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The evolution of marmot sociality:

I. Why disperse late?

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Summary. Prolonged toleration of offspring in marmots was hypothesized to be (1) a means of preventing dispersal of undersized young (Barash 1974a) or more generally (2) continued parental investment, increasing the probability of descendant survival and reproduction (Armitage 1981, 1987). These hypotheses are tested in this paper for one of the most social of marmot species, the alpine marmot. The animals studied lived in groups within territories defended by a dominant male and female, or as floaters lacking a well-defined home range. Offspring did not disperse before sexual maturity at age 2 (Fig. 1). Only territorial females bred, whereas territorial males were not able to monopolize reproduction likewise (Table 2). Dispersers had similar spring mass to nondispersers (Table 4). Hence, hypothesis 1 is not supported, at least not for adult-sized, >2 years old animals. During their residency, 19% of subordinates obtained their natal territory or a neighboring one (Fig. 2). Long distance dispersal bore a high mortality risk. Thus, toleration of mature offspring could well represent parental investment. Other results, however, suggest additional influences on the timing of dispersal. (i) Males dispersed later than females (Fig. 3), possibly because of mate sharing by territorial males (see Emlen 1982). (ii) The higher mass loss of dispersers during the previous winter indicates that weak animals were forced to leave (Table 5) despite presumably lower chances of becoming territorial (Table 3). (iii) Subordinate animals which could not be the offspring of both territorials present were not more likely to disperse (Fig. 3). (iv) Lower dispersal rates when immatures lived in the group (Fig. 3) may indicate benefits from the subordinates' presence for rearing young.

Introduction

The species of the genus *Marmota* are distributed from lowlands to high alpine regions and from semideserts to arctic tundras. Although of comparable morphology, they exhibit very different social organizations, mainly due to differences in the dispersal age of their offspring. Woodchucks (*M. monax*), for instance, living at low elevations, are solitary and highly aggressive. Offspring disperse during the year they are born and commonly reproduce as early as the next spring (Grizzell 1955; Bronson 1963, 1964; Davis 1981; Ouellet and Ferron 1986; Ferron and Ouellet 1989). Yellow-bellied marmots (*M. flaviventris*), inhabiting medium elevations to high altitudes (Frase and Hoffmann 1980), are more gregarious. The basic social units are polygynous groups frequently developing through recruitment of daughters. Most dispersal occurs after the first hibernation (for review see Armitage 1986). Olympic marmots (*M. olympus*) reside in high alpine regions in distinct social groups whose members share a common home range. Offspring disperse and reproduce at the earliest during their third season (Barash 1973). Similar social organization with natal dispersal after the second hibernation or later is also known for *M. bobac centralis* (Ismagilov 1956), *M. baibacina* (Berendyaev and Kulkova 1965), *M. marmota* (Zelenka 1965; Barash 1976; Lenti Boero and Boero 1989), *M. caligata* (Barash 1974b; Holmes 1984), *M. sibirica* (Suntzov 1981), *M. menzbieri* (Maschkin 1982), and *M. caudata* (Ebenhöh and Arnold, unpublished data).

Delayed dispersal correlates with environmental harshness, increasing with altitude and latitude. Barash (1974a) suggested the associated shortened vegetative growing season as the ultimate reason for this correlation. Animals living in severe environments require more time "to accumulate sufficient body weight for the biologically demanding acts of dispersal and reproduction". Social tolerance could have evolved to prevent dispersal of undersized young (hypothesis 1). Armitage (1981, 1987) did not regard body mass alone as the crucial variable but viewed delayed dispersal and hence sociality as a life history tactic in ground-dwelling sciurids. In species whose progeny cannot mature in one season, the parents continue to invest in their offspring beyond weaning by providing a source of food, better protection from predation, and a hibernaculum, thus increasing the probability of producing reproductive descendants (hypothesis 2).

Both hypotheses were developed in a comparative approach which included only one of the highly social species, *M. olympus*. Whether they apply to another one, the alpine marmot, was investigated in this study.

General biology of alpine marmots

Alpine marmots are large, diurnal, burrow-dwelling rodents that reside at elevations of between 600 and 3200 m (reviewed in Forter 1975). They reproduce at most once a year. Mating occurs during the first 2 weeks after emerging from hibernation, but females are receptive for a maximum of 1 day (Müller-Using 1957; Psenner 1957; Hembeck 1958; Koenig 1973). Young are born after 34 days of pregnancy (Psenner 1957). At the beginning of July, they first appear above ground and then live primarily herbivorously like adults (Psenner 1957). Alpine marmots can be sexually mature after their second hibernation but usually do not reproduce before their third summer (Psenner 1960; Kratochvil 1964; Zelenka 1965; Ratti 1970; Lenti Boero and Boero 1989).

Materials and methods

Study site and animals. The study was conducted from 1982 to 1988 in the Berchtesgaden Alps, FRG, between elevations of 1100 and 1500 m. In total, 386 animals were permanently marked upon first capture by tattooing numbers into the skin of the inguinal region. Additionally, numbers were dyed into the dorsal fur with Nyanzol-D fur dye. These fur markings allowed identification of individuals over larger distances until the annual molt. They were renewed thereafter.

