

### Further Resources

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## Social Organization

### Socioecology of Marmots

Marmots are the largest ground-dwelling squirrels. The best-known marmot is the woodchuck, which each year on February 2 predicts whether winter will be short or prolonged. Of the 14 species of marmots, the woodchuck is the earliest to emerge from hibernation in the spring and the only marmot species that is not social. This relationship raises the question of whether marmot sociality is related to hibernation. Because marmots are the largest true hibernators, could body size play a role in the evolution of sociality? To answer these questions, we must first consider the evolutionary history of marmots.

The first mammals clearly recognized as marmots lived in North America about 8 million years ago. Marmots reached Eurasia about 2 million years ago, and all existing species have evolved since that time. Marmots inhabited cool moist habitats. In general, the environment was characterized by cold winters and short, warm summers in a grassy landscape. With the general warming trend since the last glaciation, all but two species of marmots disappeared from warm, low-elevation habitats, and came to occupy cool, high-elevation meadows, often in association with rocky outcrops and talus. These environments are relatively harsh; summers are typically short, the spring season is often cold and stormy,

### The Species of Marmots (Genus *Marmota*)

Eurasia		North America	
Black-capped	<i>M. camtschatica</i>	Woodchuck	<i>M. monax</i>
Steppe	<i>M. bobak</i>	Yellow-bellied	<i>M. flaviventris</i>
Tarbagan	<i>M. siberica</i>	Hoary	<i>M. caligata</i>
Menzbier's	<i>M. menzbieri</i>	Vancouver Island	<i>M. vancouverensis</i>
Long-tailed	<i>M. caudata</i>	Olympic	<i>M. olympus</i>
Gray	<i>M. baibacina</i>	Arctic	<i>M. broweri</i>
Alpine	<i>M. marmota</i>		

and the landscape may be snow covered from September until early July. Thus, the winter season, when food is unavailable, averages 7.2 months in length for all species of marmots. Marmots are too small to migrate to lower elevations for the winter or to remain active and survive on stored fat. They are too large to store food or to seek food under the snow. The alternative adopted by marmots is to accumulate fat during the summer growing season and to hibernate. Because hibernation greatly reduces metabolism, body fat supplies all the energy required to survive the long winter. For at least six marmot species, the body fat must not only support hibernation, it must also support reproduction, which occurs in the burrow before marmots emerge above ground and before they can forage. This activity is so energy demanding that most marmot species skip one or more years between successful reproductions in order to accumulate sufficient energy for both survival and reproduction. We know very little about how marmots allocate energy to basic maintenance and reproduction or the mechanism that determines whether marmots will initiate reproduction.

These high-energy demands raise the question of why marmots are large. Large animals require more total energy than small animals; could marmots reduce their energy demands if they were smaller? The answer is yes, but large size is highly advantageous in the places where marmots live. A larger body size has a larger digestive tract relative to metabolic rate. Large animals, such as marmots, can process the fibrous diets available in their grassy environments by retaining food in their digestive tracts for longer periods of time. As long as food plants are sufficiently abundant, marmots can support their large size. The home range that a marmot utilizes for foraging varies widely among species; the largest home ranges may be at least 15 times larger than the smallest home ranges. Presumably these differences in home range reflect the abundance of food available. But marmots need not only energy, but also essential nutrients, such as protein and certain fats necessary for successful hibernation. Little is known about marmot nutrition and the quality of available food. Furthermore, how does a large home range affect foraging and antipredator behavior? Are marmots with large home ranges more vulnerable to predation? Or are they more wary? Does parental care of the vulnerable young differ among species of marmots in relation to the area over which they forage? Or do wide-ranging species dig more escape burrows so that they are never far from a refuge?

Large body size has another important advantage. Large animals accumulate fat at the same rate as small animals, but use the fat relatively more slowly. Thus, if food resources are sufficient, large animals such as marmots can accumulate large amounts of



*A hoary marmot forages in a rocky meadow in Alaska where vegetation can be scarce.*

*Courtesy of Kenneth Armitage.*



*An adult marmot ventures outside its burrow in mid-June on Vancouver Island.*

*Courtesy of Kenneth Armitage.*

fat. Because of its efficient use, marmots have sufficient energy for hibernation, for initiating reproduction, and for coping with unfavorable weather conditions until vegetation becomes available.

