ECOLOGY AND SOCIAL BEHAVIOR OF GOLDEN MARMOTS (*MARMOTA CAUDATA AUREA*)

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We studied golden marmots (*Marmota caudata aurea*), a little-studied, hibernating Eurasian sciurid, for 6 years at Dhee Sar, Pakistan, to evaluate their social behavior in light of existing thoughts about social evolution of marmots. Golden marmots most commonly were found in apparently monogamous associations (37/89 social groups consisted of one adult male and one adult female) but lived in larger groups containing up to seven adults, where group members shared a common home range and burrow system. When multiple adults lived together, contrary to the typical sciurid pattern, they lived in male-biased social groups. When multiple adult females shared a home range, only a single female in a given group lactated and weaned young. Reproduction was infrequent; >80% of social groups failed to wean a litter in any given year. Golden marmots delayed leaving their natal home range until after they had reached adult body size (≥3 years old) and were presumably sexually mature. Groups with multiple adults were largely a consequence of delayed dispersal. Resident marmots commonly tolerated adult immigrants. Golden marmots hibernated socially; the active season of all members of a group was identical. Overwinter mortality of juveniles (30%) was higher than that of yearlings or adults (<10%). Some evidence of benefits from social hibernation was found; juveniles hibernating with only parents and littermate siblings suffered lower overwinter mortality than juveniles hibernating with other individuals. While general predictions about sociality in marmots were upheld, an economic model combining defense costs and resource distribution failed to explain the mechanism of social monogamy.

Key words: *Marmota caudata aurea,* social behavior, mating system, dispersal, social hibernation

The 14 species of the Holarctic genus *Marmota,* large hibernating ground squirrels, are remarkably similar morphologically and physiologically yet are found in a variety of mating and social systems. Woodchucks (*M. monax*) typically disperse shortly after weaning as juveniles and are solitary as adults. Males apparently mate with one or more females (Ferron and Ouellet, 1989; Grizzell, 1955; Meier, 1992). Yellow-bellied marmots (*M. flaviventris*) are harem-polygynous. Dispersal typically occurs after the first hibernation as yearlings, but females may become recruited into their natal harem. Hence, females within a harem often are close relatives and then share a common home range (Armitage, 1991). Most other species of marmots are highly social with natal dispersal occurring at sexually maturity, generally after the second hibernation. Group members typically share a common home range and hibernate together (Arnold, 1990*a*). In groups of Olympic marmots (*M. olympus*) groups, a dominant male reproduces with each of two females in alternate years (Barash, 1973). A similar social and mating system has been described for southern populations of hoary marmots (*M. caligata*—Barash, 1974*a*, 1989), but some populations of hoary marmots are apparently monogamous (Holmes, 1984). Alpine marmots (*M. marmota*) have monogamous or even polyandrous mating systems characterized by a single breeding pair and adult sons who may also mate with their mother (Arnold, 1990*a*, 1993*a*; Arnold et al., 1994).

Several hypotheses have been presented to explain social variety in marmots. Barash (1974*b*, 1989) and Armitage (1981) focused on a critical body mass necessary for successful dispersal that is reached later in life in high altitude or latitude habitats with short growing seasons. Arnold (1990*a*, 1990*b*, 1993*a*) focused on harsh winter conditions in such habitats and emphasized the importance of direct fitness benefits of social hibernation and indirect fitness benefits of alloparental behavior that non-dispersers could acquire by helping warm younger siblings during winter. Holmes (1984) applied economic defensibility arguments (Emlen and Oring, 1977; Wittenberger, 1979) to contrast apparent monogamy in Alaskan hoary marmots with polygyny in other marmot populations. Arnold focused on only one of the eight Eurasian species, and the rest focused on some of the six nearctic species.

We describe the social organization of a subspecies of the Central Asian long-tailed marmot, the golden marmot (*M. caudata aurea*). Davydov (1991) reviewed studies of *M. caudata* in Tadzhikistan. Previous studies focused on geographic variation in morphology and population biology and relied extensively on trapping and collecting marmots rather than detailed observations on free-living marmots. We assessed group composition and stability, reproduction and survival, growth and overwinter loss of mass, and movements in social groups by live trapping and observing the natural behavior of marked golden marmots. We contrast social behavior of the golden marmot with other species and discuss social behavior in the context of previous models of social evolution of marmots.

The genus *Marmota* was first identified in North America in the late Pliocene and radiated into Asia and Europe during the Pleistocene (Black, 1972). *M. caudata* is accepted as an independent species and is immunologically distinct from other species of marmots (Bibikov, 1989; Zholnerovskaya et al., 1992). Golden marmots therefore provide an excellent within-genus sister group (Wiley et al., 1991) for comparative evaluation of previous models of the evolution of social and mating systems.

