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Foraging patterns of yellow-bellied marmots: role of kinship and individual variability

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Summary. Two colonies of yellow-bellied marmots (*Marmota flaviventris*) at an elevation of 2900 m in Colorado were studied to elucidate the role of various behavioral and ecological factors as determinants of spatial foraging patterns. The locations of known individuals were periodically recorded. These locality data were plotted as three-dimensional block diagrams, the peak heights representing the frequency of observation. Predation risk and vegetation distribution influenced the location of foraging areas; kinship was an important factor in the determination of the amount of foraging area shared between individual marmots. Spatial overlap tended to be greater among close kin, but this was modified by individual behavioral characteristics, reproductive state, the existence of separate burrow systems within a colony, and the age of the animal. Mothers and juveniles, and litter-mates as young and resident yearlings, had nearly identical foraging areas.

Introduction

A basic assumption of foraging theory is that fitness is enhanced by maximizing the efficiency with which an animal exploits its food resources. Efficiency usually is measured in terms of net rate of energy intake (Schoener 1971). As pointed out by Pyke et al. (1977), detailed knowledge of an animal's biology is necessary to determine how additional factors such as predation, nutritional requirements, or aggressive interactions influence foraging behavior.

An animal's decision regarding where to forage can be affected by an array of possible constraining factors. For example, the distribution of food resources might affect spatial patterns of foraging as animals feed extensively in areas rich in preferred food and spend less time where food is less desirable (e.g. blue geese, Harwood 1974; ungulates, McNaughton 1978). The way in which an animal uses space may be related to the space use patterns of its neighbors. If animals live in close proximity, foraging areas must either be shared or be partitioned as a result of agonistic or avoidance behaviors.

The yellow-bellied marmot is an animal whose spatial patterns of foraging are affected by its burrow-dwelling habit and its membership in a social group. Marmots dig burrows in or near feeding areas (Armitage 1962), but predation risk could limit the distance at which an animal can safely forage. Social interactions could also determine where a marmot feeds. For example, to what degree are foraging areas shared among colony members? What effect does social status, relatedness, or individual behavioral characteristics have on spatial patterns? This paper discusses the role of behavioral and ecological factors as determinants of spatial foraging patterns in these social animals.

Materials and methods

Yellow-bellied marmots (*Marmota flaviventris*) are large, semi-fossorial ground squirrels that are widely distributed in the western United States (Frase and Hoffmann 1980). Marmots in the study area emerge from hibernation in May, sometimes tunneling up through snow, and enter hibernation in September after 4–5 months of activity. Courtship and mating occur in the first two weeks after emergence (Armitage 1965; Nee 1969). Gestation lasts about 30 days and the young remain in the burrow for another 3–4 weeks before emerging. A marmot in

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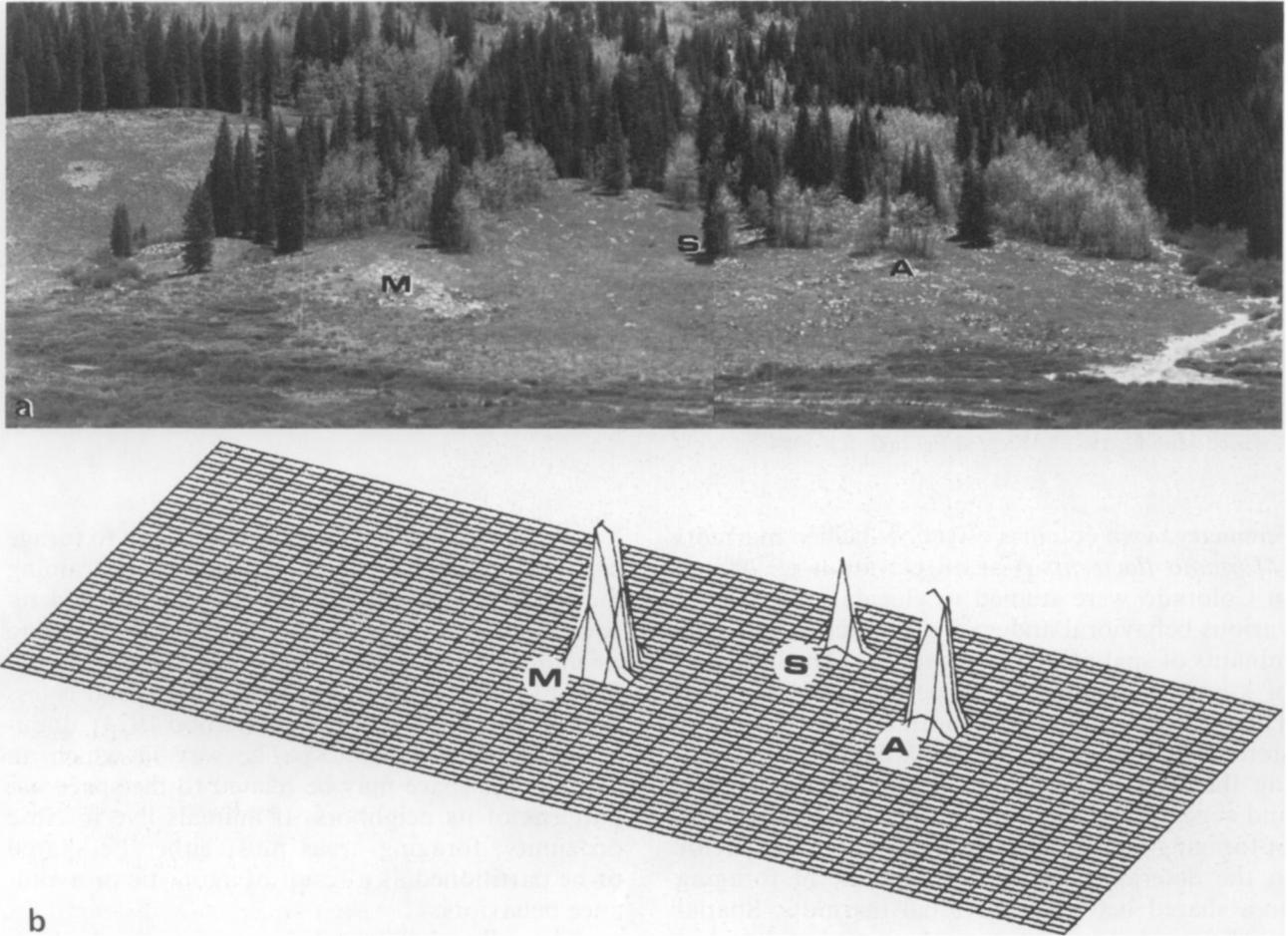


