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# REPRODUCTIVE SUCCESS OF COLONIAL AND NONCOLONIAL FEMALE YELLOW-BELLIED MARMOTS (*MARMOTA FLAVIVENTRIS*)

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Previous work comparing reproductive success of colonial and noncolonial yellow-bellied marmots (*Marmota flaviventris*) indicated that noncolonial females had lower fitness; they reproduced less often and their offspring had a lower survival to age 1 year. This work, however, may have been affected by a bias in sampling effort. We initiated a new study and found no significant differences between colonial and noncolonial females in litter size or frequency of reproduction. We did, however, recapture a lower percentage of noncolonial offspring as yearlings; this may have resulted from early dispersal, higher mortality, or both. Further, survival of noncolonial offspring from age 1 to 2 years was lower; the cause probably was a higher dispersal rate of noncolonial versus colonial yearlings, coupled with lower survival of dispersers. We suggest that lower fitness of noncolonial females, as indicated by the apparently lower survival of their offspring and their lower likelihood of recruiting daughters to form matriline, derives from lower quantity and quality of resources at localities of noncolonial females.

**Key words:** *Marmota flaviventris*, reproductive success, colony, sociality

Understanding the evolution of sociality in mammals requires an evaluation of fitness costs and benefits of group living (Alexander, 1974). One approach has been to compare social systems among closely related species living in different ecological settings (Barash, 1974; Hoogland, 1981; Jarman, 1974). Alternatively, some species of mammals exhibit variable social systems that range from solitary to group living (Lott, 1991), thereby permitting intraspecific comparisons of the fitness consequences of sociality (Boyce and Boyce, 1988; Cowan, 1987; Packer et al., 1990).

The yellow-bellied marmot (*Marmota flaviventris*) is a large, hibernating, ground-dwelling squirrel that lives in social groups called colonies. Not all marmots, however, are colonial; some lead a relatively asocial existence outside of colonies, variously described as isolated, peripheral, or satellite (Downhower and Armitage, 1971; Svendsen, 1974), herein collectively termed noncolonial. Both behavioral phenotypes, co-

lonial and noncolonial, may exist within the same population; thus, this species exhibits an intraspecific variation in social behavior (Lott, 1991).

Living in a social or a solitary setting may entail different sets of costs and benefits. Armitage and Downhower (1974) compared reproduction and survival between colonial and noncolonial individuals in a population of yellow-bellied marmots located near Rocky Mountain Biological Laboratory, Gunnison Co., Colorado. Mean litter size was similar for colonial and noncolonial females, but frequency of reproduction was about twice as great for colonial females as for noncolonial females. Further, about one-half of colonial young-of-the-year were recaptured as yearlings, whereas noncolonial young were rarely recaptured. Downhower and Armitage (1971) proposed that disappearance of noncolonial young resulted from mortality or early dispersal and concluded that noncolonial females were reproductively less successful

than colonial females. These data suggested that noncolonial females produced fewer young per year than did colonial females, and, because survival of dispersers presumably is poor (Anderson, 1989), few, if any, of their young survived to reproductive maturity.

Fitness differences between colonial and noncolonial animals suggested a difference in habitat quality as well. Immigration into colonies by females is uncommon; most colony residents are born there (Armitage 1991; Armitage and Johns, 1982; Schwartz and Armitage, 1980). In contrast, most noncolonial females are immigrants, either from colonies or from localities inhabited by noncolonial marmots (pers. obser.). This net movement of marmots from colonies, where fitness is relatively high, to localities occupied by noncolonial marmots, where fitness presumably is low, suggests a source-sink relationship (Pulliam, 1988).

Armitage and Downhower (1974), however, estimated production and survival of young-of-the-year through trapping and observation, and these results may have been affected by a bias of sampling effort toward colonies. Colonies were trapped more intensively than were localities inhabited by noncolonial marmots and were trapped earlier in the season, before most dispersal occurred. Further, intensive behavioral observations of marmots were conducted regularly at colonies, but rarely at localities inhabited by noncolonial marmots; visual observation improved trap efficiency. Both frequent trapping and intensive observations promote the detection of survival and reproduction.

Our objective was to re-evaluate reproductive success of yellow-bellied marmots near Rocky Mountain Biological Laboratory by focusing intensive sampling effort on both colonial and noncolonial marmots to assess litter size, frequency of reproduction, and survival of young until 1 year old. Further, we determined the time of dispersal of yearlings to elucidate the possible role of early dispersal in low recapture rates of

noncolonial yearlings. Finally, because evolutionary fitness can be measured as the number of offspring that survive to reproductive maturity (Armitage, 1986a), we employed radiotelemetry to determine survival of yearlings until 2 years old, the age of first reproduction.

