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HOME-RANGE SIZE AND EXPLORATORY EXCURSIONS OF ADULT, MALE YELLOW-BELLIED MARMOTS

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Home-range sizes of adult, male yellow-bellied marmots (*Marmota flaviventris*) were estimated from radiotelemetry, trapping, and visual observation. Home ranges were monitored from early May to late August in 1989, 1990, and 1991. Home-range size varied greatly among males (range, 0.06–47.51 ha). Median home-range size for all males was 1.02 ha, larger than previous estimates for the species. Distribution of females and localized fluctuations in density of males influenced home-range size of males. Home-range size was not related to number of females defended or to body mass of males. Several males made excursions from their home ranges, perhaps to locate additional mates. These results indicate that male marmots behaviorally respond to the density and distribution of females.

Key words: *Marmota flaviventris*, home-range size, exploratory excursions

Home-range size and quality commonly vary within species. The size and quality of the habitat patch in which an animal lives can profoundly influence its survival and reproduction relative to conspecifics (Hixon, 1987; Whitham, 1980). Because home-range size can affect fitness, much work has been done to quantify variation in home-range size among and within species (Grant et al., 1992; Harestad and Bunnell, 1979; Mace et al., 1983). As a result, several factors surfaced as possible determinants of home-range size.

In species where one or both sexes maintain exclusive home ranges or territories, the size of an individual's home range may depend upon the number of conspecifics with adjacent home ranges who are also competing for space and resources (Brown, 1969; Schoener and Schoener, 1982). If critical resources are limited or patchily distributed within a habitat, individual variation in home-range size may reflect attempts to sequester these resources (Broughton and Dickman, 1991; Mares and Lacher, 1987; McNair, 1987). Because energy requirements of animals are positively

related to body mass (Kleiber, 1961; McNab, 1963), home-range size may vary as a consequence of body-size variation. Individuals of large mass may have home ranges larger than those of smaller individuals in order to acquire the resources required by their higher energy demands (Harestad and Bunnell, 1979; McNab, 1963). In species that mate polygynously, the number of females with whom a male associates may greatly affect his mating success and, ultimately, his reproductive success (Clutton-Brock, 1988; Emlen and Oring, 1977; Greenwood, 1980). Hence, the number and distribution of females within the habitat may strongly influence home-range size for males. Home-range size and patterns of movement for males may vary within years and among years as males attempt to include more females within their home ranges.

Yellow-bellied marmots (*Marmota flaviventris*) are large-bodied, group-living, ground-dwelling squirrels. Marmots are polygynous, and males defend females in home ranges or territories exclusive of other adult males (Armitage, 1974, 1986; Bar-

ash, 1989). Home-range size of male marmots was examined using trapping and visual observation methods, and it varied greatly (Armitage, 1974). Armitage (1974) suggested that variation in home-range size for males is due in part to density and vigor of males and chance. The focus of the present study was to examine further the home-range sizes of males and how they may be influenced by density and body mass of males, resource abundance, and density and distribution of females. Additionally, radiotelemetry was used to produce estimates of home-range size for males possibly less biased than those generated through trapping and direct observation.

MATERIALS AND METHODS

The study area was located in the upper East River Valley of Gunnison Co., Colorado (38°56'–38°59'N, 106°58'–107°01'W; elev. 2,800–3,660 m). The vegetation of the upper East River Valley consisted of subalpine and alpine meadows interspersed with large aspen stands and coniferous forest. Subpopulations of marmots were distributed nonrandomly throughout the valley in open meadow areas that contained rocks for refugia and herbaceous vegetation for food (Armitage, 1986; Svendsen, 1974). The density of marmots within meadow habitat was partially dependent on the size of the meadow and the abundance of sites suitable for burrows (Svendsen, 1974). Large meadows often supported aggregations or colonies of marmots that consisted of one or two adult males (colonial males), two or more adult females, yearlings, and young-of-the-year. Smaller meadows generally supported fewer marmots, usually a single adult male, an adult female, few yearlings, and young-of-the-year. Marmots residing in colonial sites previously described by Armitage (1974) and smaller sites throughout the valley were observed in the present study.

Populations of marmots in the East River Valley have been the focus of extensive research since 1962 (reviewed by Armitage, 1991). Nearly all marmots in the study area were trapped annually throughout the active season that began in early May and extended into late September. Trapped individuals were examined to determine gender, weighed, ear-tagged, and dye-marked for

regular focal observations (see Armitage, 1962, 1974, for a more detailed description of trapping and handling techniques). Maternity, place of birth, and age were known for nearly all individuals born in the study area, as young were trapped soon after emergence from the natal burrow and detailed maternal pedigrees were maintained since 1962 (Armitage, 1984).

