EVOLUTION OF SOCIALITY IN MARMOTS

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The 14 species of marmots (*Marmota*) can be placed in one of four social systems: solitary; female kin matriline; adult male with two females and immature offspring; and a family group consisting of a territorial pair, subordinate adults, and immature offspring. Body size and hibernation are two critical features of marmot biology from which sociality evolves. The high correlation (r = 0.91) between immergence mass and mass loss suggests that species are heavier because they require more mass to survive the hibernation period. Marmots increase mass either by having a larger frame or by increasing the amount of mass per frame. Emergence and immergence mass are linearly related to body length; but change in mass is curvilinearly related to body length: large species use relatively more mass. An analysis of mass:length ratios reveals that species with a relatively high immergence mass use considerable mass during the hibernation period whereas species with a relatively high emergence mass use considerable mass after emergence. The consequence of large body size and a short growing season is that young in all but one species require two or more growing seasons to reach reproductive maturity. All species reach a maturity index for dispersal by age one; however, only two species disperse by that age and several species delay dispersal beyond the age of first reproduction. All species are reproductively mature by age two, but many species delay reproduction for one or more years. Delayed dispersal produces social groups of high relatedness. A cost of sociality is reproductive suppression; reproductive loss is partially compensated by increased survivorship and alloparental care. Subordinate adults also may reproduce or succeed to territorial status. Alloparental care occurs during hibernation when subordinate adults assist in social thermoregulation of closely related young. Thus, marmots have the characteristics of cooperative breeding. The following sequence of events is hypothesized to have occurred in the evolution of marmot sociality. Large size and a short growing season required the retention of offspring in their natal group for one or more additional years to reach maturity. Habitat saturation led to delayed dispersal, which in turn, increased survivorship. When subordinate adults remained in the social unit, they could participate in social thermoregulation and alloparental care.

Key words: *Marmota,* delayed dispersal, sociality, mass, delayed reproduction, mass: length ratios.

Sociality may be viewed as a life-history tactic, that, in the general sense, increases the fitness of group members (Armitage, 1981). The environmental factors that interact with other life-history traits to select for sociality are not always understood. Generally, animals are expected to aggregate to exploit a resource or to reduce predation risk (Alexander, 1974). Once social groups are formed, behaviors such as alarm calling (Blumstein et al., 1997; Sherman, 1997) and alloparental care (Arnold, 1993) can evolve. However, sociality also has costs; time to first reproduction is increased,

a smaller proportion of females breed, and litter size is reduced as social complexity increases (Blumstein and Armitage, 1998). Thus, sociality is associated with considerable reproductive skew (Blumstein and Armitage, in press; Keller and Reeve, 1994; Sherman et al., 1995). Presumably the benefits of sociality outweigh the costs, but the benefits and costs differ widely among individuals (e.g., Armitage, 1986; Clutton-Brock et al., 1988; Faulkes and Abbott, 1997). The nature of the ecological constraints that lead some individuals to accept reduced reproductive success as a consequence of living in a group and the behavioral, physiological, and ecological determinants of reproductive success within groups remain major questions of social biology (e.g., Emlen, 1997; Solomon and French, 1997).

Marmots (*Marmota*) are an excellent taxon for studying the evolution of sociality. Fourteen recognized species are distributed across the northern hemisphere (Barash, 1989). Because they are diurnal and burrow-dwelling, they can be easily located for trapping, marking, and observation. Most importantly, they have a variety of social systems. Current knowledge suggests that marmot species may be placed in one of four social systems (Armitage, 1996). Only the woodchuck (*Marmota monax*) leads a solitary existence; the mating system is polygynous. Yellow-bellied marmots (*M. flaviventris*) form female kin groups, with associated young (less than one year old) and yearlings, that may persist through time as matrilines. An adult male resides with one or more matrilines to produce a harem-polygynous mating system (Armitage, 1998). The social system of the Olympic (*M. olympus*) and hoary (*M. caligata*) marmots consists of an adult male with two females and a litter of yearlings or young; the mating system is bigamous, but some populations of the hoary marmot are monogamous (Holmes, 1984). As far as is known, all other species are characterized as living in family groups (Bibikow, 1996) consisting of a reproductive territorial pair, subordinate adults, yearlings, and young. The mating system is monogamous, but polyandry may occur in some species; e.g., *M. marmota* (Arnold, 1990*a*), *M. bobac,* and *M. baibacina* (Rymalov, 1994).

