Chapter 30 Evolution of Sociality in Marmots: It Begins with Hibernation

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IT IS NOW GENERALLY AGREED that sociality, that is, group living, has both costs and benefits. Among the benefits are increased awareness of predators through increased vigilance (Armitage et al. 1996; Blumstein 1996) and alarm-calling (Sherman 1977; Blumstein and Armitage 1997a). Major costs are a loss of reproduction; increased social complexity in ground-dwelling sciurids is associated with a smaller proportion of females breeding, a greater time to age of first reproduction, and a decrease in litter size (Blumstein and Armitage 1998). Many groups are cooperative breeders; these groups are typified by considerable reproductive skew (Keller and Reeve 1994; Sherman et al. 1995), in which only one or few mature females reproduce in a reproductive season (Solomon and French 1997; Blumstein and Armitage 1999). However, one benefit of increased social complexity and cooperative breeding is increased juvenile survival.

In this paper I describe the costs and benefits of group living in marmots (*Marmota*) and present a historical analysis of the probable evolutionary events that led to sociality.

Social Systems of Marmots

Currently, fourteen species of marmots restricted to the northern hemisphere are recognized (Barash 1989). Six species occur in western North America; only the range of the woodchuck, *M. monax*, extends into eastern Canada and the United States. Two species, the alpine marmot (*M. marmota*) and the steppe marmot (*M. bobak*), occur in Europe; the remaining six species occur in Asia. Typically marmots occur in alpine or subalpine environments, with the exception of the steppe marmot, which lives on the Eurasian prairie, and the woodchuck, which lives in low-elevation woodland/meadow habitats. Range distribution and habitat characteristics of the fourteen species are described elsewhere (Armitage 2000).

Marmot species have been placed in either three (Allainé 2000) or four (Armitage 1996b; Blumstein and Armitage 1999; Armitage 2000; Armitage and Blumstein 2002) social groups (table 30.1). The major difference between three- and four-group categories is that in the three-group system, the restricted family and extended family systems are combined into a group of "species with complex level of sociality" (Allainé 2000; p. 23). The basic social unit of this group is the family (Bibikow 1996), but my interpretation of the available literature is that family structure differs between the restricted and extended family groups, in that subordinate adults are not normally present in the restricted family groups. Information is unavailable for assigning the Himalayan marmot (*M. himalayana*) and Menzbier's marmot (*M. menzbieri*) to social groups, but they probably have extended families.

The social systems should be considered "types," as they vary considerably. In *M. monax*, in Ohio, 25% of the female offspring remained with their mother through the first hibernation, and moved to different burrows as yearlings (Meier 1992). Nearly 73% of the yellow-bellied marmot (*M. flaviventris*) matrilines consist of one female; large matrilines occur only on larger habitat patches (Armitage and Schwartz 2000). On smaller habitat patches, only a reproductive pair may be present, and mating is monogamous

Table 30.1 Social systems of *Marmota*

Social system	Species	Characteristics
Solitary	*M. monax*	Mating system polygynous; little overlap of female home ranges; disperse as young; solitary hibernation
Female kin group	*M. flaviventris*	Mother:daughter:sister groups persist through time as matrilines; territorial male defends one or more matrilines; thus mating polygynous; yearling dispersal; solitary or group hibernation
Restricted family	*M. caligata, M. olympus, M. vancouverensis*	Adult male typically with one to three females and yearlings; mating within the family; disperse as 2-year-olds; group hibernation
Extended family	*M. baibacina, M. bobak, M. broweri, M. camtschatica, M. caudata, M. marmota, M. sibirica*	Typical family of adult territorial pair, subordinate adults, and yearlings; mating monogamous or polyandrous; disperse at age three or older; group hibernation

SOURCE: Modified from Armitage 2000 and Blumstein et al. 2004.

(Armitage and Downhower 1974; Armitage 1991). However, some males achieve polygymy by expanding their home ranges to include two or more small patches with females (Salsbury and Armitage 1994). Many alpine marmot families consist only of a reproductive pair, with or without infants (Arnold 1990a, 1990b; Perrin et al. 1992; Sala et al. 1996; Lenti Boero 1999).