Most adult, male marmots (≥ 2 years of age) within the study area were equipped with radiotransmitters for the years 1985–1991. Radiotransmitters with a range of ca. 5 km were surgically inserted into the abdominal cavity (Van Vuren, 1989). Each male received a transmitter with a unique frequency for individual identification. The radiotransmitters had a battery life of ca. 27 months. Transmitters that failed prematurely were replaced whenever possible. Males equipped with radiotransmitters were located at least once daily throughout the active season when weather and other circumstances allowed. Radiolocations were obtained by triangulation and refined by moving toward areas of maximal signal strength. Locations of marmots were noted during periods of peak, above-ground activity (between 0700 and 1030 h and 1500 and 1900 h), and consecutive radiolocations for each individual male were made haphazardly throughout the daily activity periods due to the variable influences of laboratory work, weather, ease of location of individual males, and other factors. Locations of males in open or more easily accessible sites also were obtained by visual observation and routine trapping. Locations for males equipped with radiotransmitters during the active seasons of 1989, 1990, and 1991 are the focus of the study.

Locations for each focal male were plotted separately on topographic maps. Locations visited more than once by an individual were considered part of that individual's home range. Thus, one-time excursions were not used to estimate the size of a male's home range. The length or the long-axis distance of each male's home range was represented by the distance between the two most distant locations within the home range. The width or short-axis distance of each male's home range was represented by the sum of the two most distant locations, one on each side of the long axis, that connected, perpendicularly, to the long axis. Preliminary examination of the location data indicated that home ranges of males generally were elongate

and ovate in shape. Therefore, home-range size was estimated by the area (hectares) of the ellipse generated by the long and short axes. All distances were calculated by determining both the horizontal and elevational distances between two locations and using the Pythagorean theorem to solve for the hypotenuse. Thus, all distances accounted for changes in elevation.

Home-range size and movement patterns throughout the active season were compared for individual males for whom data were collected in consecutive years. The percent change in home-range size from year to year was calculated for each male as:

$$\frac{\text{new home-range size} - \text{old home-range size}}{\text{old home-range size}} \times 100.$$

Body mass for each individual male was represented by the average of the mass measurements obtained in June. Measures obtained in June are assumed to more clearly represent body size as males had not yet gained mass for hibernation (Kilgore and Armitage, 1978). A Spearman's rank correlation analysis was used to determine the relationship between mean body mass and home-range size for individual males.

Routine radiolocations of males revealed that many males made excursions from their home range throughout the active season. The distances of the excursions were measured as the distance between the final destination and the nearest location within the home range. Excursions were categorized as short ($\leq 1,000$ m from the home range) or long ($> 1,000$ m from the home range). Because excursions may reflect an effort by adult males to seek additional mates, the tendency of males to make short excursions was compared to the number of adult females they routinely associated with in their home range. Males were placed in one of two groups: males with no more than two adult females within their home range; males with at least three adult females within their home range. The number of males that did and did not make excursions were compared between groups using a chi-square test of independence.

We calculated mean and median elliptical home-range sizes for each year of the study and for all years combined. Estimates of home-range size during all three active seasons were regressed against the number of adult females

within a male's home range. Because home-range size for males may be a function of not only the number but also the dispersion of females within a male's home range, the relationship between female dispersion and home-range size for males was examined. The maximum dispersion of adult females within a male's home range was estimated by calculating the distance between the burrow areas occupied by the two most distant females. The relationship between size of a male's home range and the dispersion of females within a male's home range, estimated by maximum-interfemale distance, was examined by Spearman's rank correlation analysis. Non-parametric analyses were used whenever the variables were not assumed to be measured without error and the data were extremely variable. Long-axis distance was used as an estimate of home-range size for males in the analysis with maximum-interfemale distance to determine if the elongate shape of male home ranges is related to female dispersion. Males associating with one female were assigned a maximum-interfemale distance of zero and males with no females were omitted from this analysis.

A defensibility index, which incorporates both the number and dispersion of females, was calculated for each male's home range by multiplying the maximum-interfemale distance by the number of adult females within the home range. A greater number of females to defend from competing males and a greater distance over which the females are dispersed within a male's home range resulted in a higher defensibility index. A Spearman's rank correlation analysis was performed to examine the relationship between home-range size for males and the defensibility index. When only one female was present within a male's home range, a defensibility index of zero was assigned. Males without females in their home ranges were omitted from this analysis.