Fig. 1

its first summer is termed a juvenile or young; a yearling marmot is in its second summer and is non-reproductive. All older animals are classified as adults. A typical colony consists of one or more territorial males, each with a harem of one to several females, sometimes yearlings, and young. Marmots may also live as single individuals, pairs, or in a mother-young group (Svendsen 1974). These herbivores eat a wide variety of grasses, flowers, forbs, and seeds (Svendsen 1973; Andersen 1975; Armitage 1979; Frase 1983).

Two colonies of yellow-bellied marmots were studied in the East River Valley, Gunnison County, Colorado at an elevation of 2900 m. Marmot Meadow (locality 4, Armitage 1974) is a meadow bordered by spruce-fir forest and dense willow thickets along the East River (Fig. 1a). The meadow includes several rocky outcrops, two of which contain home burrows. Picnic (locality 5, Armitage 1974) is a multi-harem site consisting of a talus area surrounded by meadow on a steeply angled slope (Fig. 1c). Several home burrows occur in the talus and rocky outcrops. Only animals living at Lower Picnic, the area below the semicircle of spruce and aspen, were included in this study.

Data were taken from 25 June to 3 September 1978; 24 June to 16 September 1979; and 15 June to 3 September 1980. Approximately 500 h of observation were accumulated, more than half of these at Marmot Meadow. Lower Picnic data are from 1979 and 1980 only.

The marmots were live-trapped and permanently identified by numbered ear tags. Additionally each animal was marked

dorsally with black fur dye in a unique pattern of blots or stripes to permit individual identification. (See Armitage 1962 for details on trapping and marking.) Marmots were censused at 10-min-intervals (15 min at Marmot Meadow in 1980 because there were too many animals to census in 10 min) and the position of each marmot recorded from a clear numbered grid overlying a map of the area. Foraging activity also was noted at each census. An individual's home range consisted of all census data; the foraging area comprised census positions at which foraging activity was recorded. Observation hours were concentrated in the morning and late afternoon when marmots are most active (Armitage 1962).

Social interactions were recorded; these behaviors can be classified as cohesive (=amicable, Armitage 1962, 1974) or agonistic. Allogrooming, play, and greetings are cohesive behaviors; agonistic behavior includes chases, fights, and avoidance. All forms of social interaction among marmots are most frequent in early summer (Armitage 1962, 1965, 1973).

A computer program (Surface II, Sampson 1975) plotted the census data as three-dimensional block diagrams, the peak heights representing the frequency of observation in each grid square (e.g. Fig. 2). Plots of home ranges and foraging areas not included in this paper are compiled in Frase (1983). Averaging of peak heights within each plot occurred to some degree. The only situation in which averaging resulted in significant changes in peak heights occurred when the frequency of observations in one grid square was much higher than in the others. The truncated peak was usually at the burrow entrance or a

