

Costs and benefits of sociality in yellow-bellied marmots (*Marmota flaviventris*): do noncolonial females have lower fitness?

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Whether an animal lives alone or in a group may have fitness consequences. Among yellow-bellied marmots (*Marmota flaviventris*), fitness is thought to be lower for noncolonial than for colonial females because juvenile survival, as indicated by trapping, is lower. Trapping, however, may not be an accurate estimate of survival. Low recapture rates of noncolonial juveniles may result from early dispersal due to maternal behavior, or higher mortality due to predation or inadequate resources for overwinter survival. Our objective was to determine if survival was lower for noncolonial than for colonial juveniles, and to determine the cause of the low recapture rate of noncolonial juveniles. Our results show that survival of noncolonial juveniles was not lower than that of colonial juveniles. Noncolonial juveniles were not more vulnerable to predation during the active season, nor was overwinter mortality higher. Some noncolonial juveniles did disperse early, and most moved away from the natal burrow to hibernate, thereby explaining the low recapture rate reported previously. Early dispersal was not related to maternal behavior. Noncolonial females do not enjoy the benefits of group-living, especially the opportunity to form matriline; but they also do not suffer the costs, such as competition for resources.

KEY WORDS: intraspecific variation, sociality, survival, fitness, dispersal, predation, ground-squirrel, yellow-bellied marmot.

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INTRODUCTION

Many species of vertebrates exhibit intraspecific variation in their social systems. Within a species, or even within a population, some individuals live in groups while others live alone (LOTT 1991). Such variation may result from one behavioral phenotype responding to different environmental circumstances, different phenotypes responding to the same environment, or both (LOTT 1991). Whether an animal lives alone or in a group may affect fitness (HOOGLAND 1995). For example, animals living in groups may benefit from reduced risk of predation (KENWARD 1978), improved food acquisition (CARO 1994), or lower energetic costs (ARNOLD 1990). Animals living alone may benefit from reduced intraspecific competition for resources (PACKER et al. 1990), reduced aggression (LE BOEUF & BRIGGS 1977), or lower disease transmission (SHIELDS & CROOK 1987).

The yellow-bellied marmot (*Marmota flaviventris*), a large, ground-dwelling squirrel, shows intraspecific variation in its social system. Marmots hibernate 2/3 of the year and perform all maintenance, growth, and reproductive activities in the remaining third (DAVIS 1976). Marmots live in either of two social environments. Most marmots are colonial, in which two or more adult females live and mate with one polygynous male (ARMITAGE 1974, ARMITAGE & DOWNHOWER 1974). Colonial offspring remain within the colony until they are 1 year of age, when typically all males and about half of females disperse (ARMITAGE 1974, ARMITAGE & DOWNHOWER 1974, VAN VUREN 1990). Remaining female offspring then may be recruited to live permanently within the colony, potentially contributing to their mother's fitness (ARMITAGE 1988). Thus, marmot groups are formed by retention of daughters in the natal area (ARMITAGE 1984).

Some marmots, however, are relatively asocial and live away from colonies on smaller habitat patches (ARMITAGE 1974, 1986; SVENDSEN 1974; VAN VUREN & ARMITAGE 1994a). The fate of the offspring of these noncolonial marmots is poorly known. Colonial and noncolonial females do not differ significantly in production of offspring as determined by frequency of reproduction or litter size (VAN VUREN & ARMITAGE 1994a). First-year survival of noncolonial offspring, however, is thought to be lower because fewer are recaptured at age one the following year (ARMITAGE & DOWNHOWER 1974, VAN VUREN & ARMITAGE 1994a). Further, survival of offspring from age 1 year to 2 years is lower in noncolonial marmots (VAN VUREN & ARMITAGE 1994a).

Lower survival of noncolonial offspring led to the conclusion that noncolonial adult females had lower fitness than colonial females (ARMITAGE & DOWNHOWER 1974, BARASH 1989, VAN VUREN & ARMITAGE 1994a). Survival of offspring to age one, however, was estimated by trapping, and the accuracy of trapping to estimate survival is uncertain (VAN VUREN & ARMITAGE 1994a). Possibly, some marmots were alive at age one but did not enter traps. Yet, despite intensive efforts to recapture all offspring still alive at age 1 year, the recapture rate of noncolonial yearlings remained 36% lower than that of colonial yearlings (VAN VUREN & ARMITAGE 1994a).

Three explanations were advanced to account for the lower recapture rate of noncolonial versus colonial yearlings. First, noncolonial offspring may suffer higher rates of predation during their first active season, between first emergence from the natal burrow and first hibernation (SVENDSEN 1974, VAN VUREN & ARMITAGE 1994a). Marmots often emit an alarm call when a predator is detected (ARMITAGE 1962, 1982), so predation risk may be lower in colonies, where larger group size presumably results in increased probability of predator detection (SVENDSEN 1974). Further-

more, burrows of noncolonial marmots are closer to potential hiding cover for predators than are burrows in colonies (SVENDSEN 1974, VAN VUREN & ARMITAGE 1994a). Proximity of hiding cover may also increase the risk of predation (ARMITAGE 1982).

