DISPERSAL OF YELLOW-BELLIED MARMOTS

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by

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ABSTRACT

I used radio-telemetry to describe dispersal of yellow-bellied marmots (Marmota flaviventris) and to assess the fates of dispersing marmots. Transmitters were surgically implanted into the peritoneal cavity; neither surgery nor the transmitter had any discernable effect on survival, growth, or reproduction.

Marmots dispersed primarily as yearlings, although some delayed dispersal until as old as three years. Most dispersal occurred May through July. Dispersal direction was nonrandom. Dispersal distance distributions were skewed for both sexes; although marmots dispersed as far as 15.5 km, most settled within 500 m. Three patterns of dispersal were identified. Some dispersers emigrated abruptly, whereas others dispersed through a gradual process. Some marmots, mostly males, dispersed in two stages.

Dispersing females suffered higher mortality during transience, solely because of predation, than did females that remained philopatric. Thereafter, survival of dispersing and philopatric females was similar. Age at first reproduction among females was similar for dispersers and for philopatric residents, but frequency of reproduction apparently was lower for dispersers. Survival of male and female dispersers was similar except during summer the year after dispersal. Marmots that delayed dispersal until older than one year gained no survival advantage. Marmots that dispersed more than 500 m suffered higher mortality than did marmots that dispersed shorter distances.

Five predators of marmots were identified, primarily by tooth impressions left in the wax coating of recovered transmitters; coyotes (*Canis latrans*) were the principal predator. Analysis of coyote scats suggested that marmots were alternate prey sought when preferred prey were scarce. Data from scats and recovered transmitters indicated that marmots were most vulnerable to predation in July and that vulnerability of yearlings and adults was similar.

Survival rates of males and females were similar until reproductive maturity at two years of age; during the third summer of life, males suffered higher mortality than females. The female-biased sex ratio was caused solely by predation on males, primarily during the third summer.

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INTRODUCTION

Dispersal, defined as the one-way movement of an animal away from its home area (Lidicker 1975), is a widespread but poorly understood phenomenon among mammals. Previous studies of mammals usually approached dispersal as a population process, particularly focusing on its role in population regulation (e.g., Krebs it al. 1976, Gaines et al. 1979, Beacham 1981, Keith and Tamarin 1981, Boutin et al. 1985). Although some population consequences of dispersal were elucidated, the causes of dispersal and its consequences for dispersing individuals remain virtually unknown, partly because dispersers are difficult to identify and track and partly because the population approach has tended to obscure the individual nature of dispersal. Dispersal fundamentally is a behavioral attribute of certain individuals, with important implications for individual fitness; thus, an understanding of dispersal requires an evaluation of its effects on the fitness of the individuals involved. Some researchers (Murray 1967, Fairbairn 1978, Brown and Gibson 1983:196, Bondrup-Nielsen 1985, Armitage 1988) have argued that individuals disperse to increase their own fitness, but few studies attempted to assess the effects of dispersal on individual fitness.

Suggestions that some individuals disperse because they have an inherited tendency to do so (Howard 1960, Chitty 1967) have stimulated much research into the possible existence of a dispersal genotype (e.g., Hilborn 1975, Krebs et al. 1976, Keith and Tamarin 1981, Waser and Jones 1989); no convincing evidence, however, was found (Lidicker 1985). Instead, any genetic basis of dispersal may involve the inherited ability of an individual to assess prospects of success at home and to disperse when those prospects appear sufficiently poor (Grant 1978, Waser and Jones 1989)

Three premises underlie my research. First, individuals disperse to improve individual fitness. Second, dispersal, at least in part, results from a "decision" made by individuals that perceive sufficiently low chances for success in the natal area. Third, although tracking individual dispersers is logistically difficult and results in small sample sizes, detailed data from a small sample will provide valuable inferences about dispersal.