But large body size has a major consequence. The short growing season does not provide sufficient time for the young to reach maturity before their first hibernation. There is one exception, the woodchuck. The active season of the woodchuck is about 7.5 months, which is 2–4 months longer than that of any other marmot. The woodchuck disperses away from its natal burrow, hibernates alone, and may reproduce as a yearling (1-year-old). Because of large size and a short growing season, the young of all other species of marmots remain at home for one or more years. This retention of young in their natal environment forms the basic social unit of marmots.

Social behavior is tightly related to social organization. Two major types of social behavior occur; amicable behavior consists of greeting, when one marmot sniffs at the head area of another or two marmots simultaneously sniff at each other's cheeks, and grooming, when one marmot chews at the head, neck, shoulders, or flank of another. Agonistic or conflict behavior is characterized by one marmot chasing another or by one marmot fleeing or avoiding another. Amicable behavior is cohesive; it apparently enables marmots to form social bonds, which are expressed in group sharing of burrows and foraging areas. Agonistic behavior is dispersive, nongroup marmots are excluded from the group and prevented from using the burrow and food resources of the group. Thus, marmot social groups are territorial.

The woodchuck is the only asocial marmot species. Agonistic behavior characterizes social interactions; in effect, an adult forms a group of one and defends its

territory against other woodchucks. The adult male defends a territory that overlaps the territories of several females. Only during mating do adult woodchucks associate together.

In the yellow-bellied marmot, all male yearlings disperse, but about half of the female yearlings remain in their natal area to form mother–daughter social groups. These groups may persist for several generations as matriline. An adult, immigrant male associates with one or more matriline and defends them against other male intruders. The matriline defends its territory against female immigrants. Female immigrants do not join an existing matriline, but become successful residents only when some part of the habitat patch is unoccupied and open for settlement. Social behavior within matriline is primarily amicable, but between marmots from different matriline, the behavior is almost entirely agonistic.

All other species of marmots live in family groups. Within groups, behavior is primarily amicable. Intruders encounter agonistic behavior from family members of the same sex. In species such as the alpine marmot of the European Alps and the Arctic marmot of the Brooks Range in Alaska, the extended family consists of a territorial, reproductive pair, non-reproductive adults of both sexes, yearlings, and young. In the hoary, Olympic, and Vancouver Island marmots of western North America, the limited family group also consists



Two young yellow-bellied marmots greet each other above their burrow in Colorado.

Courtesy of Kenneth Armitage.

of a territorial pair, yearlings, and young. The nonreproductive adults are not present in the social group of these species. The difference in social structure is related to the age of dispersal. Dispersal occurs at the age of 2 years in the hoary, Olympic, and Vancouver Island marmots, but may be delayed to the age of 4 years in the alpine and arctic marmots. Although all marmot species are capable of reproduction by the age of 3 years, marmots living in family groups delay reproduction to an older age and those living in extended family groups actually delay dispersal to an age older than that at which they could reproduce. Why do these marmots delay reproduction and dispersal? This question is critical because evolutionary success requires producing offspring that live to reproduce; otherwise the genealogical line becomes extinct. The implication is that the benefits from living in a group are so great that it is worth delaying or possibly forgoing reproduction. If the benefits of group living are so great, why are woodchucks not social and why do yellow-bellied marmots not form family groups? To answer this question, we must first ask what are the benefits of group living?

The major benefit to group living is survivorship. The longer a marmot remains in its social group, the higher the probability that it will live to maturity. However, this benefit does not include young; the known mortality rate of young marmots is about 50%. But the probability of surviving thereafter is greater in those species that live in family groups than it is in yellow-bellied marmots. The difference in survivorship seems to be related to the age of dispersal. The mortality rate of dispersers is greater than that of nondispersers; thus more yearling yellow-bellied marmots die than yearlings of other species because about 75% of yearling yellow-bellied marmots disperse, whereas none of the yearlings disperse in the species living in family groups. Unfortunately, we do not know the mortality rate of woodchucks that disperse as young, but we would expect it to be higher than that of other marmot species. We can now note that there is a trade-off in group living; increased survivorship comes at the cost of delayed reproduction. All things being equal, an individual will have greater reproductive success and contribute more of its genes to the next generation (the criterion for evolutionary success) the earlier it reproduces. Yellow-bellied marmots are under strong natural selection to reproduce at the age of 2 years, the earliest age at which reproduction is possible, and they disperse as yearlings. Woodchucks reproduce as yearlings, and disperse as young. Thus, woodchucks and yellow-bellied marmots disperse at an early age and risk predation in order to initiate reproduction at the earliest age possible. Although marmots that form restricted family groups could disperse as yearlings, these species delay dispersal for another year and disperse at the age of 2 years. These species are larger than the yellow-bellied marmot and may require an additional year of growth to reach reproductive maturity at the age of 3 years.