Second, noncolonial juveniles may disperse early, during their first active season, and suffer high mortality due to predation (SVENDSEN 1974); such early dispersal was suspected but never confirmed (VAN VUREN & ARMITAGE 1994a). Dispersal of yearling marmots is influenced by adult behavior (DOWNHOWER & ARMITAGE 1981), thus maternal behavior could promote early dispersal of noncolonial juveniles. Colonial marmots, like other highly social species of ground-dwelling squirrels, continue to invest in offspring by allowing them to remain within the natal area until they disperse as yearlings or are recruited into the colony (ARMITAGE 1981, 1984). Cohesive behaviors between mother and offspring act to extend this association in relatively social species but end during the natal summer in asocial species (ARMITAGE 1981, MICHENER 1983, RAYOR & ARMITAGE 1991). Consequently, noncolonial female marmots may show less cohesive behaviors when compared with colonial females, thereby promoting early dispersal. Previous research showed that behavior of female marmots does differ according to social environment. SVENDSEN & ARMITAGE (1973) classified adult female marmots into different behavioral phenotypes; aggressive females were usually noncolonial, social females were primarily colonial, and avoider females either lived on the fringe of a colony or were noncolonial (SVENDSEN 1974). Aggressive behavior of noncolonial females may encourage early dispersal.

Third, overwinter survival of noncolonial offspring may be lower because of poor habitat quality (VAN VUREN & ARMITAGE 1994a). Marmots inhabit a seasonal, relatively severe environment in which juveniles must grow rapidly in order to store enough fat to survive hibernation (ARMITAGE et al. 1976, LENIHAN & VAN VUREN 1996). Marmots eat herbaceous vegetation and hibernate in burrows deep underground. Localities inhabited by noncolonial marmots are smaller in size and contain fewer burrows than localities inhabited by colonial marmots (SVENDSEN 1974). Thus, noncolonial juveniles may lack the resources necessary for rapid growth or an adequate hibernaculum.

The objective of this study was to determine if survival to age one is lower for noncolonial than for colonial marmots, and to determine the cause of the low recapture rate of noncolonial offspring. We used radio telemetry to improve the accuracy of survival estimates and to determine if noncolonial juveniles were dispersing early. We conducted behavioral observations to determine the role of maternal behavior in early dispersal, and we measured summer weight gain and overwinter weight loss to determine the influence of habitat quality on overwinter survival.

METHODS

This study was conducted from June 1991 through May 1993 in the East River Valley near the Rocky Mountain Biological Laboratory, Gunnison County, Colorado. The study area was approximately 4 km long and ranged in elevation from 2,800 to 3,050 m. Common habitats were spruce forests (*Picea* spp.), aspen woodlands (*Populus tremuloides*), and subalpine meadows dominated by tall forbs and grasses.

Distribution of marmots throughout the valley is clumped corresponding to the patchy distribution of suitable habitat (SVENDSEN 1974), which is rock outcrops or talus adjacent to meadows. The larger habitat patches are inhabited by a colony, defined as a discrete locality

supporting one adult (2 years old or more) male and two or more adult females, plus yearlings and juveniles (young of the year) (VAN VUREN & ARMITAGE 1994a). Up to 12 adult females may live in a colony, interacting socially within areas of home range overlap (ARMITAGE 1991). Noncolonial sites are smaller in area and are inhabited usually by only one adult female and occasionally an adult male (VAN VUREN & ARMITAGE 1994a). Yearlings are uncommon at noncolonial sites (SVENDSEN 1974). Nine litters at 3 colonies (localities 1, 4, and 5 in ARMITAGE 1974) and 13 litters at 11 noncolonial sites were studied.

Since 1962, marmots in the study area have been individually marked with ear-tags, and personal life histories are known for most (ARMITAGE 1991). Each year every marmot is captured, ear-tagged, weighed, and dye-marked for individual recognition. Locations inhabited by visibly pregnant females were monitored to confirm the appearance of a litter aboveground. Juveniles were trapped soon after emergence from the natal burrow, thus maternity and location of birth were identified. Weaning coincides with first emergence from the natal burrow in woodchucks (*Marmota monax*) (GRIZZELL 1951, FERRON & OUELLET 1991), so we considered date of weaning to be the day on which a litter was first observed aboveground. Juveniles were re-trapped and weighed regularly throughout the active season until entry into hibernation. The following spring intensive efforts were made to trap and weigh all offspring that survived hibernation.

