Introduction

In the early years of marmot research I was frequently asked: "what are marmots good for?" When I replied that marmots had intrinsic value as a member of the earth's biodiversity, I usually received a blank look. If I replied that marmots fed golden eagles and coyotes, I received a nod of understanding. When I stated that marmots were useful organisms for studying certain biological problems, such as what regulates animal numbers, I frequently became engaged in conversation about why animal populations did not increase without limit. As I describe in the first chapter, my interest in the yellow-bellied marmot was to use it to study the role of social behavior in population dynamics. I soon came to believe that population dynamics could be understood only in the context of marmot life history. As a consequence, the yellow-bellied marmot research program expanded to explore life-history features such as body size, habitat use, environmental physiology, social organization and dynamics, individuality, and kinship. I also came to realize that characteristics of the social and population system, such as group composition and relatedness, could be understood only by following behavioral and demographic patterns over many years. Social organization and population numbers in a marmot colony in one year were a consequence of their history, which in turn affected social composition and behavior in the years to follow. Knowing the process led to understanding the structure.

This book is written with three broad goals in mind. The first goal is to describe how one species, the yellow-bellied marmot, copes with and persists in the harsh environment where it lives. The species has to solve multiple problems; e.g., finding and processing food, finding a mate, avoiding predation, in order to evolve an integrated life history. In a broad sense, the integrated system can be thought of as all the environmental and organismal factors that enable an animal to obtain and process energy in order to produce reproductive descendents. The yellow-belled marmot system can best be understood in the context of what other species of marmots do. Thus, much of the text is a comparative biology of the 15 species of marmots.

The second goal is to present considerable new data and analyses and integrate them with material published over a 50-year span in 29 journals and 17 book chapters, symposium volumes, and conference proceedings. Extensive natural history observations are included to provide the essential foundation for integrating social and population processes.

The third goal is to relate the results of the yellow-bellied marmot research to major ecological and evolutionary theories, especially inclusive fitness and population regulation.

An overview of the book's content

This book reports the results of a 41-year empirical study of the social and population biology of the yellow-bellied marmot (*Marmota flaviventris*) in the Upper East River Valley near the Rocky Mountain Biological Laboratory in Colorado, USA. The roles played by social behavior, individual behavioral phenotypes, physiological adaptations, and resource use in reproductive strategies of males and females occupy central stage. Inclusive fitness theory provides the framework for evaluating the importance of direct and indirect fitness strategies in the formation of social groups, the sharing of critical resources, and the expression of social behavior. The significance of cooperation and competition within female kin groups is related to reproductive skew and cooperative breeding. Of special significance is relating individual reproductive strategies to the demographic factors affecting population growth and decline. A feedback model of population regulation by social behavior is evaluated and the role of population density in population dynamics is analyzed. The importance of time as a limiting factor in marmot biology is developed.

The book is organized into six topical parts. Part I includes the first seven chapters. The first chapter introduces the relationship between marmots and humans that eventually resulted in the use of marmots as experimental animals. The remaining chapters describe the evolution and diversity of marmot species, how they exploit the places where they live, the importance of a harsh environment, and the consequent evolution of sociality. Because hibernation plays a central role in marmot biology, its physiology and control receive special emphasis.

The second part (Chapters 8 and 9) describes the abiotic environment, research sites, and environmental physiology of the yellow-bellied marmot. Energy conservation is emphasized as a major adaptation enabling marmots to direct as much energy as possible to reproduction.

In the third part (Chapters 10–14) kinship provides the foundation for analyzing the functions of social behavior, resource sharing, and communication. Individual behavioral phenotypes are introduced and their effects on social play are described.

The fourth part (Chapters 15 and 16) focuses on social and demographic factors influencing reproductive success of males and females and how the strategies of one sex affect the reproductive success of the other sex.

Population dynamics is the topic of Part V (Chapters 17–20). The impact of agents, such as weather and predation, on population change through time are described and followed by an analysis of dispersal and immigration, which is followed by a discussion of metapopulation dynamics. The demographic mechanisms of population growth and decline are related to reproductive strategies of yellow-bellied marmot females living in matrilines. This section concludes with an analysis of the relevance of population-regulation and population-limitation hypotheses to marmot population dynamics.

Part VI consists of Chapter 21 in which the potential effects of climate change on marmots are evaluated. The amount and duration of snow cover are emphasized as critical factors limiting marmot distribution and reproduction and survival.

The final chapter reviews, develops, and emphasizes major life-history traits that determine the successful persistence of marmots living in a harsh, seasonal environment.

