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Home range area and shape of yellow-bellied marmots

KENNETH B. ARMITAGE

Department of Ecology and Evolutionary Biology, The University of Kansas, Lawrence, Kansas 66045-7534, USA (E-mail: marmots@ku.edu)

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Home range is the area that marmots use to obtain food and burrows necessary for growth, reproduction and survival. During regular censuses, the position of each marmot was recorded as a pair of coordinates from a calibrated grid overlain on a photograph of the colony site. Home range area was calculated as the product of the area of a grid square multiplied by the number of grid squares a marmot utilized. Clearly identified excursions were not included in the calculation of area. Shape was determined as the outline of the home range. The analysis included 24 years, four ages, two sexes, four colonies, four categories of residency, and whether an individual engaged in excursions. A general linear model ANOVA revealed that year ($P < 0.001$), age ($P < 0.001$), residency ($P < 0.001$), and colony ($P < 0.001$) significantly affected home range area but that sex ($P = 0.373$) and excursions ($P = 0.312$) did not. Shape was affected mainly by topography and the presence of other marmots. Area increased with age: adults > 2-year-olds > yearlings > young. Territorial males had the largest area followed by adult females whose area was larger than that of yearlings. Home range varied among colonies. Young and transients made the fewest excursions; adults, the most. Excursions were more frequent in the largest colonies. Residency was significantly affected by age, colony, sex, and excursions. Dispersers and transients were male-biased; residents were biased toward females and young.

KEY WORDS: *Marmota flaviventris*, residency, colony, age, sex, excursions.

INTRODUCTION

Home range is the area that an animal travels to obtain the essential resources required for growth, reproduction, and survival. For marmots, the essential resources are burrows and food. Foraging areas and burrows may be shared by members of a matriline (JOHNS & ARMITAGE 1979, FRASE & ARMITAGE 1984) and individuals may shift home ranges as a consequence of intrasexual conflict (ARMITAGE 1974, 1989, 2002). Adult males (ARMITAGE 1974) defend territories that essentially are identical to the home range. Adult females in a matriline defend the matrilineal home range, as evidenced by patterns of overlap of individual home ranges and of amicable and agonistic behavior (ARMITAGE 1989, 1998, 2002). However, there is no evidence that yearlings, young, or transients defend territories.

A short-term study revealed that mean size of home range varied among years and that the mean size of home ranges was not significantly related to the number of resident adult females (ARMITAGE 1975), but the degree of overlap of individual home ranges was significantly correlated with the number of adult females. No significant relationship was found between rates of social behavior and home range area.

This paper explores further several factors that influence home range area over a period of 24 years. I examine the variation in home range area among years, between sexes, among age groups, among colonies, and among residents. Because some marmots make excursions beyond the normal home range area, the factors associated with excursions were also examined. Because residency affected home range, the factors associated with residency were determined.

METHODS

This study was conducted from 1965 to 1989 in the Upper East River Valley, Colorado. Each year all yellow-bellied marmots in four colonies were trapped, weighed, and sexed, and their reproductive condition noted. Upon first capture, each animal received a numbered, monel metal strap tag in each ear. Age of young, yearling, and 2-year-old marmots could be determined by body mass (ARMITAGE et al. 1976). Because most adult females were first trapped as young, their ages were known. Each year the fur of each marmot was dye-marked with a unique pattern of blots and stripes for visual identification. For further details on trapping and marking, see ARMITAGE 1982a.

A grid was prepared for each colony. First, the colony was mapped by measuring distances between conspicuous landscape features such as trees, prominent and/or odd-shaped rocks, rock ledges, and large shrubs. All features were easily identified in photographs of the colony (see ARMITAGE 1974). Second, a photograph of each colony was used as a "map" and a transparent grid overlay was prepared from the measurements of distance between conspicuous objects. Third, the grid was numbered so that each grid square was identified by vertical and horizontal coordinates.

At regular intervals during behavioral observations, each active marmot was located and its position recorded as a pair of coordinates. The frequency of the censuses varied with the size of the colony and the length of time required locating animals. In general, more time to locate animals was required for the larger colonies and when vegetation grew higher in mid and late summer. In any event, censuses occurred at intervals of 20 min or less.