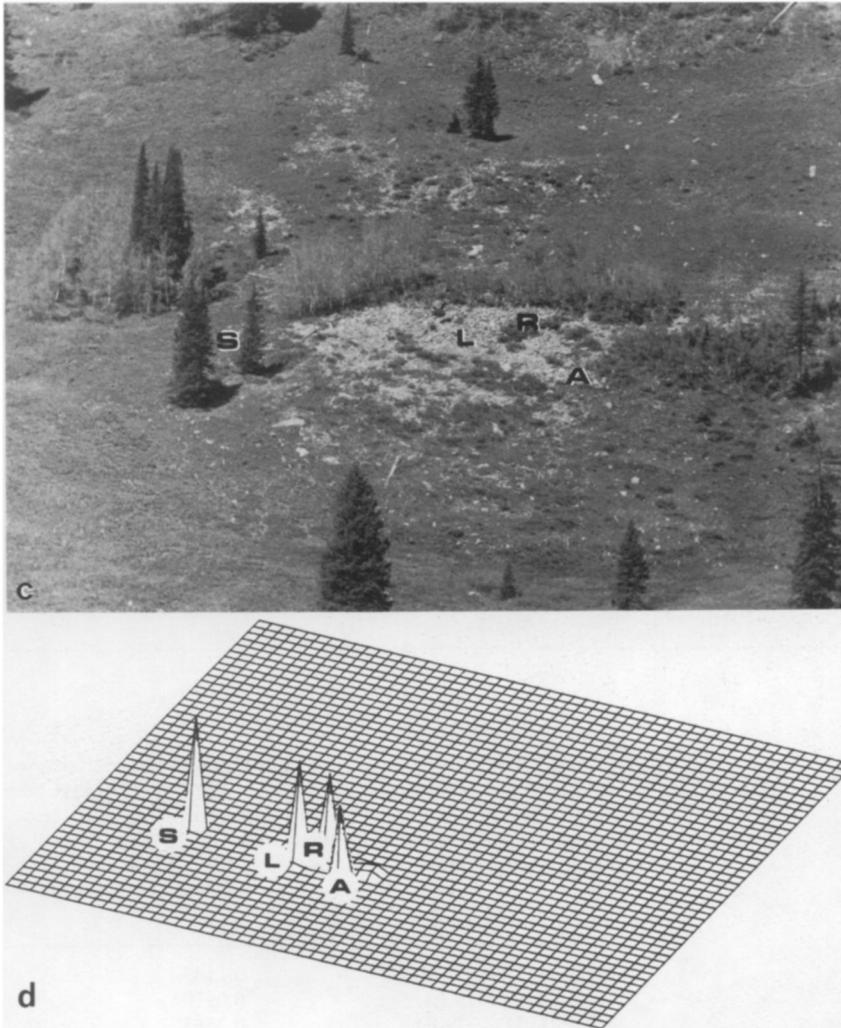


Fig. 1. Photographs (a, c) and computer-generated plots (b, d) of the study sites showing home burrow locations. *M* Main Talus; *A* Aspen Burrow; *S* Spruce Burrow; *L* Slope Burrow; *R* Split Rock. Grid squares at Marmot Meadow are 3 m square, those at Picnic are 9 m (ordinate) by 5 m (abscissa).
a Marmot Meadow from the west;
b Marmot Meadow plot;
c Picnic from the south;
d Picnic plot

heavily used sunning/observation rock, where the observation frequency might be over five times the recorded number of observations at any other point in the study area. On plots representing foraging activity, the shortening of the highest peak was slight since there were no large differences in frequencies of observation among the grid squares. For example, in Fig. 4, the top plot, the maximum observed frequency in a grid square was 9; on the plot, this value was drawn as 7.89.

Results

Social status and foraging area

Males. Adult male marmots are dominant to adult females (Armitage 1975). One male resided at Lower Picnic during the two summers of observation (Table 1). Some of the colony members foraged in areas distinct from one another, but the foraging area of the resident male overlapped the areas in which other residents fed (Fig. 2, Table 2).

No males resided at Marmot Meadow in 1978

and 1979; in 1980, three males lived there for varying lengths of time (Table 1). Dominance relations among these males were complex and changing. Male 372 and ♂374 wrestled and chased each other, were observed to allogroom, and at times lay together at the entrance to Aspen Burrow. Male 519 chased ♂372; no interactions were observed between ♂519 and ♂374.

Male 374 moved into the locality on 16 June. During his first 4 days, he spent roughly equal amounts of time around Main Talus and Aspen Burrow. On 21 June, ♂372 entered the meadow and was immediately chased by ♂374. However, ♂372 established residence at Aspen Burrow and foraged in that vicinity until he left in late July (Fig. 3); the foraging activity of ♂374 was confined to the Main Talus area during this time (Fig. 3). The third male, 519, appeared on 25 June. He first lived at Aspen Burrow, then moved into Main Talus (Fig. 3). During ♂519's stay, ♂374 shared a for-

Table 1. Population structure and home burrow use. Litter size in parentheses. Parentheses enclosing individual marmot numbers indicate a less than 2 week use of the burrow. Burrow locations shown in Fig. 1 a–d. Map distance between Marmot Meadow and Picnic is 0.9 km. Asterisk denotes reproductive female

	Marmot Meadow		Picnic			
	Main Talus	Aspen Burrow	Aspen Burrow	Split Rock	Spruce Burrow	Slope Burrow
1978	2-year-old sisters ♀911* (4) ♀918					
1979	(♀911) ♀918* (3)	(♀110*, died) litter (7) ♀911	♀1194*, 8-year-old half-niece of ♀301 ♀920*, 3-year-old daughter or niece of ♀1194 Combined litters (4)	♀301, 5-year-old ♂125, second year of residency Yearlings offspring of ♀301 or sister		
1980	♀911* ♀918* ♀179*, 2-year-old daughter of ♀911 Combined litters (15) ♂374, adult (♂519, adult)	Yearling orphans (♂372, adult)	♀920* (4)	♀1194	♀301* (6)	♂125

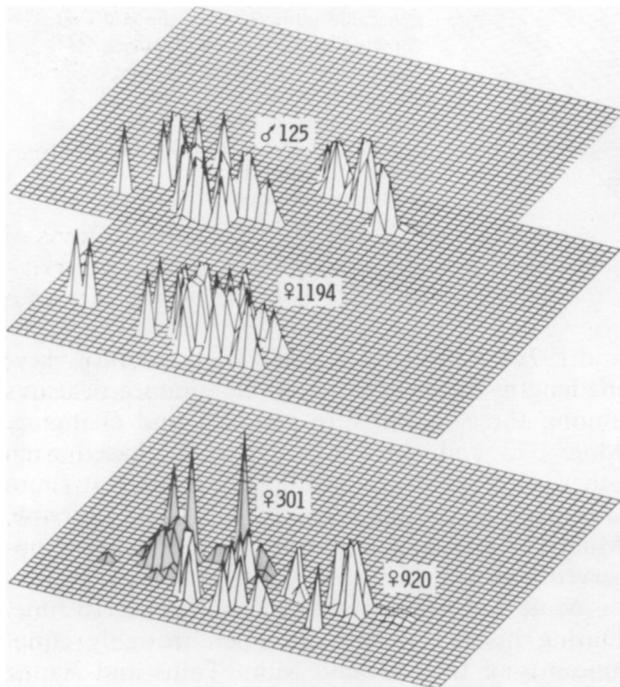


Fig. 2. Foraging areas (home range for ♀301) of adult marmots at Picnic, 1979

aging area around Aspen Burrow with ♂372 (Fig. 3). When ♂519 left Marmot Meadow 25 days later, ♂374 again concentrated his foraging around Main Talus (Fig. 3).