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Part I

The diversity and evolutionary history of marmots

1 Marmots in human culture: from folklore to research

Marmots (Fig. 1.1) are large-bodied, ground-dwelling, herbivorous squirrels (Rodentia: Sciuridae) that originated in North America, spread into Eurasia during the Pliocene and dispersed widely during the Pleistocene (Bibikov and Rumiantsev 1996). Their large size, diurnal activity, and the propensity to alarm-call at the approach of intruders would attract attention wherever humans and marmots co-existed. Their first contacts with humans were probably with nomadic hunters who populated the periglacial zone where marmots lived. Marmot fossils are not significant until the last ice age when marmots were probably an episodic game animal. The distribution and state of marmot populations during the Holocene were likely determined primarily by environmental conditions (Bibikov and Rumiantsev 1996). Evidence of marmot/human interactions dates to the Pleistocene.

Human/marmot interactions in prehistoric times in Europe are recorded in cave paintings in France (Louis *et al*. 2002). Marmots have been hunted for fur and meat in the western Alps and the southern Jura since the Late Pleistocene (Tomé and Chaix 2003). Some archaeological sites had several hundred marmot individuals indicating specialized hunting, which was uncommon because marmots are usually in low abundance. Marmot numbers and elevational range increased during cold periods and decreased during warm periods (Table 1.1). In general, hunting of marmots is clearly linked to cold periods (Tomé and Chaix 2003).

Probably all North American species (see Table 1.2 for a list of marmot species) were utilized by Native Americans. Okanagan Indians used *M. caligata* for food and clothing (Anderson 1934). A *M. flaviventris* jaw was found in Woodchuck Cave in northern Arizona associated with a burial that was dated to about AD 200 (Lange 1956). *M. vancouverensis* remains were found in four high-elevation cave sites dated from 830 to 2630 years ago (Nagorsen *et al*. 1996). Cut marks on bones and artifacts recovered at the site indicate the remains are a result of human hunting. Quite likely the aboriginal people traveled to the mountainous sites to hunt marmots.

Nagorsen *et al*. (1996) reviewed the evidence for native use of marmots along the Northwest Coast of North America. Skins of marmots, probably *M. caligata*, were reported by fur traders in the late eighteenth century as being in great abundance and they entered into the Hudson Bay Company fur trade in the mid-nineteenth century. Marmots were hunted in the fall after molt when they provided a light but finely

Table 1.1 Changes in marmot population based on information from archaeological sites (from Tomé and Chaix 2003).

Time period	Marmot status
Younger Dryas (about 14 500 to 11 500 years ago)	Marmots common during this cold period
11 000 to 10 000 BC	Marmots decreased from the Upper Paleolithic to Mesolithic because warming restricted them to higher elevations
After 7000 BC	Marmots absent from archaeological sites under 900 m

Table 1.2 The currently recognized species of *Marmota*.

Eurasia (Palearctic)		North America (Nearctic)	
M. baibacina	gray or Altai	*M. broweri*	Alaskan or arctic
M. bobak	steppe	*M. caligata*	hoary
M. camtschatica	black-capped	*M. flaviventris*	yellow-bellied
M. caudata	red or long-tailed	*M. monax*	woodchuck or groundhog
M. himalayana	Himalayan	*M. olympus*	olympic
M. kastschenkoi	forest-steppe		
M. marmota	alpine		
M. menzbieri	Menzbier's		
M. sibirica	Siberian, tarbagan or Mongolian		

Figure 1.1 A typical adult yellow-bellied marmot. (See plate section for color version.)

furred pelt prized for clothing. Marmot hides were used in potlatches (Drucker 1950). The hunters and their families went up into the mountains to their privately owned hunting grounds where they primarily used deadfall traps to capture large numbers of marmots and harvest the valuable furs. The skins were stretched and the flesh dried for winter use.

Among the Tlingit and Gitkson of the upper Skeena River, wealth was measured directly in *M. caligata* (hoary marmot) skins. Robes were made by sewing together many of the soft-furred hides (Nagorsen *et al*. 1996). Likewise, skins of *Marmota olympus* were used to make robes, bed blankets, or a seat when one had to sit on a damp or cold spot. Marmot flesh was regarded as excellent.

Humans have most certainly used marmots for food wherever humans and marmots co-existed. In *Les Miserables* Victor Hugo relates that in 1815, Jean Valjean, hungry and tired, entered an inn where he found a "fat marmot, flanked by white partridges and goose, was turning on a long spit before the fire." In Crested Butte, Colorado, during a miner's strike in 1913–14, the miners turned to hunting for meat and greatly reduced the numbers of yellow-bellied marmots (Warren 1916). The use of marmots as food continues into the twenty-first century; the old miners and trappers state that there is no better eating than a fat marmot in the fall.