The recorded grid coordinates for each marmot were plotted on grided forms (e.g., ARMITAGE 2003a). The number of grids in which the marmot was recorded was multiplied by the area of a grid (m^2) to produce the home range area. Empty grids were included in the count when those grids lay within the home range and were grids that the marmot had to use. For example, in one colony a small ravine divided the region around the burrow area from a meadow where the animals frequently foraged. The marmots had to pass through the ravine to reach the meadow, but could not be seen in the ravine. If the marmot was recorded in grids on each side of the ravine, the grid in the ravine was included in calculating home range area. Marmots sometimes made excursions from the home range area into other parts of the habitat; these excursions were not included in the calculation of home range. Sometimes individuals, especially yearlings, moved their center of activity from one area of the colony to another with a large gap of empty grids in-between. In these cases, each home range was considered separately; i.e., as two home ranges.

The analysis included the following treatments: year (24 years), age (adults, 2-year-olds, yearlings, young), sex (male or female), colony (Picnic, North Picnic, River, Marmot Meadow), excursions (yes or no), and residency (resident, disperser, territorial male, transient). Transients were marmots that either passed through a colony or lived peripherally to the resident population and made excursions into the site. Therefore, I asked the question how much of the area is visited by such animals. Presumably these animals are evaluating the area as a possible site for residency and could explore a large part of the colony as part of the evaluation process. Some of these marmots did become residents (ARMITAGE 2003b). Shape was determined by tracing the outline of the plotted grids.

A general linear model ANOVA was used to test for possible significance of the six treatments. When significance was found for treatments with more than two factors (except for year), significant differences among the factors were tested by Student's *t*. All home range areas are reported as means and standard errors.

RESULTS

Shape

The shape of home range varied considerably (Fig. 1). There is no easy way to determine all the factors that affect shape, but topography and associated resources is a major influence. For example, ♀959 at River traveled to three major foraging areas and traveled along a ridge to the top of a mound where she became vigilant and then foraged along the slope before returning to the ridge and back to her home burrow area. She also traveled directly into areas where five 2-year-old females were active; she engaged only in agonistic interactions with the females. Thus her home range consisted of linear traveling routes and broad or extensive foraging areas. By contrast, ♀918 and ♀110 lived in burrows closely adjacent to foraging areas; their home ranges are more box-like. Both females were highly agonistic and a large, unused

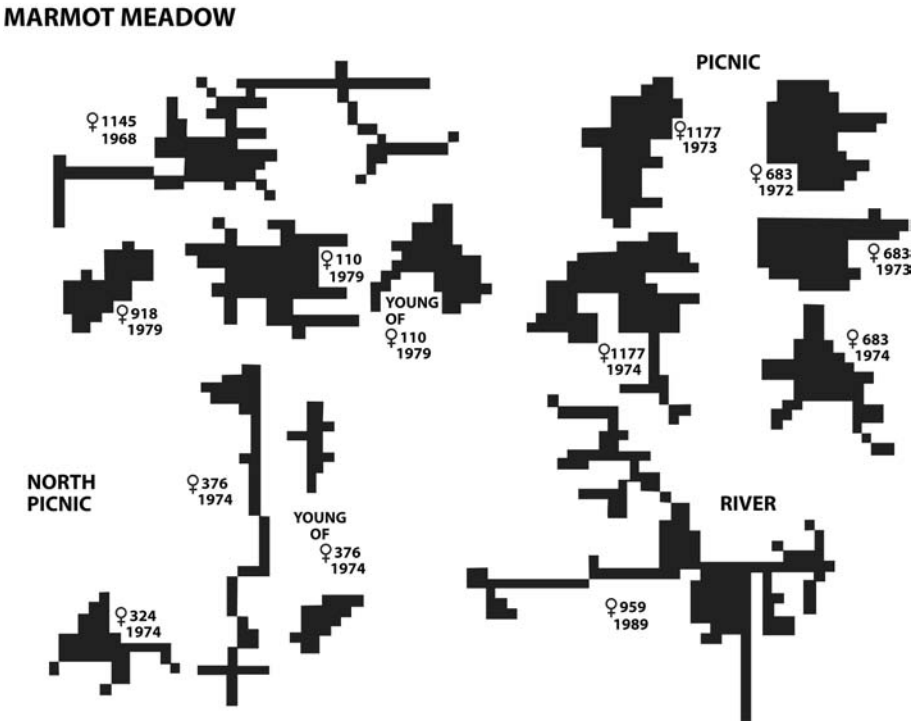

Fig. 1. — Home range shapes of yellow-bellied marmots. Colony, animal, and year are recorded by each shape.

area of the meadow separated them. The young of ♀110 utilized the same area as their mother, but ranged less widely.