This variation within social systems is primarily a consequence of demographic processes. In yellow-bellied marmots, a female immigrant to a habitat patch forms a matriline of one (Armitage 1991, 2002). Recruitment of 2-year-old daughters increases matriline size; mortality decreases matriline size, and may reduce a matriline to one adult female (Armitage 1973, 1991, 1996b, 2002, 2003a). Similar processes occur in alpine marmots, with one major exception: solitary individuals are virtually nonexistent. An immigrant becomes resident in a family either by filling a vacancy or by evicting an adult resident (Arnold 1990a; Sala et al. 1992; Lenti Boero 1999; Grimm et al. 2003). The family structure of grey marmots (*M. baibacina*) is simpler on less favorable habitat than on favorable habitat (Mikhailuta 1991).

There may be a fifth social system. In the steppe marmot (*M. bobak*) in central Kazakstan, families consisted of one mature female and male plus old nonbreeding males and subadults. Subordinate adults were not reported, and dispersal apparently occurred at age two (Mashkin 1991). Families of steppe marmots in the Ukraine consisted of an adult female with or without offspring and two or three adult males. Again, no subordinate adult females were reported (Nikol' skii and Savchenko 1999). One group had two adult females, but one soon dispersed. The black-capped marmot (*M. camtschatica*) may be a superspecies, and one or more of the three sub-species may be a separate species (Boyeskorov et al. 1996). Family groups of *M. c. camtschatica* on average consisted of 1.8 adult males, 1.7 adult females, and 4.3 young (less than half of the families produced young in any given year; Mosolov and Tokarsky 1994). Families of *M. c. bungei* usually consisted of parents and progeny; about half of the marmots lived alone or in pairs (Yakovlev and Shadrina 1996). Neither of these studies reports the presence of subordinate adults, a major characteristic of the extended family.

The uncertainty regarding the full variety of marmot social systems derives from the lack of long-term studies of social structure and dynamics. Because marmots are long-lived species, known individuals must be followed for several generations to determine the typical social system and its variability. Except for *M. marmota*, marmot research on the Eurasian marmots concentrated on population changes following exploitation of marmots for food, fat, and fur or reduction and recovery of marmot populations in programs to evaluate the role of marmots as a plague vector (Bibikow 1996). Results are presented as population averages; for example, percent of females of different ages breeding, size of families (e.g., Pole and Bibikov 1991; Shubin 1991). These studies enable one to infer the nature of the social system and its relationship to the age of first reproduction and of dispersal; some of the characteristics of social systems to be discussed later are based on such population data.

Sociality evolved at least twice (Kruckenhauser et al. 1998; Steppan et al. 1999), once in the Eurasian clade and once in the North American clade. The solitary *M. monax* has a basal position in the Eurasian clade and suggests that ancestral marmots were asocial. The female kin group and restricted family social groups occur in the North American or *caligata* clade and the extended family species occur in the Eurasian clade.

Uncertainty of the exact nature of the social system of all fourteen marmot species does not refute that this monophyletic genus (Steppan et al. 1999) has diverse social systems. This diversity raises two questions: (1) why did soci-

ality in this genus evolve, and (2) why are there diverse social systems? The attempt to answer these questions requires understanding the evolutionary history of *Marmota*.

Evolution in a Harsh Environment

Historical record

Both DNA hybridization studies (Giboulet et al. 2002) and the fossil record (Black 1972; Mein 1992) indicate that the first Sciuridae evolved in the Oligocene in North America. The first true ground squirrel, *Miospermophilus*, appeared by late Oligocene and was the ancestor of the spermophiles (*Spermophilus*), prairie dogs (*Cynomys*), and marmots. These ground-dwelling squirrels radiated in North America in the Miocene and Pliocene. Although *M. vetus* appeared in the Miocene in what is now the United States (Mein 1992), the earliest incontrovertible fossils are *M. minor* from the late Miocene, about eight million years ago (Polly 2003). One radiation led to large-bodied forms, such as *M. nevadensis* and *Paenemarmota barbouri*, the largest of the ground-dwelling squirrels (Kurtén and Anderson 1980). These large forms did not survive into the Pleistocene. Marmots reached Eurasia in the late Pliocene or early Pleistocene. All extant species evolved in the Pleistocene (Black 1972; Mein 1992).

Early marmots probably inhabited cool, moist habitats in the basin-and-range country of the North American west (Polly 2003), and occurred as far south as Mexico (Cushing 1945). In Europe, all modern species are known only from the late Pleistocene. Marmots were associated with the tundra-forest-steppe fauna, which occupied the periglacial landscape (Zimina and Gerasimov 1973; Zimina 1996). Marmots were widespread in European lower mountain ranges (Kalthoff 1999a) and are common species of the "loess fauna" of the late Pleistocene (Rumiantsev and Bibikov 1994). The environment was characterized by cold winters and short, warm summers in a grassy landscape (Zimina and Gerasimov 1973).

