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4. INTRASPECIFIC VARIATION IN MARMOTS

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Abstract

Intraspecific variation in marmots is evident in the annual cycle, physiology, genetics, body size and coloration, and alarm-calling, but not in social systems or population structure. Population differences in parasitism may reflect differences in parasite life-history rather than responses by marmots. Much of the intraspecific variation is pheno-typic, which may be the optimal solution to living in a variable environment.

Key words: intraspecific variation, marmots, genetic differentiation, phenotypic plasticity.

Resumen

La variación intra-específica en marmota es evidente en los ciclos anuales, fisiología, genética, tamaño del cuerpo, coloración y llamadas de alarma, pero no se observa en el sistema social y la estructura de la población. Diferencias poblacionales en el parasitismo pueden reflejar diferencias de historias de vida en parásitos, más que una respuesta de las marmotas. La mayor parte de la variación intra-específica es fenotípica, por lo que puede ser una solución óptima en ambientes variables.

Palabras clave: diferenciación genética, marmotas, plasticidad fenotípica, variación intraespecífica.

A current, major environmental concern is the decline in biodiversity. This decline is typically expressed as the loss of species. Although the loss of entire species is of great importance, the loss of genetically distinct populations within species is of equal importance (Ehrlich 1988). These populations contain genetic resources that could be vital to the evolutionary persistence and diversification of a species and that could be valuable for human activities. Potential loss of within species variability is more likely in wide-ranging species whose distribution is reduced because of human changes in the environment or because of climate change. Thus, from the viewpoint of maintaining biodiver-sity, it is important to document the nature of in-traspecific variability.

Intraspecific variation has been described for vertebrate social systems (Lott 1991), as patterns of geographic variation in behavior (Foster and Endler 1999), and as variation in physiological traits (Spicer and Gaston 1999). Morphological variation has been widely used in the naming of subspecies (*e.g.*, Hall 1981) and genetic variability forms the basis for evolutionary change and adaptation (*e.g.*, Maynard Smith 1989). The implication from these broad treatments of intraspecific variation is that within species diversity is a widespread and general phenomenon. Thus, from the perspectives of biodiversity resources and the evolutionary adaptation of local populations, intraspecific variation needs to be described and its underlying causes identified.

Marmots (*Marmota*), the largest true hibernators, occur in the northern hemisphere primarily in mountainous regions, but also in steppe and forest/meadow habitats (Armitage 2000). Several species

are distributed over elevational, latitudinal, or longitudinal gradients that provide opportunities for intraspecific diversification. Furthermore, populations of some species encounter different seasonal phenologies, which can markedly affect the timing of hibernation. Other populations experience different exposures to disease organisms. The purpose of this paper is to describe the intraspecific variation present in marmots and to suggest underlying ecological and/or evolutionary relationships and topics for future research. Some patterns of variation were reviewed elsewhere (Armitage 2000).

Subspecies of Marmots

The designation of subspecies usually describes a subdivision that is characterized by common morphological features within a defined geographic area (Patchen 1992). Currently, 14 species of marmots are recognized (Nowak 1999). Subspecies have not been described for three species that have restricted geographic distribution: *M. olympus* on the Olympic peninsula; *M. vancouverensis*, limited to Vancouver Island; and *M. broweri*, in the Brooks Range in Alaska. All other species of marmots have from two to 11 subspecies (Bibikow 1996; Hall 1981, Ognev 1947).

The differentiation of subspecies typically is based on skull dimensions, pelage characteristics, especially color, and body size. For example, among the three subspecies of *M. camtschatica*, there are differences in the choanal and incisive foramina. All three types of the anterior region of the choanal foramen occurred in one subspecies. However, only one type was present in another subspecies, and that type was missing in the third subspecies. Similar variation occurred for the incisive foramen (Boyeskorov *et al.* 1996). The adaptive importance, if any, of these differences is unknown. The significance of differences in size and pelage is unknown; however, some relationships between size and coloration and environmental factors have been described. The pallid yellow-bellied marmot, *M. flaviventris avara*, is a smaller and paler subspecies that lives in the lowlands of eastern Washington and Oregon, where the climate is warmer and more arid (Couch 1930). Small size and light color apparently are adaptations for living in a warm, arid climate. Similarly, the lighter and smaller *M. caudata aurea* lives in a drier climate than the larger, darker *M. c. caudata* (Davydov 1991). The alarm calls of these two subspecies differ as a consequence of glaciation that effectively separated the two populations (Nikolskii *et al.* 1999). There is no known adaptive significance to these differences. The differences between these subspecies may warrant specific designation for each.