Social behavior also was a factor in determining other shapes. At Marmot Meadow, ♀1145 was chased by her mother. She spent several days in another part of the habitat before she returned only to be chased again. Thus she traveled, typically in linear fashion, between several burrow sites where she resided and foraged in the surrounding meadow. At North Picnic, ♀376 and her young were introduced to the central burrow area. Immigrant ♀324 appeared and ♀376, followed by her young, moved up-slope along a rocky outcrop where she established residency. Her young had two home ranges; one at the introduced site and the other at the new site chosen by the adult. The home range shapes followed the distribution of vegetation in the two burrow areas. At Picnic, adult ♀683 and her yearling grand-daughter ♀1177, had home ranges of similar shape. The adult was agonistic to the yearling and the overlap in space-use was 39% (ARMITAGE 1996). The adult moved to a different burrow in 1973 and the different shapes of the home ranges of the two females reflect the burrow locations; ♀683 lived close to foraging areas whereas ♀1177 had to travel across talus to reach the foraging areas. Although the females occupied their same burrows in 1974, shapes changed as the females modified their use of foraging areas.

Area

The mean home range area for the entire sample of marmots was 2302 ± 86 m^2, N = 793. There were 24 cases of individuals shifting locations and having two different home ranges during the active season. This measured mean home range area is much smaller than the area predicted from body mass equations (CALDER 1984: 291). The ANOVA revealed that year, age, colony, and residency significantly affected home range area, but sex and excursions did not (Table 1).

Year

Mean home range area varied from 672 m^2 to 5047 m^2. Some of this variation can be attributed to sample size; e.g., the smallest mean occurred in a year for which only one value was available. Highest yearly means occurred either when wide-ranging yearlings were present or when the territory of one male included the entire colony. When several males had territories in a colony, the territories were smaller, which reduced mean territory size for that year. High yearly means also occurred when social conflict was high among adult females and the females ranged widely.

Age

Mean home range area ranged from 1169 m^2 for young to 3586 m^2 for adults (Table 2). The means for the four age groups differed significantly from each other as follows: adults > 2-year-olds > yearlings > young (t varied from 2.4 to 13.3, P varied from 0.02 to < 0.001).

Sex

The mean home range area of females was larger than that of males (Table 2), but the difference was not significant (Table 1, t = 1.1, P > 0.2).

Table 1.

General linear model ANOVA for area.

Source	df	F	*P*
Year	23	2.87	< 0.001
Age	3	17.07	< 0.001
Sex	1	0.80	0.373
Colony	3	100.32	< 0.001
Excursion	1	1.02	0.312
Residency	3	65.25	< 0.001
Error	758		
Total	792		

Table 2.

Factors affecting the home range area (m^2) of yellow-bellied marmots. All values are means and standard errors. (N).

Age		Residency	
Adults (223)	3586 ± 222	Resident (522)	2220 ± 85
Two-year-olds (97)	2821 ± 235	Disperser (153)	1688 ± 145
Yearlings (230)	2035 ± 123	Territorial male (58)	5624 ± 628
Young (243)	1169 ± 55	Transient (60)	1373 ± 202
Sex		**Colony**	
Male (355)	2199 ± 148	Picnic (308)	3770 ± 168
Female (438)	2385 ± 99	North Picnic (116)	2198 ± 191
Excursions		River (151)	1576 ± 89
Yes (194)	3190 ± 177	Marmot Meadow (218)	786 ± 36
No (599)	2014 ± 96		

Colony

The mean home range among colonies ranged from 786 m^2 to 3770 m^2 (Table 2). The means for the four colonies differed significantly (P varied from 0.01 to < 0.001) from each other in the following pattern: Picnic > North Picnic > River > Marmot Meadow.

Excursions

Although whether or not a marmot made excursions did not significantly affect home range area (Table 1), marmots that made excursions had a significantly ($P < 0.001$) larger mean home range than those that did not make excursions (Table 2).

