

Population dynamics, mating system and philopatry in a high altitude colony of alpine marmots (*Marmota marmota* L.)

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This study took place in the Parco Nazionale del Gran Paradiso (P.N.G.P.) from 1981 to 1993. Most of the observations were made from early June to late September. Marmots inhabited the concavities of the valleys above the timberline and on slopes from 0° to 35° of a transect of 4200 ha. Density was estimated by animal counts in two sample areas and ranged from 0.6 to 1.5 an/ha. Population dynamics was investigated from 1985 to 1993 in a colony at 2350 m; 57 marmots were live trapped for individual recognition. The total number of sexually mature reproductive groups observed was 27, in 18.5% a trio made of two unrelated males and one female was present. Never were two adult females found together and never were two different litters found concurrently on the same territory. Male/female ratio for immigration was 1.8, G test $P > 0.005$. Mean group size not including infants was 4.7 ± 2.9 , range 2-11. Social groups had the highest turnover rate ever reported for a colony of alpine marmots. A total of 60 infants were born during this study. Mean litter size was 4 ± 0.65 , and the median was 4. Mean number of litters sired per female was 1.5 ± 1.77 . Forty percent of the new pairs disappeared after their first overwintering with a litter. Infant mortality, ascribed both to winter stress and predation, was 77.7% when both parents, or at least the mother only, was present the following summer. No sex difference for philopatry was found, and mean age length of residence in the natal territory was 2.29, range 2-3. Predation was documented on 8.77% of all individually marked animals.

KEY WORDS: behavioural ecology, alpine marmots, population dynamics, mating system, infant survivorship.

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INTRODUCTION

Alpine marmots (*Marmota marmota* L.) are autochthonous and allochthonous winter hibernators living in European mountains (Pyrenees, Alps, Apennines, Carpathians) (GHIGI 1911; WEHRLI 1935a, 1935b; ELLERMANN 1940; ELLERMANN & MORRISON SCOTT 1951; TOSCHI 1954; COUTURIER 1964; BIBIKOV 1968, 1989, 1996; CAGNOLARO 1969; ZIMINA & GERASIMOV 1973; KRAPP 1978; SPAGNESI et al. 1979; CAGNOLARO & SPAGNESI 1981; HERRERO et al. 1987, 1994; FERRI et al. 1988; LAPINI 1989a, 1989b; MAGNANI 1992; PRELEUTHNER 1992; PRELEUTHNER et al. 1996) at elevations from 1000 to 3000 m. Density and distribution are both constrained by the life history and ecological adaptation of the species and by anthropic pressure. Distribution and habitat preference studies (BASSANO et al. 1992: 109-177, 227-268; FRIGERIO et al. 1996) indicated that woodlands and *Vaccinium* are avoided vegetation, but see MANN & JANEAU (1988), while alpine meadows are the preferred plant cover, soil with sparse rocks and detritus are uniquely found as geological substrata for settlement, and southern exposure is the primary choice (D. LENTI BOERO in prep.).

Monogamy as a mating system can be defined at the genetic level — when a female mates with only one male, and at the social level — when only a reproductive adult pair is present (WESTNEAT & SHERMAN 1993, GOWATY 1996). It was underscored that the original emphasis on the role of ecology in determining breeding systems has been overshadowed by studies on individual interactions, and that females play a more active role than previously thought by engaging in mate choice. This shows that, in terms of the distinction between genetic and social partners and the potential for genetic benefits, the two original components of breeding systems: parental care and sexual selection, do not covary as cleanly or as consistently as previously thought (REYNOLDS 1996). The alpine marmot is reported by some authors to be both genetically and socially monogamous, as are other species in the genus (PSENNER 1956; COUTURIER 1964; ZELENKA 1965; BIBIKOV 1968, 1989, 1996; LATTMAN 1973; LENTI BOERO 1991; SALA et al. 1996), while other studies suggested a bias toward polygyny (BARASH 1976, 1989; MANN & JANEAU 1988, 1990; PERRIN et al. 1996). A more recent view, however, suggests that the mating system in alpine marmots has a more complex organisation. Polyandrous mating were occasionally observed and extra-pair paternity was demonstrated (ARNOLD et al. 1994, RASSMAN et al. 1994, ARNOLD & DITTAMI 1997, GOOSSENS et al. 1997).

Other aspects of the behavioural ecology of the species studied in recent decades are hibernating strategies (ARNOLD 1990a, 1990b, 1992, 1993), group composition (ZELENKA 1965; BARASH 1976; MANN & JANEAU 1988, 1990; LENTI BOERO & BOERO 1989; LENTI BOERO 1991; SALA et al. 1996), age of dispersal (ARNOLD 1990a, LENTI BOERO 1994), biometry and size (ZELENKA 1965, LATTMAN 1973, KRAPP 1978), behavioural physiology and diet (BASSANO et al. 1996, ARNOLD & DITTAMI 1997). Taken together, they provide a patchy understanding of the behavioural ecology of

the species that requires integration. The present study is the first long term work on different aspects of the behavioural ecology of the species and aims to provide additional knowledge on distribution, density, population dynamics and mating system in a high altitude colony.