I used radio-telemetry to track individual yellow-bellied marmots (*Marmota flaviventris*) before, during, and after dispersal. My overall goal was to describe the process of dispersal and to assess the survival and reproductive success of dispersers. Tracking individual mammals was facilitated by recent technological advances in radio-telemetry; collar-mounted radio-transmitters are available for even the smallest mammals. Some species, however, including yellow-bellied marmots, are unsuited to radio-collars because of body shape or life style. Surgical implantation of the transmitter into the peritoneal cavity recently was attempted for a few species, but deleterious effects of surgery and the presence of the transmitter in the peritoneal cavity were suspected. In Chapter One I describe intraperitoneal implantation of radio-transmitters into yellow-bellied marmots and assess effects on subsequent survival, growth, and reproduction.

The age of the disperser and the date that it leaves home, the process by which it leaves, the direction it takes, and how far it moves before establishing a new home range are poorly known among mammals. Individuals are difficult to track; thus, the home range shift that constitutes dispersal seldom is well described. In Chapter Two I describe the process of dispersal in marmots from before dispersal until establishment of a new home range.

An evaluation of the consequences of dispersal is central to understanding the cause of dispersal (Waser et al. 1986, Gaines and Johnson 1987, Armitage 1988), yet the fates of dispersers are unknown for almost all mammals. In Chapter Three I evaluate the survival and reproductive success of dispersing marmots.

Predation is thought to be the major risk faced by dispersers during the period of transience between old and new home ranges (Gaines and McClenaghan 1980, Anderson 1989:11). Long-term, intensive observation, however, suggested that predation was infrequent among yellow-bellied marmots (Armitage and Downhower 1974, Armitage 1982). An assessment of predation on marmots would promote an understanding of the risks faced by dispersers. In Chapter Four I describe the predators of marmots based on evidence surrounding the deaths of instrumented marmots. In Chapter Five I assess predation on marmots by their major predator, the coyote (Canis latrans), by analyzing the contents of coyote scats.

The difficulty of determining the fates of dispersers has hindered the accurate calculation of important demographic attributes of mammals, particularly estimates of survivorship. Dispersal and death usually cannot be distinguished, survivorship of dispersers usually is excluded, and survivorship of males, because of male-biased dispersal, may be unknown. In Chapter Six I analyze survivorship of male and female yellow-bellied marmots based on both philopatric and dispersing marmots.

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CHAPTER ONE

EFFECTS OF INTRAPERITONEAL TRANSMITTER IMPLANTS ON YELLOW-BELLIED MARMOTS

Radio-telemetry is an important tool in studies of free-roaming mammals. Transmitters typically are attached to animals by external collars; radio collars, however, are impractical for some species because of life-style or body shape (Smith and Whitney 1977). Hence, surgical implantation of sealed, physiologically inert transmitters into the peritoneal cavity has been explored as an alternative. Early attempts in the 1960's produced equivocal results (Shirer and Downhower 1968), but with improved procedures and equipment, the approach has been applied successfully to several species of mammals (Smith and Whitney 1977, Melquist and Hornocker 1979, Garshelis and Siniff 1983, Davis et al. 1984, Eagle et al. 1984, Green et al. 1985, Madison et al. 1985, Koehler et al. 1987, Rosatte and Kelly-Ward 1988, Lacki et al. 1989).

Intraperitoneal surgery, however, involves a number of risks, including the stress of anesthesia and surgery (Smith and Whitney 1977, Smith 1980, Rosatte and Kelly-Ward 1988, Lacki et al. 1989), postoperative infection (Eagle et al. 1984, Green et al. 1985), incision dehiscence (Melquist and Hornocker 1979, Smith 1980, Eagle et al. 1984, Koehler et al. 1987, Rosatte and Kelly-Ward 1988), and physical blockage of internal organs by the transmitter (Guynn et al.