Due to the high frequency of disappearance of males from year to year, many of the focal males in this study were those that immigrated into the study area from other unstudied subpopulations in the valley. Thus, most focal males in this study were of unknown age, and the relationship between home-range size and age of males could not be determined.

Despite high mortality of males and immigration into the East River population, six males were resident for consecutive years. As a result,

TABLE 1.—Home-range size of adult male yellow-bellied marmots. Males that made long excursions are indicated with an asterisk. Number of fixes for each home-range estimate are given in parentheses. Colonial males are designated by C.

Tag no. of male	Home-range size (ha)			No. of females		
	1989	1990	1991	1989	1990	1991
91 C	0.39 (82)	1.65 (78)	1.34 (81)	6	6	7
122	2.28 (34)			2		
156 C	0.31 (19)			4		
227	0.06* (14)	1.29* (27)	1.15 (21)	1	2	0
276	47.51 (97)			1		
277	1.41* (51)			1		
287	26.86 (88)			3		
308	2.19 (45)			3		
408 C	0.35 (20)			6		
415	0.31 (44)	1.26 (41)		2	3	
429	0.50 (36)			1		
671 C	0.13 (76)			6		
945 C	0.34 (67)			5		
206		0.13* (37)			2	
654 C		0.12 (30)			3	
778		0.37 (45)	0.74 (39)		1	1
901		1.02 (59)			2	
913		10.68* (33)	2.47* (56)		3	3
1510		0.31 (20)			2	
1260		8.48 (17)	8.60 (45)		0	3
829			2.85 (50)			5
838 C			0.09 (52)			1
1608			0.16* (31)			0
582			4.52 (38)			0
1622			0.57* (19)			1
507 C			1.27 (52)			2
581 C			0.69 (30)			2

ca. 25% of the data in each analysis were collected from multiply sampled individuals. Independence among observations is an assumption of all statistical analyses; however, the omission of non-independent data would further decrease already small samples. Statistical results in this study must be interpreted with caution. Unless otherwise noted, the data in this study were assumed to consist of independent measures.

RESULTS

Home-range size and movement patterns were monitored for 13 males in 1989, 10 males in 1990, and 12 males in 1991 (Table 1). Two males were monitored during each year of the study, and four males were monitored for 2 consecutive years of the study; thus, the 35 home ranges determined were distributed among 27 unique individuals

(Table 1). An average of 45.0 ($SD = 22.1$) fixes/male were made, and ca. 4.3 distinct, routinely visited locations were used to delineate the home range of each male. The low number of distinct locations used to define a male's home range suggests that the data are highly autocorrelated. Autocorrelation among locations was not considered to influence the validity of the home-range estimates in this study as the estimates were calculated non-statistically (Swihart and Slade, 1985a, 1985b). Home-range size was positively related to the number of fixes made ($b = 0.20$, $r = 0.15$, $n = 35$, $P = 0.003$); however, this relationship did not appear to account for changes in home-range size of males observed in consecutive years (Table 1). Home-range size for males

TABLE 2.—Mean and median home-range size (ha) of adult male yellow-bellied marmots.

Year (<i>n</i>)	$\bar{X} \pm 1 SD$	Median
1989 (13)	6.36 \pm 14.34	0.39
1990 (10)	2.53 \pm 3.79	1.14
1991 (12)	2.04 \pm 2.43	1.21
Combined (35)	3.78 \pm 9.07	1.02

varied an average of 360% between years. The year-to-year variation was pronounced among and within individuals. For example, the home-range size of male 91 increased 320% between 1989 and 1990 and decreased 20% between 1990 and 1991 (Table 1).

Mean home-range size for all males was 3.78 ha (Table 2). Males in 1989 had the smallest median home-range size while their mean home-range size was about twice that of males in 1990 and 1991 (Table 1). The mean for 1989 was greatly influenced by the large home ranges of two individuals. Large standard deviations (Table 2) indicate that home-range size varied greatly among individuals and that mean estimates may not be representative of the home-range sizes of most males in the study. Median estimates, which are influenced little by extreme values, may better describe the general home-range size of male marmots in the current study (Table 2).

When data from all years were combined, adult males were trapped and weighed, on average, 4.35 times ($SD \pm 3.12$) throughout an active season. Home-range size was not significantly correlated to mean body mass in June when data from all seasons were combined ($r_s = 0.21$, $n = 28$, $P > 0.05$).