Adult females. Dominant females sometimes spatially displaced other females. In 1978, two sisters

Table 2. Index of similarity between space use patterns of yellow-bellied marmots. $S = 1 - 1/2 \sum_{ij} |\hat{P}^x(i, j) - \hat{P}^y(i, j)|$ where $\hat{P}^x(i, j)$ = the proportion of all foraging records of animal x occurring in the i th, j th grid square. S ranges from 0 to 1. F foraging areas; HR home ranges^a

Patterns under comparison	S
♂125, ♀1194 (1979 F)	0.1143
♂125, ♀920 (1979 F)	0.0910
♀920, ♀1194 (1979 F)	0.2565
♀301, ♀920 (1980 HR)	0.0000
♀301, ♀1194 (1980 HR)	0.0488
yearling, ♀920 (1980 F)	0.1315
yearling, ♀1194 (1980 F)	0.2293
♀911, ♀918 (1978 F)	0.3151
♀911, ♀918 (1980 F)	0.4943

^a $\sum_{ij} |\hat{P}^x(i, j) - \hat{P}^y(i, j)|$ is a measure of the distance between two vectors. The three-dimensionality of the census data is preserved by this formula

living at Main Talus in Marmot Meadow (Table 1) foraged in largely overlapping areas (Fig. 4, Table 2). Although ♀911 was reproductive, no aggressive behaviors were observed between these females. The next year, reproductive ♀918 remained at Main Talus, but non-reproductive ♀911 moved to Aspen Burrow. Female 918 chased ♀911 whenever the latter approached to within a few meters of Main Talus. Female 911 was seen only sporadically after ♀110 moved into Aspen Burrow with her litter in early July (Table 1) and was not ob-

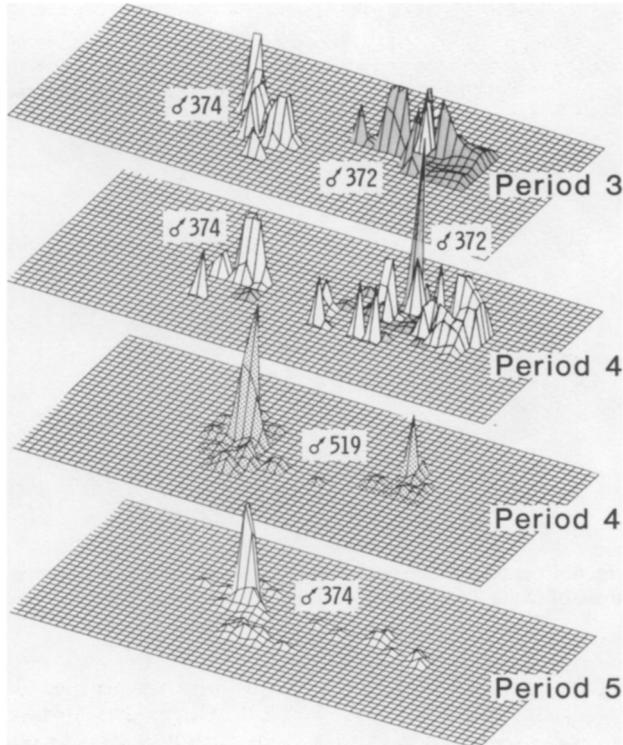


Fig. 3. Foraging areas of three adult males at Marmot Meadow, 1980. Space usage patterns changed during the summer, related to changes in male residency. Period 3: 21 June – 23 June, Period 4: 25 June – 16 July, Period 5: 18 July – 31 August

served anywhere in the meadow after 7 August. Although ♀918 inhabited a larger home range in 1979 than in 1978, her foraging again centered around Main Talus.

In 1980, three females, each with a litter, resided in the meadow (Table 1). Female 918 lived at Main Talus; ♀911 lived at Aspen Burrow until mid-June when she moved with her litter into Main Talus, despite initial agonistic behavior from ♀918. Female 179, the 2-year old daughter of ♀911, lived at Spruce Burrow until early July when she and her litter moved to Main Talus.

All three females and their combined litters lived at Main Talus for the rest of the summer. Adult females shared foraging areas extensively except that ♀179 fed in the northern extension of the meadow during the time she lived at Spruce Burrow (Fig. 4, Table 2).

At Lower Picnic also dominance relationships among females affected space use. In 1979, the foraging ranges of ♀1194 and ♀920 overlapped considerably (Fig. 2, Table 2). Frequent cohesive behaviors were observed between these closely related marmots. The third female at Lower Picnic, non-

