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The evolution, ecology, and systematics of marmots

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Abstract. The first species of *Marmota* occurred about 9.5 MYA in the United States. All modern species are known from the Pleistocene where they lived in the periglacial zone. With the retreat of the glaciers and expansion of forests, marmots became restricted to open mountain landscapes or the forest steppe or plain steppe zones. Marmots became adapted to habitats with grassland for foraging, a slope providing good drainage, southern to eastern exposure, and a soil structure appropriate for burrowing. Marmots adapted to habitats characterized by a seasonal food shortage, low temperature, and precipitation as snow by hibernating for an average among species of 7.2 months. Environmental harshness is characterized by large home ranges and reproductive skipping and the evolution of large body size, which increases the efficiency with which fat is utilized. A major consequence for this large animal living where the active season is short is that at least one additional summer of growth is necessary for young to reach maturity. Young are retained in their natal areas; this delayed dispersal results in the formation of social groups. Four types of social groups may be recognized: solitary, female kin group, restricted family, and extended family. Sociality evolved at least twice in marmots, once in North America and once in Eurasia. In those species that form extended families where dispersal is delayed beyond reproductive maturity, subordinate adults may engage in alloparental care and polyandry may occur. Evidence that marmot populations adapt to local conditions indicates that population differentiation continues and that there may be more species than the currently recognized fourteen.

Keywords: habitat, sociality, environmental harshness, hibernation, parasitism

Early evolution and systematics

Currently 14 species of marmots (genus *Marmota*), 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 (Bibikow 1996). Two species, *M. marmota* and *M. bobac*, occur in Europe; the remaining six Palearctic species occur in Asia.

Protosciurus, the first squirrel (Rodentia: *Sciuridae*), first appeared in the Oligocene in North America; *Miospermophilus*, the first of the true ground squirrels, appeared in the late Oligocene (Black 1972). During the Miocene well-developed genera of sciurids derived from *Miospermophilus* included *Marmota*, *Ammospermophilus*, *Spermophilus*, and *Cynomys* (Hafner 1984). These modern genera are grouped in the Tribe *Marmotini*. Within this tribe the marmots form a monophyletic group (Steppan *et al.* 1999) in Subtribe Marmotina along with *Paenemarmota* from the middle or late Pliocene (Hafner 1984, Mein 1992). Cladistic analysis of allozyme data indicates that marmots were derived from *Spermophilus* (Hafner 1984). The first species, *M. vetus*, occurred in the United States about 9.5 MYA (Steppan *et al.* 1999). Other fossil species include *M. minor* and *M. nevadensis*, the first giant marmot, about the size of *M. monax*; these large forms did not survive the cold crisis at the end of the Pliocene (Mein 1992). Marmots reached Eurasia at the beginning of the Quaternary via the Bering land bridge. Rapid divergence in the Pleistocene led to the present array of Palearctic and Nearctic species (Table 1). Fossil marmots were found in the Pliocene in Ukraine, Pre-Azov (Sea), western Siberia, and western Transbaikal. These fossils are rare and all modern species are known only from Pleistocene deposits (Zimina and Gerasimov 1973). An analysis of cave deposits from Italy revealed that the floor level had *M. marmota* (Aimar 1992). Other levels were dated to the late Middle or Upper Pleistocene. The skull of marmots from lower levels was more massive than the modern alpine marmot and the mandible and postcranial elements were larger. Several characters were in concordance with *M. marmota* and some with *M. bobac*. Modern molecular phylogeny does not indicate a close relationship between *M. marmota* and *M. bobac* (Kruckenhauser *et al.* 1998, Steppan *et al.* 1999); thus, these fossils most likely do not represent a common ancestor of these two species, but are indicative of ongoing microevolution in this genus.

Population differentiation and geographic variability

Geographical variability is evident in the recognition of subspecies. For example, seven sub-

Genus *Marmota*

Subgenus *Petromarmota*

M. flaviventris (yellow-bellied marmot): montane and alpine regions of western United States, north to south-central British Columbia and southern Alberta, south to southern White Mountains of California, Toquina and Pine Valley Mountains in Nevada, and the Sangre de Cristo Mountains in New Mexico (Frase and Hoffmann 1980).

M. caligata (hoary marmot): northwestern United States from northern Washington, Montana and extending through western Canada into central Alaska.

M. vancouverensis (Vancouver Island marmot): restricted to Vancouver Island.

M. olympus (Olympic marmot): restricted to the Olympic Mountains in western Washington (USA).

Subgenus *Marmota*

M. monax (woodchuck): extends from southeastern Alaska across southern Canada and southward into eastern United States east of the Great Plains and south as far as Georgia, Alabama, and Arkansas (Lee and Funderberg 1982).

M. marmota (alpine marmot): the Alps and Carpathians and reintroduced into the Pyrennes and Apennines.

M. broweri (Alaska marmot): the Brooks range of northern Alaska.

M. caudata (long-tailed marmot): western and southern Tien Shan and the Pamir Alai in addition to Kashmir, Afghanistan, and northwest Pakistan.

M. menzbieri (Menzbiers marmot): only in the mountains of western Tien Shan.

M. bobac (steppe marmot): steppe regions of Ukraine and Russia, east bank of the Volga River and southern Urals, western and southern Kazakstan.

M. baibacina (gray marmot): central Kazakstan, the Altai, Tarbagatai, Dzkungar Alatau and Tien Shan Mountains, northwestern Mongolia and western China.

M. camtschatica (black-headed marmot): eastern Siberia, Kamchatka, and mountains of northern Transbaikal.

M. himalayana (Himalayan marmot): mountains of central Asia, Tibet, western China, and the Himalayas.

M. sibirica (tarbagan): Transbaikal region, Mongolia, northern China.

Table 1. The species of marmots (modified from Steppan *et al.* 1999) and their geographical distribution. Palaearctic distributions from Zimina and Gerasimov 1973.

species of *M. monax*, 10 subspecies of *M. flaviventris*, and seven subspecies of *M. caligata* were recognized (Howell 1915). Among Palearctic species, two subspecies were described for *M. marmota*, *M. m. marmota* in the Alps and *M. m. latirostris* in the Tatras (Gasienica Byrcyn 1997); three subspecies are recognized for both *M. bobac* (Bibikow 1996) and *M. camtschatica* (Boyeskoro *et al.* 1996). The three subspecies of *M. camtschatica* differ in body and skull dimensions and fur color. All have identical karyotypes 2N = 40, NF_A = 62 (Lyapunova *et al.* 1992) but immunogenetic responses and alarm calls differ between *M. c. camtschatica* and *M. c. doppelmayeri.* The karyotype is similar to that of the Nearctic *M. caligata* and *M. vancouverensis* as the karyotype of all other Eurasian species is identical, 2N = 38, NF_A = 70 (Bibikow 1996). However, this similarity in karyotype does not mean that *M. camtschatica* and the Nearctic marmots are phylogenetically close; in fact, they belong to different subgenera (Table 1). Diversification is so extensive that Boyeskorov *et al.* (1996) suggest that the black-capped marmot should be considered a superspecies. Future work is needed to determine if one or more of these subspecies should be considered a separate species.