MATERIALS AND METHODS

Study area.—The study was conducted from 1988 to 1993 at Dhee Sar (36°81′N, 74°95′E) in Khunjerab National Park, Pakistan (Blumstein, 1995). Dhee Sar is a relatively flat high alpine meadow (4,100–4,300 m above mean sea level) surrounded by steep lateral glacial moraines and punctuated with hilly terminal moraines.

The Alpine Dry Steppe environment (Roberts, 1977) was characterized by a long cold winter with a shallow snowpack. Dhee Sar was snow-covered from late October to early November until mid-April to mid-May (N.U. Baig, pers. comm.). By the first week of May, snow depths rarely exceeded 1 m. Little precipitation fell during the short (ca. 4 month) summer, and there was substantial variation in seasonal, microclimatic, and diel temperature. In one location protected from a glacial wind, the average low temperature in summer (May–August) was 4.0°C (±1.6 *SE*, $n = 4$ monthly means of daily low temperatures for 4 years, 1990–1993), and the average high temperature was 18.9°C (±2.8 *SE*).

Study animals.—A total of 318 different marmots from at least 36 social groups was live-trapped, using Tomahawk® live traps set in burrow entrances. Marmots were permanently marked upon first capture by tattooing numbers in the skin of the inguinal region (1988–1989 by P. Ebenhöh), or by affixing small metal ear tags (1990–1993). Black numbers, dyed onto the dorsal fur with Nyanzol-D® fur dye, permitted identification of individuals from afar. Animals were recaptured and remarked when molting made numbers difficult to read. Juveniles were trapped as soon as they emerged above ground. Female reproductive status (breeding or non-breeding) was determined by nipple examination. Males became scrotal as 2-year-olds, but we were unable to determine if a male reproduced or not by external examination. We did not conduct molecular analyses to determine paternity.

Analyses on group composition were based on composition of 22 social groups at emergence from hibernation where each animal was individually known. Fourteen of those groups were studied for 5 years, three groups were studied for 4 years, one group was studied for 3 years, and four groups were studied for 1 year.

Marmots were divided into three age categories: juvenile, yearling, and adult (≥2 years old). Only juveniles and yearlings were aged on the basis of body size and pelage color. In addition to regular livetrapping, we attempted to visually locate each marmot each week beginning the first week of May from 1990 to 1993. Those observations (>2400 h) were used to identify short-term fluctuations in group compositions. Intergroup transfers were scored when a marmot was resident in a new group for >3 weeks or hibernated in a new group.

Group compositions during hibernation were inferred from the last observations or census in a year; marmots almost always emerged in groups in which they were last seen the autumn before. Russian studies (Nekipelov, 1978; Tokarsky, 1996; Vasiliev and Solomonov, 1996) that excavated entire marmot burrows found that all individuals hibernated in a single hibernaculum, and Arnold et al. (1991) remotely detected a single hibernaculum per burrow. We therefore assume that group members hibernated socially in a single hibernaculum. Plugged burrow entrances, a sign of hibernation, were seen from the second week of September onward. We did not remain at Dhee Sar to observe plugging of all burrows. Nevertheless, by the first week of September, above-ground activity of marmots was limited, and individuals in some groups remained below ground all day. Our last census week varied annually: 11–17 September 1989 and 1990; 14–20 August 1991; 28 August–3 September 1992; 4–10 September 1993.

Social group habitat use.—To determine if social structure of marmots was associated with distribution of resources and female defensibility, we estimated home-range size, studied potential food resources available in home ranges of social groups, and measured distances between hibernacula.

We estimated the amount of area that a social group used—home-range size of a social group—in 1992 (n = 16 social groups) and 1993 (n = 19 social groups) during the early season (May and June) and the late season (July and August). We drew minimum convex polygons around extreme points where individuals in a group were sighted during morning observation periods.

To study potential food resources (Holmes, 1984), we estimated standing crop (g/m^2) by systematically clipping, drying, and weighing above-ground vegetation at the height of the growing season. In 1993, we sampled six marmot groups. Briefly, in each group we clipped 20 different 0.2- by 0.2-m plots on each of four perpendicular linear arrays radiating from a group's main burrow (Blumstein, 1994; Blumstein and Foggin, 1997). Plots were 5 m from each other. Clippings were immediately sun-dried in envelopes and later oven-dried to a constant weight.

To study female defensibility by males and test Holmes' (1984) hypothesis about defensibility and mating systems, we compared the distance between hibernacula in different groups with the distance between potential hibernacula in social groups with more than one hibernacula. We measured the distance between hibernacula used in winter 1990–1991 either on the ground or from a 1:5,000 "ground-area" map drafted of the study site. Measurements from the map and the ground were statistically indistinguishable (J.E. Lopez and D.T. Blumstein, in litt.). For groups with more than one main burrow system, we measured the distance between the two farthest main burrows in that group's home range. Groups with more than one main burrow system used only one of these hibernacula annually.