Survival was determined through radio telemetry and trapping. Radio transmitters were surgically implanted into juvenile marmots shortly after weaning; neither surgery nor the transmitter had any effect on mortality or behavior (VAN VUREN 1989). Transmitted animals were monitored until hibernation in both years. In 1991, 10 noncolonial juveniles were implanted with transmitters and, in 1992, 21 noncolonial and 7 colonial juveniles were implanted. No colonial juveniles were implanted in 1991. Additionally, during 1992 transmitters were implanted in five of seven noncolonial mothers to facilitate locating them for behavioral observations. Juveniles with transmitters were located every 1 to 3 days until entry into hibernation.

Survival during the active season was calculated as the proportion of radioed juveniles that were alive at entry into hibernation. Active-season mortalities of instrumented marmots were suggested when the radio signal became invariant and were confirmed by recovery of the transmitter, often with the remains of the marmot (VAN VUREN 1990). Overwinter survival was determined for the winter of 1992-1993 only, and was calculated as the proportion of juveniles entering hibernation that survived overwinter. Juvenile littermates almost always hibernated together (LENIHAN & VAN VUREN 1996), and at least one juvenile from all litters but one carried a transmitter. Thus, radio telemetry permitted the location of each litter and its hibernaculum. Intensive trapping and observation, assisted by radio telemetry, were used to determine which marmots were alive at entry into and at emergence from hibernation. Annual survival was calculated as the proportion of juveniles marked at weaning that were recaptured the following year as yearlings. Success at recapturing yearlings was improved by trapping intensively at each hibernaculum, beginning before emergence from hibernation.

To determine if early dispersal was occurring, we recorded the locations of colonial and noncolonial juveniles regularly throughout their first active season, using radio telemetry along with observation and trapping. Locations of juveniles were recorded, and distance from the natal burrow was measured using a range finder. Because littermates remained together, distance measures were pooled within each litter over 2-week intervals after weaning. Litter means per interval were used to calculate grand means for colonial and noncolonial juveniles for each 2-week interval.

Behavioral observations were employed to describe mother-offspring interactions as well as to determine the location of juveniles. Observations commenced soon after litters were weaned (late June to mid-July) and continued until mid-August each year. Observations were conducted when marmots were most active, during morning, late afternoon, and evening (ARMITAGE 1962). Five-minute scan samples were conducted (ALTMANN 1974), recording the identity and location of all marmots within view. Social interactions were recorded during the same period by all-occurrences sampling (ALTMANN 1974). Interactions were classified as amicable (play, greet, groom) or avoidance/agonistic (rebuff, fight, chase, attack) (KING 1955,

SVENDSEN & ARMITAGE 1973, ARMITAGE 1977). The time available for interaction was considered as the amount of time that both the mother and one or more offspring were above-ground simultaneously and within 10 m of each other. A chi-square analysis was used to determine whether amicable or avoidance/agonistic behavioral interactions occurred randomly among social environments (RAYOR & ARMITAGE 1991). The expected rate (calculated from equation 7 of ALTMANN & ALTMANN 1977) of mother-offspring interactions was based on the total number of interactions and the percentage of time available for interaction within each social environment.

To assess the possible effects of differences in habitat quality between colonial and non-colonial marmots, we used data on weight at each capture to calculate and compare growth rates, weight at entry into hibernation, and overwinter weight loss of colonial and noncolonial offspring. Growth of juvenile marmots has two phases, a period of positive growth followed by a period of stable body weight until entry into hibernation (LENIHAN & VAN VUREN 1996). Growth rate was calculated for each litter and was estimated using the slope of a regression line fitted to weights of juveniles in the litter during the period of positive growth. Weight at entry into hibernation was calculated for each juvenile and was estimated using the mean of weights recorded after growth ceased. Overwinter weight loss was calculated for those juveniles that survived hibernation (LENIHAN & VAN VUREN 1996). Colonial and noncolonial sample variances were statistically different, so means were compared by a t-test for unequal variances (ZAR 1984).

RESULTS

In 1992, survival of transmitted juveniles during their first active season was identical for colonial (0.71, $n = 7$) and noncolonial (0.71, $n = 21$) offspring. No colonial juveniles were radioed in 1991, but survival of radioed noncolonial juveniles (0.90, $n = 10$) was high. Nine transmitted juveniles died during the active season (0.24, $n = 38$); all were attributed to predation. Identification of predators was determined by tooth impressions on the wax covered transmitter and circumstances of the mortality (VAN VUREN 1990); predators identified included coyotes (*Canis latrans*) and pine martens (*Martes americana*). Overwinter survival of noncolonial juveniles (0.96, $n = 26$) was higher ($\chi^2 = 7.89$, $df = 1$, $P < 0.005$) than that of colonial juveniles (0.55, $n = 11$) during the winter of 1992-1993. For 1991-1992, annual survival of noncolonial juveniles (0.70, $n = 23$) was higher ($\chi^2 = 10.36$, $P < 0.005$) than that of colonial juveniles (0.26, $n = 34$). For 1992-1993, annual survival of noncolonial juveniles (0.60, $n = 42$) did not differ ($\chi^2 = 1.18$, $P > 0.25$) from that of colonial juveniles (0.43, $n = 14$).