METHODS

Study area. The study took place from 1981 to 1993 in the Southern side of the Western Alps, on the territory of the Parco Nazionale del Gran Paradiso (P.N.G.P.), Aosta, Italy. The study site faced northeast and the planimetric surface measured 4200 ha, it included two small valleys: Grand Nomenon and Trajoz, crossed by a main stream and affluents; two wide high altitude meadows: La Valletta and Arpisson; and small clearings below the forest (Fig. 1). The geological substrate was metamorphic, with soil covering the east side of slopes and the bottom of the valleys, and taluses covering the northern side of slopes. One peak surrounded by a glacier: La Grivola (3969 m), and smaller peaks: Trajoz (3123 m), La Valletta (2726 m) and Grand Nomenon (3488 m) were present. Vegetation was identified from field books (STEFENELLI 1982) and included trees from the bottom of the valley until the timberline, shrubs, pastures and alpine meadows with monocotyledons and dycotyledons. For centuries both low and high altitude meadows were frequented by cattle and some clearings were formed within the forest by herdsmen.

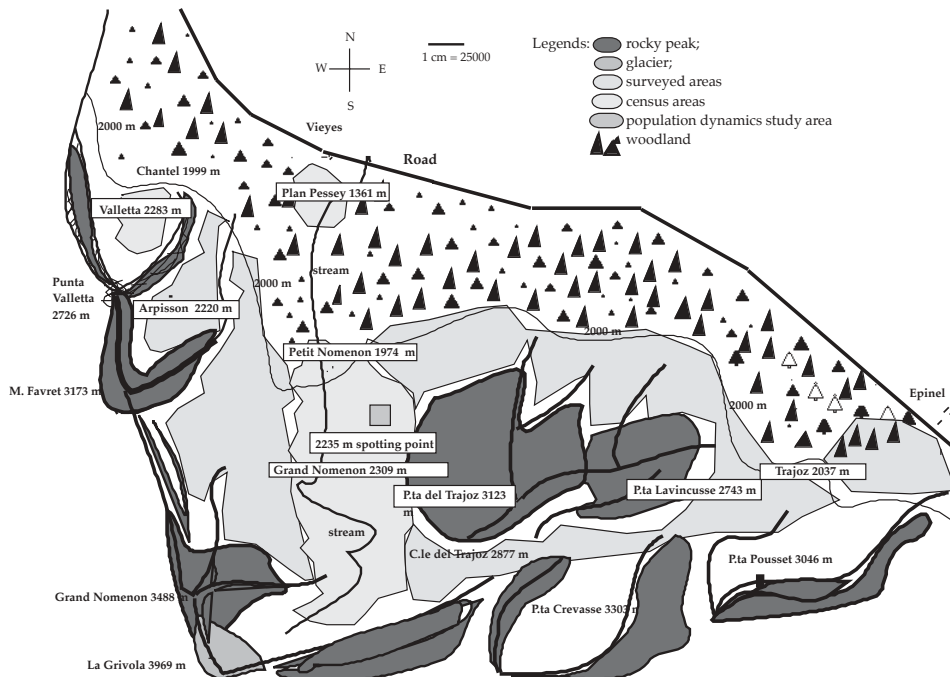


Fig. 1. — Schematic drawing of the lower portion of the Cogne Valley, Valle d'Aosta, Italy, where the study took place.

Distribution of settlements and density. Marmot distribution was assessed from 1981 to 1987 on the entire transect. From early July to late September all valleys were visited by foot, at least 10 times each, on 92 daily excursions from the bottom to the highest slopes and vice versa, or crossed on the high altitude trails of the National Park. Within stands of trees, areas surveyed extended 50 m from both sides of common hiking paths; also woodland not crossed by trails was surveyed as far much as was possible. Field notes on presence of marmots (sighted animals, whistles, freshly utilised burrows and latrines) were taken. An effort was made to be present on the surveyed areas in early morning or late afternoon, but this was not always possible for places very distant from the logistic base. Marmot settlements were considered permanent when found for at least three consecutive summers.

In 45 days of field observation from sunrise to sunset on a subsample of known settlements (La Valletta and Grand Nomenon), unmarked animals were counted every 15 min. Density (an/ha) was then calculated from the maximum number of animals counted together at least 5 times in each area (LENTI BOERO 1987, 1988). A total of 557 counts and 93 hr of ad libitum observations (ALTMANN 1974) were made at La Valletta (12 ha of inhabited surface) in 1982 and 1983; and 198 counts and 61 hr of ad libitum observations were made on four separate observable sites of the large colony at Grand Nomenon (29.6 ha of inhabited surface) in 1984.