Hibernation parameters.—Over-winter survival was determined by comparing the last week's census of one year with the first week's census from the next year. In the analysis, we assumed that our failure to see a marmot in spring indicated over-winter mortality and not late-season predation or early-season dispersal. Late-season predation could have occurred after our departure and may have inflated slightly our estimate of over-winter mortality. Our analysis of overwinter mortality of juveniles was restricted to juveniles hibernating in groups where no new adult males immigrated following emergence of juveniles. That restriction was to exclude potential mortality due to infanticide: new adult males are thought to be infanticidal (Blumstein, 1997). Less than one-half of the social groups emerged before we arrived in the first week of May. Activity in early May often was limited by snow cover. Hence, it is unlikely that dispersal occurred before our arrival.

To determine loss of mass of adults during hibernation, we estimated body mass at immergence and emergence by fitting a Gompertz growth curve, a type of logistic growth curve, to observed individual body mass (Arnold, 1986, 1990*b*). To obtain an accurate estimate of body masses (Arnold, 1986), we required: at least two mass measurements separated by ≥30 days; dates of immergence and emergence; and date of snowmelt in a group's home range (signaling the onset of the vegetative, as well as the marmot, growing season). Because immergence generally was unobserved and emergence was not always observed, we estimated unknown dates from reports of local shepherds and park rangers who visited the meadow and used known dates from surrounding groups in other years for guidance. Unless known, we assumed that groups living in south-facing slopes at relatively low elevations emerged on 21 April and immerged on 22 September. All other groups were estimated to emerge on 5 May and immerge on 29 September. Gompertz growth curves are sigmoidal and have long tails; thus, errors in estimating the exact immergence or emergence dates would thus have little effect on the resulting estimate of mass.

Statistical analyses.—Following Hoogland (1995), we generally assumed dependence of data from the same individual in the same year and treated observations of individuals from different years as independent. Analogously, we treated the individual hibernation group in a given year, or the emergence group, as the unit of analysis. For date-based measurements, days were calculated as the number of days past 1 May, weeks were numbered consecutively from the first week of May (i.e., 1–7 May = 1st week). To control for differences between years, year was entered as a categorically coded variable in the analyses.

The time to reach adult body mass was calculated on known-aged marmots. Age (i.e., juvenile, yearling, 2-year-old, etc.) was the unit of analysis; we randomly selected a single measurement of body mass from August for each individual of known age. Some individuals were represented in multiple years. Multiple comparisons were computed using Fisher's least significant differences.

Probability of over-winter survival was studied with multiple logistic regression (Norusis, 1992; Trexler and Travis, 1993). Individuals were used as the unit of analysis because the factor "group" did not explain any significant variation in over-winter survival. We studied effects of group size during hibernation on over-winter survival of juveniles and non-juveniles. For juveniles, we also considered weaning date and presence of unrelated marmots on over-winter survival. We inferred relationships by scrutinizing group composition over time. Groups inferred to consist only of relatives were: a pair of adults with juveniles, a pair of adults known to be born in the group and juveniles, or older marmots who had been resident for ≥3 years, any marmots known to be born in the group, and juveniles. For non-juveniles, we also considered the presence of juveniles on over-winter survival.

RESULTS

Social structure.—Golden marmots at Dhee Sar lived in obvious social groups where residents within groups had completely overlapping home ranges and generally behaved amicably toward each other. When we saw groups emerge from hibernation, all group members emerged from the same burrow system.

We used group composition at emergence to describe social structure of golden marmots at Dhee Sar because it was this group composition that existed during reproductive season in spring. Marmots often emerged through the snow but moved around very little during this time. Movement between groups during the breeding season was never observed. Both the median and modal group had a single adult male and a single adult female (Table 1); 52% had > 1 male and 1 female. Occasionally, over-winter mortality left a single

TABLE 1.—*Composition of 89 social groups of golden marmot after emergence from hibernation (age classes are immergence age classes).*

Character	Mean (*SE*)	Range	Median	Mode
Adults ($\geq$2 years old)				
Males	2.0 (0.13)	0–5	1.0	1.0
Females	1.4 (0.08)	0–4	1.0	1.0
Yearlings				
Males	0.2 (0.06)	0–4	0	0
Females	0.2 (0.06)	0–3	0	0
Juveniles				
Males	0.2 (0.07)	0–3	0	0
Females	0.2 (0.06)	0–3	0	0
Group size				
Adults only	3.3 (0.18)	1–7	3.0	2.0
All age classes	4.0 (0.22)	1–10	4.0	2.0
Sex ratio (proportion of adult males)				
All groups	0.6 (0.02)	0–1.0	0.5	0.5
Groups with >2 adults	0.6 (0.02)	0.25–1.0	0.67	0.67

surviving member from a previously larger social group. As long as the solitary marmot occupied the "group's" home range, we described the "group" as having a single marmot. Adult sex ratios were male biased in all groups (174 males:123 females, binomial $P = 0.004$ testing the hypothesis of a 1:1 sex ratio) and in groups with more than two adults (136 males:86 females, binomial $P = 0.002$; 32 groups male biased: 16 groups not male biased, binomial $P = 0.030$).