Likewise, the two subspecies of *M. caudata* differ; *M. c. caudata* is larger than *M. c. aurea*, *M. c. caudata* has a longer intestine than *M. c. aurea*, and *M. c. aurea* is paler (Davydov 1991). These differences can be attributed to adaptations to local conditions; the paler coloration is associated with a drier climate and the longer intestine with less nutritious plants. However, the alarm calls of the two subspecies differ (Nikolskii *et al.* 1999). The subspecific differentiation was a consequence of glaciation that effectively separated the two subspecies. The differences between these two subspecies may warrant specific designation for each. Further evidence for population differentiation comes from examining the immunogenetic responses between *M. menzbieri* and other Eurasian marmots. Intraspecific immunodiffusion differences were detected for three populations of *M. bobac* and two populations of *M. caudata* (Zholnerovskaya and Ermolaev 1996).

Not surprisingly, some patterns of variation are not clearly related to recognized subspecies. For example, the variation in the structure of the baculum of *M. baibacina* suggests a simplification of the structure in a west-east direction (Pole and Bibikov 1992). Geographical variation in the alarm call of *M. bobac* from 11 local populations was merged into four geographical populations (Nikolskii 2000a). These geographical populations only partly coincide with the conventional subspecies. The pattern of acoustic variation seems to represent differentiation in populations partly isolated by the valleys of big rivers. Whether these patterns of variation represent genetic drift or natural selection acting on local variation remains to be determined.

Further analysis of alarm calls indicates that natural selection may produce variants in alarm calls that transmit best in a particular environment. In *M. bobac* (Nikolskii *et al.* 1994) the rhythmical structure and duration and spectral structure of the elements of the alarm call change according to context and varied between two populations. Subsequent analysis of alarm calls from 11 populations revealed a strong correlation between topographic relief and the rhythmical structure of the alarm call (Nikolskii 2000b). In flat country, the rhythm of calls was slow; in hilly country, fast; and in a deeply dissected landscape, the sounds were united in sets. A similar pattern was found in an analysis of six populations of *M. baibacina* (Nikolskii 1994). When danger occurs, marmot reactivity increases, which produces a rapid series of calls. Thus, in a deeply dissected landscape a predator may suddenly appear close at hand, thus producing rapid calling. In a flat landscape, the predator may be seen at some distance, danger is not imminent, and calls are emitted slowly. Nikolskii (1994) suggests that natural selection has fixed call patterns that are optimal for the local landscape.

Some patterns of population variation probably represent phenotypic adjustments to local conditions. Much of the annual pattern of marmot activity is directed by an internal, circannual rhythm in which emergence from hibernation is followed by reproduction, growth, fattening, and immergence into hibernation (Davis 1976). This rhythm is expressed under constant conditions in the laboratory as rhythms of metabolism, feeding, and mass gain followed by a decline in metabolism, decreased feeding, and mass loss (Ward and Armitage 1981). The timing of these events varies in natural populations; e.g., *M. baibacina* emerges in early March at medium altitudes but 20-30 days later at high altitudes. The phenology can vary by 10-15 days within the same altitude belt depending on burrow location on north- or south-facing slopes (Pole 1996). Shifts of several months can occur between lowland and mountain *M. flaviventris*. In lowland valleys in eastern Washington and Oregon, yellow-bellied marmots emerge from hibernation in late February or early March, and adults immerge in June and young immerge about 20 days later (Couch 1930). By contrast, yellow-bellied marmots in the mountains of western Colorado emerge in early May and adults begin immergence in late August (Armitage 1998). That this difference in phenology is likely to be phenotypic was supported by a transfer of woodchucks from eastern United States to Australia where the animals gradually shifted their annual rhythm by about six months in agreement with the annual climate cycle of the southern hemisphere (Davis and Finnie 1975).

In recent years, genetic differentiation among marmot populations has received new interest. Earlier Schwartz and Armitage (1980) demonstrated that local populations of *M. flaviventris* did differ genetically but differences were not fixed because of gene flow among the populations. Although some gene flow was attributed to the movement of females, most of it was a consequence of the dispersal of males. All males dispersed as one-year-olds from their natal population and became resident elsewhere. Thus high levels of genetic variability were maintained. By contrast, only two polymorphic loci were found in enzyme electrophoresis in a population consisting of several families of alpine marmots (Arnold *et al.* 1994). This study revealed that the territorial male did not father 13% of the juveniles and the majority of these cases occurred in multi-male groups. Females have been observed to copulate multiply in rapid succession with various males in a group. Use of DNA fingerprinting revealed a very low degree of polymorphism. This low degree of polymorphism was attributed to low effective population size, but the number of breeding pairs was about an order of magnitude larger than one expected to lead to a low degree of heterozygosity (Rassmann *et al.* 1994). Although inbreeding was excluded as an explanation for the low polymorphism, inbreeding does occur as a mating strategy in this population (Arnold 1990). Another possible mechanism leading to low polymorphism is the occurrence of severe bottlenecks due to harsh winters. Death during hibernation is the major cause of mortality in alpine marmots and that could lead to a drastic loss of breeding pairs and loss of genetic variability (Rassmann *et al.* 1994).

Depauperated gene pools seems to characterize the alpine marmot. Only two of 50 enzyme loci showed polymorphism in 15 populations from Austria and Switzerland (Preleuthner and Pinsker 1993). This lack of variability was attributed to a severe bottleneck during the past Pleistocene withdrawal into the present alpine refuge (Preleuthner *et al.* 1995). The distribution of genetic variation revealed that the populations of western Austria are autochthonous and populations of the Eastern Alps are derived from introductions first documented in 1860. The frequencies of two alleles, Pep-1 and Sod-1, differed between the western autochthonous and eastern allochthonous populations (Preleuthner and Pinsker 1993). A parasitological survey shows that the Pep-1 genotypes differ in their degree of infestation by *Citellina alpina* (S/S genotype overrepresented among noninfected) and *Ctenotaenia marmotae* (S/F genotype higher among noninfected). The marmot-specific parasites were most abundant in the autochthonous populations (Preleuthner *et al.* 1995), which probably represents the recent history of these populations. Fossil marmots were collected primarily from caves at an altitude of 275-2,800 m. Most were from the Upper Pleistocene, but one from the Lower Pleistocene was identified as *M. primigenia*, the ancestor of the recent species (Preleuthner *et al.* 1995). During the last glaciation the marmots inhabited a wide area around the present range including the plains of central Europe. Rising temperatures forced marmots to higher elevations because of advancing forests, which may have caused local extinctions (Kruckenhauser *et al.* 1997). The current variation in the allochthonous populations probably represents the repeated introductions of small numbers of marmots from the autochthonous populations. Although genetic variation at enzyme loci remains low, new variation has been generated at VNTR-loci. The maintenance of the two allozyme polymorphisms probably reflects the ongoing attempts by alpine marmots to combat parasitical infections. However, we need to know the role played by these two enzymes and whether marmots gain resistance against parasites because of the presence of a particular genotype.