The study population was surveyed twice a year by trapping. This was done in early April, immediately after the marmots had emerged from hibernation, and in July when the infants first emerged above ground. The weaners were captured within a few days before they could intermingle with infants emerging from other burrows (Arnold 1990). Resident animals not trapped in a year (roughly 10%) were all captured in the following year. Animals were weighed to the nearest 50 g at each capture with a hand-held spring balance. Age determination was possible by body mass until the beginning of the third active season during which the animals reached adult size. Animals in their year of birth are designated as infants, after their first hibernation as yearlings, after their second hibernation as 2-year-olds and so on. In data analyses concerning age, only individuals already marked as infants or yearlings were used. Dams were easily recognized by enlarged nipples with bare skin around. The composition of the resident population was again recorded by observation during the last days prior to the onset of hibernation.

Alpine marmots do not gain mass after hibernation as long as the thaw is not complete in their home range (Arnold 1986). Reweighings of animals within 10 days gave virtually identical results (mean difference = 3 g, (SD) = 150.9, $n = 117$). Hence, weighings within this period after first emergence or after the date when a home range became free of snow (determination described in Arnold 1990) tally with the body mass at emergence from hibernation.

Hibernation mass loss. Hibernation mass loss was calculated as the difference between an individual's body mass at the end of September when entering hibernation and the emergence mass in the following spring. The mass gain of alpine marmots during their active season is best described by a Gompertz growth curve (Arnold 1986). Fall mass was estimated by extrapolating such a growth curve fitted to an individual's mass data. Estimates were sufficiently accurate if the following information was available for a given animal: (i) at least two weighings in a minimal time span of 40 days, (ii) the date of emergence from hibernation, (iii) the date when the home range became free of snow (determining the inflexion point of the growth curve), and (iv) the date of onset of the following hibernation. For a detailed description of the method and tests of its reliability see Arnold (1986).

Electrophoretic analysis. Until 1987, 2–3 ml of blood were drawn from the femoral vein from each animal marked. After about 1 h, the serum and solid fractions were separated by centrifugation, transferred into plastic vials, and stored at or below −70° C. Proteins were studied in the laboratory by horizontal starch gel electrophoresis. It is generally assumed that the allozyme phenotype of an individual reflects its genotype. Electrophoretic and staining techniques were adopted from those described in May et al. (1979). Most stain recipes were based on Harris and Hopkinson (1976). Buffers were modified from Markert and Faulhaber (1965), Ridgeway et al. (1970), Selander et al. (1971), and Clayton and Tretiak (1972). For the electrophoresis study, the solid blood fractions were homogenized after adding about 1 ml of extraction buffer [Tris(hydroxymethyl)aminoethane hydrochloride, adjusted to pH 7.1 with Tris base; approx. 0.05 molar]. Electrophoresis lasted 5 h at a current of 70 mA.

Surveying for allelic variants of proteins, blood samples from an average of 67 individuals (SD = 35) from different localities were used. Some 53 loci were investigated, and two di-allelic systems were found, a peptidase (PEP) and superoxide dismutase (SOD). All other proteins studied were monomorphic. For both polymorphic enzymes, the best pattern resolution was achieved using 0.04 molar citric acid, adjusted to pH 5.8 with *N*-(3-aminopropyl)-morpholine as electrode buffer and a 1:10 dilution of this buffer for gel preparation. The more anodally migrating variant was labeled b, the other a (Table 1). The peptidase analysed functioned with glycyl-leucine.

Statistical analysis. All statistical tests were calculated by means of SPSS × Information Analysis System, Release 3.0 (SPSS Inc.,

Table 1. Polymorphic blood protein loci used for paternity exclusion and test for goodness-of-fit of Hardy-Weinberg expectation

Locus	Allozyme variant	Variant frequency	Genotype	Observed frequency	Expected frequency	Significance
Peptidase	a	0.848	aa	228	232	$\chi^2_{(2)} = 1.9$
	b	0.152	ab	90	83	ns
			bb	4	7	
Superoxide dismutase	a	0.474	aa	68	72	$\chi^2_{(2)} = 0.8$
	b	0.526	ab	168	160	ns
			bb	85	89	

444 N. Michigan Avenue, Chicago, IL 60611). χ^2 values given are the increase in likelihood-ratio χ^2 ('G', Sokal and Rohlf 1981) due to the decrease in the fit of a hierarchical log-linear model if the interaction in question between variables is assumed to be nonexistent.

Results

Social organization of the resident population and mating system

The major part of the study population lived socially and resident on alpine meadows (about 130 individuals yearly in 19–24 groups). Typical groups comprised a dominant pair and their offspring from one or several years (see Arnold 1990 for quantitative details). A group's home range was defended against adult strangers, mainly by the dominant animal of the same sex. In the following, the dominant pair is therefore referred to as the territorial animals. Except for some adult subordinate males living peripherally until late summer, use of space and burrows was unrestricted for all group members (see also Barash 1976).

Among females, reproduction was evidently restricted to the territorial animals, even when those failed to litter [on average, 48% ($SD=8.1$, $n=7$) did so each year]. Only territorial females lactated, although mature subordinate females often showed signs of estrous (tumefaction and reddening of the vaginal mucous membranes) and were occasionally captured when already in advanced pregnancy. It is extremely unlikely that the infants born in a group ($\text{median}=3.5$, range 1–6, $n=78$) belonged to different litters. (i) They always emerged from the same burrow within 1 or 2 days, indicating equal age. (ii) Their number did not correlate with the number of mature females in a group [Spearman rank correlation coefficient $(r_s)=0.027$, $n=76$, ns]. (iii) Their weaning masses ($\text{mean}=487$ g, range 280–780 g, $n=121$) varied less than between infants from different groups (ANOVA, $F_{(33,87)}$, $P<0.001$). (iv) Their genotypes at both polymorphic loci were always compatible with the territorial female.