Marmot distribution changed dramatically with warming and advance of the forests at the end of the last glaciation. Marmot populations from Porcupine Cave, Colorado, about 750,000 to 800,000 years ago, are related to *M. monax* (Polly 2003). By about 500,000 years ago *M. monax* appeared in Pleistocene locations in the eastern United States and was prominent in fossil deposits in Missouri about 15,000 years ago. *Marmota flaviventris* now lives in Colorado; fossils were found in numerous sites in western North America dating from less than 125,000 years ago (Kurtén and Anderson 1980). Some of these sites are south of the present range of *M. flaviventris*, such as the Newberry Mountains of southern California (Goodwin 1989). The steppe marmot retreated from central Europe and the alpine marmot became restricted to the higher Alps Mountains. *Marmota primigenia*, found in middle and late Pleistocene loess deposits along with some *M. bobak* fossils in the middle Rhine region, became extinct as reforestation occurred north of the Alps (Kalthoff 1999b). In Italy, fossils from the floor level of cave deposits are *M. marmota*. Marmots from other levels (Upper or late Middle Pleistocene) have a more massive skull and a larger mandible (Aimar 1992). Several characters are in concordance with *M. marmota* and indicate a possible shift toward a smaller size as warming occurred.

This brief review of the historical record indicates that marmots have been large-bodied ground-dwelling squirrels for several million years and adapted to an open, cool landscape. Adaptation to a cool environment is evident in current species. Activity of *M. marmota* (Turk and Arnold 1988) and *M. flaviventris* (Webb 1980; Melcher et al. 1990) is much more restricted by heat than by cold during the active season.

The harsh environment

Considerable evidence supports the interpretation that currently species of marmots occupy harsh environments (Armitage and Blumstein 2002). Environmental harshness or severity is not readily defined and can include physical factors such as cold and drought and biological factors such as intense predation and disease. I will emphasize physical factors, such as length of winter and air temperature, which affect growth, reproduction, and survival of marmots. Because climatic records from marmot habitats are generally unavailable, biological features will be presented as evidence for environmental harshness.

Many species of marmots lose mass after emergence from hibernation. Heavy snow causes mass loss in the Olympic marmot (*M. Olympus*, fig. 30.1), the hoary marmot (*M. caligata*), and the steppe marmot. Mass loss typically occurs for up to several weeks in the woodchuck and in the alpine and long-tailed (*M. caudata*) marmots. Mass loss is associated with the use of fat reserves in the grey and black-headed marmots (Armitage and Blumstein 2002 and references therein).

In the long-tailed and grey marmots, up to 48% of the embryos are reabsorbed in bad years (e.g., a cold spring). Because fat accumulation is much lower in reproductive females than in barren females in many marmot species, reproduction is often not possible in successive years unless the litter is small (Bonesi et al. 1996; Armitage and Blumstein 2002). *Marmota bobak*, *M. marmota*, *M. olympus*, and *M. sibirica* usually skip 1 year between successful re-

2000) that, coupled with a metabolic rate lower than that predicted from body mass (metabolism equations and a tissue growth efficiency about five times greater than that of a typical homeotherm; Kilgore and Armitage 1978; Armitage and Salsbury 1992) allows marmots to accumulate fat reserves and use them efficiently during the hibernation and early post-hibernation seasons.

Consequences of large size

The major consequence of large size is that there is insufficient time during the active season for young to mature before their first hibernation, with the exception of the woodchuck. The active season of the woodchuck, which is about 7.5 months, is 2 to 4 months longer than that of any other marmot (Armitage and Blumstein 2002). As a result of the combination of large size and a short active season, the young of all other species of marmots remain in their natal environment for their first hibernation or longer. This retention of young forms the basic social unit of marmots (Armitage 1981, 1996b, 2000).