This diversity of social systems raises the question of what factors led to their evolution. Before we can frame hypotheses for future testing, we must consider two critical features of marmot biology. First, marmots are relatively large—they are the largest true hibernator. Thus, much of their biology revolves around the requirement of successful hibernation. There is also considerable variation in body size; the body mass at emergence from hibernation of the largest species, *M. bobak,* is 1.76 times that of the smallest species, *M. flaviventris.* Second, they have a short active season ranging among species from about 3.5 to 7.5 months ($\bar{X}$ = 4.8 months). During this limited time they must reproduce, grow, and prepare for hibernation. The interaction of these two factors establishes the basis for the evolution of sociality.

Body Mass

What accounts for the diversity of body mass? Because marmots do not store food, one possibility is that body mass is related to hibernation; e.g., those species that have longer periods of hibernation lose more mass. Note that hibernation period refers to the time from disappearance above ground in the autumn to emergence from the burrow the following spring. Hibernation refers to the period when characteristic bouts of torpor occur. This suggestion is not supported as there is no correlation among species between body mass or mass loss during hibernation and the length of the hibernation period (Armitage and Blumstein, in press). However, immergence mass (body mass at entry into hibernation) is highly correlated (r = 0.91) with mass loss during hibernation. These relationships suggest that marmots are large because they use considerable mass during the hibernation

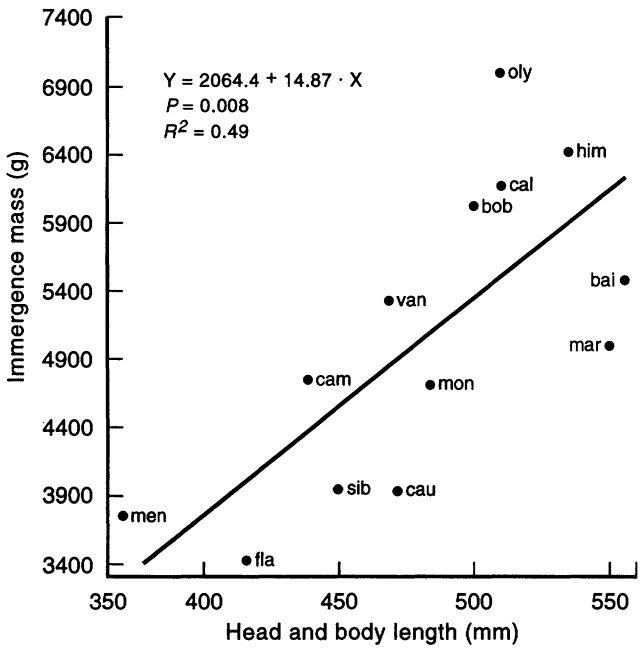

FIG. 1.—The relationship between immergence mass and head and body length for 13 species of marmots. bai = *M. baibacina,* bob = *M. bobac,* cal = *M. caligata,* cam = *M. camtschatica,* cau = *M. caudata,* fla = *M. flaviventris,* him = *M. himalayana,* mar = *M. marmota,* men = *M. menzbieri,* mon = *M. monax,* oly = *M. olympus,* sib = *M. sibirica,* van = *M. vancouverensis.* Body mass for *M. bobak* from Mashkin, 1997; for *M. menzbieri* from Mashkin and Baturin, 1993; for *M. marmota* from Mann et al., 1993; for all other species from Armitage and Blumstein, in press. Head and body length measurements for *M. flaviventris* and *M. monax* from specimens in the Kansas University Natural History Museum; for *M. vancouverensis, M. caligata,* and *M. olympus* from Lee and Funderburg, 1982; for *M. himalayana* from USNM specimens; for all other species from Ognev, 1963. Immergence mass is based on weights taken during the two weeks prior to immergence; emergence mass is based on weights taken during the first two or three weeks following emergence.

period but the use is not related to the length of the hibernation period.