Analysis of allozymes showed that 4 of 76 litters were not sired or not solely by a group's territorial male. Five of 245 offspring carried alleles not found in the natal group's territorial male (Table 2). Subordinate males with genotypes compatible with possible paternity lived in two of the four groups (Table 2) but were present in neighboring groups as well. Territorial males might well be excluded from paternity more frequently because the chance of detecting cuckoldry was low with only two informative loci available. Polyandrous matings immediately after one another promote multiple paternity of litters (Huck et al. 1985). Estrous alpine marmot females are known to copulate with all males present in rapid succession, and the males show no obvious rivalry for the mate (Müller-Using 1957; Hembeck 1958; Koenig 1973). The same was observed during this study, although copulations rarely occurred above ground. In one group, a subordinate daughter copulated several times with three sibs (or halfsibs?) as well as with the territorial male. In another group, the territorial male's littermate copulated with the territorial female, while in a third group only the territorial male copulated, despite the presence of 2-year-old males.

Floaters and their fate

The floating part of the study population consisted of animals that had dispersed from their natal site and of evicted, formerly territorial individuals. A major problem was to assess whether animals that disappeared from the resident population had died or become floaters. Infants or yearlings were never captured as floaters. These were almost exclusively ≥2-year-old, dispersed animals ($\chi^2_{(5)}=94.0$, $P<0.001$; Fig. 1, lower graph). Yearling marmots rarely disappeared from the resident population during the active season but ≥3-year-old animals overproportionally so ($\chi^2_{(5)}=86.5$, $P<0.001$; Fig. 1, upper graph). They and the disappearing 2-year-olds mainly vanished during late April and May. In contrast, disappearance of yearlings and territorials did not peak comparably. Infants disappeared most frequently during

Table 2. Genotypes of adults and infants in groups with paternity exclusion of the territorial male. Genotypes of offspring incompatible with the territorial male are shown in bold type

Group number	Year	Allozyme	Genotype of			
			Territorial male	Territorial female	Subordinate male*	Infants born in the group
11	1984	PEP	aa	aa		aa aa aa aa aa
		SOD	bb	ab		bb ab **aa** bb bb
18	1982	PEP	aa	aa		aa aa aa **ab**
		SOD	bb	aa		ab ab ab ab
19	1987	PEP	ab	aa	ab	ab aa ab
		SOD	bb	ab	ab	bb ab **aa**
22	1987	PEP	aa	aa	ab	**ab** aa **ab**
		SOD	ab	bb	ab	bb ab bb

* Subordinate adult females lived in none of these groups, a subordinate adult male in two. PEP, peptidase; SOD, superoxide dismutase

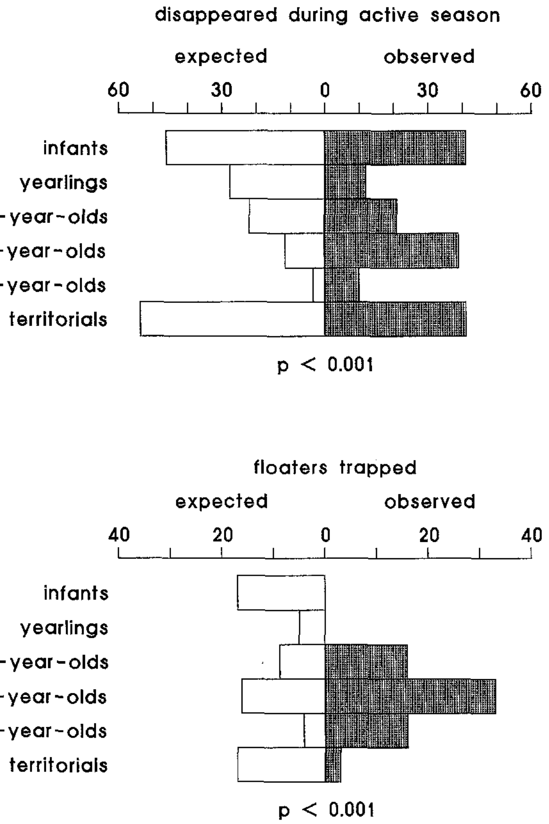

Fig. 1. Disappearance from the resident population and frequency of captured floaters of various individual classes. Expected values in the upper graph are calculated from the number of animals per individual class present in the resident population after hibernation. Expected values in the lower graph are calculated according to the number of animals per individual class that disappeared from the resident population during the active season (p = significance level of χ^2)

their first days above ground in July. Infants were very incautious during this time, and it was even possible to catch them by hand. Red foxes were seen regularly to prey upon infants, particularly during this period. Thus, the loss of infants and yearlings is most likely entirely due to mortality. Except for cases of known mortality, older animals that disappeared from the resident population during summer were regarded as dispersed or as evicted if they had possessed a territorial position.