The age of maturity may be estimated by calculating a maturity index (MI) by dividing the body mass at a specified age by the body mass of an adult. For this calculation, body mass values must be used from the same time of year to minimize the effects of fattening. Dispersal can occur when MI $\geq$ 0.5, but only *M. monax* achieves that value in its first summer (Blumstein and Armitage 1999) and disperses. The young of all other species of marmots have MI values $\leq$ 0.45 and do not disperse. However, yearlings of all species reach an MI $\geq$ 0.76, but only *M. flaviventris* disperses (Armitage 1999a). Thus, most species of marmots have delayed dispersal; that is, dispersal occurs 1 or more years beyond the year in which the MI for dispersal is reached.

A second consequence of large size is delayed reproduction. Reproduction is possible the year after an MI of about 0.65 is achieved (Blumstein and Armitage 1999). Only *M. monax* reaches that MI as a young and is the only species of marmot to reproduce as a yearling. All marmots have a MI > 0.7 as yearlings, and apparently could reproduce at age 2 years (Armitage 1999a). However, many species do not reproduce until age three. Delayed reproduction refers to those species that reproduce at least 1 year later than they otherwise could as indicated by the MI. However, for many species reproduction is delayed for more than 1 year for many members of the social group. Population means are available for some species from life table analyses; otherwise I made rough estimates based on population structure and the percentages of various age groups that reproduce (table 30.2). In all species for which data are available, the realized age of first reproduction is later than the age of reproductive maturity, even though all species have been reported to reproduce at the recorded age of maturity. Furthermore, the age of dispersal for at least three species, *M. sibirica*, *M. marmota*, and *M. bobak*, is older than the age of first reproduction (Blumstein and Armitage 1999; Armitage 1999a). Delayed dispersal and delayed reproduction characterize the more complex marmot social systems (table 30.1).

Group Living and Social Behavior

As a consequence of retaining offspring in the family or matriline, marmot social groups are based on kinship. Burrow-

Table 30.2 Age of first reproduction for female marmots

	Age (years)		
Species[a]	Reproductive maturity	Population mean	References
M. flaviventris	2	3.02	Schwartz et al. 1998
M. caudata aurea	3	>3	Blumstein and Arnold 1998
M. c. caudata	4		Davydov 1991
M. sibirica	3		Bibikow 1996
M. marmota	2	>3	Arnold 1990a
M. bobak	2, 3	>3	Mashkin 1991; Shubin 1991
M. monax	1	ca. 1.5[b]	Snyder and Christian 1960
M. vancouverensis	3	4.33	Bryant 1996
M. baibacina	2 (3)	>4	Pole and Bibikov 1991; Bibikov 1991
M. caligata	3	>3	Barash 1974d; Holmes 1984
M. olympus	3	≥3.6[b]	Barash 1973

[a]Species are listed in order of increasing body mass at immergence.
[b]Author's calculations.

mates are more closely related than a random sample of the population. Burrow-mates in *M. olympus* on average are related by 0.41 (Barash 1989); those of *M. caligata*, 0.39 (Armitage 1996b); and those of *M. flaviventris*, by 0.5 (Armitage and Johns 1982). The dynamic processes leading to patterns of relatedness have been best analyzed in *M. marmota* and *M. flaviventris*. In the alpine marmot, average relatedness between dominant and subordinate females is 0.33 (Allainé 2000); in the yellow-bellied marmot it is 0.5 (Armitage 1991). The difference in average relatedness is a consequence of the recruitment patterns of the two species.

In the yellow-bellied marmot, daughters are recruited by their mothers into the matriline. Daughters from different year classes or littermate sisters may be recruited. However, turnover in the territorial male may result in maternal half-sibs being recruited, and demographic processes may lead to grandmother–granddaughter or aunt–niece relationships. Under these conditions, average relatedness can temporarily decrease to 0.25. These matrilines divide to form two groups, with each group having an average relatedness of 0.5 (Armitage 1984, 1991). One result of the fission of matrilines is that they are small; mean matriline size measured over eleven habitat sites was 1.38 ($N = 544$) (Armitage and Schwartz 2000). Matrilines are territorial and share resources, such as burrow sites and foraging areas, with other members of the matriline—but not with members of neighboring matrilines. Use of space serves as an indirect measure of resource sharing. Space-use overlap averages about 43% for adult females related by 0.5 and is much less than predicted for all other degrees of relatedness (Armitage 1996a). For adults related as aunt–niece, space-use overlap averages about 4%.

