Ethology 93, 21—30 (1993)

ISSN 0179-1613

Laboratoire de Socioécologie et d'Ecoéthologie, U.C.B.L.1 Villeurbanne

Socio-spatial Organization and Activity Distribution of the Alpine Marmot *Marmota marmota*: Preliminary Results

CATHERINE PERRIN, DOMINIQUE ALLAINE & MICHEL LE BERRE

PERRIN, C., ALLAINE, D. & LE BERRE, M. 1993: Socio-spatial organization and activity distribution of the Alpine Marmot *Marmota marmota*, preliminary results. Ethology 93, 21—30.

Abstract

The behavioural ecology of the Alpine marmot *Marmota marmota* (Linné, 1758) was studied Jun.—Sep. 1990 in the Vanoise National Park (French Alps). We describe the socio-spatial structure of a high-altitude population, to give additional information on the formerly unclear marmot social organization.

The social unit was the family group, with a common home range between 0.9 and 2.8 ha; a slight overlapping occurred (9 to 12.5 %). Each home range had a central area of main burrows, where the hibernaculum was located, and peripheral areas.

Space utilization and distribution of activities during the season were analysed. Some activities took place exclusively in the centre area while peripheral parts were used for foraging. This latter increased in Aug. and decreased in Sep., marmots tending to remain more and more at the centre area as the hibernation period approached.

Corresponding author: C. PERRIN, Laboratoire de Socioécologie et d'Ecoéthologie, U.C.B.L.1, 43 bvd. du 11 Novembre 1918, F-69622 Villeurbanne.

Introduction

The last 20 years have seen numerous studies on social organization in North-American ground-dwelling squirrels (Rodentia, Sciuridae) (see for review BARASH 1974b; HOOGLAND 1981; ARMITAGE 1981, 1988; MICHENER 1983; MURIE & MICHENER 1984). This group is an interesting model for studying behavioural ecology because of different systems of social and spatial organization, from defense of individual territories to constitution of egalitarian harems (MICHENER 1983). The delay of sexual maturity, either because of a short growing season or low quality food, would be the main factor determining the level of sociality (ARMITAGE 1981). This results from life in open habitats, adult-subadult seasonal coincidence (MICHENER 1983, 1984) and population density (DOBSON 1984; FERRON & OUELLET 1989).

U.S. Copyright Clearance Center Code Statement: 0179-1613/93/9301-0021$02.50/0

Among ground-dwelling squirrels, the genus *Marmota* is well presented (14 species) and widespread over the whole holarctic region [6 species in North-America, 8 in Eurasia (HONACKI et al. 1982)]. The social organization of four North-American species has been extensively studied and well described: *Marmota monax* is solitary and aggressive (GRIZZELL 1955; BRONSON 1963, 1964; DAVIS 1981; OUELLET & FERRON 1986; FERRON & OUELLET 1989), *M. flaviventris* exhibits polygynous harems (ARMITAGE 1962, 1974, 1975, see 1991 for a review), *M. olympus* and *M. caligata* have distinct social groups, with members sharing a common home range (BARASH 1973, 1974a; HOLMES 1984). Nevertheless, the social organization of the Alpine marmot remains unclear (ZELENKA 1965; ARNOLD 1990a; but see BARASH 1976). Here we aim to give new information on the social and spatial organization of this species at high altitude.

Methods

Study Area

The study was conducted in the Nature Reserve of "La Grande Sassière" in the Vanoise National Park (French Alps). Altitude ranges from 1,850 to 3,757 m. The climate is typical of high mountains, with marked winter precipitation (snow). The study site, covered by subalpine and alpine vegetation, is located in the lower part of the Reserve at 2,350 m close to the Sassière mountain stream.

Observations

Marmots were captured with live traps, weighed, aged and sexed by ano-genital distances (ZELENKA 1965). Early in Jul. we were able to distinguish four age classes from body mass and body + tail length measurements (ZELENKA 1965): adult (≥ 3-yr-old), 2-yr-old, yearling and infants.

Animals were marked by attaching a numbered tag to one ear. To allow rapid identification, a piece of colored plastic was put on the other ear.