Genetic variation is also associated with exposure to plague. Mandible characteristics were used to describe four phenotypes in gray marmots (Pole and Bibikov 1991). In a plague year, phenotype 1 decreased by 14% and phenotype 3 increased by 8%. The mandible characters are certainly surrogates for some other character more directly related to plague. Hemoagglutination studies produced four phenotypes. Marmots with phenotype 4 were most sensitive to infection and those with phenotype 2 were most resistant (Pole and Bibikov 1991). Phenotype frequencies fluctuate with exposure to plague and a phenotype (genotype) that may convey resistance to plague may be less beneficial in a plague-free area. Three populations of *M. sibirica* were studied in Mongolia (Batbold 2000); one population was in an area where plague had not occurred for 15 years, and one in a plague-free area. Four polymorphic loci provided 18 phenotypes and the mean frequencies of the observed alleles varied among the three populations. There were comparatively higher frequencies of T_f^L in the low-plague and plague-free populations. The two populations with no plague were very similar in genetic structure. Observed heterozygosity was lower than expected in the high plague population. Plague acted as a strong selective force; population density decreased by 76.6%, family size by 52.7%, and male mortality was twice that of female mortality. After infection, H_P^S, T_f^M, T_f^K, and Al^B allelic frequencies decreased and frequencies of T_f^L, Al^A, and H_P^F alleles increased. Selection acted most strongly on the transferrin locus. After the epizootic, the genetic structure became more similar to the plague-free population; after eight years the genetic structure returned to the pre-epizootic condition (Batbold 2000). This study clearly reveals that selective forces modify the genetic structure of marmots and indicates that allelic frequencies that are beneficial under one selective regimen are not under another. We know little about the selective forces that direct the differentiation of marmot populations.

Ecology: marmot habitats

Marmots live in a wide variety of habitats (Appendix) ranging from wide-ranging steppe environments (*M. bobac*) to small, widely scattered alpine meadows (*M. vancouverensis*). All species are mountain dwellers except two, *M. bobac* and *M. monax*. *M. bobac* is the only species in the steppes and was widespread before a large part of its range was ploughed (Bibikov 1991a). No marmot occupies the prairie of North America; the ecological equivalent of *M. bobac* is *Cynomys ludovicianus*, the black-tailed prairie dog, that evolved in North America in the Pleistocene along with modern marmots (Hafner 1984). Bibikov argues that *M. bobac* is ecologically associated with wild ungulates whose grazing maintains a high diversity of plants suitable for marmots. Interestingly, the American bison and black-tailed prairie dogs engaged in reciprocal ecologic relationships that maintained suitable habitat for each (Koford 1958). Today, cattle and prairie dogs may have a similar relationship (Hoogland 1995: 21). By contrast, the presence of caribou and herdsmen on the grazing grounds were reported to decrease forage available to black-headed marmots (Valentsev *et al.* 1996). Where caribou grazed, marmots accumulated only 50-60% of the normal amount of fat; marmot populations declined, and fewer juveniles were produced. The relationship between ungulates and marmots should be investigated further, especially in high mountain meadows where both exist.

M. monax, the most widely ranging North American species (Table 1), is the only species restricted to low elevations and the only species associated with woodlands. Although Hamilton (1934) stated that *M. monax* was a forest species, current biology suggests that this species was associated with forest edge where the forest provided cover for burrow sites and meadows provided forages. This interpretation fits the pattern of habitat use that characterizes marmots.

An examination of habitat characteristics (Appendix) reveals the following major attributes: (1) grassland or meadow for foraging, (2) a moderate to steep slope that provides good drainage, (3) an eastern to southern exposure where snow melts earlier than on other exposures, (4) a soil structure that permits burrowing and that will support burrows, often associated with rocks, talus, or tree roots, and (5) at elevations above or near timberline or if lower, in forest openings. The altitudinal distribution emphasizes that marmots are adapted to cool to cold climates and during a large part of the year the terrain is either snow covered or cold conditions prevail such that no food is available. Marmot range became restricted where climate warmed; e.g., *M. flaviventris* (or a closely-related ancestor) skeletal remains were found in Mexico (Cushing 1945) and in the Mohave Desert of California (Goodwin 1989), far south of its current distribution.

The few physiological studies of marmots emphasize cold adaptation and that marmots are stressed by heat. Body temperature of *M. marmota* (Turk and Arnold 1988) and *M. flaviventris* (Melcher *et al.* 1990) increases to about 40˚C during activity with the result that animals enter their burrows. Warm temperatures produce a bimodal activity pattern in both species (Armitage 1962, Turk and Arnold 1988). Marmots can modify their physiology to cope with more xeric environments. *M. flaviventris* from a lowland xeric environment were smaller, had reduced metabolism at high environmental temperatures, and increased evaporative water loss to cope with heat stress at high temperatures in comparison to a montane-mesic population (Armitage *et al.* 1990). Adaptation to cope with heat stress is probably limited by the need to conserve energy at low temperatures and during hibernation (Armitage 1998).

Several studies attempted to measure habitat choice by comparing the frequency of habitat availability with habitat use by marmots. Herrero *et al.* (1994) tested whether *M. marmota* utilized the entire available food period (AFP), which was defined as the number of days between the beginning of the vegetative period (when average ambient temperature ≥ 7˚C) and the end of the freeze-thaw autumn period (when ambient temperature ≤ 0˚C). Marmots used less than expected below 1,600 m and above 2,600 m, used in proportion to availability between 1,600-1,800 m and 2,401-2,600 m and used more than expected between 1,801-2,400 m, the subalpine level. AFP was positively correlated with the number of colonies ($r^2 = 0.961$, $p = 0.003$). AFP was <135 days above 2,400 m (Herrero *et al.* 1994). This analysis indicates that growing season is only one factor that determines habitat choice; the presence of forest and possibly warmer temperatures limit use at lower altitudes and the short growing season above 2,600m probably limits colonization at these altitudes.

In the Orobic Alps, *M. marmota* occupied less habitat at 1,700-1,800 m than expected; this elevation was associated with tourist use and the fewer marmots than expected might reflect human disturbance (Frigerio *et al.* 1996). Marmots occupied northwest to northeast exposures more frequently than expected. These exposures were often associated with low human activity, good slope, and good plant cover. It seems quite likely that habitat features may interact so that some combinations are preferred over others. A univariate analysis of quadrat occupancy along a series of transects indicated that slope, sun exposure, and plant cover significantly affected habitat choice in *M. marmota* in the French Alps (Rodrigue *et al.* 1992). Altitude, human disturbance, or the number of minutes of sun per day were not related to the presence of marmots. Slope and sun exposure interacted; a southern-east-west exposure with a slope of 15-75% had a probability of 0.94 of marmot residency whatever the plant cover. The probability of marmots increased from northern exposure to southern-east-west exposure for an equal slope and plant cover. Probability also increased from extreme to middle slope for the same exposure and plant cover. Northern exposure was always poor; low slope was poor because snow thawing was often late. The most favorable situation was a southern exposure with middle slope and a middle (25-75%) plant cover; the probability of finding marmots on this complex of factors was 0.986. An additional study revealed the same complex of factors: marmots preferred sites with southern or eastern exposure (where snow melts relatively early), intermediate slopes, moderate plant cover, and a low level of human disturbance (Allainé *et al.* 1994). Population structure was also considered. The model revealed that group size was larger in large home ranges, in non-isolated groups, and with a southern exposure. The number of subordinates was larger in large and non-isolated home ranges and on south-facing slopes in the valley and on north-facing slopes. No factor affected litter size; 71.4% of the large home ranges had litters, whereas only 37.9% of the small home ranges had litters (Allainé *et al.* 1994).