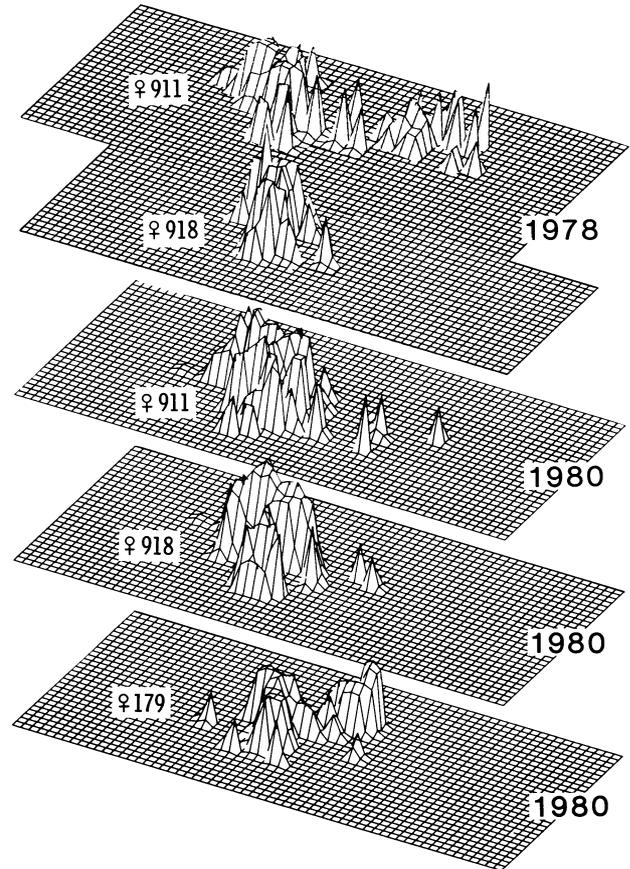


Fig. 4. Foraging area use by adult female marmots at Marmot Meadow

reproductive 301, frequented the upper regions of the slope (Fig. 2); her foraging area did not overlap that of the other females. Rare encounters with the other females resulted in ♀301 being chased.

In 1980, the same three females were present (Table 1). The foraging area of non-reproductive ♀1194 encompassed the entire width of Lower Picnic. Reproductive ♀920 foraged in the same areas as in 1979 and added an area above and to the west of the talus. Female 920 also probably foraged further upslope; frequently she disappeared into the area while foraging, but the tall vegetation there made observations difficult. Female 301 raised a litter at Spruce Burrow and her home range was again disjunct from those of the other females. The burrow itself was not visible from our observation post, and much of her activity occurred in areas not in view. There was no overlap of foraging areas between ♀301 and females 1194 and 920. Although foraging data were sparse for ♀301, the direction of trails leading from Spruce Burrow and occasional records indicate that her foraging was concentrated in the open meadow to the east of her burrow and downslope.

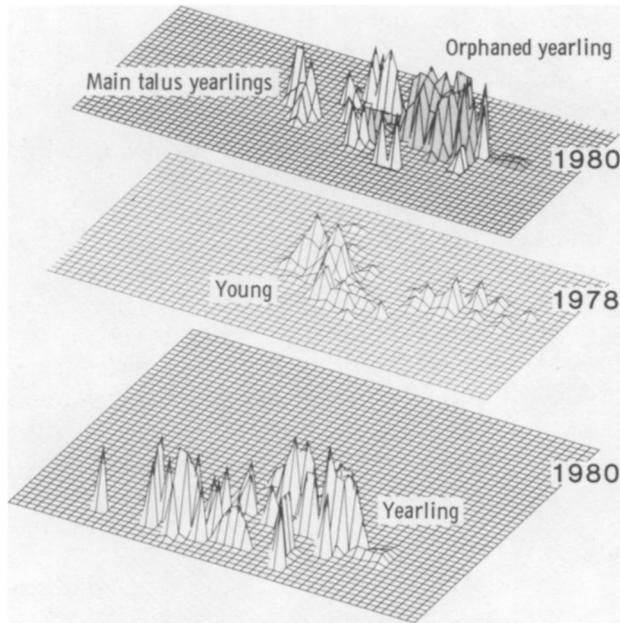


Fig. 5. Space use patterns of yearling and young marmots. *Upper:* Main Talus yearlings combined home ranges and a typical orphaned yearling foraging area at Marmot Meadow; *Middle:* Main Talus young combined foraging areas at Marmot Meadow; *Lower:* typical yearling foraging area at Picnic

Yearlings. Yearling marmots are subordinate to adults, although all social interactions between them are not agonistic (Armitage 1975; Downhower and Armitage 1981). Yearling space-use patterns were affected by the behavior of adults toward them.

In 1979, at Marmot Meadow ♀918 chased her sister's yearlings. Observations of the three yearlings decreased as the summer advanced. By August, yearling appearance was sporadic; one individual was not seen at all in the latter part of the summer. Female 918 was aggressive toward her own yearlings in 1980. They roamed widely (Fig. 5) and disappeared after 25 June. They did not occupy Aspen Burrow perhaps because four orphaned yearlings (Table 1) remained there throughout the year. The Aspen Burrow yearlings foraged in the vicinity of their burrow and to the south (Fig. 5).

In 1979, the Picnic yearlings (Table 1) frequented areas used by ♀301. These yearlings were raised as a common litter by ♀301 and her sister who disappeared in late summer of 1978. Space-use patterns of all three 1980 yearlings were similar; a typical yearling foraging area overlapped those of ♀1194 and ♀920 (Fig. 5, Table 2).

Young. At least one litter of young lived at Marmot Meadow each year of the study. In 1978 and 1979,