Population dynamics and techniques for animal identification. Population dynamics were studied on one of those sites (9 ha) at the Vallone del Grand Nomenon (2235 m) from 1985 to 1993. The site faced North, was crossed by a tiny stream, partially covered by a talus, and dominated by a projecting rock on one side. Vegetation included alpine meadow, shrubs, and some conifers.

Fifty-seven individually marked marmots (22 females and 35 males) were included in this study; 51 (89%) were trapped inside the study area from 1984 to 1993, and 7 (11%) were trapped outside the study area in 1984 and 1985, when extensive trapping was made on the whole colony of Grand Nomenon. In addition 27 non-marked infants were recognised by size and included in the survivorship analysis and 9 among 17 untrapped marmots were recognised by natural markings, consequently, from 84% to 100% marmots were individually recognisable or at least age-classified from 1985, and new immigrants from other sites of the colony were always spotted.

Social composition and age-sex structure. A typical alpine marmot family group includes a dominant reproductive pair and subordinate offspring of different ages (ZELENKA 1965; BARASH 1976; MANN & JANEAU 1988, 1990; LENTI BOERO & BOERO 1989; ARNOLD 1990a; LENTI BOERO 1991; PERRIN et al. 1993; SALA et al. 1996). In alpine marmots sex can be estimated by ano-genital distance (ZELENKA 1965, LATTMAN 1973), female parity by nipple enlargement, and four age classes are reported as distinctive: infants, yearlings, 2-year-old and adults (ZELENKA 1965; LATTMAN 1973; PERRIN et al. 1992, 1993, 1996; but see MANN & JANEAU 1988). However at Grand Nomenon biometrical parameters of yearlings of both sexes were different from 2 years old, but the latter did not differ from adult reproducers or satellites (D. LENTI BOERO submitted) and ano-genital distance of males aged two was shorter than that of adult male reproducers or satellites, as reported by ZELENKA (1965) and LATTMAN (1973). Because male offspring in a group remain sexual immature (ARNOLD & DITTAMI 1997), the difference in ano-genital distance might be considered as an indirect sign of the achievement of mature reproductive potential. All biometrical information was considered in determining the reproductive potentiality or status of individuals in the social groups. In addition, information on social interactions, marking behaviour and territory control, of interest in determining the social hierarchy, in particular when more than one potentially reproductive male was present, were gathered by means of more than 325 hr of direct observation on focal animals (ALTMANN 1974) with binoculars and telescope from an inconspicuous place. For further details see LENTI BOERO (1992, 1993, 1995).

Trapping and marking techniques. In trapping and marking the guidelines for animal research were followed (ANONYMOUS 1986) and no animal was damaged. All animals were

trapped by means of Havaharth, Tomahawk and self-made traps baited appropriately. In order to facilitate handling, marmots were sedated by means of a cocktail of ketamine (from 20 to 40 mg/kg) and xylazine (from 5 to 11 mg/kg) — mean ratio ketamine/xylazine 3.4 — according to the age and alertness of the subjects (VAN PELT 1977, MULDER & MULDER 1979, LENTI BOERO et al. 1988).

After trapping marmots were freeze branded (ROOD 1980) with market available coolers and tattooed for further recognition. Permanent marking guaranteed the recognition of marmots in the following years without trapping, and tattoo facilitated identification in cases of unsuccessful or ambiguous branding. Because marmots are small animals and only one part of the body was branded, the same part was marked for animals living in distant sites of the colony. This fact left a margin of recognition uncertainty in three cases: one male and two females who entered the study area as adult reproducers and had a recognisable permanent mark, indicating a previous trapping in a distant site, but whose tattoos were almost lost and not readable (for other details on trapping and animal handling see LENTI BOERO et al. 1988).

Data analysis. Data were analysed with Systat (WILKINSON 1989), a statistical package for Macintosh, whenever data were represent by a normal distribution, and GLIM (AITKIN et al. 1989) whenever the binomial distribution was the most accurate representation.

RESULTS

Distribution of settlements and density

Above the timberline, marmots were located in the concavities of the valleys, on slopes from 0° to 35°, in particular at La Valletta, Arpisson, Grand Nomenon and Trajoz, connected by high altitude passes. They inhabited all meadows with green vegetation, but not taluses interspersed by *Vaccinium* and *Rhododendron*. Only in Summer 1983 a solitary marmot was found inhabiting a pine wood at 2025 m. Summer burrows as high as 3000 m were encountered or located by binoculars and marmots were sighted on steeper slopes (> 35°) wedged within vertical cliffs of Mount Favret and Colle del Trajoz, but few burrows and the low frequency of alarm calls emitted for human visitors, indicated a low density.

At low elevations a stable colony made up by three families was found at Plan Pessey (1361 m), a small clearing facing North and located in a deep enclosure within two high rocky walls, with a sun-shine period lasting only from 10 a.m. to 5 p.m., in August. A second much broader area with much more sun shine hours was surveyed at the bottom of Vallone del Trajoz, but no marmot settlements were found in the years of the survey.