Unlike residents, floaters had no well-defined home ranges. They lived in a hostile habitat, which either lacked shelter (burrows and escape holes, dug by marmots) or was difficult to survey in order to detect predators (e.g., woodland). During the study period, 109 of the marmots that entered the floating part of the population failed to become resident again in the same year. Onle 4 of them were retrapped in later years, suggesting extraordinarily high mortality among wandering animals. The only way for floaters to become resident again was to obtain a territory elsewhere. Eight of 76 long distance natal dispersers and none of the 33 once territorial and later evicted animals did so within the study area. However, this proportion understates a wandering animal's chances. Successful immigration into the resident study population indicates that at least some animals born in the study area obtained territories outside. The immigration rate was estimated when all unmarked floaters could reliably be assumed to be born outside the study area. This was the case for the third and subsequent years after the beginning of the study, as floaters were unlikely to survive more than two winters. Since 1984, 8 of 43 (19%) newly established territorials in the study area were immigrants.

The ways and chances of obtaining a territory

Most animals obtained their territory for reproduction by evicting the previous tenant of the same sex ($n = 29$). The winners in fights for a territory were all of adult size (cp. Tables 3, 4) and of similar body mass after hibernation to the losers but had lost less mass during the preceding winter (Table 3). Apparently, an adult animal's competitive abilities did not depend on its body mass but on its mass loss during the last hibernation. Alternatively, marmots obtained territories by entering a group when a territorial position was vacant or by occupying abandoned sites ($n = 21$). Colonization of those parts of the study area formerly not inhabited by marmots occurred only once by one male and one female, although floaters were regularly seen there. During one season, it appeared almost impossible to dig a burrow of sufficient depth to ensure a successful hibernation. Although sites with burrows (26 in the study area) seemed to be a limited resource, on average 9% were not occupied.

Yearlings never became territorial under natural circumstances. However, two yearling females introduced into the study population experimentally in May 1984 did so. After being released, they moved distances of at least 2–3 km. In July each became resident at two different abandoned marmot sites and founded a new group, together with a male. From the 52 animals that became territorial during the study period, 5 dislodged a parent, and 1 inherited its position. Some 21 marmots became territorial in surrounding groups within approximately 500 m of the natal home range, 14 of them by expelling the former territorial animal. During short excursions from their home range in spring, the marmots frequently visited neighboring territories within this dis-

Table 3. Mass loss (g) during last hibernation and emergence mass of animals that became territorial by expelling the former territory owner and of evicted, previously territorial animals (mean ± SD, n in parentheses)

	Mass loss	Emergence mass
Newly established Territorials	1252 ± 295.7 (15)	3027 ± 292.7 (15)
Evicted, previously Territorial animals	1557 ± 246.4 (8)	3013 ± 363.3 (8)

ANOVA, effect of hibernation mass loss on subsequent fate $F_{(1,21)} = 6.2$, $P = 0.02$; effect of emergence mass $F_{(1,21)} = 0.1$, ns

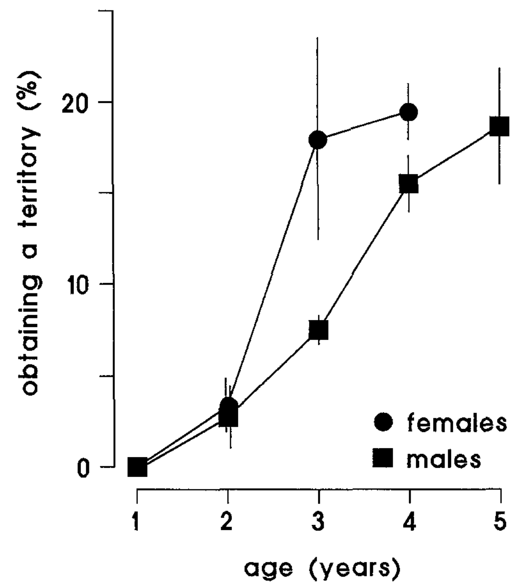

Fig. 2. Proportions of cohorts ($\bar{x} \pm$SE) that obtained during their residency as subordinate animals the natal or a neighbouring territory within approximately 500 m. Means are plotted cumulative over age (total $n=191$, mean cohort size=38, SD=11.7)

tance (see also Lattmann 1973). On average, 19% of a cohort obtained a territory without taking the risk of long distance dispersal (sex difference: $\chi^2_{(1)}=0.5$, ns; Fig. 2), mostly when 3 or 4 years old (age difference: $\chi^2_{(3)}=12.4$, $P=0.006$; Fig. 2). In these two age classes, more females than males succeeded ($\chi^2_{(1)}=3.7$, $P=0.05$; Fig. 2).

The relatedness of both partners could be assessed for 36 newly formed pairs. In 3 cases, they were half or full sibs. In 4 cases the mate of a new territorial animal was its potential father, i.e., the territorial male present in its birth year, and once it was its mother. Thus, close inbreeding could occur in 22% of the newly established pairs.

Factors influencing dispersal

After emerging from hibernation, yearlings averaged about 40% and 2-year-olds about 80% of adult mass. Older offspring were not distinguishable in mass from territorial animals (Table 4). Dispersers of both sexes were not heavier at emergence from hibernation than nondispersers, neither among 2-year-old nor among older animals (Table 4). However, mass losses during the previous winter were higher among animals that left their natal group in spring (Table 5). Furthermore, the proportion of subordinates dispersing from a group seemed to be higher the larger a group was in spring ($r_s=0.198$, $n=93$, $P=0.06$). The partial influence of four dichotomous variables on dispersal was tested jointly (Fig. 3). An individual's age (2-year-old vs. older) significantly influenced whether it dispersed or not ($\chi^2_{(1)}=69.8$, $P<0.001$). Most 2-year-old animals and about a third of the 3- and 4-year-olds spent another year at home.