Habitat use and quality.—Vegetated alpine meadows in Khunjerab were insular, and it appeared that all suitable vegetated areas in Dhee Sar were occupied by marmots. There was some annual variation in home-range size. Parts of home ranges that were not used routinely in all years appeared to provide "overflow space" used when group size increased by recruitment or intergroup transfer. Home ranges of adjacent groups overlapped. No marmots were ever observed settling in a previously unoccupied area. A few marmots spent part of the summer "floating" in peripheral parts of established home ranges. Recently vacated home ranges were resettled within the season. In one instance two groups fused, and in one instance a single group fissioned into two groups.

After snow melted, early season home ranges were larger than late season home ranges in both years ($P = 0.017$ in 1992; $P < 0.001$ in 1993). Average maximum home range size was 3.1 ha (±0.3 *SE*, $n = 16$) in 1992 and 2.9 ha (±0.4 *SE*, $n = 19$) in 1993. Home ranges provided an average of only 36 g/m^2 (±4.3 *SE*, $n = 6$ groups) of standing crop at the height of the vegetative growing season in 1993.

Most home ranges had three main burrows (range = 1–6, $n = 18$ groups studied for >1 year) with one or more openings where we saw marmots emerge in the morning. Some of those main burrows also were used as hibernacula; some groups used different hibernacula in different years. The average distance between known hibernacula in different groups was 146 m (±6.6 *SE*, $n = 18$ groups). The average distance between main burrow entrances within social groups with multiple main burrow systems was 133 m (±12.4 *SE*, $n = 15$ groups). Those distances were statistically indistinguishable (Wilcoxon matched-pairs signed rank test, $P = 0.256$, $n = 15$).

Reproduction.—Golden marmots, like most other hibernating sciurids, bred once each year. Juveniles generally emerged above ground during the last days of June or the first days of July (mode = week 9, range = 9–13, $n = 19$ groups with known emergence dates). Backdating ca. 10 weeks (30–33 days for gestation plus ca. 30–40 days for weaning—Barash, 1989; Psenner, 1957), suggested that mating occurred between the third week of April and the second week of May. We never observed a copulation; mating may have occurred underground. In some cases, the inferred date of mating was even before there was any sign of above-ground activity of marmots.

From 1989 through 1993, only 17% (15/89) of the groups produced young that survived to emerge; none produced young in 1989. All but five of those social groups contained at least one potentially reproductive female. Of those groups without reproductive females, three had only a single adult male emerge following hibernation, one had five adult males and no females emerge, and one had two males and three pre-reproductive females emerge. A single breeding female per group was virtually always responsible for that group's litters (1/15 group-years analyzed had two lactating females and weaned two litters). One female weaned young in 3 consecutive years, one female weaned young in 2 consecutive years, and two females weaned young after skipping a year. The remaining females reproduced only once during the study period. If a group weaned young more than once during the study, the same female was always the mother. Three of the 15 groups consisted only of a pair of adults. Two groups consisted of a pair of adults with previous year's offspring that were either daughters, or were too young to breed. Two groups consisted of a pair of adults with at least one breeding-aged son. The remaining eight groups consisted of multiple adults.

All juveniles of 16 litters were trapped upon emergence. Because we were unable to identify the mother of each young with certainty in the group with two lactating females, we exclude those litters from analysis. We include another group in which all juveniles were trapped but did not contribute to other analyses because some adults were untrapped. The modal and median emergence litter size in the 15 groups with a single lactating female was 4 juveniles (range = 2–6; $\bar{X} = 4.2 \pm 0.30$ *SE*). Weaning sex ratios were not significantly different from 1:1; of 63 juveniles in 15 litters, 36 juveniles were male (57%) and 27 were female (43%—binomial $P = 0.314$). The sex ratio within litters also was not biased (8 male-biased, 5 female-biased, 2 equal—binomial $P = 1$, $n = 15$).