There is further evidence to suggest that the characters used to describe subspecies may be related to climatic factors. Geographic variability in body size was examined in *M. bobac*, *M. baibacina*, *M. sibirica*, *M. camtschatica*, *M. menzbieri*, and *M. caudata* (Terekhina and Panteleyev 1994). Body mass and body length in each species increase from the south to the north and with elevation above sea level. The variability pattern conforms with Bergman's rule. Armitage and Blumstein (2002) interpreted large body size to be an adaptation for meeting heavy energy demands. Larger marmots store more fat and use it relatively more slowly. Energy demands probably increase with latitude and elevation. Possible relationships between body size and latitude and elevation in North America marmots have not been described, but evidence suggests that relationships similar to those described above for Eurasian marmots may occur. The most northerly subspecies of the hoary marmot, *M. caligata caligata*, is among the largest of the subspecies whereas the more southerly *M. c. okanagana* is smaller. The most southerly *M. c. nivaria* may be the largest subspecies, but it is found at high elevations (Howell 1915). Interestingly, *M. m. monax* is the longest and most southerly and *M. m. canadensis* is the smallest and most northerly of the woodchuck subspecies (Howell 1915). Large body size may be favored by factors other than climate, *e.g.*, defense against predators, competition for mates, and production of larger young. If food resources are available, the longer active season in southern latitudes will result in larger woodchucks. The relative importance of climatic and other factors affecting body size requires further study. Among the subspecies of *M. flaviventris*, *M. f. luteola*, which occurs over a wide range of life zones and community types (Armstrong 1972), is the largest. *M. f. nosophora* in southwestern Alberta is also large whereas *M. f. engelhardti* in southwestern Utah is the smallest or nearly the smallest subspecies (Howell 1915). Clearly *M. flaviventris* in arid areas are smaller than those from more mesic areas (Armitage *et al.* 1990). *M. f. avara* from 900 m elevation in eastern Washington exhib-

ited reduced metabolism and increased evaporative water loss to cope with heat stress at high environmental temperatures in comparison with *M. f. luteola* from 2900 m elevation in Colorado (Armitage *et al.* 1990). Thus, there are suggestions that the various subspecies of marmots reflect adaptations to local environments, but this subject requires much new and more extensive investigation.

Morphological characters other than those used to describe subspecies also vary. Initially, differences in the baculum of *M. baibacina* were related to the Tien Shan and Altai subspecies. Further analysis revealed that the structure was simplified in a west-east direction to form a cline not clearly related to the subspecies (Pole and Bibikov 1992). The incisors of two populations of *M. menzbieri* varied: they were steeply curved in Western Tien Shan where the marmots dug roots from dense, loamy soil (Bibikow 1996).

Annual Cycle

The activity pattern of all species of marmots is characterized by a circannual cycle consisting of the sequential stages of hibernation, emergence from hibernation, the active season consisting of reproduction, growth, and immergence into hibernation, thus starting a new cycle with hibernation (Armitage 1998; Davis 1976). The sequence of stages apparently is fixed and the length of the active season varies among species from 3.5 to 7.5 months (Armitage 1999). For a given species, the length of the active season (emergence from hibernation to immergence in hibernation) varies little among geographic populations, but the timing of emergence and immergence may vary widely. For example, there is trend for *M. vancouverensis* to emerge later with increasing elevation with an average difference of about 15 days between the lowest and highest elevations (Bryant, *pers. com.*).