Table 4. Body mass (g) after hibernation

Individual class	Males						Females					
	Dispersers			Nondispersers			Dispersers			Nondispersers		
	mean	SD	*n*	mean	SD	*n*	mean	SD	*n*	mean	SD	*n*
Yearlings	–	–	–	1143	268.6	70	–	–	–	1130	220.0	44
2-year-olds	2550	492.4	3	2440	300.9	53	2167	238.5	9	2257	240.1	29
3-year-olds	3080	195.9	21	2913	225.9	19	2847	205.0	17	2780	148.3	5
≥4-year-olds	3015	247.0	13	2911	362.1	9	2900	–	1	2725	35.4	2
Territorials	–	–	–	3005	306.3	94	–	–	–	2858	285.1	99

Three-way ANOVA of body mass of potential dispersers (≥2-year-old nonterritorial animals): effect on dispersal, $F=1.6$, ns; effect of sex, $F=8.8$, $P=0.003$; effect of age, $F=44.6$, $P>0.001$; all possible interactions, ns. Unplanned comparisons of individual classes in one-way ANOVA (separately conducted for males and females, identical results): differences between yearlings and 2-year-olds to all other classes, $P<0.001$; differences between 3-year-olds, ≥4-year-olds, territorials, ns

Table 5. Mass loss (g) of potential dispersers during previous winter

Individual class	Males						Females					
	Dispersed			Not dispersed			Dispersed			Not dispersed		
	mean	SD	*n*	mean	SD	*n*	mean	SD	*n*	mean	SD	*n*
2-year-olds	1043	151.5	2	911	232.0	32	1229	217.8	5	995	293.1	19
≥3-year-olds	1315	283.0	23	1301	279.5	22	1298	270.0	13	1101	384.5	6

Three-way ANOVA of mass loss: effect on dispersal, $F=4.0$, $P=0.05$; effect of sex, $F=0.03$, ns; effect of age, $F=8.5$, $P=0.004$; all possible interactions, ns

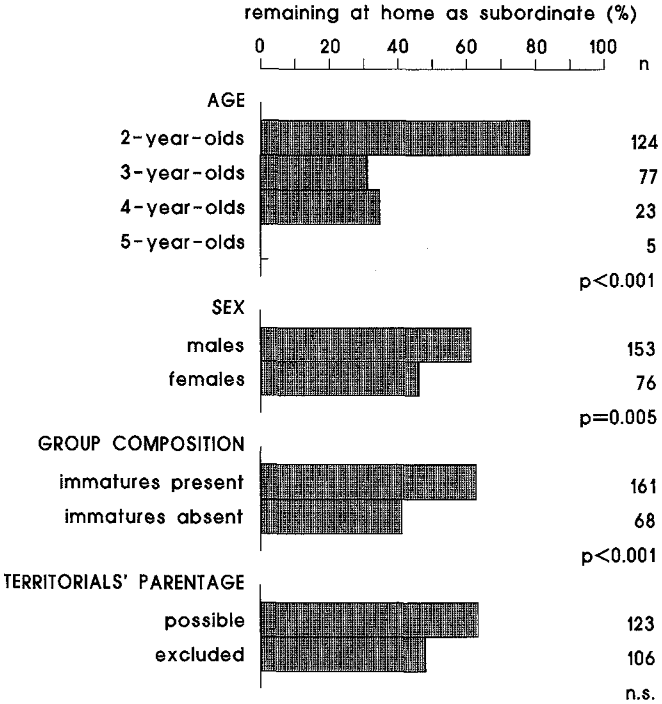

Fig. 3. Proportions of animals staying with the natal family in subordinate rank for another year according to age, sex, presence or absence of immatures (infants or yearlings) in their group, and whether the group's territorial animals could have been their parents or not (P = significance level of partial χ^2; $\geq$3-year-old animals were lumped into a single age category in the statistical analysis)

The 5-year-old animals, still present in the natal family in spring, either dispersed or took over the territorial position. A higher proportion of males than of females remained for another year ($\chi^2_{(1)}=8.0$, $P=0.005$). Dispersal was further delayed if yearlings or infants were present in the group ($\chi^2_{(1)}=11.2$, $P<0.001$). Parentage exclusion of a territorial animal, either by the allozyme analysis or because it obtained this position after the subordinates' birth, cancelled out from the model as a significant predictor of dispersal when correcting for its close association with the absence of immatures ($\chi^2_{(1)}=36.5$, $P<0.001$).

Discussion

This study confirms on a broad data basis that *M. marmota* belongs to the highly social ground-dwelling squirrels (cp. Armitage 1981; Michener 1983). Large groups developed by postponed dispersal of offspring beyond sexual maturity. As already described by other authors, only a group's dominant female produced surviving young (Zelenka 1965; Naef-Daenzer 1984; Lenti Boero 1988; but see Barash 1976). Subordinate females attempting to reproduce evidently either failed to conceive or resorbed their litter, which is common in marmots (Bibikow 1968). Alternatively, the territorial females could have killed the infants of subordinates females of their group (see also Hoogland 1985). In contrast, subordinate males may well have been the fathers of offspring not sired by the territorial male (Table 2). As is typical for social sciurids, nongroup members seemed less likely to be fathers of infants (Schwarz and Armitage 1980; Hoogland and Foltz 1982). (i) Territorial males actively defended their group's home range against adult male intruders. (ii) Both cases of cuckoldry of territorial males in the absence of subordinate group males (Table 2) occurred at sites that were already free of snow during the mating season. Usually, territories were rarely visited by floaters or by animals from neighboring groups during this time of the year because a heavy snow pack restrained movements. (iii) Polyandrous matings were observed only among group males (Müller-Using 1957; Hembeck 1958; Koenig 1973; this study).