Juvenile mortality.—First-season mortality was high. Only 50% of 72 juveniles (1990–1993) caught at emergence from their natal burrows survived their first summer. Of those that survived their first summer, 81% survived their first hibernation (22/27 in 1990–1992). Thus, only 41% of those marmots that emerged from their natal burrow in one year survived to the next. In the first summer of life, the most commonly identified or inferred sources of mortality were infanticide by new adult males entering a social group (8/36 first-season mortalities) and predation by terrestrial and aerial predators (8/36 first-season mortalities—Blumstein, 1997).

Growth.—Neither male nor female golden marmots reached adult body mass in their first active season (Table 2). A conservative interpretation of the mass data suggested that neither sex reached adult body mass until 3 years of age.

Dispersal.—While we do not know fates (dispersal or death) of all disappearing individuals ≥2 years old, observed intergroup movements and patterns of residency suggested that some golden marmots remained in their natal group for at least their first 3 active seasons (Fig. 1). One juvenile changed social groups in its first active season when it moved to a neighboring group

TABLE 2.—*Body mass (g) for known-age golden marmots in August.*

	Male[a]			Female[a]		
Age	Mean	*SE*	*n*	Mean	*SE*	*n*
Juvenile	975 a	32	16	1,013 a	54	10
Yearling	2,333 b	101	18	2,733 b	117	16
2-year-old	3,025 c	156	6	3,125 c	87	7
3-year-old	3,721 d	118	7	3,520 c	80	5
4-year-old	3,519 d	170	8			
≥5-year-old	3,508 c,d	340	3			

[a] Different letters after means indicate significant ($P < 0.05$) post-hoc Fisher's LSD comparing body masses within a sex.

with other similar-aged juveniles above ground where it was accepted by group members. No yearlings were observed changing social groups. Two males and one female left their natal social group as 2-year-olds. The remaining observed group transfers (23 males, 5 females) were made by older marmots. Some older marmots moved more than once, and we usually did not know if the first move we observed was a marmot's "natal dispersal." Nevertheless, our results suggest that dispersal occurred mostly after they reached maturity.

Intergroup movements averaged 260 m (±32 *SE*, range = 109–950 m, n = 32 observed transfers). Most movements (26/32) were to adjacent groups. Only 13% (4/32) of movements were preceded by aggression in the source group, and only 25% (8/32) of movements were associated with aggression in the destination group. Half (16/32) of the movements were preceded by investigations in other groups, while 41% (13/32) were preceded by investigations into the destination group. On five occasions, immigration by a disperser into the destination group was followed by emigration of a resident in that group; some of those emigrations were associated with aggression from the immigrant. The average source group size (including juveniles) was 5.9 (±0.47 *SE*, range = 2–13), and average destination group size was 3.8 (±0.59 *SE*, range = 0–13). Most (75%) observed transfers were to smaller groups (18 males, 6 females), 19% (6 males, 0 females) were to larger groups, and 6% (2 males, 0 females) were to equal-sized groups. We were unable to reject the null hypothesis that transfers were random with respect to group size when we calculated distribution of expected group sizes from emergence group sizes (14 groups were = 5.9, 75 < 5.9; *G*-test, P = 0.2557).

FIG. 1.—Observed intergroup transfers by age and sex. Intergroup transfers were defined as an observed movement between two groups where a marmot remained in the new group for >3 weeks. Some marmots moved multiple times; data were pooled for this figure.

Over-winter survival.—Group members hibernated in the same burrows; seasonal activity patterns of all marmots in a social group overlapped each other. Over-winter survival (Table 3) was high for yearlings and adults (≥90%) but lower for juveniles (70%). Total group size either had no effect, or a slightly negative effect, on probability of over-winter survival.

For non-juveniles, total group size (including juveniles) did not influence probability of over-winter survival (logistic regression group size coefficient = −0.1131, P = 0.190; constant coefficient = 3.0157, $P < 0.001$, n = 286). However, there was a tendency for non-juvenile survival to de-

TABLE 3.—*Number of individual golden marmots that survived or died over winter as a function of total hibernation group size and sex. Age classes are immergence age classes: at emergence juveniles become yearlings, yearlings become ≥2 years old, etc. Most marmots ≥1 year old (74%) hibernated in groups of two to six animals. Most juvenile marmots (79%) hibernate in groups of five to nine animals. Over-winter survival rates are 92% for marmots ≥2 years old, 90% for yearlings, and 70% for juveniles.*