If more mass is advantageous, how may a marmot increase mass? Two possibilities exist. More mass may be added to the skeletal frame or the frame may become bigger. Adding more mass to a frame has obvious limitations, a rotund marmot would lose both speed and agility of movement. A 1.5-fold difference in body length (head + body) among marmot species suggests that increasing the size of the frame was the major mechanism for increasing mass. Emergence mass is linearly related to body length ($P = 0.038$, $R^2 = 0.34$), but a stronger relationship exists between immergence mass and body length (Fig. 1). The change in body mass (the difference between immergence mass and emergence mass) during the hibernation season is curvilinearly related to immergence mass (Fig. 2). Larger species have a relatively larger change in mass. Although the relationships between mass and body length are highly significant, only 37 to 49% of the variation in mass is explained by body length. Species such as *M. olympus, M. caligata,* and *M. himalayana* are larger than expected (Fig. 1) and lose more mass than expected (Fig. 2) based on body length. *M. vancouverensis* and *M. bobac* have larger immergence masses than expected (Fig. 1), but mass change during hibernation is less than expected (Fig. 2). Considerable variability in

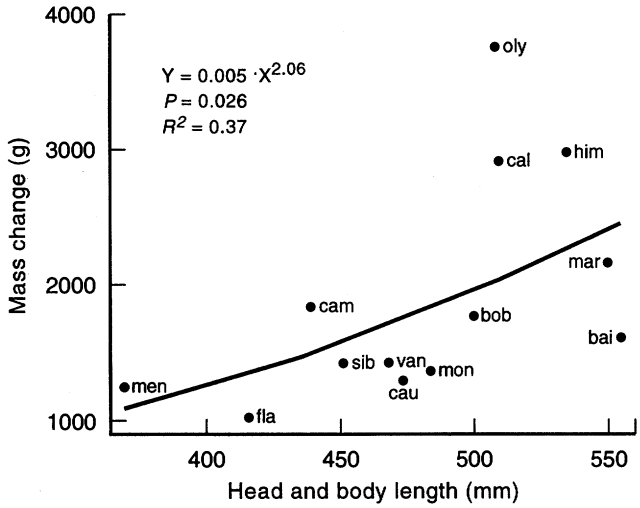

FIG. 2.—The relationship between mass change (difference between immergence and emergence mass) and head and body length of marmots. Species abbreviations as in Figure 1.

body mass remains to be explained. I will further explore body mass relative to body length.

Mass-length ratios.—I examined mass characteristics relative to body length by calculating three mass:length ratios (Table 1). Relationships among the ratios were examined by Spearman rank correlation. Immergence:length (I/L) and emmergence: length (E/L) were significantly related (r_s = 0.49, P=0.05). Essentially, this relationship states that marmots with relatively high immergence mass also have a relatively high emergence mass. This relationship is not surprising; relatively larger marmots emerge from hibernation relatively large. However, the correlation is just statistically significant and considerable variation remains unexplained. Immergence:length and change in mass:length (C/L) also were significantly related (r_s = 0.80, $P < 0.01$); immergence mass is relatively high in those species that lose relatively high mass during the hibernation season. In effect, marmots that use considerable mass during the hibernation period need to be relatively large at immergence. However, E/L and C/L were unrelated (r_s = −0.02, NS). The relative change in mass during the hibernation period does not determine the relative mass at emergence. The different relationships of E/L and I/L to C/L suggest that relative emergence and immergence masses are affected by different factors.

TABLE 1.—*Mass:length ratios for 13 species of marmots.*

Ratio		Mean	Range
Immergence: Length	I/L	10.5	8.25–13.9
Emergence: Length	E/L	6.6	5.14–8.5
Change in Mass: Length	C/L	3.9	2.43–7.4

When C/L is plotted against E/L, two major groups are distinguished based on when higher costs (as expressed in mass loss) occur (Fig. 3). Those species whose E/L ratios are above the mean for all species have emergence masses higher than expected for their body size. All live in environments where considerable mass loss regularly occurs after emergence (Armitage and Blumstein, in press). For example, both sexes of *M. baibacina* and *M. monax* lose mass for several weeks after emergence. Data on post-emergence mass loss for *M. menzbieri* and *M. vancouverensis* are unavailable. Because they have a relatively