Marmots and mythology

Marmots entered into mythology from early times and were often given names that were misunderstood. Animals reported as large ants dug up gold on the Dansar Plateau for the Persian Emperor 2500 years ago and these gold-digging ants were reported by Herodotus in the fifth century BC. The word in Persian for marmot is equivalent to "mountain ant" (Ramousse and Le Berre 2007). Local people collected earth from marmot burrows and sifted out the gold dust. This legend of gold-digging ants has a basis in reality, other legends, especially creation legends, represent mythological explanations for some aspects of marmot biology.

The following two legends are taken from accounts in Martin (1994). According to the Cherokee, in the old days animals talked and lived with people and marriages between humans and woodchucks were common. At that time, the woodchuck had a long tail. One day the woodchuck encountered a pack of wolves; in an attempt to gain time and perhaps escape from the wolves, the woodchuck offered to teach the wolves to dance. They all danced and as the woodchuck danced, it moved closer to a hole and dove in. The wolves quickly followed and grabbed the tail, which broke off. The woodchuck escaped but has had a short tail ever since.

Originally the Mohawk people and animals lived underground. One day a crack was noted and an individual went above ground and returned and told everyone what a beautiful place it was. All the people were happy to move to the surface and live above ground except the woodchuck, who was content to live in the ground.

A Pahute Indian legend tells how the whistler (marmot) and badger got their homes (Palmer 1973). The badger and the whistler were good friends. They traveled together;

the badger was stronger but the whistler was the better singer. Trouble arose when they both wanted the same wife and she preferred the badger's warm fur to the whistler's music.

But one day the whistler ran off with the wife. The badger was furious but could not run fast enough to catch them. In his anger and frustration he began to scratch and claw at the earth and dug a hole and sent rocks down the hillside. The hole caught fire and the fire grew bigger and threw out molten rocks. The badger fled the molten stream, but the whistler tried to stop it by blowing on it until the stream stopped. The whistler kept blowing all winter and the molten lava froze and broke up into big rocks.

Whistler believed his blowing had cooled and stopped the lava and led animals along the lava flow to show what he had done. He was very vain and the god Shinob decided only whistler liked all the black rocks and that they should be his home. From that time whistler's home has been in the rocks. He comes out on the big rocks and sits in the sun and whistles. As for the badger, he was punished for losing his temper and forced always to dig a hole in the ground.

The Mongolian people have a long relationship with the tarbagan (*M. sibirica*) that apparently began with cattle breeding on the Eurasian steppe (Bibikov and Rumiantsev 1996). The following legend shows that the people had excellent knowledge of tarbagan biology (Dimitriev *et al*. 2003). In ancient times there were seven suns. A drought set in, the soil became hot, domestic animals were exhausted, and it was impossible to sit or stand. The people requested a highly skilled hunter to shoot with his bow and arrows to decrease the number of suns in the sky. The hunter swore that if he couldn't strike the seven suns one by one that he would cut off a thumb and become a tarbagan that doesn't drink water or eat dry grass, and lives in a dark hole.

He began to shoot the suns, which were built in the sky from east to west. He shot six suns, but as he shot his seventh arrow, a swallow flew between him and the sun. The arrow cut a notch in the swallow's tail; ever since swallows have had forked tails. The sun, afraid of being shot, disappeared behind the West Mountains. The hunter became a tarbagan with only four fingers on the front legs and appears at his burrow at dawn and sunset to shoot the last sun. Because the sun hides to escape the hunter, day and night appeared.

One legendary behavior of the alpine marmot was described by several authors beginning in about AD 77 (Ramousse and Le Berre 2007). A marmot lying on its back, paws lifted up, holding herbs cut by other marmots, is dragged by its tail to its burrow. As a consequence of being dragged, the back is bare as the hair is worn off. Le Vasseur de Beauplan reported in 1660 that he watched the behavior several times. This legend persisted into the nineteenth century as writers used such cooperative behaviors among the animals as moral examples to humans.

The Sieur de Beauplan lived for many years in Ukraine and reported that some steppe marmots (*M. bobak*) were lazy and lay on their backs; the active marmots piled herbage on their bellies, which they held with their paws, and the active marmots dragged the lazy marmots to their burrows (Gudger 1935). There is a moral to the story; the lazy marmots were treated as slaves. Thus the dragging of marmots by their tails was used in two ways as moral lessons.