By 2 weeks after weaning all juveniles were ranging away from the natal burrow, but by 4 weeks noncolonial juveniles were moving further (Fig. 1). Noncolonial juveniles went on exploratory excursions (JOHNSON 1989, VAN VUREN 1990) away from their natal burrow area that involved overnight stays in burrows new to these juveniles. Colonial juveniles, on the other hand, remained within the colony and generally stayed in or near the natal burrow each night. Distances peaked at 10 weeks after weaning for noncolonial and at 12 weeks for colonial juveniles (Fig. 1). Thereafter colonial juveniles ranged closer to the natal burrow, but noncolonial juveniles did not. All colonial juveniles hibernated within 15 m of the natal burrow, whereas noncolonial juveniles in only 4 of 13 litters hibernated within 15 m of the natal burrow (Fig. 1).

Some noncolonial juveniles moved long distances from their natal burrow. One moved 520 m and then was killed by a coyote; another moved 350 m then

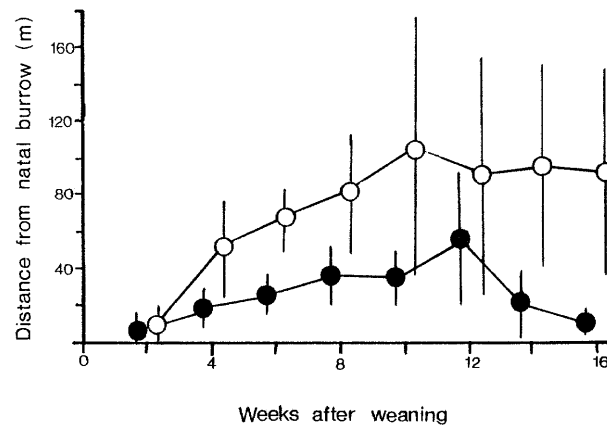


Fig. 1. — Movements from the natal burrow by colonial (solid circles) and noncolonial (open circles) juveniles from weaning until entry into hibernation. Vertical bars represent the mean $\pm$ 95% confidence intervals for each 2-week interval. Week 16 represents the location of the hibernaculum.

hibernated alone. Two litters totalling nine juveniles moved 320 m with their mothers then hibernated.

Spatial relationships of mother and juveniles differed between social environments. Noncolonial mothers and their offspring were recorded together up to 425 m from the natal burrow, whereas the furthest distance recorded for a colonial mother with offspring was 170 m. At least two noncolonial mothers temporarily abandoned their litters. One moved 555 m away from her litter 5 weeks after weaning, then returned 2 weeks later and hibernated with her litter. The other left her litter 2 weeks after weaning; when she returned 5 weeks later most of her litter had disappeared. In addition, 3 of 13 noncolonial mothers were killed by predators, leaving orphaned litters behind.

Mother-offspring interactions were recorded during 227 hr of behavioral observations. Interaction rates were 2.56 interactions/hr for colonial females and 3.24 interactions/hr for noncolonial females. Amicable interactions between mother

Table 1.

Frequency analysis of amicable and avoidance/agonistic interactions by colonial and noncolonial female yellow-bellied marmots towards their offspring.

	Amicable		Avoidance/Agonistic	
	expected	observed	expected	observed
Colonial	47.35	40	3.9	3
Noncolonial	136.65	144	11.10	12
χ^2	1.54		0.28	
P	> 0.10		> 0.75	

Table 2.

Growth rate, weight at entry into hibernation, and overwinter weight loss for colonial and noncolonial juvenile yellow-bellied marmots. Growth rates are based on litters, and weight at entry into hibernation and overwinter weight loss are based on individuals.

	Colonial	Noncolonial	<i>P</i>
Growth rate (g/day)			
Mean	17.0	22.2	0.03
SD	3.13	6.15	
n	9	10	
Weight at entry into hibernation (g)			
Mean	1321	1746	< 0.001
SD	188	422	
n	31	41	
Overwinter weight loss (g)			
Mean	383	593	< 0.001
SD	152	213	
n	13	30	

and offspring predominated; 92% ($n = 144$) were amicable for noncolonial females and 93% ($n = 40$) for colonial females. The rate of amicable and avoidance/agonistic interactions between mother and offspring did not differ from expected ($P > 0.10$) for either colonial or noncolonial marmots (Table 1).

Growth rates ($t = 2.36$, $df = 14$, $P = 0.03$), weight at entry into hibernation ($t = 5.74$, $df = 58$, $P < 0.001$), and overwinter weight loss ($t = 3.66$, $df = 32$, $P < 0.001$) were all significantly higher in noncolonial offspring compared with colonial offspring (Table 2).