The fact that marmots occupy a location should not be used to infer that the site is preferred or that it will sustain viable populations. In the Orobic Alps, marmot populations increased between 1985-1992. Density increased at all altitudes and on all slopes; there was increased use of steep slopes and a greater increase in the low sun-exposure class (Panseri and Frigerio 1996). Use of northwest exposure also increased, but western exposure was not used. Thus expansion was associated with use of habitat characteristics that several studies revealed to be less favorable. The lack of favorable habitat may make marmot populations vulnerable to extinction. In the Jura, where alpine marmots were reintroduced, the habitat is fragmented and highly limited (Neet 1992). None of the habitat patches were at >40% probability of being favorable. Marmots had been absent from these mountains since the last glaciation and their capacity to persist is questionable.

Clearly, the habitat characteristics that marmots prefer have been determined by the presence of marmots. This technique must be used with care because marmots occupy habitats of varying quality and marmots may persist on these habitats for many generations. Many

Species	Home range area (ha)	Vegetation biomass (g/m ^{2})	Reference
M. flaviventris	0.13-1.0	383	Armitage 1975
M. caligata	13.8	117	Holmes 1984a
	9.2 (foraging area)		
M. vancouverensis	3.0		Heard 1977
M. olympus	2.0	206	Barash 1973
M. monax	1.3 (summer)		Meier 1992
M. marmota	1.4-5.7		Sala *et al.* 1992
	2.8		Bassano *et al.* 1996
	2.3-2.8		Perrin *et al.* 1993
M. caudata aurea	2.9-3.1	36	Blumstein and Arnold 1998
M. bobac	3.2		Mashkin 1991
M. baibacina	3.0		Dudkin, per. com.
M. camtschatica	13		Tokarsky 1996
M. sibirica	3-6 (favorable)		Suntsov and Suntsova 1991
	2 (unfavorable)		
	1.7		Seredneva 1991

Table 2. Home range area of the genus *Marmota*. Vegetation biomass from Armitage and Blumstein (2000).

studies have related population density, reproductive output, or other measures to habitat quality. One measure of habitat quality is home range area (Table 2). Home range areas are large and there is a rough relationship between vegetation biomass and home range area; home range areas are smaller when biomass is greater (Table 2). For *M. marmota* in the Polish Tatra Mountains, home range size was negatively correlated with vegetation cover (r = -0.959); marmots had larger home ranges (up to 7.2ha) where plant cover was lower (Gasienica Byrcyn 1997). Large home ranges is one indication that marmots live in harsh environments (Armitage and Blumstein 2000). Home range movements of *M. monax* average 337 m on marginal habitat and 246 m on good habitat (de Vos and Gillespie 1960). Both quality and quantity of food affect marmot use of space and population density. *M. flaviventris* avoided areas where dense growths of *Geum rossi*, a plant not used for food, were located (Andersen *et al.* 1976). Use of habitat patches by *M. flaviventris* in California was explained by high food biomass (Carey 1985a). Less food results in larger home ranges in *M. sibirica* and the earlier in the season vegetation begins growth, the higher the population density of tarbagans (Seredneva 1991). When foraging areas were fertilized, patch use by *M. caligata* was 62.5% greater than before fertilization (Holmes 1984b). However, food is not the only determinant of patch use. When frequency of selected plants was chosen as the forage factor and number of burrows/patch and distance to talus served as risk factors, risk factor was more important (Holmes 1984b). The linear correlation of the three variables accounted for 77% of the variance in patch use; only distance to talus entered the model as a significant independent variable. Thus, both food and predation risk contribute to use of a patch. For *M. caudata aurea*, food resources were not associated with group size or marmot density, but were related to the probability that a group weaned young (Blumstein and Foggin 1997). The probability of a group weaning young was related to the log of available food the previous year.

Kinship and social structure affect use of resources. In those marmots whose social structure consists of family groups (Table 4), the family has exclusive use of its home range (e.g., Blumstein and Arnold 1998, Holmes 1984, Arnold 1990, Barash 1973, Perrin *et al.* 1993, Sala *et al.* 1992). Among yellow-bellied marmots, space-use overlap and the consequent sharing of resources occurs only among closely-related kin (Armitage 1996a), but the degree of overlap is affected by individual behavioral characteristics, age, and reproductive state (Frase and Armitage 1984).

A number of studies report population characteristics on favorable vs unfavorable habitat. Generally, these studies do not report the factors that distinguish favorable from unfavorable habitat. On favorable habitat, 84.6% of *M. baibacina* families produced litters averaging 4.8 young per litter. On unfavorable habitat 75% of the families had litters averaging 3.6 young per litter (Mikhailuta 1991). Mean family size was 7.8 in the favorable habitat and varied from 4.6-5.1 in less favorable habitats. On favorable habitats, family density of *M. bobac* was 0.4/ha; on marginal habitat, family density was a maximum of 0.1/ha (Tokarski *et al.* 1991). Family structure of *M. sibirica* is unstable, consists of 2-6 animals, and is short-lived in unfavorable conditions and is long-lived and consists of 13-18 animals in stable families under favorable conditions (Suntsov and Suntsova 1991). Average population density of *M. camtschatica* in northeastern Yakutia is 9/100km^2 but varies from 3/100km^2 to 19/100km^2. On the most favorable habitats the number is 9 to 13/10km^2 (Yakovlev and Shadrina 1996).

A dramatic example of the effect of habitat quality on reproduction and persistence was described for the endangered *M. vancouverensis* (Bryant 1996). Colonies inhabit natural subalpine meadows and recently logged clear cuts. Persistence of marmots at natural sites was higher than at logged sites (65 vs 48%). Females lived longer on natural sites; maximum age was 9 years vs 5 years in clear cuts. No adult female inhabiting a clear cut weaned more than one litter; whereas five of 14 females in natural habitats produced at least two litters during the nine years of the study. Bryant believes that the logged sites act as dispersal sinks that capture dispersing marmots and prevent them from recolonizing natural habitats. Interestingly, these sites have the characteristics that marmots seem to choose when settling on a habitat patch: moderate to steep slope, south or southwest facing aspect, with a meadow or meadow-like area for foraging and soil suitable for burrows. Quite possibly marmots use all or some sub-set of these habitat characteristics as a rule of thumb of when to terminate dispersal and assume residency. It is unlikely that marmots use particular plant species as cues for settlement as species composition changes through the season and varies among sites. Thus the life form of the vegetation (meadow) is the likely cue. Females in particular may settle at the first favorable, unoccupied spot that they encounter. Indeed, female yellow-bellied marmots seem to settle on the first available site they encounter after dispersing from their natal home range (Van Vuren 1990).

Differences in habitat quality can be inferred from differences in survivorship and net reproductive rate, which were calculated for mean matriline size for each of 12 habitat sites occupied by *M. flaviventris* (Armitage and Schwartz manuscript). The sites supported a range of mean matriline sizes and survivorship and net reproductive rate differed among sites with similar mean matriline sizes. The difference among sites was not attributable to the area of the sites, thus some other, unmeasured factor or factors, was responsible for differences in quality.