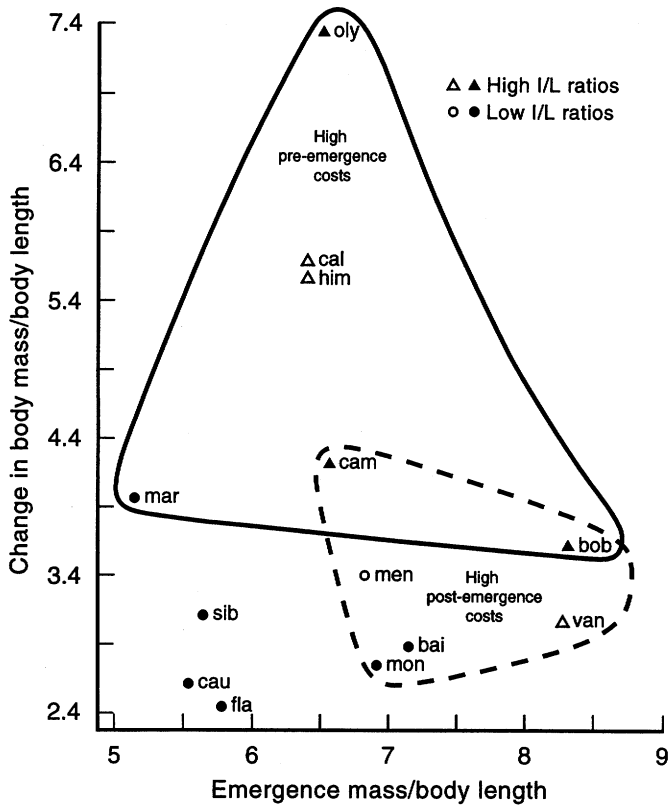

FIG. 3.—The relationship between the ratio of change in body mass:body length to the ratio of emergence mass:body length. Those species enclosed within the solid line have C/L ratios greater than the mean. Those species enclosed within the dashed line have E/L ratios greater than the mean. Species with open symbols are predicted to have the costs associated with their respective grouping. Species abbreviations as in Figure 1.

high E/L ratio, I predict that they also have high post-emergence mass loss.

Species with high I/L ratios (greater than the mean) (Fig. 3) have higher immergence masses than expected for their body size. These species have high pre-emergence costs. Both *M. camtschatica* and *M. bobac* mate and initiate gestation before emergence (Armitage and Blumstein, in press). This period of euthermy requires considerably greater energy expenditure than that of a torpor bout (Armitage et al., in litt.; Heldmaier et al., 1993). Other species in this group; e.g., *M. marmota* and *M. olympus,* have high hibernation costs (costs that occur before terminal arousal from hibernation). Reasons for these costs will be discussed later. *M. himalayana* and *M. caligata* have high I/L ratios; therefore, I predict that they also have high pre-emergence hibernation costs (Fig. 3).

Those species with a C/L greater than the mean have a greater change in mass than expected for their body size (Fig. 3). All have high hibernation costs (as evidenced by mass loss during the hibernation period) and may also have high post-emergence costs. *M. olympus, M. caligata,* and *M. marmota* typically lose mass, especially in years of snow cover, after emergence (Armitage and Blumstein, in press).

The mass characteristics of marmots are

a consequence of living in a harsh environment with a short growing season. Because of the short growing season, there is a trade-off between the timing of reproduction and survival. An adult female must initiate reproduction as early as possible so that the young have sufficient time for growth and so that the young and the adult female can prepare for hibernation. If the female initiates reproduction before she can forage, she will be euthermic with a high metabolic rate and must rely on her fat. If she becomes euthermic too soon, she may die of starvation before she can forage. If she delays reproduction until she is certain of food, time may be insufficient for either the young or her to accumulate sufficient fat to survive the next hibernation. Thus, fat resources become critical for successful reproduction. Because with an increase in body size fat is added at a rate greater than it is used, the female can increase her net gain in the use of fat by becoming larger, but this tactic has consequences for juvenile development. She can also accumulate relatively more fat for her body size (Fig. 2). In the evolution of marmots, both an increase in size and a relative increase in fat have occurred.

Reproductive stress.—Reproduction early in the year is stressful, especially for females. In part, early reproduction represents a gamble that future conditions, such as food and weather, will sustain reproductive effort. Stress is evident in embryo absorption by *M. caudata* and *M. baibacina,* which occurs in bad years, and reduced fattening, which is a consequence of lactation and the short active season (Armitage and Blumstein, in press). During lactation female marmots fail to gain mass and may actually lose mass. Thus, they begin to gain mass at least three weeks later than barren females and there is insufficient time for the reproductive females to catch up. Interestingly, *M. sibirica* and *M. caudata,* two species with reduced fattening by reproductive females, have I/L ratios below the mean for all species (Fig. 3). Summer drought also produces reproductive stress; young *M. bobac* and young and reproductive female *M. flaviventris* suffer high mortality during hibernation as a consequence of being unable to accumulate fat (Armitage, 1994).