Nevertheless, three lines of evidence suggest that becoming territorial is the best option for males to maximize reproductive success. (i) In most groups, the territorial male was the only mature male present (Arnold 1990), and its paternity should then be more secure. (ii) Territorial males reside longer and hence are able to reproduce longer than subordinates. Some males were already territorial when marked in 1982 and still possess this status, whereas subordinate males dispersed at the latest during the fourth year after reaching sexual maturity (Fig. 3). (iii) The dominant males may allow subordinates to copulate only with subordinate females, which never reproduced. The copulation of a territorial female with an individual other than the territorial male was observed only once while the territorial male was in a burrow.

If reproducing, the subordinate males had inbred with their mother in most of the groups (Arnold 1990). Inbreeding could additionally occur when animals became territorial at or close to their natal site. The practical lack of variability found in the enzymes studied may indicate a high degree of inbreeding (see also Faulkes and Abbott 1990). Preliminary results from DNA-fingerprinting of alpine marmots showed similar limited variability (Raßmann, pers. comm.). On the other hand, the frequencies of heterozygotes at the two polymorphic loci agree with the Hardy-Weinberg expectation (Table 1), contradicting close inbreeding. Avoidance of inbreeding is known for species that live in groups of close kin (Schwartz and Armitage 1980; Hoogland 1982; Brooker et al. 1990). Therefore, low genetic variability in the alpine marmot could also be the result of a recent evolutionary bottleneck. However, both the exact degree of inbreeding and the reproductive success of subordinate males remains to be quantified by analysis of paternity with more sensitive methods.

If remaining at home beyond sexual maturity prevents or impairs reproduction, other benefits must exist if delayed dispersal is adaptive. Possibly, an alpine marmot has a higher chance of obtaining a territory for reproduction if it is large and strong and hence should not disperse before reaching sufficient size. The failure of yearlings to disperse and the low dispersal tendency in 2-year-old animals supports this point of view. However, many alpine marmots of adult size remained longer, and dispersers were not heavier than nondispersers in any age class (Table 4). Dispersal peaked during the first month after emerging from hibernation. It seems unlikely that significant mass differences arose in the meantime, considering that no food was available for up to 53 days, as long as the home ranges remained snow covered (Arnold 1990). The lack of influence of emergence mass on the chance of obtaining a territory (Table 3) and the higher mass loss of dispersers during the previous hibernation (Table 5) also contradict hypothesis 1.

Nevertheless, remaining at home could still be beneficial, though in a different manner. The survival chances of floaters seemed to be low, as indicated by the extremely few recaptures in subsequent years. High mortality due to predation and, presumably more important, the inability to find a suitable hibernaculum were most likely the reasons. Although any winter burrow on a mewdow was easily detected in spring, the hibernaculum of a wandering animal was never found. Thus, floaters either hibernated in forested areas or on meadows like residents but did not emerge again the following year. On the other hand, there was a fair chance of becoming territorial at the natal site or close to it (Fig. 2). The marmot territories encompassed by the subordinate animals' frequent and short excursions in spring could be checked for the possibility of a take-over year after year without resigning the safety of the natal territory and hibernaculum. Thus, offspring may postpone dispersal because the higher survival probability at home increases their chances of obtaining a territory. If so, it remains to be answered why many animals left their natal site although they did not become territorial in the neighborhood.

Not all of the marmot territories in the study area were occupied each year, and a number of territorial positions were vacant in the spring. About half of all animals that became territorial established themselves at such sites. Even yearlings could find abandoned burrows and start new groups. Thus, being successful in the search for a territory seems to a considerable degree to be a matter of scanning a large area. Dispersed animals travel over large distances (Arnold 1986; Hottinger 1989). Compared with nondispersers, they should therefore have a higher probability of finding a site whose former inhabitants had died or with a weak territorial animal which can be expelled. Considering that most floaters do not survive more than 1 year, the relatively high proportion of long distance dispersers among the newly established territorial animals (25 of 52) supports this idea. Hence per time unit, long distance dispersers are expected to have a higher chance of becoming territorial than those animals remaining at home. Avoidance of the high risk of long distance dispersal is likely to be beneficial as long as time is not a crucial variable, but the cost of forfeited or reduced reproduction due to remaining increases with age, since an individual's future reproductive span is proportionately reduced. Beyond a certain age, it should be advantageous for a subordinate to disperse, despite the involved risk, in order to increase the probability of becoming territorial soon. Altogether, an animal is expected to leave its natal unit at the age when its future reproductive success would be lower by further delaying dispersal.

Dispersal of subordinate alpine marmots can also be elicited by aggression of the territorial animals (Naef-Daenzer 1984; Hottinger 1989). By definition, parental investment in one offspring is accomplished at the expense of the parent's ability to invest in other offspring (Trivers 1972). If tolerance of older offspring is parental investment, then parents should try to expel them from the territory at that time when it becomes more beneficial to devote the available resources to younger progeny. Relatively more dispersal with increasing group size seems likely and might indicate the parents' interest in expelling subordinates from too large groups.