DISCUSSION

Intraspecific variation within a population may reflect environmental influences (DOBSON & MURIE 1987). Thus, social variation in yellow-bellied marmots may represent phenotypically plastic responses to environmental conditions such as availability of space, food resources, and hibernaculum quality. Models relating resources to sociality show that group size should increase with increasing resource abundance (SLOBODCHIKOFF & SCHULZ 1988). Accordingly, marmot group size is positively correlated with habitat patch size (SVENDSEN 1974). Variation in behavioral phenotypes also influences social variation in marmots; a highly aggressive female can exclude all other adult females from a habitat patch that otherwise supports a colony (ARMITAGE 1975).

Predation is an important source of mortality affecting the behavior of prey species. Protection from predators is cited not only as an important benefit of colonial living but often as an impetus towards the evolution of sociality (BERTRAM 1978, HOOGLAND 1981, CAMPAGNA et al. 1992). Evidence from other vertebrate species suggests that small groups incur a higher cost of predation (BIRKHEAD 1977, KENWARD 1978, HOOGLAND 1981, CAMPAGNA et al. 1992, YOUNG & ISBELL 1995) than

large groups. Likewise, previous research on marmots suggested that predation risk was higher in noncolonial marmots (ARMITAGE & DOWNHOWER 1974, SVENDSEN 1974). Because noncolonial groups are small, adult females spent more time in an alert posture while feeding than did colonial females (SVENDSEN 1974). Further, noncolonial sites contain fewer burrows in which to take cover from predators, and these burrows are often located close to cover where predators may hide (SVENDSEN 1974). Nonetheless, we detected no difference in vulnerability to predation between colonial and noncolonial juveniles.

Three noncolonial litters were orphaned after the death of their mother and one was deserted for 5 weeks, while no colonial litter was orphaned or deserted during this study. Desertion by noncolonial mothers was also observed twice by SVENDSEN (1974). Despite the absence of the mother in 4 of 13 litters, noncolonial juveniles did not suffer higher predation. Apparently, noncolonial mothers did not play an important role in predator detection or defense.

Both colonial and noncolonial juveniles showed a pattern of exploratory movement away from the natal burrow after weaning, followed by a return toward the natal burrow as hibernation approached. Noncolonial juveniles, however, moved significantly farther. Moreover, noncolonial juveniles often remained overnight in areas far from the natal burrow and were less likely than colonial juveniles to return to the natal area to hibernate. Noncolonial juveniles may have moved more because they had more freedom to do so. Space within colonies is subdivided by groups of related females called matriline (ARMITAGE 1991). Members of a matriline share common home ranges and may occupy the same burrow system, but members of different matrilines never share burrows and show little home range overlap (ARMITAGE 1991). Conversely, noncolonial localities are relatively isolated, thus juveniles can range farther without encountering aggressive conspecifics.

Dispersal is the one-way movement of an animal away from its home area (LIDICKER 1975). No colonial juveniles dispersed, but some noncolonial juveniles did. Home ranges of noncolonial adult females averaged about 300 m in length (D. VAN VUREN unpub. data), so dispersal was defined as a one-way movement more than 300 m away from the natal burrow. Two noncolonial juveniles from different litters made such a move alone. Nine juveniles comprising two litters made such a move accompanied by their mothers, thereby undergoing locational dispersal, in which they left a familiar area but maintained social contact with their mother and litter mates (ISBELL & VAN VUREN 1996). These results document early dispersal by noncolonial juveniles, which has long been suspected (DOWNHOWER & ARMITAGE 1971) but never confirmed (VAN VUREN & ARMITAGE 1994a).

Greater mobility of noncolonial juveniles provides an explanation for the low recapture rates of yearlings reported in previous studies. Most colonial juveniles hibernated in or near the natal burrow; those that survived were trapped upon emergence the following spring. In contrast, most noncolonial juveniles hibernated away from the natal burrow at locations that were known during this study only because of radio telemetry. Thus, trapping efforts the following spring that focused only on the natal area would have missed noncolonial yearlings that were alive but living elsewhere.

The hypothesis that maternal behavior promotes early dispersal of noncolonial juveniles was not supported. Mother-offspring behavior did not differ between colonial and noncolonial marmots. For both social environments, almost all interactions were amicable. Similarly, ARMITAGE (1986) observed only amicable behaviors between colonial mothers and their offspring. If mother-offspring interactions

are an appropriate measure of maternal care (RAYOR & ARMITAGE 1991), then colonial and noncolonial mothers appear to be investing similarly in offspring during the juvenile phase.