The major factor that reduces average relatedness in alpine marmots is that only 15% (Vanoise, France; Allainé 2000) to 18.3% (Berchtesgaden, Germany; Arnold 1993) of the territorial females inherited the territory of their birth. On average, 17.5% to 21.5% of the females take over a neighboring territory. In an 8-year study of a high altitude colony in northern Italy, no female became reproductive in her natal family, one female was an immigrant from an adjacent family, and three female immigrants from outside the colony successfully reproduced (Lenti Boero 1994, 1999). Similarly, immigrant males replaced resident males; no resident male was known to have two successive female partners (Lenti Boero 1999). Regardless of the degree of relatedness within alpine marmot families, territories are stable and overlap is slight (Perrin et al. 1993; Lenti Boero 1996; Sala et al. 1996). Transfer among groups commonly occurs in golden marmots (*M. caudata aurea*); most transfers are from larger to smaller groups (Blumstein and Arnold 1998). Translocations from one family to another also occur in *M. menzbieri*, *M. c. caudata*, *M. baibacina*, *M. bobak*, *M. sibirica*, and *M. camtschatica* (Mashkin 2003 and references therein). Intergroup transfer occurs more frequently in golden marmots than in alpine marmots (Blumstein and Arnold 1998), but the dynamics of intergroup transfer are generally unknown. Long-term studies of the demographic characteristics of the immigrating animals and of the residents and the consequences of such transfers on the lifetime reproductive success of all the participants are needed. Some consequences of the variable kinship in extended families will be discussed later.

In general, rates of amicable and agonistic behavior (Armitage 1977) are related to the social system. Amicable behavior among woodchucks is mostly limited to mother–offspring interactions; agonistic behavior characterizes the social interactions of this solitary species. The rate of greetings is much higher in the species in the restricted family groups than in the yellow-bellied marmot. Agonistic behavior in the restricted family groups is rare and occurs primarily when the adult male repels intruders or chases peripheral males (reviewed in Armitage 2003a). In the extended families, agonistic behavior occurs primarily between members of different groups, and amicable behavior predominates within groups (Armitage 1996b). However, when a territorial takeover occurs, subordinates may be chased and subsequently disappear (Lenti Boero 1994). The territorial pair defends against adult same-sex intruders (Arnold 1993; Lenti Boero 1999) and fighting may occur, with the loser being expelled almost immediately after the fight (Hackländer and Arnold 1999). Sometimes the intruder male does not expel the old territory owner and both males remain in the group. Because of variable relatedness in the extended family groups, the relationship of rates of social behavior and nearest neighbor associations, such as during foraging, should be determined. This study would be especially interesting, because evidence suggests that reproductive suppression (to be discussed subsequently) is kin-biased.

The relationship between kinship and social behavior has been most intensively studied in the yellow-bellied marmot. Mother–daughter and sister–sister amicable behavior greatly exceeds agonistic behavior, whereas aunt–niece agonistic behavior greatly exceeds amicable behavior in three colonies observed for 30 years (Armitage 2002). Mothers, daughters, and sisters typically associate in the same matriline; their aunts and/or nieces live in different matrilines. The same pattern is evident when social behavior of adult females in four colonies is analyzed as a function of the degree of relatedness (r). Amicable behavior exceeds agonistic behavior by 5.5 times when $r = 0.5$; at all $r \leq 0.25$, agonistic behavior exceeds amicable behavior by an average of 5.4 times (Armitage 2002). Behavior is related to recruitment of female yearlings; recruitment is more likely when the amicable/agonistic ratio is high and when amicable behaviors predominate among adult females (Armitage 1986a, 1996b).

Benefits of Group Living

Delayed dispersal in marmots with a family social structure is associated with increased survivorship. After the first year, survivorship of the golden marmot did not differ significantly from that of the Olympic and Vancouver Island marmots, and was significantly greater than that of the yellow-bellied marmot (Blumstein et al. 2002). The life table of the steppe marmot (Shubin 1991) is similar to that of the golden marmot and indicates higher survivorship, similar to that of the other family social groups. Only for the yellow-bellied marmot did males have lower survivorship than females (Schwartz et al. 1998; Blumstein et al. 2002). Lower survivorship in males is associated, in part, with much higher rates of dispersal by male yearlings and extensive movements by older males, either searching for females or defending a very large territory (Van Vuren and Armitage 1994b; Schwartz et al. 1998).