In 1990, 325 h of observation were conducted from Jun. to the end of Sep. Four neighbouring groups (A, B, C and D) were observed directly using scan sampling (ALTMANN 1974). Only one group was observed on a particular day. In observation periods, the location of each group member was noted at 10-min intervals, mapped approximately, and activities recorded as follows:

Foraging (F): marmots foraged lying down and crawling through vegetation, but sometimes sat and used forepaws to manipulate food such as *Poaceae* and thistle *Carlina acaulis*.

Postures (P): sitting, lying down, half out of a burrow, adopted during rest, visual exploration.

Locomotion (L): all movements not associated with food intake.

Social interactions (SI): recognitive (greetings, KING 1955), cohesive (allogrooming, play-fighting, BARASH 1989) and agonistic (threat, chase, fight, BARASH 1989) behaviours.

Selfgrooming (SG)

Alert (A): characterized by two kinds of upright posture, squatting on haunches or standing on hindlegs. Alarm calls are often emitted.

Marking (M): active marking behaviour is performed by muzzle rubbing on stones, rocks, or burrow mounds or directly on the ground, previously scratched.

Defecation (D)

Other (O): all other behavioural patterns observed, such as gathering and carrying nest materials, digging burrow . . .

Home range for the whole group was calculated according to the convex polygon method (MOHR 1947) and using the technique described by ARMITAGE (1975).

Statistical analyses were performed using χ^2 tests. Relative contributions (rc) higher than the average contribution to the total χ^2 were interpreted.

Results

Group Composition

Groups B, C and D each contained a pair of adults, subadults and/or juveniles from one or several years (Table 1). Group A contained two unidentified animals: a female captured in 1991 and an adult male subordinate that left the group in 1991 (unpubl. data).

Except in group C, the three non-adult age classes were not all present at the same time in a group.

Group composition changed during the season because of mortality, new births and dispersal.

Reproduction occurred in three of the four groups studied in 1990, one litter in each breeding group (Table 1). Infants emerged between 24 Jun. and 14 Jul. (Table 2). This variability among groups could have been due to differences in the date of emergence from hibernation.

Disappearances were also noted. Subadults and adults vanishing from groups A, B and C (Table 1) were assumed dispersed. Infants also disappeared during the summer (Table 2) but dispersal cannot account for such cases (ARNOLD 1990a), which were more likely due to diseases, predation (by the golden eagle, *Aquila chrysaetos,* or red fox, *Vulpes vulpes*) or to infanticide (SHERMAN 1981; MICHENER 1982; BALFOUR 1983; MCLEAN 1983; BRODY & MELCHER 1984; HOOGLAND 1985).

Home Range

The home range size of groups A, B and C varied from 2.4 to 2.8 ha (Table 3). Group D's smaller home range may have been slightly underestimated because of a rocky barrier. Home ranges overlapped 9 to 12.5 % and overlaps were similar for each group (Table 3).

A home range comprised a main burrow system (MBS) and peripheral areas. The MBS exhibited a high density of burrow entrances, outside latrines, and contained both the hibernaculum and birth burrow. Burrows in peripheral areas, used in emergencies, were much shallower than main burrows. Conspicuous trails occurred between the most frequently used burrows and the most used areas.

Facies of home ranges (Fig. 1) have been described from topography and types of vegetation (GENSAC & ROTHE 1974).

Groups A and C occupied subalpine meadows (M) edged by taluses (T) with a gentle slope and few rocks. The MBS were located in the talus. Members of groups A and C also used a riparian area (RA).

The group B MBS and an auxiliary burrow system (ABS) were located in two mounds overhanging the river. The density of rocks was relatively important and rocks on top of mounds were often used for watching and/or rest. This group of marmots occupied a peat bog (PB) and a subalpine meadow (M).

Group D occupied a steeply sloping subalpine meadow (M) with an area of rockslides overhung by a rocky barrier.