Colonial and noncolonial marmots inhabit localities with significantly different physical structure (SVENDSEN 1974), suggesting that habitat quality may differ. Noncolonial juveniles, however, did not exhibit lower growth rates or hibernation weights than colonial juveniles. Indeed, noncolonial offspring showed higher growth rates and hibernation weights, suggesting that food resources may actually be greater in noncolonial habitats. Noncolonial juveniles range over larger distances than colonial juveniles and as a result may be able to search out high quality foods. Conversely, colonial juveniles range over smaller distances within the subdivided space of the colony, foraging within the limits of their mother's matriline. Heavier weight at entry into hibernation results in a higher probability of overwinter survival (LENIHAN & VAN VUREN 1996), explaining the higher overwinter survival of noncolonial offspring.

Overwinter survival may also be influenced by hibernaculum quality. Because there are fewer burrows at noncolonial sites, good hibernacula may be limiting, thus contributing to higher overwinter mortality (SVENDSEN 1974). Noncolonial juveniles lost more weight during hibernation than did colonial juveniles. This difference may result, in part, because noncolonial juveniles weighed more at entry into hibernation; in Alpine marmots (*Marmota marmota*), the absolute magnitude of overwinter weight loss was greater in larger marmots (ARNOLD 1990). But, higher weight loss could also indicate lower hibernaculum quality (ARNOLD 1990). Noncolonial juveniles, however, did not suffer higher overwinter mortality; possibly, higher weight gain during the active season compensated for any negative effects of hibernaculum quality on overwinter weight loss. Further, noncolonial juveniles, despite ranging widely during the active season, remained together and hibernated as a group. Joint hibernation in groups of Alpine marmots resulted in increased survival of juveniles (ARNOLD 1990).

CONCLUSION

Juvenile survival among marmots in the East River Valley varies from year to year (ARMITAGE 1991), in part because of variation in environmental factors. For example, predation pressure on marmots during summer varies among years (VAN VUREN 1991), and overwinter survival of juveniles may be reduced by summer drought during the active season (ARMITAGE 1994) or persistent snow cover the following spring (ARMITAGE & DOWNHOWER 1974). Previous estimates of survival of colonial offspring to age 1 year range 0.47 to 0.55 (ARMITAGE & DOWNHOWER 1974, VAN VUREN & ARMITAGE 1994a). Survival of colonial offspring born in 1991 (0.26) was substantially lower, leading to the unexpected result that survival of noncolonial offspring was significantly higher than that of colonial offspring. Especially low rainfall during the summer of 1991 and its effect on overwinter survival may be the cause. Effects on survival varied geographically (ARMITAGE 1994), and colonies, perchance, may have been more severely affected.

Our results show that survival of noncolonial juveniles to age one was not lower than that of colonial juveniles. Noncolonial juveniles were not more vulnerable to predation during the active season, nor was overwinter mortality higher.

Noncolonial juveniles may have hibernated in poorer quality burrows, but the resultant energetic cost apparently was balanced by higher growth rates. Some noncolonial juveniles did disperse, and most moved away from the natal burrow to hibernate, thereby explaining the low recapture rate of noncolonial yearlings reported in previous studies.

An important benefit for females in colonies is the opportunity to form matriline, groups of close kin which result from recruitment of daughters (ARMITAGE 1988). Members of a matriline may cooperate in defense of the home range against conspecifics and in detection of predators (ARMITAGE & JOHNS 1982), although a lower risk of predation in colonies has not been demonstrated. Matriline formation is a form of parental investment; because dispersal has a survival cost (VAN VUREN & ARMITAGE 1994b), females may improve their own direct fitness by retaining daughters in the natal area (ARMITAGE 1988).

Coloniality, however, has several costs. Females compete for resources, especially burrows and foraging areas (ARMITAGE 1989), and reproductive success may suffer because of reproductive suppression (ARMITAGE 1986) or infanticide (BRODY & MELCHER 1985). Disease has long been considered a potential cost of sociality (ALEXANDER 1974); although parasites decreased the fitness of Alpine (ARNOLD & LICHTENSTEIN 1993) and yellow-bellied marmots (VAN VUREN 1996), parasite loads did not differ between colonial and noncolonial yellow-bellied marmots (VAN VUREN 1996).

Noncolonial females rarely form matrilines, primarily because of insufficient space (ARMITAGE 1988). Instead, almost all their offspring eventually disperse. A higher rate of dispersal, coupled with lower survival of dispersers (VAN VUREN & ARMITAGE 1994b), resulted in lower survival of noncolonial offspring from age one to age two (VAN VUREN & ARMITAGE 1994a). Thus, noncolonial females do not enjoy the benefits of matriline formation, but they also do not suffer the costs associated with living in close proximity to conspecifics.

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REFERENCES

- ALEXANDER R.D. 1974. The evolution of social behavior. *Annual Review of Ecology and Systematics* 5: 325-383.
- ALTMANN J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49: 227-267.
- ALTMANN S.A. & ALTMANN J. 1977. On the analysis of rates of behaviour. *Animal Behaviour* 25: 364-372.