Populations of the gray marmot, *M. baibacina*, in Tien Shan at 1600 to 1800 m elevation emerge in early March and immerge in late August; those at 3200 to 3400 m emerge in April and immerge in early September. The red marmot, *M. caudata*, is active from early March to late July at low elevations, from late March to late August at medium elevations, and from late April to late September at high elevations (Bibikow 1996). Immergence of *M. bobac* depends on the local climate; immergence occurs later in a hot, dry summer and earlier in a cooler, humid summer. Steppe fires initiate the earliest immergence (Soroka 2000). The seasonal phenology of *M. baibacina* can vary 10 to15 days at the same altitude depending on whether burrows are located on north- or south-facing slopes (Pole 1996). This difference in phenology likely results from differences in the length of snow cover. In the East River Valley in Colorado, the mean date of 50% snow cover differed by as much as 21 days between down valley populations of *M. flaviventris* at an elevation of about 2867 m and up valley populations at an elevation of about 2995 m (Van Vuren and Armitage 1991); the difference in mean date of 50% snow cover was 12 days (Van Vuren, *pers. com.*). Up valley marmots on average wean young 12 days later than down valley young (Armitage, unpublished data). Thus, a 12-day average shift in snow phenology is associated with an average 12-day shift in marmot phenology.

The active season of yellow-bellied marmots in eastern Washington and Oregon and in Capitol Reef National Park, Utah, all low elevation, dry, and warm environments, begins in late February or early March and terminates in June (young immerge about 20 days later) (Couch 1930; Hopkinson, *pers. com.*) whereas high elevation yellow-bellied marmots in Colorado emerge in late April or early May and immerge in late August or early September (Armitage 1998). Note that the length of the active seasons is essentially the same in the low and high elevation populations; the phenology shifts so that marmots are active when the season is most favorable to reproduction and growth. An active season that is as long as possible enables marmots to prepare adequately for hibernation and to reproduce more frequently; that is, marmot species with relatively short growing seasons typically skip reproduction for one or more years (Armitage and Blumstein 2002).

For the woodchuck, *M. monax*, the active season is longer where winter is shorter. Thus, woodchucks hibernate for about 5.5 months in Canada, for about five months in upstate New York, for about 4.0 to 4.5 months in Pennsylvania and Missouri, and for 3.5 to 4.0 months in Maryland. Woodchucks may be active in any month when weather conditions are mild (Armitage 2003).

Two experiments strongly indicate that the phenology of the active season is a phenotypic response that enables a marmot population to adjust to local

environmental conditions. Woodchucks were transferred from the eastern United States to Australia where they gradually shifted their phenology by about six months in agreement with the climatic cycle of the southern hemisphere (Davis and Finnie 1975). Three yellow-bellied marmots were translocated from a population that emerged in early May to outdoor enclosures in a population that emerged by early March. After three years, the phenology of the translocated marmots had shifted to conform to that of the local population; *i.e.*, emergence occurred in early March rather than in early May (Thompson 1979). Photoperiod probably entrains the shift in phenology (Concannon *et al.* 1997).

Physiology and Genetics

Lowland yellow-bellied marmots have a lower hematocrit (ml of red blood cells/100 ml of blood) value than high elevation yellow-bellied marmots. When high elevation marmots are maintained near sea level, hematocrit values decrease and do not differ from those of lowland marmots (Armitage 1983). Thus, hematocrit values also are a phenotypic response to local conditions. However, differences in metabolic rate and water budgets of montane mesic and lowland xeric populations of *M. flaviventris* probably are genetic as the differences persist when the marmots are acclimatized to the same laboratory conditions (Ward and Armitage 1981).

All species of Eurasian marmots have a chromosome number $2N = 38$ (Bibikow 1996) except for *M. camtschatica* $2N = 40$. Recently *M. baibacina kastschenkoi* from western Siberia was described as having $2N = 36$ (Brandler 2000). This subspecies is darker than other *M. baibacina* and differs in cranial and *os penis* structure. It inhabits the forest-steppe and appears to be a relict population (Galkina and Taranenko 2002). The possible adaptive significance of the differences in morphology and chromosome numbers are unknown. Brandler and Galkina and Taranenko suggest that this subspecies should be elevated to specific status.