Table 1: Composition of the 4 family groups of Alpine marmot (number of individuals by age and sex classes) in 1990

	Group A		Group B				Group C				Group D			
Age and sex classes	15 Jun.	16 Aug.	11 Jun.	8—14 Jul.	14 Jul.	Aug.	20 Jun.	27 Jun.	6 Jul.	Aug.	early Jun.	24 Jun.	Jul.	Aug.
Adult m	2	2	2	1	1	1	1	1	1	1	1	1	1	1
Adult f	—	—	1	1	1	1	1	1	1	1	1	1	1	1
Unident.	2	2	—	—	—	—	2	2	1	1	—	—	—	—
2-yr m	2	—	—	—	—	—	—	—	—	—	—	—	—	—
2-yr f	1	—	—	—	—	—	1	1	1	1	—	—	—	—
Yearling m	2	1	4	4	4	4	1	1	1	1	—	—	—	—
Yearling f	—	—	1	1	1	1	1	1	1	1	—	—	—	—
Infants	—	—	—	—	3	3	—	5	4	3	—	4	2	2
Total	9	5	8	7	10	10	7	12	10	9	2	6	4	4

m = male, f = female, unident. = unidentified individuals. Group compositions did not change in Sep. for the four groups.

Table 2: Reproductive parameters in three family groups of Alpine marmot

Group	fecondation	Dates of birth	emergence	Litter size (no. infants)	Disappeared
B	3/4 May	5 Jun.	14 Jul.	3	0
C	16/17 Apr.	19 May	27 Jun.	5	2
D	13/14 Apr.	16 May	24 Jun.	4	2

Table 3: Home range size and density of marmots on the study site

Group	Home range size ha	Overlapping ha (% of home range) A	B	C	Total no. of marmots	Density (no./ha)
A	2.4	—	0.3 (12.5)	0	9 (5)	3.8 (2.1)
B	2.6	0.3 (11.5)	—	0.26 (10)	8 (10)	3.1 (3.9)
C	2.8	0	0.26 (9)	—	7 (9)	2.5 (3.2)
D	0.9	0	0	0	2 (4)	2.2 (4.4)
Total area	8.7				26 (28)	3 (3.2)

no.: number and density of marmots at the beginning of the observation period early Jun., in brackets from Aug. onwards

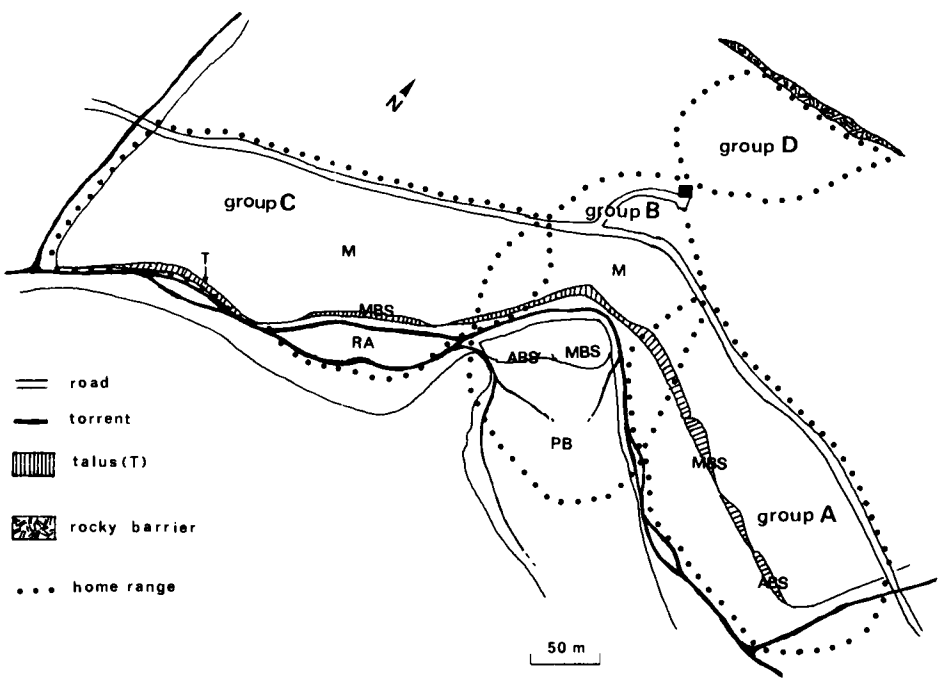

Fig. 1: Study area: home ranges of 4 family groups (A—D) of Alpine marmots and parts of the home ranges of groups B and C. MBS: main burrow system, ABS: auxiliary burrow system, peripheral areas = M: subalpine meadow, T: talus, RA: riparian area, PB: peat bog

Utilization of Space and Distribution of Activities

Analysis of space utilization and distribution of activities were performed only on groups B and C.