With the above interpretation, the data so far seem to be in accordance with hypothesis 2. However, it cannot explain several other results of this study. (i) Males dispersed later than females although they reached adult size at the same age (Table 4). Furthermore, an equal proportion of both sexes obtained territories without long distance dispersal, but males mostly at an older age than females (Fig. 2). This again reflects most likely the subordinate males' higher tendency to remain, since there is no reason to assume a sex difference in the chance of becoming territorial nearby. There was no evidence for higher mortality or a higher eviction rate of territorial females than of males (Arnold 1990). On the other hand, existing reproductive chances of subordinate males might be the reason why they dispersed later than females (see Emlen 1982), but mate sharing is definitely not continued paternal care. (ii) It was more usual for offspring with high mass loss during hibernation to disperse (Table 5). They may have been unable to withstand the territorial's aggression in spring (see Barash 1976; Naef-Daenzer 1984) and hence be forced to leave the group. Under hypothesis 2 one would expect the opposite – predominant dispersal of offspring with low mass loss during the previous hibernation, since they probably have better chances of becoming territorial (Table 3). (iii) If tolerance of older animals in the group is purely parental investment, more pressure to disperse on those subordinates that could not be descendants of both territorial animals present is to be expected. This was apparently not the case. More dispersal of these individuals turned out to be an epiphenomenon of the less frequent presence of immatures in such groups (Fig. 3), which in turn was due to virtually no reproduction in years when a territorial animal changed (Arnold 1986). (iv) Dispersal was less likely in years when immatures lived in the group (Fig. 3, see also Barash 1973). Why should parents invest for longer in their already adult offspring in such a situation? This result suggests that adult subordinates could be tolerated at least in part because of benefits arising from their presence or help in rearing young (Arnold 1990).

Whether dispersal in the alpine marmots occurs at the age when the reward in future fitness from remaining at home becomes less than that of dispersal cannot be proven at this stage. The chances for long distance dispersers of becoming territorial are quantitatively unknown because the amount of successful emigration from the study area cannot be inferred reliably from the immigration rate. However, the results of this study strongly suggest that postponed dispersal in this species cannot be viewed solely as prolonged parental investment.

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References

Armitage KB (1981) Sociality as a life-history tactic of ground squirrels. Oecologia 48:36–49

Armitage KB (1986) Marmot polygyny revisited: determinants of male and female reproductive strategies. In: Rubenstein DS, Wrangham RW (eds) Ecological aspects of social evolution. Princeton University Press, New Jersey, pp 303–331

Armitage KB (1987) Social dynamics of mammals: reproductive success, kinship and individual fitness. Trends Ecol Evol 2:279–283

Arnold W (1986) Sozioökologie des Alpenmurmeltieres. Dissertation, Ludwig-Maximilians-Universität München

Arnold (1990) The evolution of marmot sociality: II. Costs and benefits of joint hibernation. Behav Ecol Sociobiol 27:239–246

Barash DP (1973) The social biology of the olympic marmot. Anim Behav Monogr 6:171–249

Barash DP (1974a) The evolution of marmot societies: a general theory. Science 185:415–420

Barash DP (1974b) The social behaviour of the hoary marmot (*Marmota caligata*). Anim Behav 22:256–261

Barash DP (1976) Social behaviour and individual differences in free-living alpine marmots (*Marmota marmota*). Anim Behav 24:27–35

Berendyaev SA, Kulkova NA (1965) On intraspecies relations of grey marmots. Zool Zh 44:110–116

Bibikow DI (1968) Die Murmeltiere. Die neue Brehm Bücherei. Ziemsen, Stuttgart

Bronson FH (1963) Some correlates of interaction rate in natural populations of woodchucks. Ecology 44:637–643

Bronson FH (1964) Agonistic behaviour in woodchucks. Anim Behav 12:470–478

Brooker MG, Rowley I, Adams M, Baverstock PR (1990) Promiscuity: an inbreeding avoidance mechanism in a socially monogamous species? Behav Ecol Sociobiol 26:191–199

Clayton JW, Tretiak DN (1972) Amine-citrate buffers for pH control in starch gel electrophoresis. J Fish Res Board Can 29:1169–1172

Davis DE (1981) Mechanism for decline in a woodchuck population. J Wildl Manage 45:658–668

Emlen ST (1982) The evolution of helping: 2. The role of behavioral conflict. Am Nat 119:40–53

Faulkes CG, Abbott DH (1990) Investigation of genetic diversity in wild colonies of naked mole-rats by DNA fingerprinting. J Zool (London) 221:87–97

Ferron J, Ouellet JP (1989) Temporal and intersexual variations in the use of space with regard to social organization in the woodchuck *Marmota monax*. Can J Zool 67:1642–1649

Forter D (1975) Zur Ökologie und Verbreitungsgeschichte des Alpenmurmeltieres im Berner Oberland. Dissertation, Universität Bern

Frase BA, Hoffmann RS (1980) Marmota flaviventris. Mammalian Species 135:1–8

Grizzell RA (1955) A study of the southern woodchuck, *Marmota monax monax*. Am Midl Nat 53:257–293

Harris H, Hopkinson DA (1976) Handbook of enzyme electrophoresis in human genetics. American Elsevier, New York