Group size affects fitness, measured as survivorship and net reproductive rate (NRR), in yellow-bellied marmots. Mean matriline size for eleven habitat sites varied from 1.17 to 2.24. Survivorship and NRR increased as mean matriline size increased, decreased slightly in large matrilines, and varied between sites with similar mean matriline sizes. Although there was no direct measure of site quality, survivorship, but not NRR, was closely related to the area of the habitat patch (Spearman rank correlation = 0.45, $0.1 > P > 0.05$). The number of females was directly correlated with habitat area; possibly the larger number of females on a patch provides increased detection of predators (Armitage and Schwartz 2000). Marmots usually alarm-call when a predator is detected. Alarm-calling is not altruistic; we have never observed a caller to become a victim. Similarly, callers did not suffer predation in other marmot species (Barash 1975b). Variation in the rate of alarm-calling by yellow-bellied marmots was best explained by direct parental care (Blumstein et al. 1997). More females on a habitat patch is associated with more litters, hence the likelihood that alarm-calling will occur increases. Although a female may call to warn the offspring, other marmots will also be alerted.

When matriline size was considered over all habitat sites and the average per year calculated, both survivorship and NRR were significantly related to matriline size. The relationships were curvilinear; survivorship was only slightly affected by matriline size, but the relationship explained most of the variation ($R^2 = 0.97$). Matriline size explained less of the variation ($R^2 = 0.67$) when sites were treated separately. The difference between the amounts of variation in survivorship explained by the two analyses suggests that there is a major effect of habitat quality on survivorship. NRR was strongly affected by matriline size; NRR increased as matriline size increased to a maximum at three, then decreased in matrilines of four and five (Armitage and Schwartz 2000).

Although the optimal matriline size is three, matrilines of this size occur only 4.7% of the time. The low frequency of the optimal matriline size raises the question of why it does not occur more often. The three major reasons seem to be habitat size, demography, and reproductive competition. Small habitat patches never develop large matrilines; 55% of the large matrilines (≥ 3) occurred at three localities. Although these are among the larger localities, size is a necessary but not a sufficient condition for the development of large matrilines. These localities have numerous burrow sites and large meadows with abundant forage (Svendsen 1974; Kilgore and Armitage 1978; Frase and Armitage 1989); larger areas with widely spaced, small resource patches have smaller matrilines. Demography affects the formation of large matrilines as follows. Assume that a female first reproduces at age 3 years (the population mean). She would be five years old when her first daughter would become an adult at age 2, and 6 years old when she could recruit her second daughter. Only 31% of the 3-year-old females reach age 6 years (Schwartz et al. 1998), and a female's first 2-year-old has a 66% probability of reaching age three. Thus there is a 0.22 probability that both these demographic events will occur within a matriline. However, even if favorable demographic events occur in a favorable habitat, matriline size may be limited by reproductive competition (Armitage 2003d), which will be discussed as a cost of group living.

In marmots with a family social system, there is no indication that group size affects NRR. Regardless of group size, only the dominant territorial female reproduces (Bibikow 1996; Blumstein and Armitage 1999; Armitage 1999a). However, group size may affect survivorship through social thermoregulation during hibernation (Arnold 1988, 1993). In the alpine marmot, mortality may be high when parents hibernate with juveniles; the entire group may die (Arnold 1990b; Lenti Boero 1999). Mortality results from a greater loss of mass when juveniles are present, and is especially severe in hibernacula of low quality (Arnold 1990b).

Increased survivorship occurs under two conditions: (1) the absence of juveniles and (2) the presence of subordinate adults with the territorial pair and juveniles. When juveniles were absent, loss of mass was lower and survivorship greater the larger the number hibernating together. When juveniles were present, there was no influence of group size on winter mortality (Arnold 1993), but the presence of older, subordinate animals significantly reduced mortality. Only potential full sibs engaged in alloparental care by warming infants; mass loss of the subordinates was greater but survivorship of infants was greater. Overall, there was almost no mortality when territorials, subordi-

research is needed to evaluate the role and evolution of social thermoregulation in marmots.