Both groups used parts of the home range differentially (group B: $\chi^2 = 153.55$, df = 6, $p < 0.001$; group C: $\chi^2 = 46.73$, df = 6, $p < 0.001$) (Fig. 2). In these two cases, the MBS was more used than any other part, particularly in Sep. (group B: rc = 16.54; group C: rc = 8.26). Although the MBS area is small, more than ⅓ of all activities took place there. This highlights the functional importance of the MBS. In group B, use of the ABS decreased as the season progressed (rc = 38.78). In group C, use of meadows and talus increased in Aug. (meadows: rc = 5.16; talus: rc = 7.7) and then decreased in Sep. (meadows: rc = 6.8; talus: rc = 4.6).

Most frequent activities were foraging, then postures, locomotion and social interactions. The distribution of activities varied with the season (group B: $\chi^2 = 99$, df = 16, $p < 0.001$; group C: $\chi^2 = 156.9$, df = 10, $p < 0.001$) (Fig. 2). In both cases foraging increased in Aug. (group B: rc = 12.6; group C: rc = 37.1) whereas social interactions decreased (group B: rc to $\chi^2 = 8.7$; group C: rc =

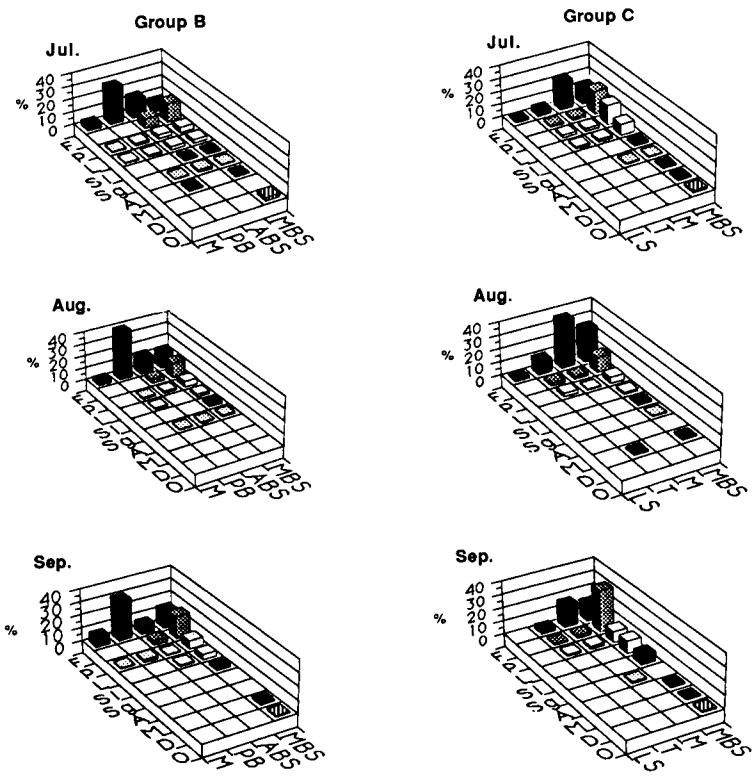

Fig. 2: Spatial distribution of activities of Alpine marmots from Jul. to Sep. (in % of observations). Activities: F: foraging, P: postures, L: locomotion, SI: social interactions, Sg: selfgrooming, A: alert, M: marking, D: defecation, O: other. Parts of home range: see Fig. 1

12.3). In group B, foraging was infrequent in Jul. (rc = 6.3) whereas social interactions were frequent (rc = 5). Alert decreased in Sep. (rc = 5.8). In group C, social interactions increased in Sep. (rc = 22.8).

For both groups spatial distribution of activities changed during the season (Fig. 2). Some parts were less used in Aug. Some activities observed in a given part of the home range in Jul. were no longer observed in the same place in Aug. Social interactions, locomotion and postures were mainly confined to the MBS in both groups, whereas foraging was performed everywhere, although mainly in peripheral areas.

Discussion

Group Composition

The social unit of *Marmota marmota* is a family group in which individuals share a common home range and hibernate together (BARASH 1976; ARNOLD 1990b). The typical social unit is a dominant pair of adults and their offspring (ARNOLD 1990a).

Considering that monogamy is a mating system and not a social system (see WICKLER & SEIBT 1983), breeding by only one adult pair in a family group characterizes monogamy (KLEIMAN 1977). Our results supported the hypothesis that the mating system of *Marmota marmota* is monogamy (ARNOLD 1990a; but see BARASH 1976).

