most numerous one during the whole study. Stability also is an important factor, because the social dynamics show that marmots do not reproduce in the year of their first settling in a new territory or when a pair is disrupted by the arrival of a newcomer (Lenti Boero, 1991c) and data show that FamGia, the most unstable territory, was also the least productive one.

Local social factors, however, did not influence the size of litters in the colony and in the surrounding area (Lenti Boero, 1991a). Though data are scanty and difficult to compare a litter size of four is reported by Zelenka (1965) in Switzerland in an area located not more than 30 km by air from my study area, and apparently not dissimilar in pedology, vegetation and exposition, by Arnold (1990a) in the Bavarian Alps, by Perrin *et al.* (1993) in three family groups in the French Alps. However litter sizes of 2.5 and of 1.7 are reported by Mann & Janeau (1988) and Barash (1976) respectively, for 4 social groups in the French Alps. It can be hypothesized that macroenvironmental factors might influence the size of litters in alpine marmots.

Survivorship and permanence in the natal area. Yearlings can easily be distinguished from other age classes because of their smaller

dimensions and body size (Zelenka, 1965; Lattmann, 1973), thus indicating that adult size is not reached at this age. Moreover, no author reports dispersal at one year of life for alpine marmots. Consequently, disappearance from the natal area of animals in their first year of life should be attributed to death, caused by predators and by the stress due to the first overwintering. This pattern is similar to what happens in other geographical areas (Arnold, 1990a, 1993).

All animals that survived the first winter spent their second and third summer in the natal territory: the only missing animal in this time span was a documented victim of a fox (Lenti Boero, 1991c). Biometrical data collected on all the animals trapped (Lenti Boero, unpublished data) indicated that marmots reached adult size, in particular length, at two years, similar to what happens in other areas (Psenner, 1957; Lattmann, 1973; Arnold, 1993). Disappearance from the colony was documented again after this age was reached. And, because it is expected that overwinter mortality is reduced for adult animals, due to accumulation of body reserves (Zelenka, 1965) and experience in avoiding predators, disappearance from the natal area after two years of age should be attributed, at least in part, to active dispersal that was accomplished in the third and fourth year of life for all animals.

Arnold (1990a, 1992), in a large sample of marmots studied in Berchtesgarden National Park, Bavarian Alps, Germany, found that

20% of animals dispersed when two years old and that more than 30% of animals were still living in their natal group when four years old, and some of them until five years old, consequently giving rise to larger social groups. It seems that in the Bavarian Alps, marmots have a wider choice in age of dispersal than the marmots in the Gran Nomenon area. However, it could also be that a larger sample taken in a wider area both in the microhabitat of Gran Nomenon or in the macrohabitat of Gran Paradiso and of the Aosta Valley might document more behavioural choices in the South Western Alps as well.

Retention in the natal territory. Permanence in the natal group should be examined from the point of view of dispersing animals and of the social groups, and both at the genetic and the somatic level. For an individual delayed dispersal is a loss of genetic fitness but might be a gain in inclusive fitness because kin act as helpers in the burrow (Arnold, 1990b). From the point of view of the family group retention is an advantage until a threshold number of individuals is reached and competition for resources begins. Armitage (1975) proposed a population behavioural system related to population density and to the cyclic variation in behavioural characteristics of cohorts successively recruited in the colony, with amicable social interactors recruited when population density was low and agonistic interactors recruited when population density was high. Alpine marmots have a completely different social system, and present data are too scanty to formulate a complete model. Preliminarily, it might be said that the proximate causes of retention in the family group seem to be related both with individual characteristics of dispersers and of the members of social group, apparently related with the density of individuals in each group. In fact when data for each territory are considered, it can be seen that rate of permanence is highly variable: 50% of the few animals born in FamGia territory were retained even when their parents had disappeared, and were tolerated by the newcomers, no agonistic interactions were observed in this group (Lenti Boero, unpublished data). Conversely, all animals born in Tanab territory disappeared at the same time as their parents and other members of the group, and the newcomers seemed very aggressive and highly intended to protect their territory from intruders (Lenti Boero, 1991b; Lenti Boero, in press). Only 24% of the animals born in

FamGenz territory were retained in the natal group and chasing away three year olds was very frequent (Lenti Boero, 1985, 1992 and unpublished data).

Fate of dispersing animals. The ultimate cause of dispersal is to enhance the genetic flow within a population and to avoid excessive breeding (Shields, 1987). My study sample was taken from a wider area where hibernating burrows were known and monitored each year (Lenti Boero, 1988 and unpublished data). The total number of animals dispersing from the whole colony was six, because two settled within the colony, conversely, the total number of animals coming into the colony was nine, but only seven were successful breeders. Because genes travel within bodies, it seems that the balance of individuals moving in and out the colony guarantees avoidance of at least extreme inbreeding.

5. Conclusions

General theory suggests that populations adapted to different geological, vegetational and biological environments might show behavioural differences in setting the age of dispersal and, accordingly, the degree of sociality and the size of social groups (Barash, 1974; Krebs & Davies, 1978). The colony investigated in this study has the highest rate of turnover of adult reproducers ever documented for an alpine marmot colony in the Alps (Zelenka, 1965; Barash, 1976; Mann & Janeau, 1988; Lenti Boero, 1991; Perrin *et al.*, 1993). Among the causal factors of those results are high altitude, northern exposition, long lasting snow cover, the grazing cattle, all factors that reduce the energy intake, and heavy predatory pressure. All the above factors have been reported to reduce the number of marmot populations in the Aosta Valley (Grimod *et al.*, 1991; Bassano *et al.*, 1992) and in other areas of the Alps as well (Chiesura Corona, 1992; Macchi *et al.*, 1992; Panseri, 1992; Rodrigue *et al.*, 1992). Due to lack of stability for reproducing pairs, this high turnover rate indirectly influences the entire productivity of the colony, which was lower than the one reported by Mann & Janeau (1988), notwithstanding the fact that their average litter size was less than in the litter size in the Gran Nomenon area.

The mortality rate was similar to the one reported by Arnold (1990b, 1993), however retention in the natal group was longer in his study area, this might also be correlated to greater stability of the reproducers.

In fact high turnover, and consequently the augmented probability of finding or gaining an empty hibernating burrow for settling, might be a major factor in setting dispersal at an earlier age than in the Berchtesgarden area. In conclusion the major differences found in this study in reproduction rates and the age of dispersal are related to the high turnover rate and, indirectly the harshness of the environment causing it.

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