Sereological differences among populations probably represent genetic differences. The immunogenetic method determines the degree of similarity in antigen systems. Immunodiffusion differences are revealed by the absorption of rabbit antisera with sera of marmot populations. These differences are expressed in the number of precipitin lines, which, in turn, reveals differences among the populations. When the serum from *M. menzbieri* was tested against sera from populations of *M. caudata* and *M. bobac*, clear intraspecific differences were detected. A clear precipitation line was formed with Uljanovsk bobac, but not with Kharkov and Tselinograd bobacs. There was a reaction with *M. caudata* from Tadjikistan, but not with serum from Kazakstan red marmots (Zholnerovskaya and Ermolaev 1996). Further analyses revealed intraspecific differences in the formation of precipitation lines for *M. sibirica*, *M. bobac*, *M. baibacina*, and *M. camtschatica*. Other studies further reveal population differentiation among bobac marmots (Zholnerovskaya *et al.* 1992) and among populations of *M. camtschatica* (Boyeskorov *et al.* 1996). The adaptive significance, if any, of this variation is unknown.

Some patterns of genetic variation have been related to disease or parasitism. Western and eastern populations of *M. marmota* differ significantly in the frequencies of two alleles, Pep-1 and Sod-1 (Preleuthner and Pinsker 1993). The Pep-1 genotypes differ in their degree of infestation of the nematode *Citellina alpina* and the cestode *Ctenotaenia marmotae*; the genotype S/S was overrepresented among individuals not infected with *C. alpina* and the S/F genotype occurred in a higher frequency in individuals not infected with *C. marmotae*. The polymorphism at the Pep-1 locus may be maintained by balancing selection (Preleuthner *et al.* 1995). Allelic frequencies of peptidase with glycyl leucine-4 and phosphogluconate dehydrogenase of woodchucks in Delaware, where woodchuck hepatitis virus is endemic, differed from those of woodchucks in New York, where the virus apparently is absent (Wright *et al.* 1987).

The patterns of genetic variation among marmot populations fluctuate in response to the incidence of disease. The characteristics of the holes of nerves of the mandible of *M. baibacina* form four phenotypes. In a plague year, phenotype 3 increased by 8% and phenotype 1 decreased by 14%. The other two phenotypes fluctuated independently of disease exposure. Hemo-agglutination patterns formed four phenotypes; gray marmots with phenotype 4 were most sensitive to infection and those with phenotype 2 were most resistant (Pole and Bibikov 1991). Fluctuations of these two characters were hypothesized to reflect unequal resistance to plague of the different marmot phenotypes.

Four polymorphic loci provided 18 phenotypes whose mean frequencies varied among three populations of the tarbagan, *M. sibirica*. 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% and male mortality was twice that of female mortality. After infection, frequencies of four alleles (Hp^S, Tf^M, Tf^K, Al^B) decreased and frequencies of three alleles (Tf^L, Al^A, Hp^F) 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 2002).

Allozyme variation was measured in 15 populations of *M. marmota* in Austria and Switzerland. Only two of 50 enzyme loci were polymorphic, no rare alleles were detected and average heterozygosity was low (Preleuthner and Pinsker 1993). The lack of genetic variation probably represents a loss of variation when widespread populations became restricted during the post-glacial warming in Central Europe. Many populations went extinct in the face of advancing forests. A severe bottleneck occurred during this time, which greatly reduced genetic variation as only a small founder population survived and eventually spread to occupy Austria. The bottleneck is still present at the protein level (Preleuthner *et al.* 1995). However, genetic differentiation has occurred at the VNTR *loci*. Eight populations from western Austria were polymorphic (Kruckenhauser *et al.* 1997). Populations in eastern Austria and Switzerland are variable; these populations are derived from multiple introductions from western Austria and probably represent variation in the source populations from which the introductions were made.

Local populations of *M. flaviventris* differ genetically, but the differences are not fixed because of gene flow among the populations (Schwartz and Armitage 1980). Most of the gene flow was a consequence of the dispersal of males as all males disperse from their natal population whereas many females are philopatric (Armitage 1998). However, genetic differentiation has occurred on isolated mountain ranges in the Great Basin of western United States. These ranges have been separated for 7000 to 10,000 years. Genetic variation is very high and mean heterozygosities are much higher than reported for other populations of yellow-bellied marmots (Floyd, *pers. com.*). Presently the mechanism for maintaining the high heterozygosities is unknown; there is no relationship between geographic distance and the genetic difference between populations or between mountain range area and genetic diversity (Floyd *et al.* 2002).