			Juveniles		Yearlings		≥2 year	
n Groups	Group size	Sex	Survived	Died	Survived	Died	Survived	Died
2	1	M					1	0
	1	F					1	0
22	2	M					22	0
	2	F					21	1
12	3	M					19	2
	3	F			1	0	14	0
6	4	M			0	1	11	2
	4	F					7	3
12	5	M	2	1	2	0	27	2
	5	F	2	0	4	0	19	1
10	6	M	4	0			32	2
	6	F	3	0			17	2
3	7	M	2	0	4	1	6	1
	7	F	3	0			4	0
3	8	M			2	0	12	0
	8	F	0	2			6	2
3	9	M	3	2	2	0	9	2
	9	F	0	2			7	0
1	10	M	2	1			3	0
	10	F	0	1			3	0
1	11	M	2	0	1	0	1	1
	11	F	0	1	2	0	2	1
	Total		23	10	18	2	244	22

crease as the number of non-juveniles in the hibernacula increased (logistic regression group size coefficient = −0.2009, $P = 0.061$; constant coefficient = 3.4209, $P < 0.001$, $n = 286$; Fig. 2). Presence or absence of juveniles in the hibernacula, per se, did not influence over-winter survival of non-juveniles (model $P = 0.710$, $n = 286$; Fig. 2).

Juveniles obligately hibernated with older animals. Juveniles hibernating in groups that consisted only of parents and littermate siblings suffered less over-winter mortality than juveniles hibernating in groups containing other animals (logistic regression "relatives only, yes-no" coefficient = 3.0756, $P = 0.015$; constant coefficient = −0.5108, $P = 0.484$, $n = 22$). Total hibernation group size did not influence overwinter survival of juveniles (logistic regression group size coefficient = −0.4391, $P = 0.152$; constant coefficient = 4.3025, $P = 0.078$, $n = 22$), but when we excluded juveniles from the hibernation count of group size, we found that overwinter survival of juveniles decreased when hibernating in groups with more non-juveniles (logistic regression group size coefficient = −0.9316, $P = 0.013$; constant coefficient = 5.1508, $P = 0.011$, $n = 22$). There was a tendency for survival to be lower for those juveniles weaned later in summer (logistic regression weaning day coefficient = 0.4042, $P = 0.059$; constant coefficient = 78.1044, $P = 0.057$, $n = 22$). There was no association between sex and overwinter survival of juveniles (Fisher's Exact $P = 0.257$).

Overwinter mass loss.—Golden marmots

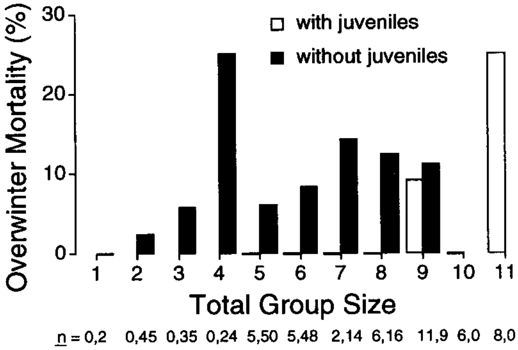

FIG. 2.—Over-winter mortality of non-juvenile marmots in relation to total hibernation group size and presence or absence of juveniles in the hibernacula. Sample sizes (bottom of figure) refer to the number of hibernation events in marmot-years; individuals known to have hibernated in several years were included in each year (*n* = 286).

lost on average 41% (±2.7 *SE*, $n = 16$) of their body mass during hibernation. There were no significant sex differences in the estimated proportion of body mass lost during hibernation (Mann-Whitney $z = -0.170$, $P = 0.865$; $\bar{X} = 42.4\%$ ±3.3 *SE*, $n = 11$ males, and $\bar{X} = 37.3\%$ ±4.8 *SE*, $n = 5$ females). Similarly, presence/absence of juveniles had no significant effect on mass loss (Mann-Whitney $z = -1.111$, $P = 0.266$; $\bar{X} = 35.0\%$ ±3.9 *SE*, $n = 2$ individuals in groups with juveniles, and $\bar{X} = 42.1\%$ ±3.0 *SE*, $n = 14$ individuals in groups without juveniles). Group size was also not significantly correlated with estimated mass loss in the entire data set ($r_s = -0.07$, $P = 0.784$, $n = 16$).

DISCUSSION

Comparison with other sciurids.—Golden marmots at Dhee Sar generally were found in apparently monogamous associations. When multiple adult females shared a home range during our study, at most only one female weaned young. This pattern is in apparent contrast to polygynous yellow-bellied marmots (Armitage, 1991) but appears similar to alpine marmots (Arnold, 1993*a*). When groups of golden marmots had more than two adults, in contrast to the typical sciurid pattern (Armitage, 1981; Michener, 1983), additional marmots were generally males. This social structure also is similar to the typically monogamous alpine marmot that, to some degree, lives and mates polyandrously (Arnold, 1990*a*, 1993*a*). Finally, unlike the highly social Olympic and hoary marmots (Barash, 1973, 1974*a*; D.T. Blumstein, in litt.), but like alpine marmots, golden marmots in a social group shared sleeping burrows; home ranges were truly "group home ranges."