Costs of Group Living

One potential cost of group living is increased disease transmission. A group of four Vancouver Island marmots hibernated together and all died from a bacterial infection (Bryant et al. 2002). Female yellow-bellied marmots that failed to reproduce had more fleas than those that reproduced, and marmots that died during hibernation had more fleas than the survivors. Yearlings with greater flea infestations grew more slowly (Van Vuren 1996). Infant winter mortality of alpine marmots increased with the ectoparasite load of the family, but there was no relationship between ectoparasite load and group size or marmot density (Arnold and Lichtenstein 1993). Both of these reports suggest that ectoparasites affected individual fitness, but neither found evidence that the parasitism was a cost of sociality. Plague foci—concentrations of infected marmots—occur regularly in marmots such as *M. baibacina* and *M. sibirica*. Plague apparently is most detrimental when associated with drought or food shortage. Mortality during plague epizootics is small, and may reach 10 to 15%; populations quickly recover (Bibikow 1996). Some populations of *M. sibirica* develop genetic resistance to plague, which is reflected in a difference in gene frequencies and the level of heterozygosity between plague-free and infected populations (Batbold 2002). There is no evidence that plague infections are a cost of sociality; plague is present in many other nonsocial species in the same geographic area (Bibikow 1996). Thus available evidence does not support disease as a cost of sociality; in fact, some of the severe viral infections seem to be restricted to the asocial *M. monax* (Armitage 2003a).

The major cost of sociality is decreased reproduction. In yellow-bellied marmots, reproductive competition occurs between adjacent matrilines. A numerically dominant matriline reduces reproductive frequency in the numerically inferior matriline. Within a matriline, adults may chase yearlings, even when the yearlings are full sibs, from the colony. This activity results in resources becoming available to the offspring of the adult rather than to other individuals (Armitage 1986b, 2003c).

The primary cause of decreased reproduction is reproductive suppression. Evidence indicates that reproductive suppression occurs in every marmot species (Armitage 1996b; Blumstein and Armitage 1999). For example, in the biennial-breeding hoary marmot a female skips an additional year if her coresident breeds. When subordinate females breed, they produce half as many young as dominant females (Wasser and Barash 1983).

In the alpine marmot, *M. marmota*, the dominant territorial female suppresses the reproduction of the subordinate females, even in those years when the dominant female skips reproduction. Although subordinate females copulate, they fail to wean a litter (Arnold 1990a; Perrin et al. 1993; Lenti Boero 1999). Reproductive suppression in alpine marmots apparently is mediated through social behavior. Social interactions were most frequent during gestation, and the dominant females initiated most of the agonistic behavior (Hackländer et al. 2003). Subordinate females were not denied access to males; some copulated and developed nipples, which indicates pregnancy (Armitage and Wynne-Edwards 2002). Social status was unrelated to estradiol concentrations during mating; glucocorticoids increased in all adult females, with higher levels in subordinates (Hackländer et al. 2003). The authors suggest that suppression occurs by the negative effects of stress acting on the hypothalamic-pituitary-gonadal axis. Dominant females apparently pay a cost for reproductive suppression; reproductive success decreased as the number of adult subordinate females in the family increased.

But what of males? Extended family groups often contain several adult males, but only one is a dominant territorial. Among adult subordinate male alpine marmots at least 3 years old, sons had androgen levels as high as the territorial male, whereas non-sons had significantly lower levels, similar to those of 2-year-olds (Arnold and Dittami 1997). Corticosteroid and androgen levels were positively correlated in territorial males and negatively correlated in subordinate males. Corticosteroids were negatively correlated with body mass in sons and were high regardless of body mass in non-sons. High corticosteroid levels are associated with less mass gain; only those individuals with sufficient summer mass gain are capable of both surviving hibernation and sustaining the energetic costs of reproduction. Thus, suppression of competitive males may act through direct conflict during the mating season and through impairment of energetic processes needed to sustain reproduction.

Male suppression is kin-biased. Non-sons received more injuries from fighting, and large sons are tolerated. Large sons are critical for social thermoregulation and may also be more competitive for taking over an adjacent territory (Arnold and Dittami 1997). Although there may be fitness gains from the favorable treatment of sons, there is a possible fitness cost. Sons compete with their fathers for reproductive success, such that the territorial male does not father all the offspring (Arnold et al. 1994).

In alpine marmots, males may cause reproductive failure of females. Territory takeover by males impaired reproduction of dominant females if the takeover occurred after the mating period, despite clear evidence of pregnancy in the form of enlarged nipples and late molt (Hackländer and

through its effect on the age of first reproduction is a major demographic mechanism of population dynamics. Retrospective analyses of a life table response experiment revealed that age of first reproduction made a major contribution to annual changes in the projected population growth rate (Oli and Armitage 2004).

Why Remain in the Group, Given Suppression?