Density. At La Valletta 7 infants, 11 adults and subadults; and 7 adults and subadults with no infants were counted respectively in 1982 and 1983. This gives a density of 1.5 an/ha and 0.6 an/ha, in the two years respectively. In 1984, 30 animals were counted on four separate sites of the large colony at Grand Nomenon, with a density of 1 an/ha.

Population dynamics and group structure

Immigration, emigration, and philopatry of sexually immature subadults, and sexually mature adult reproducers or potential reproducers are shown in Figs 2-4 for each territory in the study colony. Although the territories were apparently simi-

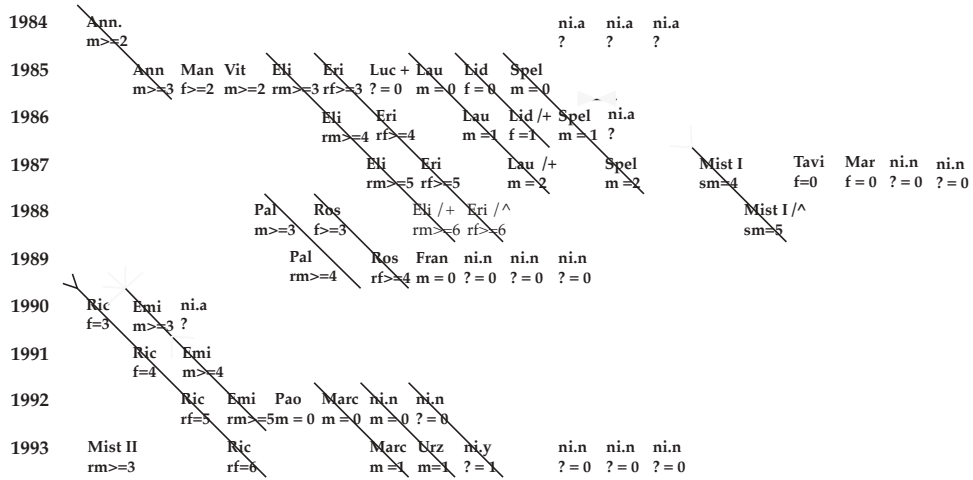


Fig. 2. — Population dynamics in Tanab territory at Grand Nomenon, P.N.G.P. Valle d’Aosta, Italy (1984-1993). Sex and age are indicated below the name of the marmot: “m” and “f” indicate male and female, “rm” and “rf” indicate reproductive male and female, respectively, “sm” indicate the satellite males immigrated from adjacent families or from distant sites of the colony, the definition of reproductive and satellite was made on the basis of previous residency and on the amicable interactions and mutual grooming within the reproductive pair (D. LENTI BOERO unpublished data), “n.i.a” indicate an adult or subadult not individually identified by trapping, “ni.n” indicate an infant not individually identified by trapping. Age is indicated with “=” followed by a number, when known, or “>=” (more or equal to), when estimated; sex of untrapped marmots is indicated with “?”. Ascertained death is indicated with “/+”, and ascertained emigration to another site with “/^”. Black lines connect the same individual through years. Arrows at start indicate immigration from adjacent family groups, arrows at end indicate emigration to adjacent family group.

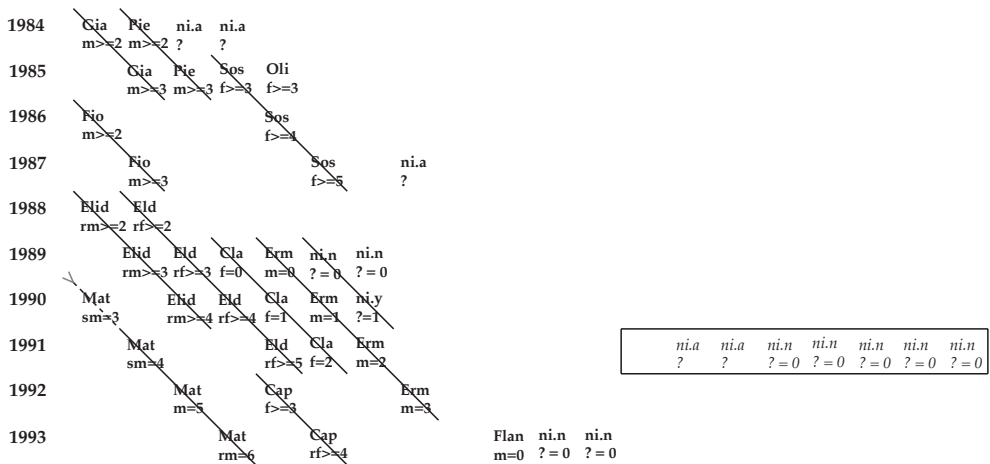


Fig. 3. — Population dynamics in Fam. Gia territory at Grand Nomenon, P.N.G.P. Valle d’Aosta, Italy (1984-1993). For further explanation see Fig. 2.