Ecology: habitat and food quality

One obvious possible factor that contributes to differences in habitat quality is the quality of the food plants. *M. marmota* was absent from meadows where the predominant plants were *Nordus stricta*, *Carex sempervirens*, *C. curvula* and *Sesleria* sp. (Vita 1992) and avoided areas in the home range where bilberry (*Vaccinium myrtillus*) was extensive (Sala *et al.* 1992). *M. sibirica* seldom was found outside the distribution limits of *Astragalus*, *Bupleurum*, *Poa*, *Allium*, *Oxytropis*, *Festuca*, and *Stipa* (Suntsov and Suntsova 1991). Food consumption and assimilation decrease when cellulose content is too high; *M. sibirica* feeds on growing plants (normal diet 20-25% cellulose). In the first half of the active season the tarbagans eat grasses and some herbs and in the second half, mainly herbs. Habitats dominated by grasses are less favorable (Seredneva 1991). Several studies report that marmots eat a wide variety of plants and may be considered to be generalist herbivores (Frase and Armitage 1989). *M. camtschatica* ate 80 of 125 plant species present and preferred leaves and flowers (Solomonov *et al.* 1996). *M. monax* ate 37 species of plants of which three were grasses (Hamilton 1934); 24 different food stems were found in stomachs from woodchucks in Maryland, red clover, white clover, grass, chickweed and alfalfa were eaten most often and in the largest amounts (Grizzell 1955). *M. vancouverensis* utilized 26 of 88 species, but four species in the spring and nine species in the summer accounted for the most highly used items and these items were not chosen on the basis of relative abundance (Milko 1984). Similarly, *M. marmota* utilized 16 of 70 species, but dicots, especially legumes, predominated (Bassano et al. 1996); for *M. caligata*, 28 kinds of food were identified, but vetches (*Oxytropis-Astragalus*), sedges, fleabanes (*Erigeron*) and fescues made up more than 80% of the diet (Hansen 1975). These hoary marmots also selected particular plant species and did not forage in proportion to relative abundance. Although grasses are an important component of marmot diet, forbs (herbs) may be essential for a normal diet. Forbs were preferred over graminoids, especially in mid and early summer, by *M. flaviventris* in California (Carey 1985b) and by *M. flaviventris* in Colorado (Frase and Armitage 1989); native grasses with the exception of ryegrass (*Elymus*) were chiefly consumed by lowland yellow-bellied marmots (Couch 1930). Woodchucks in Pennsylvania consumed 45 species and selected dicots, especially clover, much more frequently than monocots (Arsenault and Romig 1985). *M. bobac* preferred succulent plants of the *Fabaceae* and *Asteraceae* (Ronkin and Tokarsky 1993). Selectivity experiments support a preference for forbs. The woodchuck in Missouri preferred wild lettuce (*Lactuca*), white clover, red clover and grasses in that order (Twichell 1939); in New England, dandelion (T*araxacum officinale*) and common plantain (*Plantago major*) were most commonly selected in cafeteria-style feeding trials (Swihart 1990). In one set of feeding trials, the most preferred species was removed each time. Eight species of forbs ranked above the median in terms of consumption more frequently than expected by chance and grasses ranked lower than expected by chance (Swihart 1990). Woodchucks were observed to feed on leaves of trees (Weeks and Kirkpatrick 1978, Swihart and Picone 1991). Red mulberry was highly palatable and peach and hackberry had moderate palatability. Norway maple, along with orchard grass, had low palatability (Swihart and Picone 1991). I conclude that forbs are a major food of choice of marmots and that grasses are eaten, in part because of availability.

Food choice doubtlessly is based on other considerations. Yellow-bellied marmots in food choice experiments reject plants containing defensive compounds (Armitage 1979). Food plants may be chosen to meet minimal needs. Woodchucks use small mineral licks and lick road surface for residues of winter-applied NaCl (Weeks and Kirkpatrick 1978) and I have observed yellow-bellied marmots licking the mud surface at salt licks, which were also visited by deer, ground squirrels, porcupines, and chipmunks. When woodchucks were provided with salt-impregnated wooden pegs, pegs containing Na compounds were more highly gnawed than pegs with Ca, Mg, or K. Water-soaked pegs were not gnawed (Weeks and Kirkpatrick 1978). Two principal forbs eaten by *M. flaviventris* had a calcium content 2-3 times greater than any other plant species and forbs are significantly higher in phosphorus, calcium and sodium and significantly lower in cellulose than graminoids (Carey 1985b). In addition, food choice may be based on protein (Frase and Armitage 1989) or essential fatty acid (Florant 1998) content. Much more needs to be learned about the role of nutrition in habitat use by marmots.

Ecology: modification of the environment

Because marmots dig burrows and may consume several hundred grams of vegetation a day during their active season, they could impact the environments where they live. Quantitatively, marmots have little impact on the vegetation as they consume from 2.0 to 6.4% of plant production or 10-12% of plant biomass (Kilgore and Armitage 1978, Bibikow 1996). Where marmots live on or near agricultural lands they can cause considerable damage; e.g., *M. monax* on crops and hay meadows (Thompson 1979) and *M. bobac* and *M. himalayana* on crops (Bibikow 1996).

Even though marmots may not markedly reduce the plant biomass, they may have localized effects on plant biomass and species composition. In an old field inhabited by *M. monax*, total plant cover increased with distance from burrows. Species richness was low near and distant from burrows and relatively high at intermediate distances (English and Bowers 1994). Horse nettle (*Solanum carolinense*), Kentucky bluegrass (*Poa pratensis*) and fescue (*Festuca elatior*) increased and orchard grass (*Dactylis glomerata*) decreased with distance from burrows. The strongest effects were limited to a 4m radius around the burrows. Woodchucks are important agents in creating a vegetational mosaic. Species of plants close to burrows tended to be mostly unpalatable, early successional, and early colonizing annual and biennial species. I have observed the same phenomenon around yellow-bellied marmot burrows where unpalatable composites, fireweed (*Epilobium angustifolium*, Rocky Mountain pentstemon (*Pentstemon strictus*) and nettle (*Urtica dioica*) are conspicuous.

In hayfields, grass biomass decreased and forb biomass increased as a function of distance from *M. monax* burrows. Overall, in a grass hayfield orchard grass (*Dactylis glomerata*) increased about 2.6% by woodchucks (Swihart 1991). In a hayfield with alfalfa (*Medicago sativa*) the biomass of orchard grass increased an average of 7.4% and the biomass of alfalfa decreased by 2.5% because of woodchuck activity. In feeding trials, alfalfa was selected more often than orchard grass (mean was ten times greater). Orchard grass was lush around burrows (Swihart 1991). Alfalfa stem totals were about three times greater 20 feet or more from a woodchuck burrow than they were within five feet of a burrow. Grass stems increased only about 20% beyond eight feet from the burrow. Grass stems were 5.5 times more numerous than alfalfa stems near the burrow but only 2.3 times more numerous distant from the burrow. Because woodchucks prefer legumes, the differences in grass vs alfalfa stems can be attributed to selective grazing (Merriam and Merriam 1965). A lush, green zone occurred next to the burrow similar to that reported above by Swihart. Soil nitrogen was 1.7 times more concentrated near the burrows than in the field. Both authors reported that considerable feces were deposited in the burrow area and no doubt urine was also deposited. Feces and urine are most likely the source of nitrogen, which in turn produces the lush growth.