Because of the difference in mean home range area between those marmots making excursions and those that did not, the factors associated with excursions were analyzed by ANOVA. Year, age, colony, and residency, but not sex, significantly affected excursions (Table 3). Adults made significantly ($0.05 > P > 0.02$) more excursions than 2-year-olds who made significantly ($0.05 > P > 0.02$) more excursions than young, as did yearlings ($0.01 > P$ 0.001). Thus, young made fewer excursions than all other age groups, adults made more excursions than all other age groups, and 2-year-olds and yearlings made excursions at the same frequency ($P > 0.9$).

Among the colonies, excursions occurred significantly (P varied from < 0.01 to < 0.001) more frequently in the two larger colonies (Picnic and North Picnic) than in the two smaller colonies (River and Marmot Meadow). There was no significant difference in the frequency of excursions between the two larger colonies ($P > 0.9$) or the two smaller colonies ($P > 0.5$).

Residency strongly affected the occurrence of excursions (Table 3). Transients made significantly fewer excursions than territorial males ($P < 0.001$),

Table 3.

General linear model ANOVA for excursions.

Source	df	F	*P*
Year	23	2.81	< 0.001
Age	3	7.40	< 0.001
Sex	1	0.67	0.413
Colony	3	6.56	< 0.001
Residency	3	11.57	< 0.001
Error	759		
Total	792		

residents ($P < 0.001$), and dispersers ($0.01 > P > 0.001$). Excursions did not differ significantly between residents and territorial males ($P > 0.4$). Although territorial males made excursions more frequently than dispersers, the difference was marginally significant ($0.1 > P > 0.05$). Finally, residents made more excursions than dispersers ($P = 0.05$). To summarize, those marmots who were present for only part of the active season either as dispersers or transients made fewer excursions than those marmots present throughout the active season.

Residency

The mean home range area ranged from 1373 m^2 for transients to 5624 m^2 for territorial males (Table 2). Home range area of territorial males was significantly larger ($P < 0.001$) than that of residents, which had the second largest mean home range (Table 2). Residents included adult females, yearlings, and young. Because young and yearlings had smaller home ranges than older animals, the overall mean of residents was reduced compared to that of adults. The home range area of residents was significantly greater ($P = 0.001$) than that of dispersers, but mean home range areas of dispersers and transients did not differ significantly ($P = 0.2$).

Because residency strongly affected mean home range area (Table 1), factors associated with residency were analyzed. Age, sex, colony, and excursions significantly affected variation in residency (Table 4). All ages older than young were more likely to be dispersers or transients than young (all $P < 0.001$), but residency did not differ among the other age groups (all $P > 0.5$). Females were more likely to be residents than males and residency was higher in those groups not making excursions. Residency scores did not differ significantly ($P > 0.5$) between River and Marmot Meadow, and the residency score for River was significantly lower than that of Picnic ($0.05 > P > 0.02$) and North Picnic ($P < 0.001$). The residency score for Marmot Meadow was marginally significantly lower than that of Picnic ($0.1 > P > 0.05$) and significantly lower than that of North Picnic ($P < 0.001$) and the residency score for Picnic was significantly lower ($P < 0.001$) than that of North Picnic. These dif-

ferences indicate that patterns of residency; e.g., numbers of dispersers and transients differed among colonies.

The percentage of individuals in each category of residency was determined for each colony (Table 5). There is little difference in the distribution of percentages among the categories of residency between River and Marmot Meadow (Table 5), which accounts for the lack of difference in their residency scores. However, Picnic and especially North Picnic had much higher percentages of transients and somewhat higher percentages of territorial males. In addition, North Picnic had a smaller proportion of residents and Picnic, of dispersers. The high proportions of territorial males and transients, and low proportions of dispersers or residents account for the higher residency scores of Picnic and North Picnic.

Sex ratios

Although sex did not significantly affect home range area (Table 1), an examination of the data indicated that there was a possible variation in sex ratio with age and/or residency. Both age and residency significantly affected sex ratios, but not colony or excursions (Table 6). Thus, males and females were equally likely to make excursions and the pattern of sex ratios was similar across all colonies.

Table 4.

General linear model ANOVA for residency.

Source	df	F	*P*
Year	23	1.11	0.327
Age	3	54.79	< 0.001
Sex	1	186.65	< 0.001
Colony	3	5.07	0.002
Excursion	1	30.75	< 0.001
Error	761		
Total	792		

Table 5.

The percentage of individuals in each category of residency. Residency scores in parentheses.