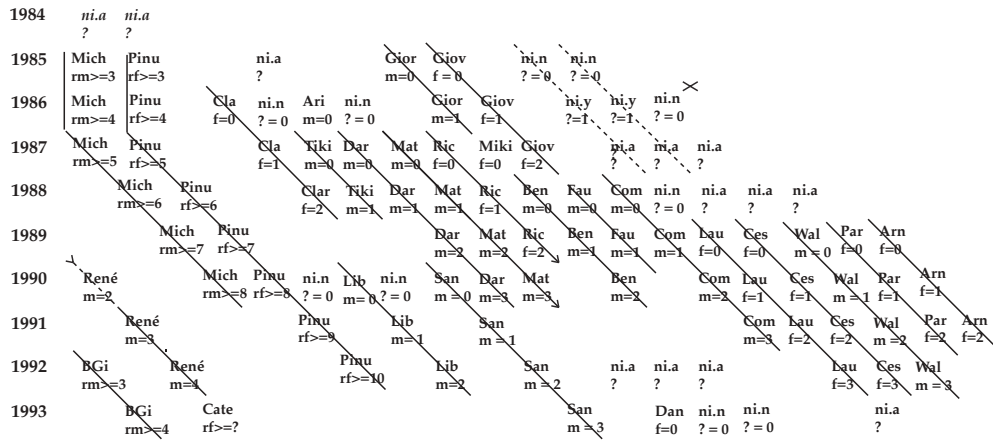


Fig. 4. — Population dynamics in Fam. Genz territory at Grand Nomenon, P.N.G.P. Valle d'Aosta, Italy (1984-1993). For further explanation see Fig. 2.

lar, the groups living on them had very different population dynamics. In Tanab territory four different sexually mature dominant males, one subordinate sexually mature male satellite and three different females in the reproductive status were residents from 1985 to 1993. One of those females, Ricky, was the daughter of the female who occupied the adjacent territory named Fam. Genz from 1988 to 1992, Ricky immigrated in Tanab at age three, weaned her first litter at age five, and a second litter with a different partner, who had replaced the previous one, in the following year, without skipping a reproductive year, as did her mother (see Fig. 4). Fam. Gia territory had a more marked turnover of residents because four different males and four different females inhabited it as sexually mature adult reproducers, however litters were found only twice. Only in spring 1991 a new hibernaculum appeared at the edge of this territory, it was inhabited by a couple, which intruded the previous year. This couple weaned a litter of five young, but the whole family disappeared during winter 1991-1992, and the hibernaculum was abandoned in the following years (D. LENTI BOERO submitted) (trapping of those marmots was always unsuccessful, but the two adults were well recognised by natural marking, consequently they were included in the statistics of reproductive output, and their infants in the computation of litter size and philopatry). The social group in Fam. Genz territory enjoyed more stability: it was inhabited by a stable couple for six years, in 1991 the male was substituted by René, a male aged three, who intruded into the territory in the previous year and was born in an adjacent group not included in this study (Fig. 4). René did not sire any viable offspring in the territory, because the resident female skipped 2 years of reproduction in 1991 and 1992. She disappeared in 1993, and was substituted by a female trapped in 1985 outside the colony, who weaned three youngs with a very aggressive male immigrant in 1992, who apparently displaced René.

From 1985 the total number of male-female groups observed was 27, in 18 cases they consisted of a pair; in 9 cases (33%) a trio was found made of previous adult residents and immigrants from other sites of the colony or from adjacent families, thus probably unrelated with the guesting group; in 5 cases (18.5%) of success-

ful identification of all marmots, the trio consisted of two sexually mature males and one female. Two litters were never found on the same territory. The male/female ratio for all known sexually mature adults was 1.3 males for each female. In three cases the satellite substituted the resident male and was the only sexually mature male in the territory the following year. No resident male was known to have two successive female partners. Male/female ratio for immigrants, 1.8, was significantly biased toward the male sex (G test = 7.916, df = 1, $P > 0.005$). Mean group size, calculated for each year as all sexually mature and immature animals not including infants, was 4.714 ± 2.9 , range 2-11. Group size was related to the number of infants born in the previous year (Regression, $F = 8.4$; df = 1,26; $P = 0.008$).

Reproductive output

Sixty infants distributed in 15 litters were weaned in the colony during this study. Mean litter size was 4 ± 0.65 , and the median was 4. Mean number of litters weaned per each sexually mature female was 1.9 ± 1.72 . If we conservatively suppose that litters were sired by the dominant sexually mature males, the mean number of litters sired by males, was 1.5 ± 1.33 . Those figures are not significantly different. Females' and males' reproductive success in term of the number of litters sired was related to the number of years of residence (Regression, $F = 27.3$; df = 1,6; $P < 0.002$ and $F = 18.9$; df = 1,7; $P = 0.003$, respectively for females and for males).

Infant mortality and philopatry

Hibernation emergence always happened within the first week of May, and observations started at the end of June, consequently it is not possible to disentangle overwintering mortality, migration and early season predation pressure in this study.