Home-range size for males was not strongly related to the number of adult females within a male's home range ($b = -1.21$, $r = 0.089$, $n = 35$, $P = 0.598$; Table 1). Home-range size for males, as estimated by long-axis distance, was significantly correlated to the maximum distance between females within a male's home range ($r_s =$

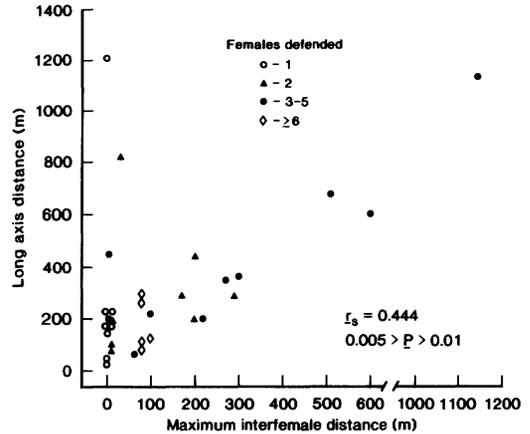


FIG. 1.—Relationship between home-range size of male yellow-bellied marmots and the dispersion of females within a male's home range. Home-range size for males is estimated by long-axis distance. Female dispersion is estimated by maximum-interfemale distance.

0.44, $n = 31$, $0.05 > P > 0.01$; Fig. 1). While home-range size increased with an increase in maximum-interfemale distance, some males with a few, closely spaced females had large long-axis distances, and data for these males greatly reduced the strength of the correlation (Fig. 1). Home-range size for males was significantly correlated to the defensibility index ($r_s = 0.37$, $n = 31$, $0.05 > P > 0.01$), but the relationship was not as strong as that between home-range size and maximum-interfemale distance. This result is understandable as the defensibility index incorporates not only interfemale distance but also number of females, which alone was not related to home-range size.

Because of transmitter failure and loss of males, only 26 of the 35 home ranges were routinely monitored throughout the active seasons. Frequent radiolocations indicated that, for 18 of the 26 cases of monitoring through the season, males made one ($n = 9$) or two ($n = 9$) short excursions ($\leq 1,000$ m) from their home ranges. Males made short excursions throughout the active season, with 70% occurring in May and June. All short excursions were made after the

snow melt and nearly all occurred well after the breeding season. The occurrence of short excursions was statistically independent of the number of females within a male's home range ($\chi^2 = 0.11$, *d.f.* = 1, $0.9 > P > 0.5$).

Six males made long excursions (>1,000 m) from their home ranges; two males did so in different years. The longest excursion was ca. 4,270 m. Long excursions were made during middle to late July and August. Males making long excursions were all of unknown age and origin as they entered the study area from unstudied subpopulations. One-half of the time, males that made long excursions returned to the home range from which they moved prior to hibernation the same year or at the start of the following active season. The remainder of the time, males did not return to the home ranges they deserted, and their fates were unknown. All males located after long excursions had moved to areas that contained several other marmots. All but two long excursions were made by males associating with two or fewer adult females in their home range. In 2 consecutive years, however, one male, who associated with three widely dispersed females, made long excursions to the same location ca. 1,500 m away. The number of females within a male's home range did not significantly influence the tendency of adult males to make long excursions ($\chi^2 = 0.89$, *d.f.* = 1, $0.5 > P > 0.3$), however. Males that made long excursions were not more likely to have made short excursions earlier in the active season than those males that did not make long excursions ($\chi^2 = 1.81$, *d.f.* = 1, $0.2 > P > 0.1$).

DISCUSSION

Mean home-range size for males in this study (Table 1) was significantly larger than previous estimates for yellow-bellied marmots ($\bar{X} = 0.67$ ha—Armitage, 1974). The median estimate generated in this study, however, was similar to the mean estimate observed by Armitage (1974). The discrep-

ancy between the mean estimates may be due to the different methods used to estimate home-range size and the different males observed. Armitage (1974) primarily observed males living at colonial sites and did not include males defending isolated, widely-spaced females. Colonial males in this study had home ranges comparable in size (range, 0.09–1.65 ha; Table 1) to those observed by Armitage (1974—range, 0.35–1.90 ha).

The density and distribution of females within the habitat may strongly influence home-range size. Reproductive success of male marmots is positively correlated with the number of females defended (Armitage, 1986, 1991). A strategy of male marmots may be to increase home-range size to include as many females as can be economically defended (Armitage, 1986). Home-range size for males, however, was not positively related to the number of females defended. In fact, males that associated with two or three solitary females had some of the largest home-range sizes (Fig. 1). The absence of a positive relationship is likely due to the uneven density of females throughout the habitat; females reside in meadows at densities appropriate to the abundance and suitability of burrow systems (Armitage, 1986; Svendsen, 1974). Also, the home-range sizes of males that defended no females were extremely variable.