Residency	Colony			
	River	Marmot Meadow	Picnic	North Picnic
Residents (1)	70.9	70.2	69.5	43.1
Dispersers (2)	20.5	21.6	14.0	26.7
Territorial males (3)	6.6	5.5	7.5	11.2
Transients (4)	2.0	2.8	9.1	19.0

Table 6.

General linear model ANOVA for sex.

Source	df	F	*P*
Age	3	38.3	< 0.001
Colony	3	0.5	0.653
Excursions	1	0.6	0.442
Residency	3	108.0	< 0.001
Error	782		
Total	792		

The sex ratios of young and yearlings did not differ from each other ($P > 0.5$) and fit a 1:1 ratio. Similarly, the sex ratios of adults and 2-year-olds did not differ ($P > 0.4$), but were female biased and differed significantly from the sex ratios of young and yearlings (P varied from 0.02 to < 0.001). These results agree with previously published sex ratios (ARMITAGE 1991, SCHWARTZ et al. 1998).

Residents were strongly biased toward females; dispersers and transients were male-biased. Thus the sex ratio of residents differed significantly from that of dispersers ($P < 0.001$) and transients ($P < 0.001$) whereas the sex ratios of dispersers and transients did not differ significantly ($P > 0.5$).

DISCUSSION

Both area and shape are affected by topographical features such as location of rocky sites for burrows and their proximity to foraging areas. At Marmot Meadow, the colony with the smallest mean home range, the main burrows are located in a rocky outcrop in the meadow. Marmots need to travel only a few meters to begin foraging. At Picnic, the colony with the largest mean home range, major burrows may be located in the midst of a large talus slope such that marmots may travel 30 m or more before reaching a foraging area.

Previous research reported that adult females shifted their home ranges in the early weeks following emergence from hibernation and mating, as females moved out from the center of the colony to other areas (ARMITAGE 1965). The movement was attributed in part to the avoidance of dominant by subordinate animals. Because this study began after the early mating season, reproductive-related shifts were not detected. However, shifts in home range area were clearly documented during the summer. Of the 24 recorded shifts, fourteen were by eventual dispersers (nine male and three female yearlings, and one male and one female 2-year-old). These marmots fit the two-stage dispersal patterns in which individuals left their natal area and established a new home range a short distance away before a final dispersal from the colony area (VAN VUREN 1990).

Other shifts in area occurred when six transients used different areas in multiple visits to a colony. These transients lived near a colony for part or all of a summer and some became residents in subsequent years (Armitage 2003b, 2004a). No excursions were recorded for transients; in effect, transients were making excursions when they entered the area from a location outside the colony. Presumably transients were assessing the possibility of becoming immigrants in the colony they visited. The remaining shifts in home range involved one female from Marmot Meadow. She moved over a wide area, even spending some time at a nearby satellite site (Svendsen 1974). In 2 years she evidently shifted her home range to avoid conflict with an older, reproductive female. In the 3rd year, she was the only adult female resident and weaned a litter. For an unknown reason, she and her litter shifted home ranges in late summer. The surviving young and the adult female had returned to their original home range areas in the following year.

Territorial males had the largest mean and variation in home range area (Table 2). This result was not unexpected as the typical home range of a territorial male includes the home ranges of one or more matrilines (Armitage 1991, 2004a). In large colonies, such as Picnic, the entire area was dominated by one male, who had a very large home range. On the other hand, the same area could be divided into three territories (Armitage 1974), resulting in smaller home ranges and producing a high variation in home range area. Non-colonial males, not included in this study, had much larger home ranges; the home ranges varied from 0.06 to 47.51 ha ($x \pm SE = 5.24 \pm 2.84$ ha, calculated from Salsbury & Armitage 1994). Thus, on average, the home ranges of non-colonial males were about 10 times larger than that of colonial males. Territory size of all males was significantly correlated with the distance between females (Salsbury & Armitage 1994).

Transients had the smallest home range for residency (Table 2). The relatively small home range of transients indicates that they frequented a relatively small proportion of the colony site and were unable to travel widely at a site when seeking possible permanent residency. Most transients were present for only a few days and avoided social contact. When social interactions with residents occurred, they were agonistic (K.B. Armitage unpub. data) and the transient usually disappeared.