- ARMITAGE K.B. 1962. Social behaviour of a colony of the yellow-bellied marmot (*Marmota flaviventris*). *Animal Behaviour* 10: 319-331.
- ARMITAGE K.B. 1974. Male behaviour and territoriality in the yellow-bellied marmot. *Journal of Zoology, London* 172: 233-265.
- ARMITAGE K.B. 1975. Social behavior and population dynamics of marmots. *Oikos* 26: 341-354.
- ARMITAGE K.B. 1977. Social variety in the yellow-bellied marmot: a population-behavioural system. *Animal Behaviour* 25: 585-593.
- ARMITAGE K.B. 1981. Sociality as a life-history tactic of ground squirrels. *Oecologia* 48: 36-49.
- ARMITAGE K.B. 1982. Marmots and coyotes: behavior of prey and predator. *Journal of Mammalogy* 63: 503-505.
- ARMITAGE K.B. 1984. Recruitment in yellow-bellied marmot populations: kinship, philopatry, and individual variability, pp. 377-403. In: Murie J.O. & Michener G.R., Edits. *Biology of ground-dwelling squirrels: annual cycles, behavioral ecology, and sociality*. Lincoln: University of Nebraska Press.
- ARMITAGE K.B. 1986. Marmot polygyny revisited: determinants of male and female reproductive strategies, pp. 303-331. In: Rubenstein D.I. & Wrangham R.W., Edits. *Ecological aspects of social evolution: birds and mammals*. Princeton: Princeton University Press.
- ARMITAGE K.B. 1988. Resources and social organization of ground-dwelling squirrels, pp. 131-155. In: Slobodchikoff C.N., Edit. *Ecology of social behavior*. San Diego: Academic Press.
- ARMITAGE K.B. 1989. The function of kin discrimination. *Ethology Ecology & Evolution* 1: 111-121.
- ARMITAGE K.B. 1991. Social and population dynamics of yellow-bellied marmots: results from long-term research. *Annual Review of Ecology and Systematics* 22: 379-407.
- ARMITAGE K.B. 1994. Unusual mortality in a yellow-bellied marmot population, pp. 5-13. In: Rumiantsev V.Y., Edit. *Actual problems of marmot investigation*. Moscow: A.B.F. Publishing House.
- ARMITAGE K.B. & DOWNHOWER J.F. 1974. Demography of yellow-bellied marmot populations. *Ecology* 55: 1233-1245.
- ARMITAGE K.B., DOWNHOWER J.F. & SVENDSEN G.E. 1976. Seasonal changes in weights of marmots. *American Midland Naturalist* 96: 36-51.
- ARMITAGE K.B. & JOHNS D.W. 1982. Kinship, reproductive strategies and social dynamics of yellow-bellied marmots. *Behavioral Ecology and Sociobiology* 11: 55-63.
- ARNOLD W. 1990. The evolution of marmot sociality: II. Costs and benefits of joint hibernation. *Behavioral Ecology and Sociobiology* 27: 239-246.
- ARNOLD W. & LICHTENSTEIN A.V. 1993. Ectoparasite loads decrease the fitness of Alpine marmots (*Marmota marmota*) but are not a cost of sociality. *Behavioral Ecology* 4: 36-39.
- BARASH D.P. 1989. Marmots: social behavior and ecology. Stanford, California: Stanford University Press.
- BERTRAM B.C.R. 1978. Living in groups: predators and prey, pp. 64-96. In: Krebs J.R. & Davies N.B., Edits. *Behavioural ecology: an evolutionary approach*. Oxford: Blackwell Scientific Publications.
- BIRKHEAD T.R. 1977. The effect of habitat and density on breeding success in the common guillemot (*Uria aalge*). *The Journal of Animal Ecology* 46: 751-764.
- BRODY A.K. & MELCHER J. 1985. Infanticide in yellow-bellied marmots. *Animal Behaviour* 33: 673-674.
- CAMPAGNA C., BISIOLI C., QUINTANA F., PEREZ F. & VILA A. 1992. Group breeding in sea lions: pups survive better in colonies. *Animal Behaviour* 43: 541-548.
- CARO T.M. 1994. Cheetahs of the Serengeti Plains: group living in an asocial species. Chicago, Illinois: University of Chicago Press.
- DAVIS D.E. 1976. Hibernation and circannual rhythms of food consumption in marmots and ground squirrels. *The Quarterly Review of Biology* 51: 477-514.
- DOBSON F.S. & MURIE J.O. 1987. Interpretation of intraspecific life history patterns: evidence from Columbian ground squirrels. *The American Naturalist* 129: 382-397.