Thus, we note a tendency for a marmot species to disperse the summer before it is capable of reproduction, but we also noted that marmots living in extended family groups do not disperse until one or more years after they are capable of reproduction. We have come full circle and again ask the question, why do these species lose reproductive opportunities by remaining in their family instead of dispersing at a younger age? The answer apparently lies in the probability that a disperser can survive its first hibernation. A young woodchuck can either find an old burrow to occupy or readily dig a new one. A dispersing yearling yellow-bellied marmot can find many places where unoccupied burrows exist, and they survive hibernation as well as those yearlings that remain in their natal colony. But the situation differs drastically for such marmots as the alpine and steppe marmots. Their environments appear to be saturated with existing families. An alpine marmot has almost no chance either of finding an unoccupied burrow or of digging a new one for hibernation.

The only chance for survival is for the disperser to find a family in which the same sex territorial adult is no longer present and replace the missing adult or to successfully invade a family and drive out the current resident. The loser of such brief, intense conflict will almost certainly die. A small marmot would have almost no chance of winning a conflict; thus alpine marmots remain at home until they are large and strong enough to have a chance of winning the conflict for a territorial position. Also, by remaining at home they have some chance of replacing the same-sex territorial adult of their family. Whatever the nonreproductive adults eventually do, their only chance for eventual reproduction is to remain at home, forego reproduction, and gain size and strength for the eventual conflict over who will reproduce.



*A gray marmot in a vigilant posture outside its burrow in Kazakhstan.*

*Courtesy of Kenneth Armitage.*

The conflict over who will reproduce characterizes marmot societies and will be discussed more fully later. For now, let us consider how living in groups increases survivorship.

In yellow-bellied marmots, survivorship increases as group size increases. Marmots are vigilant and they commonly sit up on their haunches and scan the environment. When foraging, they look up or stand up while chewing and scan their surroundings for predators or agonistic marmots. When a predator is sighted, the marmot may give an alarm call and run to a nearby burrow or may run to the burrow and then call. The high-pitched, whistle-like cry alerts other marmots to the danger and perhaps informs the predator that it has been detected and might as well go elsewhere. The more marmots that are present in the social group, the more likely one of them will detect the approaching predator.

Survivorship may also be increased by group hibernation. Two or more marmots huddling together in the same hibernation nest can share heat and reduce the heat loss of each individual. Reducing heat loss reduces the use of fat, which extends the time that marmots can hibernate or makes more fat available for mating and reproduction after emerging from hibernation.

Although all species of marmots except woodchucks could benefit by the social group hibernating together, very little is known about whether marmots benefit from group hibernation. Only the alpine marmot has been studied extensively. In this species, the survivorship of young is greater when the family has several nonreproductive adults who are closely related to the young. The 3- and 4-year-old adults provide heat to the young, which reduces the use of fat by the young. In effect, these adults provide a form of parental care for their younger brothers and sisters. The adults incur a cost; they lose more body mass when hibernating with related young than when related young are not present.

In contrast to those species that form family groups in which only the territorial, dominant female reproduces, in yellow-bellied marmot matriline, commonly more than one female reproduces. Reproductive success increases as matriline size increases up to a size of three, then decreases in larger matriline of four or five. Reproduction is enhanced as the density of the social group increases. This relationship implies some kind of social facilitation of reproduction, but nothing is known about a possible mechanism. Reproductive enhancement is most likely when a female is living with same-age kin or with younger kin

(i.e., sisters or daughters). Thus, we could predict that adult females should recruit their daughters to become members of their matriline, and that yearling females should attempt to become residents. But only about 50% of the yearling females remain in their natal matriline; the others disperse. As is so often true in biology, recruitment is complex.