One correlate of monogamy is the parental manipulation of progeny (ALEXANDER 1974) whereby the older offspring care for subsequent litters of their parents while their own reproduction is inhibited. This was observed in Alpine marmots. Only territorial females reproduced; subordinate females failed to conceive or resorbed their litters (ARNOLD 1990a). Our results confirmed that the presence of more than two adults in a group is not rare. ARNOLD (1990a) found that about ⅓ of the 3- and 4-yr-old individuals spend one more year in the natal home range.

ARNOLD (1990a) showed that often females did not reproduce the next year, after giving birth. In our groups we estimated that females could reproduce two years consecutively, but not three. Additional data are required.

Our results confirm the high level of sociality of *Marmota marmota.* Its social system is close to that of North-American species such as *M. olympus* and *M. caligata,* which have short growth seasons (BARASH 1974b, 1976).

Home Range

ZELENKA (1965) and MANN & JANEAU (1988) described two different kinds of spatial organization in Alpine marmots:

1) isolated family group. Home range size from 2 to 5.75 ha.

2) colony, composed of several family groups, with a slight home range overlap. Size of home range for a family in the colony is from 0.9 to 2 ha.

The home-range sizes of groups A, B and C belong to the first category. Conversely, home-range overlap between groups in our study belongs to the second category.

The term "colony" should be clarified. ARMITAGE (1962) used it first for *Marmota flaviventris* to describe a social group with an adult male and a harem. In ZELENKA (1965) and MANN & JANEAU (1988) it denoted several family groups, and BARASH (1976) used it for one family group, but adopted "colony town" for *M. olympus* and *M. caligata* (1989), similar to the meaning of "colony" used by ZELENKA (1965) and MANN & JANEAU (1988) for the Alpine marmot. Marmot populations studied by ARMITAGE (1986) were clumped on habitat patches. Therefore the term "colony" involves limits such as natural barriers that reduce exchanges. In our study we preferred to use only the term family group and to avoid the term "colony". Indeed, in the Reserve of "La Grande Sassière", groups are not patchily distributed but form a continuum over more than 5 km without any natural barriers. Therefore it was not possible to identify colonies. For the same reason, isolated family groups were not observed. In our study, one colony could then correspond to the population.

Distribution of Activities

The activity budget of the Alpine marmot was characterized by foraging, postures, locomotion and social interactions.

Foraging increased in Aug. whereas other activities such as postures and social interactions decreased, but foraging decreased in Sep. while other activities increased. This fluctuation in foraging was expected. It was strongly correlated with weight gain and hibernation. As summer proceeded, both *Marmota caligata* and *M. olympus* became lethargic but continued to gain weight, despite reduced foraging (BARASH 1989). The rate of weight gain and food consumption by *M. monax* changed seasonally even when fed ad lib. (BAILEY 1965, DAVIS 1967). Similarly, captive *M. flaviventris* showed roughly annual cycles in food consumption, body mass and metabolic rate (WARD & ARMITAGE 1981). It seems that under natural conditions, hibernation is induced by food deprivation and facilitated by the presence of large amounts of fat (LYMAN & DAWE 1960). Moreover, the seasonal decrease in metabolism rate may well facilitate weight gain and create a physiological predisposition for hibernation. This also allows fat deposition without increased food intake (BARASH 1989).

Utilization of Space

The MBS was the most frequently used area. Activities such as postures frequently occurred there. Such activity is related to the different functions of postures and to the configuration of the MBS. For instance, when marmots rested, reducing vigilance, the proximity of numerous deep burrows permitted rapid escape in an emergency. Postures could also be associated with visual exploration because the MBS was always a high point permitting a more efficient surveillance of the area to detect predators and intruders. Finally, the rocks (e.g. in group B) in this area served behavioural thermoregulation (TÜRK & ARNOLD 1988). Social interactions were observed more often on the MBS. This could result from frequent use of this area anyway, but scarcity of interactions between social groups could also be involved.

Peripheral areas were mainly used for foraging. At the end of the season most marmots tended to stay in the MBS, and occupied peripheral areas least. This was related to changes of activity (decrease of general activity and foraging, increase of MBS-related activities). Thus the distribution of activities and utilization of space by Alpine marmots changed notably during the season. The timing of hibernation could be the determinant factor.