- DOWNHOWER J.F. & ARMITAGE K.B. 1971. The yellow-bellied marmot and the evolution of polygamy. *The American Naturalist* 105: 355-370.
- DOWNHOWER J.F. & ARMITAGE K.B. 1981. Dispersal of yearling yellow-bellied marmots (*Marmota flaviventris*). *Animal Behaviour* 29: 1064-1069.
- FERRON J. & OUELLET J.P. 1991. Physical and behavioral postnatal development of woodchucks (*Marmota monax*). *Canadian Journal of Zoology* 69: 1040-1047.
- GRIZZELL R.A. 1951. Life history, ecology and management of the southern woodchuck. *Ph.D. Dissertation, University of Michigan, Ann Arbor*.
- HOOGLAND J.L. 1981. Evolution of coloniality in white-tailed and black-tailed prairie dogs (Sciuridae: *Cynomys leucurus* and *C. ludovicianus*). *Ecology* 62: 252-272.
- HOOGLAND J.L. 1995. The black-tailed prairie dog: social life of a burrowing mammal. *Chicago, Illinois: University of Chicago Press*.
- ISBELL L.A. & VAN VUREN D. 1996. Differential costs of locational and social dispersal and their consequences for female group living primates. *Behaviour* (in press).
- JOHNSON M.L. 1989. Exploratory behavior and dispersal: a graphical model. *Canadian Journal of Zoology* 67: 2325-2328.
- KENWARD R.E. 1978. Hawks and doves: factors affecting success and selection in goshawk attacks on wood-pigeons. *Journal of Animal Ecology* 47: 449-460.
- 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. *Contributions of the Laboratory of Vertebrate Biology, University of Michigan* 67: 1-123.
- LE BOEUF B.J. & BRIGGS K.T. 1977. The cost of living in a seal harem. *Mammalia* 41: 167-195.
- LENIHAN C. & VAN VUREN D. 1996. Growth and survival of juvenile yellow-bellied marmots (*Marmota flaviventris*). *Canadian Journal of Zoology* (in press).
- LIDICKER W.Z. JR 1975. The role of dispersal in the demography of small mammals, pp. 103-128. In: Golley F.B. et al., Edits. *Small mammals: their productivity and population dynamics*. London: Cambridge University Press.
- LOTT D.F. 1991. Intraspecific variation in the social systems of wild vertebrates. *Cambridge: Cambridge University Press*.
- MICHENER G.R. 1983. Kin identification, matriarchies, and the evolution of sociality in ground-dwelling sciurids, pp. 528-572. In: Eisenberg J.F. & Kleiman D.G., Edits. *Advances in the study of mammalian behavior: American Society of Mammalogists Special Publication No. 7*.
- PACKER C., SCHEEL D. & PUSEY A.E. 1990. Why lions form groups: food is not enough. *American Naturalist* 136: 1-19.
- RAYOR L.S. & ARMITAGE K.B. 1991. Social behavior and space-use of young of ground-dwelling squirrel species with different levels of sociality. *Ethology Ecology & Evolution* 3: 185-205.
- SHIELDS W.M. & CROOK J.R. 1987. Barn swallow coloniality: a net cost for group breeding in the Adirondacks? *Ecology* 68: 1373-1386.
- SLOBODCHIKOFF C.N. & SCHULZ W.C. 1988. Cooperation, aggression, and the evolution of social behavior, pp. 13-32. In: Slobodchikoff C.N., Edit. *Ecology of social behavior*. San Diego: Academic Press.
- SVENDSEN G.E. 1974. Behavioral and environmental factors in the spatial distribution and population dynamics of a yellow-bellied marmot population. *Ecology* 55: 760-771.
- SVENDSEN G.E. & ARMITAGE K.B. 1973. Mirror-image stimulation applied to field behavioral studies. *Ecology* 54: 623-627.
- VAN VUREN D. 1989. Effects of intraperitoneal transmitter implants on yellow-bellied marmots. *The Journal of Wildlife Management* 53: 320-323.
- VAN VUREN D. 1990. Dispersal of yellow-bellied marmots. *Ph.D. Dissertation, University of Kansas, Lawrence*.
- VAN VUREN D. 1991. Yellow-bellied marmots as prey of coyotes. *American Midland Naturalist* 125: 135-139.
- VAN VUREN D. 1996. Ectoparasites, fitness, and social behaviour of yellow-bellied marmots. *Ethology* (in press).

- VAN VUREN D. & ARMITAGE K.B. 1994a. Reproductive success of colonial and noncolonial female yellow-bellied marmots (*Marmota flaviventris*). *Journal of Mammalogy* 75: 950-955.
- VAN VUREN D. & ARMITAGE K.B. 1994b. Survival of dispersing and philopatric yellow-bellied marmots: what is the cost of dispersal? *Oikos* 69: 179-181.
- YOUNG T. & ISBELL L.A. 1995. Minimum group size and other conservation lessons exemplified by a declining primate population. *Biological Conservation* 68: 129-134.
- ZAR J.H. 1984. Biostatistical analysis. *Englewood Cliffs, New Jersey: Prentice Hall*.