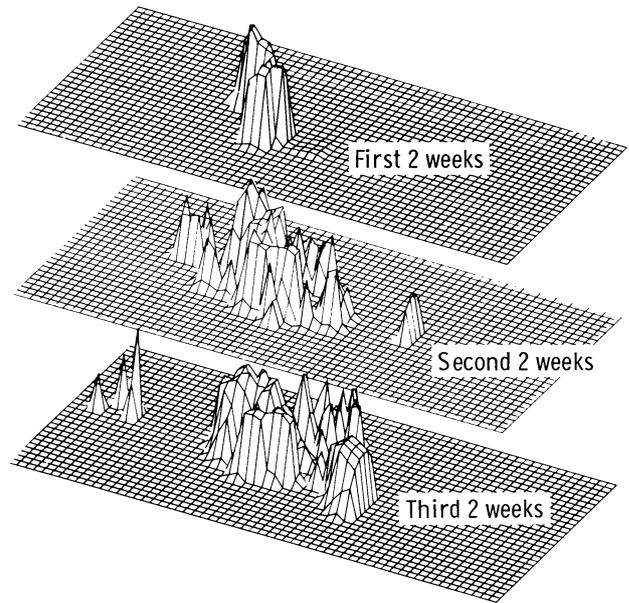


Fig. 6. Post-emergence temporal changes in combined foraging areas of Main Talus young at Marmot Meadow, 1980

the Main Talus young fed in the same area as their mother (e.g. Figs. 4, 5). In 1979, a weaned litter was brought from outside the meadow to Aspen Burrow by ♀110 (Table 1). Four days after their arrival, this adult female was killed. Her orphaned young remained at Aspen Burrow and foraged mostly in the eastern section of the meadow. The areas of most intensive use by this orphaned litter were disjunct from those areas most used by ♀918's litter, although individuals from both litters did feed in the meadow between the two burrow systems. Although ♀918 did visit Aspen Burrow, she did not molest any orphan. No evidence of fostering behavior by ♀911 was observed.

The foraging area of the three litters at Main Talus in 1980 (Table 1) was more extensive than that of any previous litter in this study, and included the meadow above Main Talus and to the north, an area little used in other years (Fig. 6). Foraging was more frequent in that area than our figures indicate. The tall vegetation and uneven topography made it impossible to census every young. The heavy use of these areas was indicated by a newly-created marmot trail leading northward from Main Talus and by the observation of young entering that area only to "disappear" for several censuses and to reappear at some visible point nearby. There were only a few excursions to the Aspen Burrow area.

The four young at Picnic in 1979 fed in much the same areas as their mother. Similarly to the litters occupying separate burrow systems in Marmot Meadow, there was no overlap between the areas frequented by the two Picnic litters in 1980.

Seasonal changes in foraging area

At Marmot Meadow, the newly emerged juveniles stayed close to the burrow site. Subsequently, they gradually enlarged their home range and added to their foraging area. For example, in 1980, during the first 2 weeks after emergence, the young moved only as far as the rocks just west of Main Talus. During the second 2 weeks, they expanded their usage of the meadow considerably. There was little change in their range in the next 2 weeks, except for the addition of a fairly distant foraging area to the north (Fig. 6).

Picnic young did not exhibit quite the same pattern. Due to the topography of the site, foraging is not possible in the immediate vicinity of most home burrows, and thus these young animals had to move to fairly distant points to feed soon after emergence. The areas in which they foraged changed little as the summer progressed.

The emergence of the young had negligible effect on the spatial foraging patterns of other resident marmots. Commonly, there were no material differences between the mothers' foraging areas pre- and post-emergence of a litter, although the post-emergence foraging areas of the mothers appeared to be larger than during pre-emergence in most cases (Frase 1983). This difference, in part, resulted from the greater number of locality records from the usually longer post-emergence interval. Importantly, however, there was no marked shift in space usage that would segregate the feeding areas of a female from her litter. Occasionally, definite, within-summer changes in the space use patterns of a yearling were temporally correlated with young emergence (Frase 1983). Because such spatial changes did not occur universally among the sibship or within one sex, the cause of the changes probably was not emergence of a litter.

Vegetation

The vegetation in Marmot Meadow is characteristic of a *Festuca thurberi* grassland community (Langenheim 1955). Dominant species included the grasses *Bromus richardsonii* and *Stipa lettermani*, cinquefoil (*Potentilla gracilis*), and dandelion (*Taraxacum officinale*) (Kilgore 1972; Frase 1983). The vegetation was distributed fairly uniformly and was of low diversity. Grasses, cinquefoil, and dan-

delion ranked highest in importance value (IV) (Svendsen 1973). Together, these three constituted 88.9% of the summed IV's for Marmot Meadow's herbaceous vegetation.

Choice of foraging areas by marmots at Marmot Meadow probably was not affected by plant distribution to any great degree. In 1980 it was noticed in late summer that the vegetation for several meters around Main Talus was unusually sparse and short. A zone of biodeterioration around a central refuge is not uncommon (Hamilton and Watt 1970), and in this instance was no doubt due to the combined effects of trampling and foraging by 22 marmots, perhaps exacerbated by an exceptionally dry summer. Animals continued to forage around the burrow, but it was at this time that the young began to utilize the area to the northwest (Fig. 6).

Picnic vegetation was more diverse and clumped. Large, showy perennials such as columbine (*Aquilegia caerulea*) and fireweed (*Epilobium angustifolium*) were abundant. Grasses, cinquefoil, columbine and fireweed had the highest IV's, constituting 75% of the summed IV's of the herbaceous vegetation.

At Picnic, marmots were observed to cross the slope to feed in an area particularly rich in a preferred plant species (Frase 1983). Picnic animals occasionally foraged in the talus on ripe raspberries or columbine flowers growing between the rocks.

Predation and foraging

Marmots may forage long distances from their burrow. At Marmot Meadow, the young frequently fed over 40 m from the nearest burrow. Typically, the distance between a foraging marmot and any burrow was less than 20 m. At Picnic, home burrows were in the talus where little foraging was possible. There are upwards of 70 burrows in the colony area (Svendsen 1974); consequently, a marmot usually was not far from a refuge. In most cases, a foraging animal responding to an alarm call by a colony member, runs from the outlying meadow toward its home burrow, or at least to the talus to sit alertly on a rock. If danger were imminent, these animals would take refuge in the closest burrow and not run all the way to the talus.