The eligible cohort for calculation of infant survivorship in the first year of life numbered 49 infants, that is all the ones born from 1985 to 1992, minus the animals lost to predation in their first summer (Figs 2-4). In 1988 in Tanab territory the adult male was predated by an eagle in early May (Fig. 3), the female emigrated or died before the summer observations started, and all the young were lost. In 1988 Fam. Gia territory and in 1990 in Tanab the previous year's resident reproductive pair was already substituted by a new pair at the end of June, when regular observations started, and their fate is unknown. Infant survivorship in the first year was heavily affected by or correlated with the presence of their parents in the natal territory: 77.7% of infants whose parents were still present in their territories were found in the following year as yearlings, but none of the orphaned infants were found ($\chi^2 = 26.4$, df = 10; $P < 0.003$).

The eligible cohort for the calculation of philopatry of 2-year-olds included all the yearlings from 1985 to 1991 minus the one predated in his first summer (Fig. 2), that is 24 animals. No parent disappeared from this cohort and 83.3% of the animals were retained in their natal family groups when 2-years-old.

The eligible cohort for 3-year-olds included all marmots from 1985 to 1990 minus the one predated in his second summer (Fig. 2), that is 17 animals. For 3 of them, one female and two males, the disappearance of one or both parents and their substitution with new dominant individuals was documented: only one of the males was still retained in his natal area for an additional year by the new pair (see

Fig. 3, year 1992). Seven of the 14 animals (50%) whose parents were still present were philopatric in their third year. No animal of four years of age was found in the natal group independent of their parents' presence, but two marmots, a male, Matteo and a female, Ricky, born in Fam. Genz, migrated at age 3 to the adjacent territories of Fam. Gia and Tanab respectively, where they successfully became adult reproducers (Figs 2-4). No sex difference for philopatry was found and mean age of residence was 2.25 ± 0.866 and 2.33 ± 0.516 , respectively for males and females surviving the first hibernation.

Predation

Predation episodes observed and/or documented in the study area and surroundings included 8.8% of all individually marked subjects: remains of an adult male, predated by an eagle (*Aquila chrysaetos*), were found in spring 1988, (see above); one predation by a female goshawk (*Accipiter gentilis*) on an infant was observed; remains of fox predation on three marked animals — an infant, a yearling and a 2-year-old — were found in the study area or in the surroundings.

Outside the study area a successful attack on an adult marmot by a fox was observed by the author, and three episodes of fox predation and one by an eagle were reported by local rangers.

DISCUSSION

Distribution and density

Most studies conducted in different parts of the European mountains indicate southern exposure as the most preferred (BASSANO et al. 1992: 109-177, 227-268), in the few studies where this was not observed, authors indicated human pressure on the southern slopes as a possible factor counterbalancing the tendency for privileged southern occupation (FRIGERIO et al. 1996). In a survey based on censuses hibernacula as a density estimate (PERACINO et al. 1987) in the Gran Paradiso National Park, it was found that southern slopes were preferred. Consequently the area surveyed in this study can be considered a suboptimal one as regards exposure. Elevation, slope and preferred vegetation found in the Cogne Valley are in accord with other studies (BASSANO et al. 1992: 109-177, 227-268). The fact that at least a few instances of marmots on steep slopes ($> 35^\circ$) and on the passes connecting high altitude prairies above 2800 m suggests an interchange among all populations in the transect, and indicates that high altitude colonisation consists of sparse or absent settlements interspersed with more important concentrations. The latter could be the greater barrier for dispersing animals, due to the strong territorialism of the species (ZELENKA 1965; LENTI BOERO 1993, 1995; BEL et al. 1995). Below the woodlands, at less than 1400 m, marmots were only located in a shady clearing, which was preferred to a broader and more sunny pasture, suggesting that at lower elevations a brief period of sun-shine is preferred, due to thermal constraints (TURK & ARNOLD 1988).

Studies on density are difficult to compare: some authors report the number of colonies as census units (HERRERO et al. 1994, PANSERI & FRIGERIO 1996); others

the number of individuals. When individuals are censused, the carrying capacity is higher in southern habitats with medium slopes (SOLARI 1988, LEONI et al. 1993). At the Parco Naturale Orsiera Rocciavré, western Alps, in locations comparable to my study area, VITA (1992) found a density of 0.2 marmots/ha. A density from 0.24 to 0.36 marmots/ha was found in the entire territory of the Parco Nazionale del Gran Paradiso (PERACINO & BASSANO 1992). Densities reported in this study are higher than those reported above for the western Alps, and comparable with those reported for optimal habitats by SOLARI (1988). However, it should be noted that the density estimate may change according to the methods used (LENTI BOERO 1987, 1988; PERACINO et al. 1987), the ecofacies and whether only the suitable habitat or the whole planimetric surface is considered (LENTI BOERO 1988).