In meadows utilized by *M. olympus*, plants on the mounds formed when marmots excavate the soil are mainly unpalatable species. Overall species richness was greater in the meadow than on the mounds (Del Moral 1984). Vegetation analysis indicated that the marmots fed selectively and enhance plot diversity and reduce the dominance of common species. Eurasian marmots have similar effects on vegetation abundance and diversity (Bibikow 1996).

Marmot burrowing activity creates particular assemblages of invertebrates that inhabit the burrows or nests or utilize the "lavatories" where feces are deposited. Many species of small mammals, birds, reptiles and amphibians use marmot burrows for shelter or nesting (Bibikow 1996).

Marmots can affect soil structure. *M. bobac* digging affects soil solinization by both desalinization and by creating local salt concentrations which increases salinization and raises the carbonate content, thus producing a mosaic structure in an area (Rumiantsev 1992). Marmot modifications of the landscape can be extensive. Burrowing in high density settlements formed typical landscapes as excavated earth forms small hills (up to 1.5m high). The burrows and mounds may exist for several thousand years (Zimina 1996). A burrow may be 63m (*M. baibacina*) to 75m (*M. caudata*) long and the amount of excavated earth may be as much as 150m^3/ha. An active marmot may deposit 15kg of feces (air dry weight) and 7.5kg of urine. Nest materials can reach 8kg (wet weight). Thus marmots enrich soil both organically and inorganically. Soil excavated from tunnels is richer in carbonates, sulfates, and chlorides and poorer in organics. Different plant associations develop. A more xerophytic vegetation may develop on the top of mounds along with weed species (Zimina 1996). The native vegetation is slow to replace mound vegetation; thus ongoing marmot activity maintains diverse plant associations.

Ecology: effects of weather

Sixteen measures of variation in survival and reproduction of *M. flaviventris* were correlated with 15 measures of weather. Litter size, colony size, and survival were the life-history traits most affected by weather and length of winter, length of the growing season, and precipitation were the major weather factors affecting survival and reproduction (Schwartz and Armitage 2000). For example, colony size was larger the earlier snow-melt occurred and the longer the growing season lasted. No measure of temperature was significantly correlated with life-history variables. When growing-season phenology, as indexed by the time of snow melt, was related to variation in reproduction, the number of litters per female and litter-size decreased the later snow melt occurred (Van Vuren and Armitage 1991). The population density of *M. sibirica* was higher the earlier vegetative growth started (Seredneva 1991), which appears to be similar to the effect of early snow-melt reported for *M. flaviventris*. Conversely, late snow-melt decreased reproduction by *M. camtschatica* (Mosolov and Tokarsky 1994) and unfavorable weather is associated with a decrease in the number of breeding females and increased embryo mortality in *M. caudata* and a long, cold spring increases juvenile mortality in *M. bobac*, which breeds before emergence (Shubin 1991). Also, body mass of juvenile yellow-bellied marmots is smaller on 1 August the later snow melt occurs (Van Vuren and Armitage 1991).

Rainfall markedly affects marmot populations. Extensive reproduction by *M. sibirica* (Seredneva 1991), *M. flaviventris* (Schwartz and Armitage 2000) and *M. baibacina* (Bibikov 1991b) occurs in the year after a rainy year. Drought negatively affects marmots. *M. bobac* may migrate in response to drought (Rudi *et al.* 1994). Drought reduces growth of young *M. monax* (Hamilton 1934) and young and adult *M. flaviventris* (Armitage 1994). Survivorship of young and reproductive females decreased markedly during the hibernation that followed the summer of low rainfall; reproduction decreased the following summer (Armitage 1994). Migration during drought seems to be a common response in Eurasian marmots (Bibikow 1996) and I have documented one case of a reproductive female and two cases of juvenile yellow-bellied marmots migrating late in a dry summer.

Ecology: the role of parasitism

Many diseases affect marmots (Bibikov 1992), but the importance of disease is little known (Bassano 1996). Among the endoparasites, nematodes and tapeworms are widespread; among the ectoparasites, fleas, mites, and ticks predominate (Bibikov 1992, Bibikow 1996, Bassano 1996). Marmots may be widely infected with large cestodes in the autumn, but only small cestodes occurred in marmots killed in the spring (Prosl et al. 1992). Marmots eliminate roundworms (*Ascaris*) and tapeworms (*Ctenotaenia*) at the time of hibernation (Calliat *et al.* 2000) when the stomach and intestine contract (Rausch and Rausch 1971). Some studies report that parasitized marmots are in good condition (Prosl *et al.* 1992) and that mass gain was unaffected by the presence of parasites (Calliat *et al.* 1996). However, we haveseveral instances of young marmots that had very low or no mass gain. When treated with a vermifuge, they passed large numbers of ascarids and thereafter mass gain was normal.

Two recent studies investigated the cost to fitness of ectoparasites. Yearling *M. flaviventris* with greater flea infestations grew more slowly, animals that died during hibernation had more fleas than survivors, and adult females that failed to reproduce had more fleas than those that reproduced (Van Vuren 1996). For *M. marmota*, infant winter mortality increased with the ectoparasite (a mite) load of the family (Arnold and Lichtenstein 1993). Although group living should favor parasite transmission (Bassano 1996), neither of the two studies considered parasitism to be a cost of sociality.

The importance of parasitic infections may depend on environmental conditions. Epizootics in *M. baibacina* living in alpine meadows occurred after periods with low summer temperature and surplus rainfall whereas in populations in the arid high mountains, epizootics occurred after several dry summer seasons (Bibikov 1992). *M. baibacina* seemed more resistant when normal mass gain occurred before hibernation. The weather conditions described above decrease food availability; hence marmots in good condition may resist infections whereas marmots in poor condition may be susceptible to infections. We witnessed several instances of mortality from a pneumonia-like disease. In each instance, the marmot was subjected to additional stress, either environmental (low temperature, wet conditions) or social, which seemed to induce the expression of the disease.

Bacterial and viral diseases are little known. Several viral diseases have been identified in *M. monax*; viral hepatitis causes mortality in laboratory animals, but the effect of viral diseases on wild populations is unknown (Bassano 1996). Plague (*Yersinia pestis*) is especially prevalent in *M. sibirica*, *M. baibacina*, and *M. bobac* (Bassano 1996, Bibikow 1996). The plague occurs in foci;

even when the plague epizootic spreads over 10-30 km^2, ill animals occur only in local spots (Bibikow 1996). In the foci up to 22% of the individuals in a family may become ill. Although death decreases numbers and changes family structure (Bibikov 1992), death due to plague is far less important than other factors, such as lack of food and the poor accumulation of fat (Bibikow 1996). The interaction between ecological conditions and parasitism needs more intensive study, especially the effects on individual fitness.

Environmental harshness and the evolution of marmot sociality

Environmental harshness or environmental severity, is not easily defined, but includes such factors as rainfall (drought), environmental temperature, length of growing season (length of winter), and snow cover (Armitage and Blumstein 2000). Several lines of evidence support the interpretation that marmots live in harsh environments: mass loss may be high following emergence from hibernation (Armitage 1999, Armitage and Blumstein 2000), large home range areas (Table 2), mating in the burrow before emergence above ground from hibernation (Armitage and Blumstein 2000), the frequency of reproduction or reproductive skipping (Table 3), the effects of precipitation on reproduction (Armitage and Blumstein 2000), and reproductive stress, which is evidenced by embryo reabsorption and less fat accumulation in reproductive than in barren females. *M. monax* and mid elevation (2900 m) *M. flaviventris* do not skip reproduction; all high altitude species that live in family groups do skip from one to five years (Table 3).