First, a yearling female is very unlikely to join a matriline if her mother is not present. In the mother's absence, older, nonlittermate sisters chase their younger sisters from the colony. Marmots prefer to recruit daughters rather than other kin; females that chase their younger sisters one year may recruit their daughters the next year. Second, recruitment is strongly related to the social environment. If most of the social behavior in the group is amicable, the yearling female is more likely to remain. But if agonistic behavior is common, the yearling female is more likely to disperse. Third, yearling recruitment is markedly affected by the "personality" or behavioral phenotype of the adults and yearlings. One way to measure a behavioral phenotype is by mirror image stimulation. A marmot in an arena is exposed to a mirror and its behavior with the mirror image is recorded. For example, a marmot may approach the image, attempt to greet or groom it or may remain in the back of the arena, chirp at the image, adopt a threat posture, or even attack the image. Each marmot receives an individual score, which represents its behavioral phenotype. Marmots that attempt to contact the image may be categorized as "more sociable," and those that avoid or threaten the image may be categorized as "more agonistic." The "more sociable" adult females are more likely to recruit yearling females, whereas the "more agonistic" yearling females are more likely than the "more sociable" yearlings to be recruited. This process produces an adult population in which individuals vary in their degree of sociability. Interestingly, once a yellow-bellied marmot becomes a resident, its behavioral phenotype minimally affects its reproductive success.

The major reason that the behavioral phenotype does not affect reproductive success is that reproductive suppression of younger adult females by older, dominant females is widespread. For example, a 2-year-old female, regardless of behavioral phenotype, has only about a 20% probability of reproducing if an older adult female is present, but that probability increases to about 48% when the no older adult is present. The major reason that reproductive success decreases in large matriline is that they consist of a high percentage of young adults that are reproductively suppressed. The mechanism of reproductive suppression is unknown, but available evidence suggests that agonistic behavior disrupts the normal endocrine processes of reproductive physiology.

Although yellow-bellied marmots are reproductively mature at age 2, reproductive suppression increases the average age of first reproduction to 3 years. Similar patterns of reproductive suppression occur in all social marmots. For example, the dominant, territorial female alpine marmot reproduces every other year. Even in the year in which she does not reproduce, she suppresses the reproduction of the other adult females in the family. In gray marmots, only 3% of the 2-year-old females breed, but 70% of females aged 5 years or older breed. In the Vancouver Island marmot, most females do not breed until age 4 or older. But what do males do? Male yellow-bellied marmots exclude other males from their territories, and the territorial males do all the breeding. In those marmots, such as the alpine marmot, where subordinate, mature males are present, some of these males may also mate with the territorial female. The territorial male attempts to suppress the reproduction of the subordinate males, especially when these males are not his sons. Because his sons are critical for warming the young during hibernation, their reproduction may not be suppressed. The sons are more likely to warm the young if there is some likelihood that they fathered some of the young. In fact, the sons of the dominant male father about 13% of the young in alpine marmot families. We may conclude that one characteristic of marmot societies is competition for reproduction.

In conclusion, the physiological adaptations associated with hibernation enabled the large-bodied marmots to live in harsh environments with a short growing season. The physiological adaptations in turn required behavioral and social adaptations leading to the retention of young with their parents to form social groups characterized by both competition and cooperation. Cooperation occurs primarily in the detection of predators and defense against marmot intruders. Competition occurs primarily in determining who will reproduce. In general, the older, dominant males and females reproduce, and reproduction by subordinates is suppressed. Fundamentally, the competition is a contest to determine which individuals achieve evolutionary success by producing offspring. The alternative to remaining in the social group and being reproductively suppressed is dispersal at a body size that has almost no chance of surviving hibernation alone or gaining access to an established territory. Only those species where unoccupied habitat is available have a reasonable probability of successful dispersal. Also, the marmots that remain at home have the possibility of reproducing (not all reproductive suppression is successful), of inheriting the territory and becoming a dominant, reproductive individual, of budding off a new adjoining territory and establishing a new family, or of gaining residency in an adjoining territory either by displacing a territorial resident or by filling a vacancy resulting from the death of a resident. Each individual adjusts its behavior (i.e., to be amicable or agonistic) to its local situation. Ultimately such behavior may lead to reproductive and evolutionary success.

*See also* Lemurs—*Behavioral Ecology of Lemurs*

Social Organization—*Dispersal*

Social Organization—*Monkey Families and Human*

*Families*

Social Organization—*Social Dynamics in the Plateau*

*Pika*

Social Organization—*Territoriality*

### Further Resources

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## ■ Social Organization

### Territoriality

Territory is one of many terms in animal behavior which has been borrowed from common usage, and as such, it is easy for us to assume that we know more about the territorial behavior of animals than is actually the case. According to Webster, territory is defined as “the land or waters under the jurisdiction of a nation, state, or ruler.” This definition captures