Social groups and mating system

Multiple mating has been observed in many species of tree and ground squirrels (FARENTINOS 1980; HOOGLAND & FOLTZ 1982; MICHENER 1983; SHERMAN & MORTON 1984; SCHWAGMEYER 1984, 1986; TAMURA 1995; MICHENER & MCLEAN 1996; LACEY et al. 1997; HOOGLAND 1998), and electrophoretic and DNA studies have documented multiple paternity in many cases (HANKEN & SHERMAN 1981, FOLTZ & SCHWAGMEYER 1989, SHERMAN 1989, BOELLSTORFF et al. 1994, VAN STAADEN et al. 1994, MURIE 1996), but considerable interspecific variation was found in patterns of sperm precedence within different species (LACEY et al. 1997). In the closely related genus of marmot (GIBOULET et al. 1997) analogous studies are scantier and provide contrasting results: in the yellow-bellied marmot (*Marmota flaviventris*), that has a polygynous mating system with a dominant male defending a territory occupied by smaller female home ranges (DOWNHOWER & ARMITAGE 1971, ARMITAGE 1991), it was found that the young were without exception produced by colony residents (SCHWARTZ & ARMITAGE 1980). However in the alpine marmot polyandrous mating was occasionally observed and subordinate males were reported to sire offspring (ARNOLD et al. 1994). Earlier studies on the alpine marmot reported both a sex ratio of one male to one female (PSENNER 1956; COUTURIER 1964; ZELENKA 1965; BIBIKOV 1968, 1989, 1996; LATTMAN 1973; LENTI BOERO 1991; SALA et al. 1996) and a sex ratio of one reproducing male and two adult females (ZELENKA 1965; BARASH 1976; MANN & JANEAU 1988, 1990). This indicates the coexistence of different strategies: the most frequent monogamy, then social polygyny and genetic polyandry in the sense of WESTNEAT & SHERMAN (1993). The present data add another perspective: social monogamy was indeed the most frequent mating strategy in the Grand Nomenon colony, but social polyandry was adopted in 18.5% of the resident groups and thus can be considered an alternative strategy.

Alpine marmots have the potential to reproduce when 2-year-old. The social structure described in other studies (ARNOLD 1990a, 1990b) and in the present study indicate that alpine marmots remain in the natal family beyond this age, and this seems to happen with parental consent (WASER 1988). However this consent for philopatry implies the cost of reproductive suppression for the younger generations (ARMITAGE 1996). Female steppe marmots (*Marmota bobac*) kept in captivity show breeding suppression when two or more animals are caged with a male, but not when two males and one female are put together (RYMALOV 1997 and personal communication). ARNOLD & DITTAMI (1997) found that subordinate males had a low testosterone level and hypothesised a role of the dominant male in the breeding sup-

pression of competitors. Although I did not measure testosterone levels in this study, the ano-genital distance was significantly shorter in 2-year-old than in adult dominant males for both resident and immigrants, and in a 3-year-old before and after emigration (LENTI BOERO submitted). This finding may support the hypothesis of sexual immaturity in subordinate philopatric males.

Present data point to a female role in the breeding suppression of daughters: although the reported known age for female reproduction in alpine marmots is two (MANN & JANEAU 1990; PERRIN et al. 1992, 1993; SALA et al. 1992; ARMITAGE 1996) throughout this study eleven potential female breeders aged two or more were recorded as living in the same territory and in presence of their mothers, but none of them had a litter, even when a satellite sexually mature male was present. The only female born in the colony who had a litter did so 2 years after emigrating in a territory adjacent the natal one, and she actively defended her new territory from the intrusion of her mother (D. LENTI BOERO personal observation). Females were probably also active in keeping out of the territories unrelated female competitors, as the male biased sex-ratio for immigration may prove. In fact marmots are biennial breeders and all groups, but an exceptional one, skipped a reproductive year and neither did a second female alternate reproduction as happens in *M. olympus* and *M. caligata* (BARASH 1989). This situation with females stood in contrast to the apparently more socially tolerated satellite males which were present 18.5% of the time. Analogously to reports from the French Alps (BEL et al. 1995), at Grand Nomenon adult females marked their territories for the entire season (LENTI BOERO 1995), this behaviour might be related with territory defence from intruding female competitors, but does not explain the male biased sex ratio for the presence of satellites. Male marmots at Grand Nomenon seemed more tolerant of competitors than females were, or simply they had a less refined way of getting rid of them. Although preliminary, the present data provide a stimulus for further research on female breeding strategies.

Litter size, infant mortality and philopatry

In the present study I observed five new pairs undergoing their first hibernation alone with their infants. Two of those pairs and their litter were not found the following summer. In addition, four yearlings and a 2-year-old descendant of the two animals inhabiting Tanab territory in 1987 disappeared after the death of their father and the disappearance of their mother. Infant survival thus seems strictly related to the survival of the reproducing pair. Being a parent for the first time is risky for alpine marmots, because in the first overwintering with the litter the entire burden of thermogenesis falls on the two adults (ARNOLD 1990a, 1990b, 1992, 1993). The infant mortality rate reported in my study is comparable to other geographical areas (ARNOLD 1990a, 1993).