#### MATERIALS AND METHODS

The study was conducted from 1983 through 1989 in the upper East River Valley near Rocky Mountain Biological Laboratory. Elevation ranged from 2,850 to 3,900 m; common plant communities were spruce (*Picea*) forests, aspen (*Populus tremuloides*) woodlands, and subalpine meadows dominated by tall forbs and grasses.

Yellow-bellied marmots were common in the upper East River Valley and were studied since 1962 (Armitage, 1991). Marmots lived at discrete habitat patches, usually rock outcrops or talus adjacent to meadows. Larger patches were inhabited by a colony, defined here as a circumscribed locality that typically supported one adult ( $\geq 2$  years old) male and two or more adult females, many of whom had overlapping home ranges and interacted socially. Colonies contained as many as 12 adult females (Armitage, 1991). Smaller patches were inhabited by noncolonial marmots, typically only one adult female and sometimes an adult male. Six colonies and 14 localities inhabited by noncolonial marmots were studied. Marmots hibernated from September until early May.

Fieldwork began each year in early May, when marmots first emerged from hibernation. All marmots at each locality were live-trapped several times during the summer active season; individuals were identified with numbered ear tags. Successful reproduction in females was suggested by swollen nipples during gestation and lactation and subsequently was confirmed when a litter appeared aboveground, typically late June through mid-July. Frequency of reproduction was computed by dividing the total number of litters by the number of possible pregnancies, defined as the number of adult females present each year, summed over the 7 years of the study. Litter size at emergence from the natal burrow was determined by trapping and by observation. Litters whose size was not accurately known were excluded from analysis.

Survival of young from first emergence at the

natal burrow until emergence from the hibernation burrow at age 1 year (first-year survival) was evaluated by intensive trapping at all localities, of both colonial and noncolonial marmots, beginning before yearlings emerged from hibernation and continuing for several weeks. Time of dispersal and survival from 1 to 2 years old (second-year survival) were evaluated by surgically implanting radiotransmitters (Van Vuren, 1989) in yearlings, both colonial and noncolonial. Transmitters had a range of ca. 5 km and an expected life of  $\geq 1$  year. Surgery and the implanted transmitter had no discernable effect on subsequent survival, growth, or reproduction (Van Vuren, 1989). Instrumented marmots were radiolocated every 1–3 days until entry into hibernation, then again upon emergence from hibernation when 2 years old.

We defined a disperser as a marmot that permanently left its natal home range to establish a new, non-overlapping home range; most dispersers emigrated during their yearling summer (Van Vuren, 1990). Time of dispersal was defined as the midpoint of the interval, usually 1–3 days, that was bounded by the last day the yearling was located in its natal home range and the first day it was located elsewhere.

Mortality of instrumented marmots during the active season was suggested by an invariant radiosignal and subsequently confirmed by recovery of the transmitter, usually with remains of the marmot (Van Vuren, 1990). Mortality over winter was indicated by failure of the marmot to emerge from its hibernaculum. Because transmitters of some marmots expired prematurely, overwinter mortality sometimes could not be distinguished from early-season dispersal. Such instances, and any others in which status (either dead or alive) was uncertain, were excluded from analysis.

## RESULTS

We detected no differences in mean litter size ( $t$ -test,  $t = 0.07$ ,  $P > 0.90$ ) or frequency of reproduction ( $G$ -test of independence,  $G = 0.26$ ,  $P > 0.50$ ) between colonial and noncolonial females (Table 1). Because some females were responsible for more than one litter during the 7 years of the study, the assumption of independence of observations was violated for both tests. We doubt, however, that this violation unduly

TABLE 1.—*Reproductive success of colonial and noncolonial female yellow-bellied marmots near Rocky Mountain Biological Laboratory, Gunnison Co., Colorado, 1983–1989. Litter size and successful reproduction were determined when offspring first emerged from the natal burrow. First-year survival of offspring was determined by intensive trapping, and second-year survival of offspring was determined by radio-telemetry.*

Reproductive measure	Colonial	Noncolonial	<i>P</i>
Litter size			
$\bar{X}$	4.20	4.18	>0.90
<i>SD</i>	1.34	1.42	
<i>n</i>	49	33	
Frequency of reproduction			
Litters/female	0.64	0.60	>0.50
<i>n</i>	105	70	
First-year survival			
Recapture rate	0.55	0.35	<0.005
<i>n</i>	233	139	
Second-year survival			
Survival rate	0.78	0.59	<0.10
<i>n</i>	86	27	>0.05

influenced the biological significance of the results.

A higher proportion of colonial young was recaptured as yearlings than of noncolonial young ( $G = 13.68$ ,  $P < 0.005$ ; Table 1). Time of dispersal of noncolonial yearlings (median = 17 June,  $n = 21$ ) was earlier in the season (Mann-Whitney test,  $W = 1,855$ ,  $P = 0.02$ ) than was time of dispersal of colonial yearlings (median = 7 July,  $n = 48$ ). Second-year survival of noncolonial marmots was substantially lower than that of colonial marmots; the difference approached statistical significance ( $G = 3.46$ ,  $0.10 > P > 0.05$ ; Table 1).