Discussion

Foraging area and competition for food

Reproduction in female marmots may be food limited to varying degrees (Andersen et al. 1976). For

such animals, food availability is particularly important in the first weeks after emergence from hibernation. For all marmots, sufficient food resources are necessary for adequate fat deposition prior to hibernation. Overwinter survival of young in particular is strongly affected by their ability to gain at least a minimum weight by emergence (Armitage and Downhower 1974; Armitage et al. 1976). If food were a limited resource, marmots should exhibit some form of competitive behavior.

By foraging in a different area from her young, a mother marmot might minimize food competition between herself and her litter. She could forage further from the burrow to allow her offspring adequate forage nearer to safety. However, mothers and young have similar foraging areas and a mother's relative use of near-burrow foraging areas does not decrease after her litter emerges.

A female might attempt to obtain exclusive use of a foraging area (as do some female hoary marmots, Barash 1974) to ensure sufficient forage for herself and her young. Of the nine females with litters observed during this study, only two had exclusive foraging areas. The isolation of ♀301 at Picnic in 1980 was not self-imposed, but resulted from intolerance by the other resident females. By contrast, highly aggressive ♀918 at Marmot Meadow in 1979 shared a foraging area only with her litter and actively excluded other marmots from her home range. In a marmot population consisting of several contiguous harems, exclusive use of forage areas was only 10% for individual animals (Johns and Armitage 1979). All of the above indicate that competition for food is not responsible for the foraging patterns observed in yellow-bellied marmots. Indeed, marmot population density is probably not restricted by food abundance (Kilgore and Armitage 1978); marmots consume only 0.9 to 3.1% of the aboveground primary production in a year. However, because marmots forage selectively (Armitage 1979; Frase 1983), vegetative distribution might affect the spatial foraging patterns.

Vegetational distribution

In an alpine area, the only parts of the basin not within the foraging area of some individual were those in which *Geum rossii*, a plant not utilized by marmots, was abundant (Andersen et al. 1976). Marmots at Lower Picnic foraged more in some parts of their foraging areas, spatially shifting throughout the summer in response to seasonally-changing abundance of patchily distributed preferred plants. Plant distribution and marmot selec-

tivity, can influence spatial foraging patterns, although these factors are not the major determinants of where an individual feeds. Vegetation patterns may restrict foraging to within certain areas, but because marmots do not forage in all vegetationally suitable places, other factors must be responsible for an individual's spatial foraging pattern.

Location of refugia

The intensity of predation on a forager may affect the distance it can travel from a refugium (Covich 1976). Predation on marmots seldom has been observed (Frase and Hoffmann 1980; Armitage 1982) and there is no good measure of the strength of predation pressure as a selecting factor. Foraging does tend to occur in areas close to a home burrow (e.g. Marmot Meadow) or another refuge burrow; other factors being equal, predation risk probably precludes foraging further afield.

Space sharing and kin selection

Marmot colonies may be largely occupied by matriarchal lineages of females (Schwartz and Armitage 1980). Thus, some harem-mates are closely related. In an alpine population of yellow-bellied marmots, a higher rate of cohesive behavior was observed among closely related animals than among relatively unrelated individuals (Johns and Armitage 1979). Most marmots do not maintain exclusive use of either foraging areas or burrow (Armitage 1965, 1975; Johns and Armitage 1979, this study), but knowing the degree of relatedness between individuals might allow us to predict with whom these resources are most likely to be shared.

All young born to colony residents remain with their mother at least through the first winter; many disperse the following year (Armitage and Downhower 1974). A female and her litter occupy the same burrow which may be shared with other marmots. In Olympic (*M. olympus*) and hoary (*M. caligata*) marmots, a parous female and her litter maintain exclusive use of a burrow; other adults and yearlings may live together (Barash 1973, 1974). Burrows are not shared among adult European marmots, *M. marmota* (Barash 1976).

In yellow-bellied marmots, mothers and young have similar home ranges as expected. Kinship, however, is only a partial predictor of the amount of space sharing among other individuals, although closely related adults did share space.

Aggressiveness may increase in reproductive female marmots (*M. flaviventris*, Armitage 1962, 1965; Downhower 1968; *M. monax*, Bronson

1964; *M. caligata*, Barash 1974), and this heightened aggressiveness may explain ♀918's intolerance of her non-reproductive sister. Her intolerance was not due to a lack of adequate resources at Main Talus to support herself, her litter and her sister, since in other years, two or three adults and three to fifteen young lived at Main Talus without conflict (Table 1). Female 918's failure to exclude her sister and her niece in 1980 may be due to the increased aggressiveness of these now reproductive females. The agonistic encounters between ♀918 and the dominant adult males that appeared may have reduced ♀918's general level of aggressiveness at the time the other two females with litters were attempting to move into the better burrow system. (It appears that the Main Talus burrow system is superior to the Aspen Burrow system. In 19 years of observation at this site, when only one of the two areas was inhabited, it was always Main Talus, and in other years, yearlings or subordinate adults lived at Aspen Burrow.) On the other hand, ♀1194 and ♀920 shared space at Picnic regardless of their respective reproductive conditions. However, even when reproductive, ♀301 did not attempt to move into a burrow occupied by another female; her use of space did not overlap with the other females, whether she had a litter or not. She was more distantly related to ♀1194 and ♀920 than the latter two were to each other (Table 1) and she had shared a burrow with her sister prior to 1979.