The major reason for remaining in the group is the high cost of dispersal. In the alpine marmot, dispersers and evicted, former territorials form the floating part of the population. As many as 50% of the floaters may be killed by predators; survival of those floaters that do not establish territorial residency is virtually nil, whereas annual mortality of subordinates living with resident territorials is about 4% (Arnold 1993; Grimm et al. 2003). By contrast, mortality of dispersing yearling yellow-bellied marmots is only 14% more than that of philopatric yearlings, and overwinter survival does not differ between dispersing and philopatric yearlings (overall mean = 89.3%).

Why the difference between the two species? Alpine marmots live in open habitat in forests; all available space is filled with family territories of about 2.5 ha (see fig. 13 in Arnold 1999). Similarly, steppe marmot families occurred over millions of hectares until about the 11th century (Tokarski et al. 1991). In effect, the only available habitat was occupied, and a disperser had almost no probability of surviving unless it found a vacant territorial position or was sufficiently large and strong to displace a resident territorial. Presumably older and larger marmots had a much higher probability of success. By contrast, radio-tracking of yellow-bellied marmots revealed that unoccupied patches of habitat were widely available (Downhower 1968; Van Vuren 1990). Although many of these sites did not have resources sufficient for long-term residency, they did provide shelter and hibernation sites during dispersal. Marmots that delayed dispersal until age two did not have increased survival, presumably because increased size was not an advantage for utilizing the widely available habitat patches. Similarly, burrow sites are readily available to dispersing young woodchucks, and young individuals readily dig new burrows (Armitage 2003b). Thus delayed dispersal does not occur in these species, as there is no known competitive advantage that can be gained by delay. By contrast, alpine marmots cannot dig a hibernaculum in 1 year (Arnold 1993), and delay dispersal until they are competitive for obtaining a territorial position in a saturated environment (Armitage 1996b). I believe that differences in the probability of successful dispersal, which results in delayed dispersal in many species of marmots, is the major factor leading to the diversity of social systems.

Furthermore, marmots may gain direct fitness in a variety of ways. Subordinate male alpine marmots may father some of the offspring (Arnold et al. 1994; Goossens et al. 1998). In addition, males gain indirect fitness benefits from alloparental care, which leads to a male-biased population sex ratio (Allainé et al. 2000) and polyandry. A subordinate female may reproduce in the family group (Mikhailuta 1991; Goossens et al. 1998) or may bud off to form a new group or matriline, or ascend to the territorial position in her natal group (Arnold 1990a; Armitage and Schwartz 2000; Oli and Armitage 2003). She may also mate in one group and escape suppression by the territorial dominant by joining a neighboring group (Goossens et al. 1996). Finally, by being a member of a matriline of two or three adult females, her reproductive success is higher than that of living alone (Armitage and Schwartz 2000).

Summary

Marmots evolved as large-bodied, ground-dwelling squirrels that occupied cool, moist, open landscapes. Large size allowed marmots to use more fibrous diets and to efficiently store and use fat during hibernation. Warming and the advance of the forests at the end of the last glaciation restricted the distribution of most species of marmots to high elevations, harsh environments that are characterized by a short growing season. Thus all species of marmots except the woodchuck require at least one additional growing season for young to reach maturity. The retention of young in their natal environment for their first hibernation or longer forms the basic social unit of marmots. Thus the evolution of adaptations for hibernation led to the evolution of sociality.

Marmot sociality evolved twice in two subgenera to form four social groups: solitary and extended family groups in the subgenus *Marmota*, and female kin groups and restricted family groups in the subgenus *Petromarmota*. Social behaviors are generally amicable within social groups and agonistic between social groups. Behaviors are kin-biased, with closely related kin treated more favorably than more distantly related kin. Most social groups are characterized by delayed dispersal and reproduction.

Delayed dispersal occurs because habitat saturation provides almost no opportunity for a small animal to survive by becoming resident as an immigrant in a social group. Only large individuals have a high probability of successfully competing for the dominant position within a family. Delayed reproduction is the result of reproductive competition; the dominant female (or male in extended families)

suppresses the reproduction of subordinates. This loss of reproduction is the major cost of sociality. A major benefit is increased survivorship. In yellow-bellied marmots, net reproductive rate increases as the number of matrilineal members increases, but decreases in the largest matrilines. Reproductively suppressed subordinates apparently choose the best alternative available to them by remaining in the social group until they can escape suppression, bud off to form a new group, or take over the dominant position within their group or an adjoining group.