Inability of females to maximize fattening leads to reproductive skipping (failure to wean young), which occurs normally in most species of marmots. Ten of 14 species regularly skip one or more years; only *M. flaviventris* and *M. monax* are known not to regularly skip reproduction (Armitage and Blumstein, in press).

Dispersal and Reproductive Maturity

Recall that large body size has a developmental consequence. Only *M. monax* has a growing season of sufficient length to enable young to reach reproductive maturity and to reproduce after their first hibernation. All other species require one or more additional years. In order to determine if dispersal and reproduction are delayed beyond maturity, an estimate of maturity is needed. For this purpose, a maturity index (MI, Barash, 1989) may be calculated by dividing the body mass at a specified age by the body mass of an adult. For this calculation, emergence mass is used to minimize the effects of fattening. For example, the emergence mass of young at the end of their first hibernation is divided by the emergence mass of adult females.

Dispersal is possible when MI $\geq$ 0.5 (Blumstein and Armitage, in press). Only young *M. monax* reach a MI of 0.5 in their first summer and disperse as young. All other species reach the MI for dispersal one year later as yearlings, but only *M. flaviventris* disperses in that year (Table 2). Thus, all other species delay dispersal; some delay beyond the age of first reproduction. Therefore, delayed dispersal is applied only to those species that disperse one or more years beyond the year in which the threshold MI (0.5) for dispersal is reached.

Reproductive maturity is possible in the year after an MI of at least 0.65 is achieved (Blumstein and Armitage, in press). Only

TABLE 2.—*Maturity index, age of first reproduction (for females), and age of dispersal (for both sexes) for eight species of marmots for whom data are available. References are in Blumstein and Armitage, in press.*

Species	Maturity index		Age of first reproduction (years)	Age of dispersal (years)
	Young	Yearling		
M. monax	0.67	0.87	1	<1
M. flaviventris	0.39	0.76	2	1
M. olympus	0.42	0.77	3	2
M. caligata	0.37	0.71	3	2
M. vancouverensis	0.38	0.86	3	2
M. marmota	0.39	0.79	2	3 or 4
M. sibirica	0.26		2	3 or older
M. bobac	0.45	0.88	3	3 or older

M. monax reaches this level as a young and it is the only species of marmot that reproduces as a yearling. Apparently all species could reproduce at age two, but most species delay reproduction one or more years (Table 2). Thus, delayed reproduction refers only to those species that reproduce at least one year later than the year after the threshold MI (ca. 0.7) for reproduction is reached. The foregoing discussion raises two questions: Why delay dispersal? Why delay reproduction?

DELAYED DISPERSAL AND REPRODUCTION

I hypothesize that dispersal is delayed because of ecological constraints. Evidence indicates that for most species of marmots, habitats are saturated. Saturation occurs either when a local patch is fully occupied or a large habitat patch is occupied by several families (Armitage, 1996). A marmot must either displace a resident or find a vacancy (e.g., a territorial male or female who dies during hibernation creates a vacancy). Presumably the chances for success improve with age and size. When population reduction occurs, the empty spaces are filled by younger animals dispersing form the core areas (Bibikow, 1996). A major consequence of delayed dispersal is that marmots form social units consisting of kin groups. However, relatedness within kin groups may vary because of immigration, such as when the territorial male is displaced by an immigrant (Arnold, 1990*a*).

Reproductive delay is probably imposed; i.e., reproductive suppression occurs. Reproductive suppression is the failure of reproductively mature, usually younger, animals to reproduce in the presence of reproductive, usually older, individuals. Either sex may be suppressed (Arnold and Dittami, 1997). Evidence indicates that reproductive suppression in marmots is widespread (Armitage, 1996) and may be a universal feature of marmot biology. Thus, a cost of sociality is reproductive loss; i.e., a loss of fitness.

Are there compensatory gains in fitness that at least partially offset the loss due to reproductive suppression? Three possibilities exist. First, survivorship is increased in species with delayed dispersal (Armitage, 1998; Blumstein et al., in press). Second, there is an opportunity to mate as a subordinate; i.e., an individual may escape suppression. Some subordinate male *M. marmota* breed (Arnold, 1993) and subordinate female *M. vancouverensis* (Bryant, 1996), *M. baibacina* (Mikhailuta, 1991), *M. caligata* (Wasser and Barash, 1983), and *M. caudata aurea* (Blumstein and Arnold, 1998) may produce litters. Third, there is an opportunity to gain indirect fitness through alloparental care.