## DISCUSSION

Unlike results of earlier study on the same population of yellow-bellied marmots (Armitage and Downhower, 1974), we found that production of young, as indicated by frequency of reproduction and litter

size, did not differ between colonial and noncolonial females. We attribute the difference in results between studies to a bias in sampling effort toward colonies in the earlier study; apparently, many noncolonial females were producing litters that were not being recorded.

Frequency of reproduction overall was somewhat higher in our study ( $\geq 0.60$ ) than in the earlier study ( $\leq 0.48$ ), probably because snow in the upper East River Valley melted unusually early during some years of our study. Date of snow melt is negatively correlated with frequency of reproduction among localities in the study area; apparently, earlier snow melt means a longer growing season and greater access to resources and, thus, a higher likelihood of successful breeding by females (Van Vuren and Armitage, 1991).

We recaptured substantial numbers (35%) of 1-year-old offspring from localities of noncolonial marmots. As hypothesized by Downhower and Armitage (1971), many of these yearlings dispersed earlier than did colonial yearlings, thereby explaining, in part, the low recapture rate of noncolonial yearlings reported previously (Armitage and Downhower, 1974). Other noncolonial yearlings that we trapped had not yet dispersed, but were difficult to observe or trap; we discovered them only after intensive effort. Nonetheless, survival of noncolonial young to age 1 year, as indicated by rate of recapture, remained significantly less than survival of colonial young.

Second-year survival was substantially lower among noncolonial (59%) than among colonial (78%) marmots; although the difference was not statistically significant, we suspect that it was biologically significant. Most males, whether colonial or noncolonial, dispersed before 2 years old (Van Vuren, 1990). Most noncolonial females also dispersed before 2 years old, but most females born at colonies did not disperse (Van Vuren, 1990). Thus, the rate of dispersal from localities inhabited by noncolonial marmots was higher. Because sur-

vival during the summer active season was lower for dispersers than for nondispersers (Van Vuren and Armitage, 1994), the higher rate of dispersal among noncolonial marmots should result in a somewhat lower survival rate to age 2 years.

Our results indicate that colonial living conferred no advantage to females in production of offspring. Young of colonial females, however, had a higher probability of being recaptured at age 1 year and of surviving from age 1 year to age 2 years. Also, yearling daughters of colonial females were more likely to become recruited as adult residents of their natal colony (Armitage and Downhower, 1974).

Localities of noncolonial marmots were significantly smaller in area and contained significantly fewer burrows than did localities of colonies (Svendsen, 1974). We suggest that lower recapture rates of noncolonial yearlings may have occurred because resources, such as suitable hibernacula, food, and space, were insufficient to support a female and her offspring on a long-term basis. Some young may have perceived this limitation and dispersed during their summer of birth; others may have remained and hibernated, only to suffer high overwinter mortality. Further, because burrows of noncolonial marmots were closer to potential hiding cover for predators than were burrows in colonies (Svendsen, 1974), noncolonial young may have been more vulnerable to predation. Almost all noncolonial young that survived to yearling age dispersed (Van Vuren, 1990). Dispersal during the first summer of life has been suspected on a few occasions, but never confirmed; hence, the effects of first-summer dispersal and mortality on recapture rates cannot be distinguished, and first-summer dispersal may account, in part, for the lower recapture rate of noncolonial yearlings.

Noncolonial females seldom recruited their daughters (Van Vuren, 1990), presumably because of lack of resources. This low likelihood of forming matriline, and the loss of direct fitness benefits that accrue

from matriline formation, may be an additional fitness cost of a noncolonial existence (Armitage, 1988). The lower fitness of noncolonial females suggests that they should seek residency in a colony. Immigration into colonies was uncommon, probably because colony residents are highly aggressive toward strangers (Armitage and Johns, 1982); those few instances of successful immigration usually occurred when the disappearance of a colony resident left vacant space (Armitage, 1984).

The demonstrated reproductive success of noncolonial females suggests the possibility of intraspecific variation in the mating system. Yellow-bellied marmots have a harem-polygynous mating system that derives from the clumped distribution of colonial females (Armitage, 1986b). Because harem males rarely leave their territories (Armitage, 1974), most litters born outside of colonies apparently were fathered by noncolonial males. Thus, males that do not acquire a territory within a colony have other opportunities for reproductive success. These opportunities, however, may be limited; the clumped distribution of colonial females probably facilitates territorial defense by males, and noncolonial males may have difficulty defending territories large enough to include more than one noncolonial female.

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