Hembeck H (1958) Zum Paarungsverhalten der Murmeltiere. Z Jagdwiss 4:40–41

Holmes WG (1984) The ecological basis of monogamy in Alaskan hoary marmots. In: Murie JO, Michener GR (eds) The biology of ground-dwelling squirrels. University of Nebraska Press, Lincoln, pp 250–274

Hoogland JL (1982) Prairie dogs avoid extreme inbreeding. Science 215:1639–1641

Hoogland JL (1985) Infanticide in prairie dogs: lactating females kill offspring of close kin. Science 230:1037–1040

Hoogland JL, Foltz DW (1982) Variance in male and female reproductive success in a harem-polygynous mammal, the black-tailed prairie dog (Sciuridae: *Cynomys ludovicianus*). Behav Ecol Sociobiol 11:155–163

Hottinger J (1989) Abwanderungsverhalten und dessen soziale Ursachen beim Alpenmurmeltier. Diplomarbeit, Technische Universität München

Huck UW, Quinn RP, Lisk RD (1985) Determinants of mating success in the golden hamster (*Mesocricetus auratus*) IV. Sperm competition. Behav Ecol Sociobiol 17:239–252

Ismagilov MI (1956) Material on the ecology of the Tien-Shan marmot. (*Marmota bobac centralis* Thom.) Zool Zh 35:908–915

Koenig L (1973) *Marmota marmota* (Sciuridae) Paarungsverhalten. Wolf G (ed) Encyclopaedia cinematographica E 459/1962. Institut für den wissenschaftl. Film, Göttingen

Kratochvil J (1964) Das männliche Genitalsystem des europäischen Bergmurmeltieres *Marmota marmota* latirostris. Z Säugetierk 29:290–304

Lattmann P (1973) Beiträge zur Ökologie und zum Verhalten des Alpenmurmeltieres (*Marmota marmota*). Ergebnisse der wissenschaftlichen Untersuchungen im Schweizerischen Nationalpark 11:273–347

Lenti Boero D (1988) Distribuzione degli insediamenti e stima della densita' di marmotta alpine (*Marmota marmota* L.): metodi di indagine per zone campione. In: Atti del 1 Convegno dei Biologi della Selvaggina. Supplemento alle Ricerche di Biologia della Selvaggina, vol 14, Tipolitografia F.G., Savignano sul Panoro, Modena, pp 253–264

Lenti Boero D, Boero E (1989) Dati preliminari sulla dispersione e predazione nella marmotta alpine (*Marmota marmota* L.): uno studio a lungo termine. In: Atti dell'8 Congresso della Divisione Ricerca di Base in Psicologia. Imprimatur, Padova, pp 57–59

Markert CL, Faulhaber I (1965) Lactate dehydrogenase isozyme patterns of fish. J Exp Zool 159:319–332

Maschkin VI (1982) New materials on ecology of *Marmota menzbieri* (Rodentia, Sciuridae). Zool Zh 61:278–288

May B, Wright JE, Stoneking M (1979) Joint segregation of biochemical loci in salmonidae: results from experiments with *Salvelinus* and review of the literature on other species. J Fish Res Board Can 36:1114–1126

Michener GR (1983) Kin identification, matriarchies, and the evolution of sociality in ground-dwelling sciurids. In: Eisenberg JF, Klieman DG (eds) Advances in the study of mammalian behavior. American Society of Mammalogists, Shippenburg, PA, Spec Publ, No 7, pp 528–572

Müller-Using D (1957) Die Paarungsbiologie des Murmeltieres. Z Jagdwiss 3:24–28

Naef-Daenzer B (1984) Sozialverhalten und räumliche Organisation von Alpenmurmeltieren. Dissertation, Universität Bern

Ouellet JP, Ferron J (1986) L'utilisation de l'espace par la marmotte commune (*Marmota monax*). Naturaliste can (Rev Ecol Syst) 113:263–273

Psenner H (1957) Neues vom Murmeltier, *Marmota m. marmota* (Linne, 1758). Säugetierk Mitt 5:4–10

Psenner H (1960) Welche Erkenntnisse brachten die Murmeltierforschungen in den letzten Jahren. Proc Int Symp Methods Mamm Invest: 259–263

Ratti P (1970) Beitrag zur Kenntnis des Alpenmurmeltieres (*Marmota m. marmota*). Schweizer Archiv für Tierheilkunde 112/6: 283–295

Ridgeway GJ, Sherburne SW, Lewis RD (1970) Polymorphism in the esterase of atlantic herring. Trans Am Fish Soc 99: 147–151

Schwartz OA, Armitage KB (1980) Genetic variation in social mammals: the marmot model. Science 207: 665–667

Selander RK, Smith MH, Yang SY, Johnson WE, Gentry JB (1971) IV. Biochemical polymorphism and systematics in the genus *Peromyscus*. I. Variation in the old-field mouse (*Peromyscus polionotus*). Studies in Genetics VI. Univ Texas Publ 7103: 49–90

Sokal RR, Rohlf FJ (1981) Biometry. Freeman, San Francisco

Suntzov VV (1981) The territorial structure of the population and intraspecies relations of mongolian bobaks (*Marmota sibirica*) in Tuva. Zool Zh 60: 1394–1405

Trivers RL (1972) Parental investment and sexual selection. In: Campbell BG (ed) Sexual selection and the descent of man. Heinemann Educational Books, London, pp 136–179

Zelenka G (1965) Observations sur l'ecologie de la marmotte des alpes. La Terre et la Vie 19: 238–256