Acknowledgements

This work is part of the research program "Dynamics of space occupation by Alpine Marmots" supported by a grant from the French Ministry of Environment (EGPN 90-294). We thank the Vanoise National Park for allowing us to work in the Reserve. We thank Pr L. LE GUELTE, Pr R. GRANTHAM and S. J. SALEK for their critical readings of this manuscript.

Literature Cited

ALEXANDER, R. D. 1974: The evolution of social behavior. Ann. Rev. Ecol. Syst. **5**, 325—383.

ALTMANN, J. 1974: Observational study of behavior: sampling methods. Behaviour **49**, 227—265.

ARMITAGE, K. B. 1962: Social behaviour of a colony of the yellow-bellied marmot (*Marmota flaviventris*). Anim. Behav. **10**, 319—331.

— — 1974: Male behaviour and territoriality in the yellow-bellied marmot. J. Zool. Lond. **192**, 233—265.

— — 1975: Social behavior and population dynamics of marmots. Oikos **26**, 341—354.

— — 1981: Sociality as a life-history tactic of ground squirrels. Oecologia **48**, 36—49.

— — 1986: Marmot polygyny revisited: determinants of male and female reproductive strategies. In: Ecological Aspects of Social Evolution. (RUBENSTEIN, D. I. & WRANGHAM, R. W., eds.) Princeton Univ. Press, Princeton, pp. 303—331.

— — 1988: Resources and social organization of ground-dwelling squirrels. In: The Ecology of Social Behavior. (SLOBODCHIKOFF, C. N., ed.) Acad. Press, New York, pp. 131—155.

— — 1991: Social and population dynamics of yellow-bellied marmots: results from long-term research. Ann. Rev. Ecol. Syst. **22**, 379—407.

ARNOLD W. 1990a: The evolution of marmot sociality: I. Why disperse late? Behav. Ecol. Sociobiol. **27**, 229—237.

— — 1990b: The evolution of marmot sociality: II. Costs and benefits of joint hibernation. Behav. Ecol. Sociobiol. **27**, 239—246.

BAILEY, E. D. 1965: Seasonal changes in metabolic activity of non-hibernating woodchucks. Can. J. Zool. **43**, 905—909.

BALFOUR, D. 1983: Infanticide in the Columbian ground squirrel, *Spermophilus columbianus*. Anim. Behav. **31**, 949—950.

BARASH, D. P. 1973: The social biology of the Olympic marmot. Anim. Behav. Monogr. **6**, 171—249.

— — 1974a: The social behaviour of the hoary marmot (*Marmota caligata*). Anim. Behav. **22**, 256—261.

— — 1974b: The evolution of marmot societies: a general theory. Science **185**, 415—420.

— — 1976: Social behaviour and individual differences in free-living Alpine marmots (*Marmota marmota*). Anim. Behav. **24**, 27—35.

— — 1989: Marmots: Social Behavior and Ecology. Stanford Univ. Press, Stanford.

BRODY, A. K. & MELCHER, J. 1984: Infanticide in yellow-bellied marmots. Anim. Behav. **33**, 673—674.

BRONSON, F. H. 1963: Some correlates of interaction rate in natural populations of woodchucks. Ecology **44**, 637—644.

— — 1964: Agonistic behaviour in woodchucks. Anim. Behav. **12**, 470—478.

DAVIS, D. E. 1967: The annual rhythm of fat deposition in woodchucks (*Marmota monax*). Physiol. Zool. **40**, 391—402.

— — 1981: Mechanism for decline in a woodchuck population. J. Wildl. Manage. **45**, 658—668.

DOBSON, F. S. 1984: Environmental influences on sciurid mating systems. In: The Biology of Ground-Dwelling Squirrels. (MURIE, J. O. & MICHENER, G. R., eds.) Univ. of Nebraska Press, Lincoln, pp. 227—249.

FERRON, J. & OUELLET, J. P. 1989: Temporal and intersexual variations in the use of space with regard to social organization in the woodchuck (*Marmota monax*). Can. J. Zool. **67,** 1642—1649.

GENSAC, P. & ROTHE, B. 1974: Carte de la végétation de la Réserve de la Grande Sassière. Trav. Sci. Parc nation. Vanoise **5,** 77—103.