Young had the smallest home range area. Young are weaned at about the time the standing crop of vegetation is near maximum (Kilgore & Armitage 1978, Frase & Armitage 1989); possibly young need not travel as far for foraging as adults do earlier in the active season. Yearling home ranges are also smaller than those of adults and 2-year-olds. Many yearlings have a small home range and disperse early in the year. The home range of yearling dispersers is significantly lower ($t = 4.8$, $P < 0.001$) than that of yearling residents. The home range of yearling residents (2889 ± 212 m^2) is significantly lower ($t = 2.27$, $0.05 > P > 0.02$) than that of adults (Table 2). However, if the effect of territorial males is removed from the adult home range calculation, the home range of yearling residents is almost identical to that of adult females (2869 m^2). Thus, the smaller mean home range of yearlings compared with adult females is a consequence of the smaller home range of dispersers. Likewise, when the effect of male home range is removed from

that of adults, the home range areas of adult and 2-year-old females do not differ. Thus, resident females 1-year-old or older on average have the same home range area. This similarity indicates that each of these age groups requires about the same amount of space to meet its requirements for necessary resources. The larger home range area of territorial males includes the required resources of food and burrows and in addition is a consequence of the polygynous reproductive strategy whereby the male may defend more than one matriline of females.

The home range of yellow-bellied marmots is smaller than that of any other marmot species (reviewed in ARMITAGE 2000, 2003c). Different populations of a species may have different sized home ranges. For example, home ranges of an alpine marmot (*M. marmota*) population for three family groups over an 8-year period varied from 1.52 to 1.92 ha (LENTI BOERO 2003), whereas other populations ranged from 1.4 to 5.7 ha in Italy, 2.3 to 2.8 ha in France (references in ARMITAGE 2000), and 2.1 to 7.2 ha in the Polish Tatra Mountains (GASIENICA BYRCYN 1997). Median home range of the Olympic marmot (*M. olympus*) ranged from 3.59 ha for adult females to 12.06 ha for adult males (GRIFFIN 2007). Home range generally exceeds 2.0 ha and may be as large as 13.0 ha in other marmot species (ARMITAGE 2000).

Why, then, is the home range of yellow-bellied marmots so much smaller than that of other marmot species and considerably smaller than that predicted from body-mass equations? A major factor is the standing crop of available vegetation in the marmot habitat. Data are scarce, but indicate that home range increases as vegetation biomass decreases (ARMITAGE & BLUMSTEIN 2002). Home range of the Upper East River Valley marmots is associated with the highest standing crop of vegetation recorded for marmot habitats (ARMITAGE 2000). This relationship between home range and food resources is supported by the variation in home range of woodchucks (*M. monax*) and alpine marmots (*M. m. latirostris*); woodchucks had smaller home ranges where food resources were greater (ARMITAGE 2003c): and vegetation cover and home range size were significantly correlated ($r = -0.96$) in the alpine marmot (GASIENICA BYRCYN 1997).

I tested the relationship between home range and food resources by examining home range and vegetation biomass in North Pole Basin, Colorado, at an elevation of 3400 m where no adult female was known to wean a litter in successive years (JOHNS & ARMITAGE 1979). I calculated a midsummer standing crop of vegetation of 23.9 g/m^2 from ANDERSEN (1975), which is much less than the 247 to 350 g/m^2 reported in the East River Valley at about 2960 m elevation (KILGORE & ARMITAGE 1978, FRASE & ARMITAGE 1989). Foraging area, which is smaller than home range area, of North Pole Basin adults (0.62 ± 0.055 ha) was significantly larger ($t = 11.4$, $P < 0.001$) than the home range (0.36 ± 0.022 ha) of East River Valley adults. The difference in the two areas is minimal because I compared total home range area of East River Valley marmots with a smaller sub-set of the home range of the North Pole Basin marmots. The precise relationship between home range (foraging area) and the standing crop of vegetation is unknown, but this comparison supports the interpretation that vegetative biomass is a major factor affecting home range area in marmots. I conclude that the relatively small home range of yellow-

bellied marmots is a consequence of their living in or adjacent to meadows with a dense food supply.

In conclusion, home range is significantly affected by food resources, age, colony (habitat), residency, and topography. Although predation may affect where in the home range a marmot forages (ARMITAGE 1982b, 2004b), there is no evidence that predators affect home range size. Marmots may feed selectively (ARMITAGE 1979, 2003d) but it is unknown if this behavior affects home range size. The possible effects of selective feeding and predation on home range area require further study.

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