Patterns of space use might affect the amount of aggression among marmots in such a way that proximity rather than relatedness becomes an important determinant of which animals coexist in a colony. For example, ♀918 may have tolerated the orphans but not her own yearlings because the former lived at Aspen Burrow while the latter did not have any similarly distant burrow system to occupy. Aspen Burrow could serve as a "refuge" for individual marmots not tolerated by Main Talus residents. In 1979, ♀911 was chased by ♀918 only when ♀911 approached Main Talus closely; she was not harassed in the vicinity of Aspen Burrow. At Picnic, the relative infrequency of agonism between ♀301 and females 1194 and 920 probably resulted from their spatial separation.

Kinship, then, is one factor in the determination of the amount of foraging area overlap between individuals. In a large alpine population of marmots, exclusive use of foraging areas among burrow groups (on the average closely related to each other) was 41%; exclusive use increased to 88% if all harem members (degree of relatedness much less than among burrowmates) were consid-

ered (Johns and Armitage 1979). In this study, space sharing among close kin was modified by individual behavioral differences and the existence of separate burrow systems within a colony site. The only consistent patterns were forage area sharing between a mother and her young and the nearly identical patterns of space usage within a litter, as young or as resident yearlings.

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References

- Andersen DC (1975) Socio-ecology of *Marmota*. Reproductive strategies of female yellow-bellied marmots (*M. flaviventris*). Master's thesis, University of Kansas, Lawrence
- Andersen DC, Armitage KB, Hoffmann RS (1976) Socioecology of marmots: female reproductive strategies. *Ecology* 57:552-560
- Armitage KB (1962) Social behaviour of a colony of the yellow-bellied marmot (*Marmota flaviventris*). *Anim Behav* 10:319-331
- Armitage KB (1965) Vernal behaviour of the yellow-bellied marmot (*Marmota flaviventris*). *Anim Behav* 13:59-68
- Armitage KB (1973) Population changes and social behavior following colonization by the yellow-bellied marmot. *J Mammal* 54:842-854
- Armitage KB (1974) Male behaviour and territoriality in the yellow-bellied marmot. *J Zool (Lond)* 172:233-265
- Armitage KB (1975) Social behavior and population dynamics of marmots. *Oikos* 26:341-354
- Armitage KB (1979) Food selectivity by yellow-bellied marmots. *J Mammal* 60:628-629
- Armitage KB (1982) Marmot and coyote: behavior of prey and predator. *J Mammal* 63:503-505
- Armitage KB, Downhower JF (1974) Demography of yellow-bellied marmot populations. *Ecology* 55:1233-1245
- Armitage KB, Downhower JF, Svendsen GE (1976) Seasonal changes in weights of marmots. *Am Midl Nat* 96:36-51
- Barash DP (1973) The social biology of the Olympic marmot. *Anim Behav Monogr* 6:171-245
- Barash DP (1974) The social behavior of the hoary marmot (*Marmota caligata*). *Anim Behav* 22:256-261
- Barash DP (1976) Social behavior and individual differences in free-living alpine marmots (*Marmota marmota*). *Anim Behav* 24:27-35
- Bronson FH (1964) Agonistic behaviour in woodchucks. *Anim Behav* 12:470-478
- Covich AP (1976) Analyzing shapes of foraging areas: some ecological and economic theories. *Annu Rev Ecol Syst* 7:235-257

- Downhower JF (1968) Factors affecting the dispersal of yearling yellow-bellied marmots. PhD dissertation, University of Kansas, Lawrence
- Downhower JF, Armitage KB (1981) Dispersal of yearling yellow-bellied marmots (*Marmota flaviventris*). *Anim Behav* 29:1064–1069
- Frase BA (1983) Spatial foraging patterns and diet selectivity in the social yellow-bellied marmot. PhD dissertation, University of Kansas, Lawrence
- Frase BA, Hoffmann RS (1980) *Marmota flaviventris*. *Mammal Spec* 135:1–8
- Hamilton WJ III, Watt KEF (1970) Refuging. *Annu Rev Ecol Syst* 1:263–286
- Harwood J (1974) Grazing strategies of blue geese *Anser caerulescens*. PhD dissertation, University of Western Ontario, London
- Johns DW, Armitage KB (1979) Behavioral ecology of alpine yellow-bellied marmots. *Behav Ecol Sociobiol* 5:133–157
- Kilgore DL jr (1972) Energy dynamics of the yellow-bellied marmot (*Marmota flaviventris*): a hibernator. PhD dissertation, University of Kansas, Lawrence
- Kilgore DL jr, Armitage KB (1978) Energetics of yellow-bellied marmot populations. *Ecology* 59:78–88
- Langenheim JH (1955) Flora of the Crested Butte Quadrangle, Colorado. *Madroño* 13:64–78
- McNaughton SJ (1978) Serengeti ungulates: feeding selectivity influences the effectiveness of plant defense guilds. *Science* 199:806–807
- Nee JA (1969) Reproduction in a population of yellow-bellied marmots (*Marmota flaviventris*). *J Mammal* 50:756–765
- Pyke GH, Pulliam HR, Charnov EL (1977) Optimal foraging: a selective review of theory and tests. *Q Rev Biol* 52:137–154
- Sampson RJ (1975) Surface II graphics system. Kansas Geological Survey, Lawrence, pp 1–240
- Schoener TW (1971) Theory of feeding strategies. *Annu Rev Ecol Syst* 2:369–404
- Schwartz OA, Armitage KB (1980) Genetic variation in social mammals: the marmot model. *Science* 207:665–667
- Svendsen GE (1973) Behavioral and environmental factors in the spatial distribution and population dynamics of a yellow-bellied marmot population. PhD dissertation, University of Kansas, Lawrence
- Svendsen GE (1974) Behavioral and environmental factors in the spatial distribution and population dynamics of a yellow-bellied marmot population. *Ecology* 55:760–771