The male bias among adults in our study population may stem from a slightly, although not significantly, biased weaning sex ratio. A similar male-biased weaning sex ratio was also found in a much larger sample of recently weaned alpine marmots (58% males, $n = 476$) which deviated significantly from a 1:1 sex ratio (binomial $P = 0.001$, W. Arnold, in litt.). In contrast, Davydov (1991) reported that in harvested alpine populations of *M. caudata* in Tadzhikistan, 2-month-old marmots were slightly female-biased (48% male, $n = 206$), and marmots ≥2-years old also were female-biased (46% male, $n = 513$).

Because of our limited knowledge about dispersal, we could not test if groups of golden marmots were male-biased because males dispersed later than females, as they do in alpine marmots (Arnold, 1990*a*, 1993*a*). However, we know that in contrast to the general sciurid pattern (Holekamp, 1984), golden marmots often delayed leaving their natal home range until after attaining adult size when presumably sexually mature. Groups with multiple adults resulted either from delayed-dispersal or from adult intergroup transfer. Immigration of adults into a group was not uncommon and often occurred without the expulsion of a resident and often without much overt aggression. Such tolerance of adult immigration is atypical for marmots. Similar tolerance is known to exist only in alpine marmots, but even in this highly social species, it is much less frequent than in golden marmots (W. Arnold, in litt.).

Golden marmots live in a harsh environment. Marmots did not reach adult body mass until they were 3-year-olds, and reproduction was infrequent. In the harvested alpine population of *M. caudata,* Davydov (1991) reported that a few (4%, $n = 237$) female marmots first bred as 3-year-olds; most required more years to mature. Like Davydov's (1991) alpine population, not all females at Dhee Sar breed annually and reproduction was infrequent, perhaps because it took time to regain body condition following a successful breeding.

Overwinter mortality of juvenile golden marmots approximated that in alpine marmots and was less than that in Olympic and yellow-bellied marmots; overwinter mortality of adults was greater than that in gray marmots (*M. baibacina*), approximated that in yellow-bellied, alpine, Mongolian (*M. sibirica*), and Menzbier's (*M. menzbieri*) marmots, and appeared less than that in Olympic marmots (Arnold, 1993*b*; Barash, 1973; Van Vuren and Armitage, 1994). Adult golden marmots lost an average of 1.3 times more body mass than reported for adults of other marmot species (Arnold, 1993*b*). Analyses of mass loss may have failed to find significant effects of sex and group composition because they were based on a small samples and on immergence and emergence estimates that inevitably produced considerable scatter. Standing crop at the height of the growing season at Dhee Sar in 1993 (36 g/m^2) was about one-third less than, or about equal to colonies of hoary marmots (Hansen, 1975; Holmes, 1984). Dhee Sar had only 6% of the peak standing crop found at colonies of yellow-bellied marmots ($\bar{X} = 555$ g/m^2, $n = 5$ colony-years—Frase and Armitage, 1989; Kilgore and Armitage, 1978). Over-winter mortality and mass loss may be a response to the combination of a long winter, a relatively depauperate snow-pack (and therefore potentially lower burrow temperatures), and limited summer vegetation.

Like most other marmots, golden marmots at Dhee Sar hibernated socially; seasonal activity patterns of all individuals in a group overlapped and all animals emerged from the same hibernacula at the same time. Despite availability of other potential hibernacula (some groups used different hibernation burrows in different years), all group members always hibernated in the same burrow system. Like other marmots (Armitage et al., 1976; Arnold, 1993*b*; Barash, 1973), juvenile golden marmots had a higher probability of dying during hibernation than older marmots; juveniles weaned late in the season were the least likely to survive winter. Overwinter survival of juveniles was higher if only parents and littermate siblings were present in the hibernacula, suggesting a benefit from social thermoregulation by relatives (Arnold, 1993*b*). Unfortunately, because adult immigration reduced our certainty about relationships between all social group members and successful reproduction was rare, we were unable to test Arnold's (1993*a*) key prediction about alloparental thermoregulatory care by older relatives.

Evaluation of previous models.—Did previous models of social evolution of sciurids predict social organization of golden marmots? Because it took more than one active season for juveniles to reach adult body mass, environmental-harshness hypotheses (Armitage, 1981; Barash, 1974*b*) successfully predicted delayed dispersal in golden marmots. To completely evaluate these hypotheses, we need to compare body masses and survival of natally dispersing and non-dispersing animals (Arnold, 1990*a*), but we were unable to do so.