Social Thermoregulation and Alloparental Care

The best evidence suggests that alloparental care may occur during hibernation. Because most species of marmots hibernate in a common hibernaculum (Bibikow, 1996), the potential for social thermoregulation is widespread. Social thermoregulation is best documented in the alpine marmot, *M. marmota* (Arnold, 1990*a*, 1990*b*, 1993).

Social thermoregulation has costs and benefits. The major benefit is that loss of mass is lower and survivorship greater the larger the number hibernating together in the absence of juveniles. The presence of juveniles imposes a cost: the loss of mass of the territorial pair and related subordinate adults is greater when hibernating with juveniles. If only the territorial pair is present with juveniles, loss of mass results in high winter mortality. Thus, successful social thermoregulation with juveniles requires the presence of subordinate adults. When subordinate adults are present, group survivorship increases as the number of closely related adults in the group increases. The role of subordinate adults is biased by kinship; loss of mass of subordinate adults less closely related to juveniles is not affected by the presence of juveniles.

Thus, alloparental care by subordinate adults increases the survivorship of related juveniles and their parents. Increased survivorship of juveniles provides some indirect fitness benefits to the non-reproductive adults. Family members of both *M. olympus* (Barash, 1973) and *M. caligata* (Holmes, 1984) occupy the same hibernaculum. If social thermoregulation occurs in these species, the cost of providing heat to the young in the absence of subordinate adults may account for their large body size and the relatively high change in mass during hibernation. In effect, the Olympic and hoary marmots may accomplish with large size and greater fat resources what the smaller Alpine marmot achieves by alloparental care.

Finally, it should be noted that among marmot species the attributes of cooperative breeding, delayed dispersal, reproductive suppression, and alloparental care, occur (Solomon and French, 1997). These attributes differ among marmot species (Blumstein and Armitage, in press), which makes this taxon an excellent one for the study of the evolution of cooperative breeding.

Evolution of Marmot Sociality: A Scenario

The evolution of marmot sociality begins with large body size that is required for the accumulation of resources for existing in a harsh environment that typically has a short growing season. As a consequence of the short growing season, young of all species except *M. monax* require one additional summer to reach a size that increases the probability of successful dispersal. The retention of offspring in their natal group as a consequence of delayed dispersal results in the formation of social groups. In *M. flaviventris,* only the females are philopatric; in those species that form family groups, both sexes are retained. Because of habitat saturation, dispersal may be delayed beyond reproductive maturity. The major cost of delayed dispersal is delayed reproduction, which is a consequence of reproductive suppression of younger, subordinate individuals by older, dominant individuals, who typically are kin of the younger subordinates.

Once individuals are members of a social group, several benefits are possible. First, survivorship increases. Second, a subordinate marmot of either sex may breed in its natal family. Thus, there is the potential for both polyandry and polygyny. Third, both males and females may become dominant, territorial reproductives. Fourth, all age groups may participate in social thermoregulation, which is not required, but which increases survivorship. Fifth, there is an opportunity of alloparental care once dispersal

has been delayed. Alloparental care is energetically costly, but because survivorship of juveniles increases, indirect fitness benefits accrue to the helpers.

Eventually many, if not most, individuals disperse. Dispersal should occur when benefits of dispersing exceed the benefits of remaining philopatric. In other words, dispersal should occur when the probability of reproducing after dispersal is greater than the probability of reproducing when remaining (Armitage, 1992). In terms of fitness, dispersal should occur when inclusive fitness of a disperser is greater than the inclusive fitness that individual could gain by remaining philopatric.

Future Research

Marmots are a superb group of mammals for studying the evolution of sociality and cooperative breeding. Although I believe that the broad outline that I sketched is correct, there are enough unanswered questions to occupy a generation of mammalogists. Let me express a few of them.