GRIZZELL, R. A. 1955: A study of the southern woodchuck, *Marmota monax*. Am. Midl. Nat. **53,** 257—293.

HOLMES, W. G. 1984: The ecological basis of monogamy in Alaskan hoary marmots. In: The Biology of Ground-Dwelling Squirrels. (MURIE, J. O. & MICHENER, G. R., eds.) Univ. of Nebraska Press, Lincoln, pp. 250—274.

HONACKI, J. H., KINMAN, K. E. & KOEPPL, J. W. 1982: Mammal Species of the World: a Taxonomic and Geographic Reference. Allen Press Inc. Ass. Syst. Coll., Lawrence, pp. 354—356.

HOOGLAND, J. L. 1981: The evolution of coloniality in white-tailed and black-tailed prairie dogs (Sciuridae: *Cynomys leucurus* and *Cynomys ludovicianus*). Ecology **62,** 252—272.

— — 1985: Infanticide in prairie dogs: lactating females kill offspring of close kin. Science **230,** 1037—1040.

KING, J. A. 1955: Social behavior, social organization, and population dynamics in a black-tailed prairie dog town in the Black Hills of South Dakota. Contr. Lab. Vert. Biol. Univ. Michigan **67,** 1—123.

KLEIMAN, D. G. 1977: Monogamy in mammals. Qu. Rev. Biol. **52,** 39—69.

LYMAN, C. P. & DAWE, A. R. 1960: Mammalian hibernation. Bull. Mus. Comp. Zool. **124,** 1—549.

MANN, C. S. & JANEAU, G. 1988: Occupation de l'espace, structure sociale et dynamique d'une population de marmottes des Alpes (*Marmota marmota* L.). Gibier Faune Sauvage **5,** 427—445.

MCLEAN, I. G. 1983: Paternal behaviour and killing of young in Arctic ground squirrels. Anim. Behav. **31,** 32—44.

MICHENER, G. R. 1982: Infanticide in ground squirrels. Anim. Behav. **30,** 936—938.

— — 1983: Kin identification, matriarchies and the evolution of sociality in ground-dwelling squirrels. In: Recent Advances in the Study of Mammalian Behavior. Spec. Publ. no. 7. (EISENBERG, J. F. & KLEIMAN, D. G., eds.) Am. Soc. Mammal., Shippenburg, pp. 528—572.

— — 1984: Age, sex and species differences in the annual cycles of ground-dwelling sciurids, implications of sociality. In: The Biology of Ground-Dwelling Squirrels. (MURIE, J. O. & MICHENER, G. R., eds.) Univ. of Nebraska Press, Lincoln, pp. 81—107.

MURIE, J. O. & MICHENER, G. R. 1984: The Biology of Ground-Dwelling Squirrels. Univ. of Nebraska Press, Lincoln.

MOHR, C. O. 1947: Table of equivalent populations of North American small mammals. Am. Midl. Nat. **37,** 223—249.

OUELLET, J. P. & FERRON, J. 1986: L'utilisation de l'espace par la marmotte commune (*Marmota monax*). Naturaliste Can. **113,** 263—273.

SHERMAN, P. W. 1981: Reproductive competition and infanticide in Belding's ground squirrels and other animals. In: Natural Selection and Social Behavior: Recent Research and New Theory. (ALEXANDER, R. D. & TINKLE, D. W., eds.) Chiron Press, New York, pp. 311—331.

TÜRK, A. & ARNOLD, W. 1988: Thermoregulation as a limit to habitat use in Alpine marmots (*Marmota marmota*). Oecologia **76,** 544—548.

WARD, J. M. & ARMITAGE, K. B. 1981: Circannual rhythms of food consumption, body mass and metabolism in yellow-bellied marmots. Comp. Biochem. Physiol. **69,** 621—626.

WICKLER, W. & SEIBT, U. 1983: Monogamy: an ambiguous concept. In: Mate Choice.(BATESON, P., ed.) Cambridge Univ. Press, Cambridge, pp. 33—50.

ZELENKA, G. 1965: Observations sur l'écologie de la marmotte des Alpes. Terre et Vie **112,** 238—256.

Received: June 5, 1992

Accepted: September 21, 1992 (W. Wickler)