Given the extremely limited food resources found at Dhee Sar, Holmes' (1984) hypothesis would have predicted a single adult male and a single adult female social and mating system. Our data are consistent with this prediction because the median and modal group size was a single adult male and a single adult female marmot. However, apparent support for this prediction, and in fact Holmes' original relationship, may be spurious. Overall standing crop may not be the appropriate way to measure food resources. Because marmots may have food preferences (Blumstein and Foggin, 1997; Carey, 1985), or may avoid certain foods (Armitage, 1979), overall standing crop may overestimate actual food availability.

Holmes (1984) explained the hoary marmot's monogamy in Alaska by suggesting that males are unable to defend more than one female's home range and hibernaculum against other males. If we assumed that each main burrow system of a golden marmot could potentially be associated with a single female, distance between main burrow systems in those groups of golden marmots that had more than one main burrow should be a metric of male-defense costs. Intergroup distances at Dhee Sar (146 m) were indistinguishable from intragroup distances (133 m) and were shorter than intergroup distances that Holmes (1984) reported for hoary marmots (259 m), suggesting that hoary marmots had greater defense costs than golden marmots.

Holmes (1984) assumed that home ranges were large because of low food availability. Low food availability would require females to obtain access to large home ranges to support themselves and potential litters. While golden marmots and hoary marmots lived in areas with similar standing crop, foraging ranges of female hoary marmots ($\bar{X} = 9.2$ ha, range = 8.9–10 ha, $n = 4$ social groups over 2 years; W.D. Holmes, pers. comm.) were much larger than group home ranges of golden marmots. Interestingly, golden marmots at Dhee Sar had apparently larger litters than hoary marmots in Alaska (4.2 versus 2.8) and therefore might be expected to require larger foraging areas. Yet some fitness correlates of golden marmots were influenced by natural variation in forage availability (Blumstein and Foggin, 1997). Probability of weaning young in 1 year was associated with food availability in a female's home range in the previous year and early-season resources in the same year. Weaning date, a correlate of juvenile overwinter survival, was associated with food availability in the home range in the same year. Nevertheless, despite an apparent paucity of food resources at Dhee Sar, home ranges of some golden marmots supported multiple adults without evidence of a polygynous mating system. We therefore reject the hypothesis that limited food resources influence female distribution and thus defensibility of females by males to explain the observed mating system in golden marmots.

Past models have assumed that sociality of sciurids evolved along female kin-lines (Armitage, 1981; Michener, 1983), and there are no models of social behavior of sciurids that predict polyandry. From a male's perspective, cooperative polyandry may be favored when a male's reproductive success when sharing a mate is greater than otherwise (Gowaty, 1981). Kin-selected benefits may enhance the probability of polyandry (Maynard Smith and Ridpath, 1972—but see Gibbs et al., 1994). From a female's perspective, polyandry may be favored when female reproductive success increases with the number of brood caring males (Davies, 1992; Goldizen, 1987). Cooperative polyandry may evolve from already cooperative social systems (Faaborg and Patterson, 1981).

For marmots living in habitats with severe winter conditions, cooperative brood care by additional males can increase juvenile over-winter survival. Unlike spermophiline ground squirrels, marmots are unable to tolerate extremely low body temperatures during hibernation. For most of the winter they must maintain energetically costly heat production to prevent their body temperature from dropping below a critical threshold (Arnold, 1993*b*; Arnold et al., 1991). Coordinated bouts of social thermoregulation and warming of juveniles has been demonstrated in hibernating alpine marmots where it is important for juvenile survival (Arnold, 1988, 1990*b*, 1993*b*). Winter mortality of juveniles and breeding pairs decreases with increasing numbers of adult sons in a hibernation group (Arnold, 1993*b*). Interestingly, these sons may either be helpers, warming young sibs, or brood caring fathers because adult sons may well have reproduced with their mother (Arnold and Dittami, 1997; Arnold et al., 1994). The need to hibernate in groups and to thermoregulate socially seems to be an important selective force in marmots living at high elevations that leads to evolution of delayed dispersal and possible polyandry. All marmot species that experience harsh overwinter conditions that have been studied so far hibernate communally and natal dispersal does not occur before sexual maturity (Arnold 1990*a*, 1993*b*; D.T. Blumstein and K.B. Armitage, in litt.). A critical re-examination of data from Olympic marmot data (Barash, 1973:194–195) and hoary marmots (Holmes, 1984:255) shows that potentially reproductively mature offspring (≥2 years old) remained in some groups.

Social organization of golden marmots is more-or-less consistent with this story. Winter in golden marmot habitats is severe, and group members always hibernated together. Adult thermoregulatory care increases juvenile survival. Adult sex ratio within groups was male-biased, suggesting the opportunity that sons may delay dispersal and help thermoregulate younger relatives. While we acknowledge that genetic evidence of paternity ultimately is required for stronger support of the hypothesis, fitness benefits from group hibernation may be a crucial factor in explaining evolution of marmot sociality.

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