One response to environmental harshness is hibernation. Marmots are the largest true hibernators and hibernate from 4.5 to 8.5 months (mean = 7.2 months). Hibernation clearly is a response to a seasonal lack of food rather than to temperature per se. The need to hibernate is a major determinant of marmot biology that affects factors such as body size, reproductive frequency, and habitat choice. Body size, in turn, affects the age of dispersal, age of first reproduction, and sociality (Armitage 1999). The pervasive influence of hibernation on marmot biology suggests that this trait was present in the ancestral marmots.

Marmots were more widely distributed in the latter part of the Quaternary and in the late Pleistocene were associated with a fauna characteristic of cold and also with a tundra-forest-steppe fauna (Zimina and Gerasimov 1973). Marmots were widespread in the periglacial, the zone marginal to the glacial ice. The climate was charaterized by a cold winter with little snow, short, bright and warm summers and with a deep permafrost with periodic summer ice-melting. The landscapes were open with grassy vegetation consisting of tundra and meadow-steppe elements (Zimina and Gerasimov 1973). These conditions favored the evolution of hibernation and the selection of open habitats with herbaceous vegetation. By this time, if not sooner, marmots must have evolved physiological adaptations to cold such as the circannual cycle, a metabolic rate lower than that predicted from

Species	Reproductive frequency	Reference
M. flaviventris	No female at a high elevation population bred in successive years	Johns and Armitage 1979
M. caligata	Females breed biennially	Barash 1974
	Mean of 3.3 years between breedings	Holmes 1984
M. vancouverensis	Mean of 1.83 years between litters	Bryant 1996
M. olympus	Adult females bore young in alternate years	Barash 1973
M. marmota	48% of territorial females failed to breed	Arnold 1990
M. caudata	More than 80% of social groups failed to wean a litter in any given years, only 2 females weaned in successive years, many weaned once in 4 years	Blumstein and Arnold 1998
	Usually skipped 1-2 years after breeding	Davydov 1991
M. menzbieri	Large number of nonbreeding females	Bibikow 1996
M. bobac	55% of 103 females bred once in 1-3 years, 28% did not breed for 4 years running	Mashkin 1991
	Most families with litters in one year did not breed the next year	Rudi *et al.* 1994
M. baibacina	Alternation of barren and breeding years	Pole and Bibikov 1991
M. camtschatica	Rarely do pairs have cubs in successive years	Yakovlev and Shadrina 1996
M. sibirica	Number of breeding females in a year varies from 17-77%, mostly does not exceed 50%	Bibikow 1996

Table 3. Environmental harshness and the frequency of reproduction in the genus *Marmota*.

Social system	Species	Comments
Solitary	*M. monax*	Disperse as young; mating system polygynous; little overlap of female home ranges; solitary hibernation
Female kin group	*M. flaviventris*	Disperse as yearlings; mother:daughter kin groups persist through time as matrilines; adult male territorial and defends one or more matrilines, thus mating polygynous; hibernation usually solitary
Restricted family	*M. caligata, M. olympus,* *M. vancouverensis*	Disperse as two-year-olds; adult male typically with one to three females and yearlings; typically one litter per year; mating within the family; group hibernation
Extended family	*M. broweri, M. marmota,* *M. caudata, M. bobac,* *M. siberica, M. baibacina,* *M. camtschatica*	Disperse at age three years or older; typical family consists of reproductive territorial pair, subordinate adults, yearlings, and young; polyandry may occur; group hibernation; alloparental care may occur

Table 4. Social system of *Marmota* (modified from Armitage 1996b, Armitage and Blumstein 2000).

body size, effective insulation that reduces heat loss, especially after the summer molt prior to hibernation (Armitage and Salsbury 1993), reduced evaporative water loss, which not only reduces heat loss but also results in metabolic water supplying water requirements during hibernation (Armitage *et al.* 1990), and low conductance (Armitage *et al.* 1990, Armitage 1998). The conditions of the periglacial zone probably lasted 40-50,000 years, ample time for adaptations to the open, herbaceous environment to evolve. Recent climate change resulted in the spread of forests and the migration of marmots from the periglacial plains to mountains in western North America and Eurasia and into the continental steppes of eastern Europe (Zimina and Gerasimov 1973, Rumiantsev and Bibikov 1994).

During the period of modern speciation, two major lineages evolved. One lineage, *Petromarmota*, evolved in North America and the other lineage, subgenus *Marmota*, evolved in Eurasia, but may have originated in the Nearctic of which *M. monax* is a remnant. Although *M. broweri* occurs in the Nearctic, it is not clear whether it represents a late recrossing from Eurasia or is also a remnant of the earlier Nearctic radiation prior to the invasion of the Palearctic (Steppan *et al.* 1999).

The evolution of large body size as an adaptation for hibernation in a harsh environment had consequences for the evolution of sociality. Only *M. monax* does not live in a social group (Table 4). The long growing season of about 7.5 months or longer enables young to become independent in their year of birth. In all other species, the young require at least one more summer of growth before reaching maturity. Thus, retention of young in their natal area for their first hibernation and for one or more years of additional growth leads to the development of sociality (Armitage 1999). Sociality evolved separately in the two major lineages of modern marmots (Kruckenhauser *et al.* 1998, Steppan *et al.* 1999). In the subgenus Marmota, all species except *M. monax* live in extended family groups (Table 4). In the subgenus *Petromarmota*, *M. flaviventris* forms female kin groups and the other species occur in restricted family groups (Table 4). In the species living in extended family groups, dispersal is delayed beyond the age of first reproduction (Blumstein and Armitage 1999). This retention of adult individuals in the social group provides an opportunity for the evolution of alloparental care. For example, subordinate *M. marmota* help warm their juvenile relatives during hibernation (Arnold 1993). In addition, the retention of adult males provides an opportunity for polyandry as several males may mate with the territorial female (Arnold *et al.* 1994). The evolution of sociality had other consequences. In addition to loss of reproduction because of physiological stress, reproductive loss occurs because of reproductive suppression, especially in those species living in family groups (Wasser and Barash 1983, Armitage 1992, Armitage 1996b, Blumstein and Armitage 1998, 1999). For example, in a captive population of *M. broweri* consisting of a territorial pair and other individuals of both sexes up to five years old, only the original pair bred for six consecutive years (Rausch and Bridgens 1989). The loss of reproduction is partially compensated by increased survivorship in the highly social species (Armitage 1996, Blumstein *et al.* 2000). Because a loss of reproduction represents a loss of evolutionary fitness, we would expect individuals to escape reproductive suppression. However, the data indicate that opportunities for independent reproduction is limited because where marmot populations are thriving, the habitat appears to be saturated. Thus individuals remain in their natal families waiting for a chance to become reproductive by becoming a territorial dominant either in their family of birth or in another family in the same habitat patch (Armitage 1996b). Eventually the individual may disperse to seek a reproductive opportunity in some other habitat patch.