Forty-three percent of the animals weaned in the area were sired by a couple with a high quality female that reproduced for 6 consecutive years. As other pairs in this study, this couple simply started with a litter of four infants and no elder helper (Fig. 4: 1985). Then the annual breeding accelerated the stabilisation of the group, with more individuals guaranteeing alarm signalling, territorial defence and possibly helping of the young during hibernation (ARNOLD 1990a, 1990b; LENTI BOERO 1992, 1995). This sustained breeding effort might be ascribed both to high microenvironmental quality of the territory (LENTI BOERO 1996) and to high genetic

quality of the female. The first factor cannot be ruled out, because no vegetation study was performed, but the high genetic quality of the female is supported by the fact that her daughter weaned two litters in two consecutive years in an adjacent territory. Although in domesticated animals the heritability of fecundity is very low, we know very little about the genetic variation of this trait in natural populations (RICKLEFS 1980), and the reported finding should be considered with caution. This high reproductive rate clearly enhanced the fitness of this female, because she sired the only animals which became successful reproducers in the same study area, though not in their natal home range.

Published data on litter size are scanty and difficult to compare. In the present study a mean or median litter size of four is reported; analogous sizes are reported by ZELENKA (1965) in Switzerland, ARNOLD (1990a) in the Bavarian Alps, PERRIN et al. (1993) in the French Alps, and SALA et al. (1996) in the Apennines. Litter size of 2.5 and 1.7 are reported respectively by MANN & JANEAU (1988) and BARASH (1976) in the French Alps. This allows us to hypothesise that macroenvironmental factors might influence the size of litters in alpine marmots, but further data are needed.

Population dynamics, animal turnover and predation

In ground dwelling hibernating sciurids the impact of extrinsic environmental factors such as detrimental weather, food resources and predation on population dynamics has been reported by many authors (MORTON & SHERMAN 1978; DOBSON 1984; PHILLIPS 1984; DOBSON & KJELGAARD 1985a, 1985b; VAN VUREN & ARMITAGE 1991, 1994; HUBBS & BOONSTRA 1997). In the yellow-bellied marmot demographic changes occur primarily as a result of overwinter mortality of all age groups, dispersal of yearlings, and recruitment of highly related female reproducers (daughters and full sisters) while immigration is relatively unimportant, and the role of intrinsic social behavioural factors on population dynamics has been emphasised (ARMITAGE & DOWNHOWER 1974; ARMITAGE 1975, 1991). Because *M. flaviventris* is a polygynous species the turnover of colonial males has little effect on the number of resident animals (ARMITAGE 1974). In effect, in the yellow-bellied marmot the mating system and demography reinforce each other (ARMITAGE 1996). Present data for the alpine marmot show a markedly different pattern: due to reproductive suppression (see above) recruitment of younger generations is virtually non-existent and fitness success is related to the progeny's successful dispersal and ownership of a territory. This in turn is affected by predation pressure (VAN VUREN & ARMITAGE 1994) and availability of food resources and hibernacula, that are believed to be limiting factors for population expansion in alpine marmots (LENTI BOERO 1988, 1996, submitted). An estimation of habitat availability and of the demographic pressure can be made by surveying the number of hibernacula across years and extrapolating the number of potential 2 or 3-year-old dispersers produced each year in the area from data gathered in the present study on population dynamics (LENTI BOERO 1988, submitted). During this study the number of hibernacula lasting at least 4 years (theoretically two generations) rose from 10 to 13, although the number of all hibernacula found in springtime had a wider fluctuation: from 10 to 21 (LENTI BOERO submitted). I considered that half the population gave birth to four young each year, that the probability of survival of those youngs in the first winter was 77.7% and multiplied this by the number of permanent hibernacula each year.

This gave a figure of 0.88 male and female potential immigrants per year per each territory at Grand Nomenon, that is a total of 23.74 animals for the whole study. The real number of immigrants observed was 17. This discrepancy might be explained by the fact that some animals do not choose the strategy of conquering a territory evicting the resident owner, but try to dig new hibernacula for themselves, and sometimes are successful in making them permanent hibernacula to be added to the colony pool (LENTI BOERO submitted).

Present data suggest that predators might influence demography in opposite ways, when killing sexually immature animals or sexually mature reproducers: in the first case they lower the population pressure by eliminating animals that may compete for territories, but in the second case, they make territories available for new immigrants: in fact the killing of the adult dominant male in Tanab in the spring of 1988 (Fig. 2) led to the disappearance of the whole family group and created a vacuum which was immediately filled by a new pair.

Consequently, although the figure of 8.77% of known animals killed by predation is probably an underestimated, because very few observations occurred in springtime after emergence, when the fox and the eagle, the most important predators for alpine marmots, are more active, the role of predators on population dynamics is unpredictable. The high turnover rate recorded in this study, the highest ever reported for a colony of alpine marmots, has yet to be explained (ZELENKA 1965; BARASH 1976; MANN & JANEAU 1988, 1990; PERRIN et al. 1993).

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