Alarm Calling

Each species of marmot has a distinctive alarm call (Nikol'skii 1996, Blumstein and Armitage 1997). No significant intraspecific variation was found for *M. flaviventris*, *M. marmota*, *M. caudata aurea* (Blumstein and Daniel 1997), *M. olympus*, *M. caligata*, and *M. vancouverensis* (Blumstein 1999). However, variation occurs among populations of *M. bobac* (Nikol' skii 2002a) and *M. baibacina* (Nikol'skii 1994). Variation may also occur among populations of *M. camtschatica* and *M. sibirica*, but further investigation is required (Nikol'skii 1996). Spectral analysis of the alarm call of 11 populations of *M. bobac* permitted the merging of 11 populations into four geographical populations that coincided only partly with conventional subspecies. Six populations of *M. baibacina* were merged into three groups. For both species, variation in the alarm call was related to the vertical irregularity of the landscape; *i.e.*, the distance from the valley floor to the valley top. Low verticality was related to alarm calls occurring in sets; *i.e.*, groups of sounds widely spaced. High verticality was associated with a rapid series of calls, which corresponds to a call given when danger is close. Apparently natural selection has fixed the pattern of alarm-calling for a population that is optimal for its landscape (Nikol' skii 1994, 2002b). In particular, natural selection would favor rapid calls where high verticality occurs as in that landscape predators are likely to appear suddenly at close range. Because rapid calls infer danger, marmots should immediately seek refuge even if they can not see the predator. Seeking refuge in a burrow means that the marmot loses track of the predator and may lose considerable time that could be allocated to other activities; *e.g.*, foraging. Widely-spaced sounds indicate low danger and the marmot can invest time in the low verticality habitat to locate the predator, keep track of it, and decide whether it is

necessary to enter a burrow. Usually a predator that has been detected leaves the area; thus a marmot may be able to resume foraging much sooner than if it fled below-ground, when such flight was unnecessary.

Parasitism and Habitat

Marmots are infected by a wide range of parasites, especially ascarids, tapeworms, fleas, mites, and ticks (Bassano 1996). Other than studies mentioned previously, there is little examination of the variability in parasitism among marmot populations of the same species. For example, sensitivity to plague by *M. baibacina* is related to blood characteristics, but it is not clear if the distribution of the blood types is associated with particular populations (spatial distribution of phenotypes formed a mosaic pattern) or represents short-term variation in response to plague (Aikimbaev and Pole 1996).

Parasites were enumerated for four populations of *M. caudata* and one population of *M. baibacina*. The population of *M. caudata* inhabiting East Pamir and the population of *M. baibacina* from Tien Shan were infested primarily by the flea *Oropsylla silantiewi* whereas *M. caudata* populations from Gissar and Alai were infested primarily by the flea *Citellophilus lebedewi* and that from Tolas was characterized by the abundance of the flea *Pulex irritans* (Ageev and Pole 1996). In a separate study (Davydov 1991), a long-tailed population from Gissaro-Darvaz was characterized by the abundance of *P. irritans* (reported in low numbers by Ageev and Pole) and the population from Pamir had mainly *O. silantiewi* (similar to the report of Ageev and Pole). Most likely the distribution of fleas does not result from intraspecific marmot responses, but results from altitudinal zonality. Thus, *O. silantiewi* predominates on marmots in cold alpine belts (Pamir and Tien Shan) while *C. lebedewi* predominates in the meadow-forest-steppe belts of lower elevations (Alai, Gissar, and Tolas). Dry, lower elevations are preferred by *P. irritans* (Ageev and Pole 1996). This flea/marmot relationship illustrates that care must be taken when trying to determine if an intraspecies pattern depends on characteristics of the marmot population or on characteristics of the parasite. However, the report that the helminth *Citellina alatau* is specific to the *M. caudata* population of Gissaro-Darvaz and the nematode *Ascaris tarbagan* is specific to the population from Pamir appears to be a characteristic of the marmot populations, and not the endoparasites (Davydov 1991).