How is the use of mass allocated to different activities; e.g., thermoregulation, reproduction, alloparental care, during the hibernation period? We have clues, such as alloparental care in *M. marmota* and reproduction in *M. bobac,* but we really do not have a mass-utilization budget for any marmot species. What is the frequency of breeding by subordinate adults? What social dynamics are employed by successful breeders that enable them to avoid reproductive suppression? What are the mechanisms of reproductive suppression? How widespread is social thermoregulation and alloparental care? How do we quantify "harsh environment" and measure the availability of habitat? What is the success rate of dispersers and how does success vary with the age of the disperser? What rule of thumb is used by a marmot when it decides to disperse? Do marmots use the natal group as a base for exploring residence and/or reproductive possibilities in nearby groups, thereby gaining information that leads to a decision of whether to stay or emigrate? How critical is kinship in the social dynamics and reproductive success within the social group? Many more questions could be raised, but these should suffice to make clear that marmot research is in its infancy and some species, such as *M. broweri,* the Arctic marmot, are virtually unknown.

Marmots are warm, furry, boisterous, intelligent, enigmatic creatures that live in beautiful places. What more could one ask for! I hope to see all of you at the next International Marmot Conference in Austria in the year 2000. There is no more fitting way to end the millenium.

Acknowledgments

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Literature Cited

Alexander, R. D. 1974. The evolution of social behavior. Annual Review of Ecology and Systematics, 5:325–383.

Armitage, K. B. 1981. Sociality as a life history tactic of ground squirrels. Oecologia, 48:36–49.

———. 1986. Individuality, social behavior, and reproductive success in yellow-bellied marmots. Ecology, 67:1186–1193.

———. 1992. Social organization and fitness strategies of marmots. First International Symposium on Alpine Marmot (*Marmota marmota*) and on Genus *Marmota,* 89–94.

———. 1994. Unusual mortality in a yellow-bellied marmot population. Pp. 5–13, *in* Actual problems of marmots investigation (V. Yu. Rumiantsev, ed.). ABF Publishing House, Moscow.

———. 1996. Social dynamics, kinship, and population dynamics of marmots. Pp. 113–128, *in* Biodiversity in marmots (M. Le Berre, R. Ramousse and

L. Le Guelte, eds.). International Marmot Network, Moscow-Lyon.

———. 1998. Reproductive strategies of yellow-bellied marmots: energy conservation and differences between the sexes. Journal of Mammalogy, 79:385–393.

ARMITAGE, K. B., AND D. T. BLUMSTEIN. In press. Body-mass diversity in marmots. Pp. 000–000, *in* Holarctic marmots as a factor of biodiversity (K. B. Armitage and V. Yu. Rumiantsev, eds.). International Marmot Network, Moscow.

ARNOLD, W. 1990*a*. The evolution of marmot sociality: I. Why disperse late? Behavioral Ecology and Sociobiology, 27:229–237.

———. 1990*b*. The evolution of marmot sociality: II. Costs and benefits of joint hibernation. Behavioral Ecology and Sociobiology, 27:239–246.

———. 1993. Social evolution in marmots and the adaptive value of joint hibernation. Verhandlungen der Deutschen Zoologischen Gesellschaft, 86:79–93.

ARNOLD, W., AND J. DITTAMI. 1997. Reproductive suppression in male alpine marmots. Animal Behaviour, 53:53–66.

BARASH, D. P. 1973. The social biology of the Olympic marmot. Animal Behaviour Monographs, 6:173–245.

———. 1989. Marmots. Social behavior and ecology. Stanford University Press, Stanford, California.

BIBIKOW, D. I. 1996. Die Murmeltiere der Welt. Westarp Wissenschaften, Magdeburg, Germany.

BLUMSTEIN, D. T., AND K. B. ARMITAGE. 1998. Life history consequences of social complexity: a comparative study of ground-dwelling sciurids. Behavioral Ecology, 9:8–19.

———. In press. Cooperative breeding in marmots. Oikos, 74:000–000.

BLUMSTEIN, D. T., AND W. ARNOLD. 1998. Ecology and social behavior of golden marmots (*Marmota caudata aurea*). Journal of Mammalogy, 79:873–886.

BLUMSTEIN, D. T., J. C. DANIEL, AND W. ARNOLD. In press. Survivorship of golden marmots (*Marmota caudata aurea*) in Pakistan. Pp. 000–000, *in* Holarctic marmots as a factor of biodiversity (K. B. Armitage and V. Yu. Rumiantsev, eds.). International Marmot Network, Moscow.