There is an evolutionary trajectory leading from the harsh environment to sociality. To summarize, the evolution of marmots in harsh landscapes led to adaptations to open landscapes with herbaceous vegetation and the development of hibernation to cope with periods of food shortage or absence. The evolution of large body size as a means of maximizing storage and use of fat (note: body size may have other advantages such as predator defense) coupled with a short growing season resulted in young requiring one or more additional years of growth to reach maturity. The retention of offspring in their natal area resulted in delayed dispersal which in turn led to the evolution of sociality with all of its consequences in all marmot species except *M. monax*. Once sociality developed, the potential for cooperative breeding was present. Many questions about marmot ecology remain unanswered; e.g., the role of nutriton and parasitism, extent and mechanisms involved in cooperative breeding, and the allocation of fat to maintenance and reproduction.

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Species	Habitat	Reference
M. flaviventris	Grass-forb meadows with rock outcrops or talus, avoid meadows where rocks too tightly packed for digging or where large subsurface rock volume occurs, colony sites with mean slope of 33°	Svendsen 1974
	Meadow dominated by graminoids, some forbs, vegetative cover over 90%	Carey 1985
	Grassy meadows and flats in lowland inland valleys	Couch 1930
M. caligata	Valley at 900m, 300m above timberline, relatively flat meadow, short mesophytic grass-land vegetation	Holmes 1984
	Rock ledge and talus slope with adjacent sub-alpine meadow	Barash 1974
M. vancouverensis	81% of marmots at elevations between 1000-1400m in clear-cuts or grass-forb alpine meadows mostly (74%) on south- to west-facing slopes; natural habitat patches small and scattered, typically in avalanche bowls	Bryant and Janz 1996
M. olympus	Subalpine to alpine meadows and talus slopes just above and below timberline, which varies from 1500-1750m, most colonies oriented between southeast and southwest	Barash 1973
M. monax	Meadow-forest edge, meadow hedgerow, burrows in woods, meadows, hillsides; hiber-naculum usually on southern exposure in or at edge of woods	Hamilton 1934
	Old field associations interspersed with small woodlots	Davis *et al.* 1964
	Mixture of pasture and grazed woodlots	de Vos & Gillespie 1960
	Old fields, hedgerows, burrows in well-drained soil in woods or meadows; hibernation den in wooded or brushy locations	Grizzell 1955
	Fields, small woodlots, cultivated crops	Ferron and Ouellet 1989
	Second-growth woodlands and grazed fields; burrows in field or woodland, hibernacula in woodland	Meier 1992
M. marmota	Aosta valley: mainly between 2100-2500 m on slopes facing southeast to southwest, woods avoided, most burrows on alpine open grassland, preferred slopes 20°-30°	Bassano *et al.* 1992
	Southeastern Alps: open areas characterized by rich alpine pasture, preferred altitude 1700-2100 m, southern exposure, medium to steep slopes (11°- >30°?)	Chiesura-Corona 1992
	Western Italian Alps: 52% of den systems above timberline, 2200-2600 m, south facing slope of 10-30?or more	Macchi *et al.* 1992
	Eastern Italian Alps: colonies between 1900-2400 m, 27% had southern exposure, 80% on average slope	Ventura Luini 1992
	Apennines: areas above timberline regardless of exposure; flat and less steep areas where substrate composed primarily of earthy deposits rarely colonized, very rocky parts not inhabited, grassy banks and slopes	Sala *et al.* 1992
	Orobic Alps: 68% of colonies between 1700-2100 m in siliceous area on slopes facing south to east; favored south-east or east at higher altitudes	Panseri 1992
	Orobic Alps: colonize open space without trees, colony distribution peak where plant cover 40-60%	Frigerio *et al.* 1996
	French Alps: subalpine meadows edged by talus, gentle slope	Perrin *et al.* 1993
	Southern or eastern exposure, intermediate slopes, moderate plant cover	Rodrigue *et al.* 1992 Allainé *et al.* 1994
	Pyrennes: 67% of colonies found between 1800-2400 m, lower edge coincides with current forest limit, upper limit probably set by available food	Herrero *et al.* 1994
	Tatras: mostly in alpine zone, some in meadow patches in mountain pine zone; 40% of colonies on slopes of 31°-35°, exposure mostly east to south, some on north at lower elevations	Gasienica Byrcyn 1997
	Swiss Alps: alpine pastures	Solari & Capriasca 1988

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Species	Habitat	Reference
M. broweri	Hibernaculum on exposed ridges that become snow free relatively early in the spring	Rausch and Rausch 1971
M. caudata aurea	Flat, high alpine meadow at 4100-4300m surrounded by glacial moraine and punctuated with hilly terminal moraines	Blumstein 1992
M. menzbieri	Alpine and subalpine meadows at altitudes of 2400-3400m	Red Data Book 1996
M. bobac	Historically steppe, forest steppe; presently occupies gullies, small flat-bottom valleys, pastures, forest edges; penetrate agricultural fields; south-facing slopes	Tokarski *et al.* 1991
	Not found in Turgai Hollow with high levels of subsoil waters; none near Islim River where layer of bedrock close to the surface; none lived where soils fine	Rumiantsev 1991
	Flat stream valleys, slopes of hills and low mountains, few marmots on dry stony watersheds or on hilltops	Mashkin 1991
	Maximum density in perennial grasses, least in fields of annual crops	Le Berre *et al.* 1994
	Open fields with good visibility, lush vegetation available for entire active season; frost-proof ground, deep groundwater	Mashkin *et al.* 1994
M. baibacina	Occupy tops of ridges with alpine vegetation, typically at elevations above 3000m	Rogovin 1992
	High mountain meadows, meadow-pastures	Pole and Bibikov 1992
M. camtschatica	Middle mountain zone above timberline, west to south slopes	Zheleznov 1991, 1996
	Cirques above timberline, alpine meadows, boulder fields	Tokarsky and Vasiljev 1991
	Mountain tundra, tundra steppe, permafrost zone	Lukovtsev and Yasiliev 1992
	Old lava flows covered with mountain tundra vegetation with fireweed and graminoid vegetation	Mosolov and Tokarsky 1994
	Inhabit permafrost zone tundra and tundra steppe, hibernacula on terrace-like ledges, made on level plots or gentle slopes on southern or western sides	Solomonov *et al.* 1996 Tokarsky 1996
	Well-watered alpine meadows, hibernaculum where soil layer more than 1m thick	Valentsev *et al.* 1996
	Cirques, subalpine meadows and stony fields, rocky seashore covered with alpine plants	
M. himalayana	In rocky, alpine meadows at 4200-4650m	Allen 1940
	High mountain grasslands	Zhi and Cheng-Xin 1984
M. sibirica	Steep lowland valleys, hills and mountain slopes, also in the alpine	Rogovin 1992
	Steppe areas, gently sloping uplands with forb-grass vegetation, not on steppe with sagebrush or forested slopes; low limit set by desert steppes, upper limit in high mountains; marmots on well-drained relief in swampy river valleys and south-facing slopes	Suntsov and Suntsova 1991
	Steppe plant associations, vegetation present 100-150 days	Seredneva 1991

Appendix. Habitat characteristics of the genus *Marmota*.