The relationship between the linear size of a male's home range and the maximum distance between defended females is understandable given that most males routinely patrol their home ranges, presumably to visit their females and to ward off males competing for access to their females (Armitage, 1974; Van Vuren, 1990). With the exception of occasional excursions, the relationship between home-range size for males and maximum-interfemale distance indicates that many males do not move routinely through areas of the habitat known to be empty of adult females. Males may minimize movements beyond those necessary

to defend females because movement increases vulnerability to predation (Van Vuren, 1990). Some males had home ranges larger than those predicted by the maximum-interfemale distance. Those males routinely visited nearby vacant habitats perhaps to gain knowledge of potential male competitors or female mates that may settle there.

Contrary to other rodent species that display an inverse relationship between population density and home-range size of males (heteromyid rodents—Maza et al., 1973; *Peromyscus californicus*—Ribble and Salvioni, 1990; *P. leucopus* and *P. maniculatus*—Wolff, 1985), population density is not a likely factor influencing home-range size of males in this study. Population density of males fluctuated little during the course of this study; all suitable sites generally were occupied each season by adult males. Local fluctuations in density of males, however, may account for a portion of the year-to-year variation in individual home-range size. In the absence of competing males, males might expand their home-range size, or males might decrease their home-range size, as there is little need to defend or patrol surrounding areas (Armitage, 1974). Generally, the home-range size of males in this study was inversely related to local density of males. However, changes in local density of males did not account for the year-to-year increases in home-range size for those males isolated from other males.

Neither resource abundance nor body-mass differences among males were factors contributing to the variation in home-range size of males. Suitable burrow sites are the primary limiting resource for marmots in this population (Armitage, 1988; Svendsen, 1974). Burrow abundance and dispersion likely only indirectly influence home-range size of males because it is in these burrow areas that females reside. Male marmots of large body mass were not more prone to defend large home ranges than were smaller males. Apparently, males of varying body

mass met their energy needs in even the smallest home ranges.

Monitoring the locations of male marmots revealed that many individuals make exploratory excursions from their home ranges. Short excursions were common among males, but no individuals made more than two short excursions within a single active season. One possible explanation for the rarity of multiple short excursions by individuals within a season is that traveling outside a familiar area is risky. If so, males should make excursions when the benefits gained outweigh the associated costs of high predation risk. A benefit of moving may be increased reproductive success as males encounter additional females. The value of making excursions is likely greater for males that associate with few or no females. The prediction that males defending few females are more likely to risk the costs of excursions was not supported, however. Either the benefit of finding additional mates consistently outweighed the risks of moving, or males made short excursions for reasons other than location of mates. For some males, short excursions were an effective strategy to locate potential mates; 50% of the time, males encountered additional females, and, the remainder of the time, it is not known whether females were encountered. Many males that made short excursions also obtained information regarding nearby male competitors; the majority of females encountered were resident in another male's home range.

Long excursions were peculiar not only in their rarity but also because they were made by adult males with established home ranges containing reproductive females. Factors motivating males to make such moves were not clearly evident from the results of this study. Despite the inconclusive nature of the data, a few possible explanations for the occurrence of long excursions can be eliminated. It is unlikely that males made long excursions to avoid inbreeding or intense competition for resources or

mates. Some males that made long excursions returned to their abandoned home ranges, and no males originated from subpopulations within the study area and, therefore, were not likely to be closely related to the females deserted. Also, there was no indication that resources, either food (Kilgore and Armitage, 1978) or burrows (Andersen et al., 1976), were limited in the habitats deserted by males making long excursions. Finally, with the exception of one male, males that made long excursions had isolated home ranges and made no observable contact with other adult males prior to moving. Additional observation of long excursions by males is necessary to assess the possible relationship between the number of females defended and the frequency of excursions.

In conclusion, the home-range sizes of adult male marmots vary greatly and are unlikely to be influenced by a single factor. The local density of males within a habitat patch may account for some of the variation in home-range size among males. The dispersion of females within a habitat patch most profoundly influences home-range size of males. The influence of female dispersion agrees with previous findings that mating success and, ultimately, reproductive success for males are highly dependent on the number and distribution of females within the habitat. Finally, behavioral phenotypes of individuals vary greatly among marmots (Svendsen and Armitage, 1973) and also should be considered as possible factors influencing variation in home-range size of males.

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