BLUMSTEIN, D. T., J. STEINMETZ, K. B. ARMITAGE, AND J. C. DANIEL. 1997. Alarm calling in yellow-bellied marmots: II. The importance of direct fitness. Animal Behaviour, 53:173–184.

BRYANT, A. 1996. Reproduction and persistence of Vancouver Island marmots (*Marmota vancouverensis*) in natural and logged habitats. Canadian Journal of Zoology, 74:678–687.

CLUTTON-BROCK, T. H., S. D. ALBON, AND F. E. GUINNESS. 1988. Reproductive success in male and female red deer. Pp. 325–343, *in* Reproductive success. Studies of individual variation in contrasting breeding systems (T. H. Clutton-Brock, ed.). The University of Chicago Press, Chicago, Illinois.

EMLEN, S. T. 1997. Predicting family dynamics in social vertebrates. Pp. 228–253, *in* Behavioural ecology: an evolutionary approach (J. R. Krebs and N. B. Davies, eds.). Blackwell Science, Inc., Malden, Massachusetts.

FAULKES, C. G., AND D. H. ABBOTT. 1997. The physiology of a reproductive dictatorship: regulation of male and female reproduction by a single breeding female in colonies of naked mole-rats. Pp. 302–334, *in* Cooperative breeding in mammals (N. G. Solomon and J. A. French, eds.). Cambridge University Press, Cambridge, United Kingdom.

HELDMAIER, G., S. ORTMANN, AND G. KÖRTNER. 1993. Energy requirements of hibernating alpine marmots. Pp. 175–183, *in* Life in the cold: ecological, physiological, and molecular mechanisms (C. Cary, G. L. Florant, B. A. Wunder, and B. Horwitz, eds.). Westview Press, Boulder, Colorado.

HOLMES, W. G. 1984. The ecological basis of monogamy in Alaskan hoary marmots. Pp. 250–274, *in* The biology of ground-dwelling squirrels: annual cycles, behavioral ecology, and sociality (J. O. Murie and G. R. Michener, eds.), University of Nebraska Press, Lincoln, Nebraska.

KELLER, L., AND H. K. REEVE. 1994. Partitioning of reproduction in animal societies. Trends in Ecology and Evolution, 9:98–102.

LEE, D. S., AND J. B. FUNDERBERG. 1982. Marmots (*Marmota monax* and allies). Pp. 176–191, *in* Wild mammals of North America: biology, management, and economics (J. A. Chapman and G. A. Feldhamer, eds.). The Johns Hopkins University Press, Baltimore, Maryland.

MANN, C. S., E. MACCHI, AND G. JANEAU. 1993. Alpine marmot (*Marmota marmota,* L.) Ibex. Journal of Mountain Ecology, 1:17–30.

MASHKIN, V. I. 1997. The European bobac: ecology, conservation and use. (In Russian).

MASHKIN V. I., AND A. L. BATURIN. 1993. Menzbier's marmot (*Marmota menzbieri*). Professor B. M. Zhithov Research Institute of Game Management and Fur Farming, Kirov, Russia. (In Russian).

MIKHAILUTA, A. A. 1991. Family structure in grey marmots. Pp. 172–187, *in* Population structure of the marmot (D. I. Bibikov, A. A. Nikolski, V. Ju. Rumiantsev, and T. A. Seredneva, eds.). USSR Theriological Society, Moscow. (In Russian).

OGNEV, S. I. 1963. Mammals of the U.S.S.R. and adjacent countries. Rodents. Israel Program for Scientific Publications, Jerusalem, Israel, 5:185–286.

RYAMALOV, I. V. 1994. On social structure and behavior of steppe marmots during breeding period. Pp. 225–235, *in* Actual problems of marmots investigation (V. Yu. Rumiantsev, ed.). ABF Publishing House, Moscow, Russia.

SHERMAN, P. W. 1977. Nepotism and the evolution of alarm calls. Science, 197:1246–1253.

SHERMAN, P. W., E. A. LACEY, H. K. REEVE, AND L. KELLER. 1995. The eusociality continum. Behavioral Ecology, 6:102–108.

SOLOMON, N. G., AND J. A. FRENCH (EDS.). 1997. Cooperative breeding in mammals. Cambridge University Press, Cambridge, United Kingdom.

WASSER, S. K., AND D. P. BARASH. 1983. Reproductive suppression among female mammals: implications for biomedicine and sexual selection theory. Quarterly Review of Biology, 58:513–538.

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