A similar problem arises in interpreting variation in population composition. There is considerable variation in the nature of marmot settlements, age and sex structure of the populations, population size of families, age of maturity, and frequency and nature of social interactions (*e.g.*, Armitage 1977, Shubin 1991, Bibikow 1996, Pole 1996). Most studies do not compare different populations. However, two populations of *M. caudata* were compared, one from Gissaro-Darvaz (G-D) and one from Pamir (P). The population from G-D had small families and females typically began breeding at age four; P populations had large families and some females initiated breeding at age three (Davydov 1991). A higher percentage of P females than of G-D females bred each year. Several differences characterized Vancouver Island marmots inhabiting natural and clear-cut habitats: mean age of first reproduction was earlier, survival rates were lower, and no female produced a second litter on clear-cut habitats (Bryant 1996a). Probably these differences represent phenotypic responses to the different environments (G-D lives in heavily dissected mountain relief, and P lives in steppe or flat relief) occupied by these populations rather than genetic differentiation.

Social Systems

Yellow-bellied marmot females form social groups of one to five females known as matrilines. The mating system may be monogamous or polygynous (Armitage 1991). Both mating systems occur in the population at the same time and in the same social group at different times. Thus variation occurs because of changes in the number and size of matrilines. For example, the number of females may be reduced to one because of mortality and a failure to recruit replacements. Thus a male has no alternative except to be monogamous. Small habitat patches typically support only one reproductive female and male; hence, a monogamous system occurs. However, radiotelemetry recently revealed that some males in those situations may have expanded home ranges and are actually polygynous (Salsbury and Armitage 1994). Thus, there is no evidence of intraspecific differentiation in *M. flaviventris* social systems; variation is facultative and a consequence

of demography and habitat differences (Armitage and Schwartz 2000).

The Vancouver Island marmot (*M. vancouverensis*) typically inhabits small, subalpine meadows. The social system consists of one pair of adults plus juveniles of various ages. Thus, the mating system is monogamous (Bryant 1996b). However, a habitat patch may have as many as three litters in a year when one male is present. Thus, polygyny is facultative and does not represent intraspecific differentiation.

Hoary marmots, *M. caligata*, are monogamous in Alaska (Holmes 1984) and bigamous in Washington (Barash 1974). These differences appear to be phenotypic responses to local conditions; resources in Alaska do not support more than one adult pair. The social structure of *M. marmota* varies from a territorial pair to a territorial pair with subadults, yearlings, and young (Perrin *et al.* 1993; Sala *et al.* 1996). This variation also is a function of demographic processes and may occur on the same territory. There is no evidence that different geographic populations have different social systems (Arnold 1990; Lenti Boero 1999).

The woodchuck, *M. monax*, is the only species of marmot that is asocial and has the widest geographic range in North America (Armitage 2000). Some differences in spacing behavior, dispersal, and social behavior among woodchucks from different geographic areas were summarized by Meier (1992). These differences generally represent small, quantitative shifts in the character under consideration. For example, all juveniles disperse from some populations whereas in other populations up to 25% do not disperse until they are yearlings (Meier 1992). The reported differences among woodchuck populations appear to be phenotypic responses to local habitat and climatic conditions. There is no evidence that these differences are associated with genetic differentiation.

Conclusions

Much of the intraspecific variability of marmots is phenotypic. Marmots maintain considerable plasticity in response to environmental variation; *e.g.*, the onset of the active season. This phenotypic plasticity is adaptive and is considered the optimal solution in a variable environment (Schlickting and Pigliucci 1998). However, when the environmental condition is consistent and predictive through time, then genetic differentiation is expected. Thus, the different phenotypic responses in warm, arid environments compared to those in cool, mesic environments are a consequence of genetic variation. Much remains to be learned about the genetic basis of phenotypic plasticity and the amount of intraspecific variability in marmots that has a direct genetic basis or represents phenotypic plasticity with an underlying common genotype.

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