1987, Koehler et al. 1987). Moreover, effects of implanted transmitters on survival, growth, and reproduction have been suspected, although these suspicions appear unfounded for some species (Smith and Whitney 1977, Smith 1980, Eagle et al. 1984, Reid et al. 1986, Madison et al. 1985, Guynn et al. 1987, Koehler et al. 1987).

Since 1983 I have used intraperitoneally implanted radio transmitters to study dispersal in the yellow-bellied marmot (Marmota flaviventris). Previous attempts to attach transmitters to marmots, by collars, harnesses, or subcutaneous implants, were problematic (Downhower 1968, Thompson 1979). My purpose is to describe a successful surgical procedure and assess the effects of implants on survival, growth, and reproduction of marmots.

METHODS

I implanted transmitters in marmots living near Rocky Mountain Biological Laboratory (2900 m elevation), Gunnison County, Colorado. Marmots in this area have been the subjects of a long-term study (Armitage 1986); each summer since 1962, marmots were live-trapped, weighed, dye-marked for individual recognition, and released. Young of the year were trapped soon after emergence from their natal burrow and identified permanently with numbered ear tags. Most animals were retrapped and reweighed periodically through the summer.

In my study, marmots were trapped and taken to a nearby laboratory maintained at 16-18°C, then weighed, given an intramuscular injection of antibiotic, and anesthetized with an intramuscular injection of ketamine hydrochloride (dosage = 100 mg/kg). After immobilization, animals were secured in a dorsal recumbent position, all hair was shaved from the area around the site of the incision, and the skin was cleaned thoroughly with povidone-iodine scrubs. Tools and transmitter were soaked in povidone-iodine solution for 12 hours before surgery, and sterile gloves were worn.

I made a 4-cm diagonal incision in the skin low on the left side of the abdomen, over the juncture between the rectus abdominis and external oblique muscles. A 3-cm incision was then made between these two muscles and into the peritoneal cavity. This site offered several advantages, including little or no bleeding, protection from contact with the substrate during healing, and an alternate entry site on the right side of the abdomen that facilitated subsequent surgery to replace transmitters. The transmitter was inserted and floated freely in the peritoneal cavity. Each incision was closed with a simple interrupted pattern of 3-0 synthetic, absorbable sutures spaced 4 mm apart, then irrigated liberally with povidone-iodine solution. Additionally, the skin closure was coated with an antibiotic ointment. Animals were held overnight, then examined for loose sutures and signs of infection, given another injection of antibiotic, and released.

Two transmitter designs were used, both of them constructed as sealed cylinders with internal antennas. Transmitters implanted in 1983 and 1984 (Wyoming Biotelemetry Inc., Longmont, Colorado) measured 16 x 88 mm, had a mass of 31 g, and were sealed in clear epoxy; all these transmitters failed shortly after implantation. Transmitters implanted thereafter (Custom Telemetry and Consulting Inc., Athens, Georgia) measured 21 x 90 mm, had a mass of 35 g, and were coated with surgical-grade beeswax. Transmitter mass never exceeded 4% of animal mass. Post-1984 transmitters had an expected life of 30 months (pulse rate = 30/min) and a range, under excellent conditions, of 2-5 km using a hand-held four-element Yagi antenna.

I located marmots usually every 1-3 days following release. Survival was calculated on the basis of number of animals alive 30 days after implantation, allowing ample time for complete recovery from surgery. Most implanted animals were yearlings, and calculations of growth rates were restricted to animals of this age class that were recaptured at least 20 days after surgery but before onset of hibernation. The difference between body mass at recapture and at surgery, less transmitter mass, was divided by the number of days elapsed to determine mean daily growth rate. Most yearlings captured from 1983 to 1989 were implanted, so for a control group I used yearlings captured in the study area from 1979 to 1982 that were weighed two or more times at least 20 days apart (K. B. Armitage unpubl. data). Reproduction of mature ($\geq$2 years old) females that carried transmitters during pregnancy was indicated by emergence of a weaned litter at the female's burrow.

RESULTS

I implanted transmitters in 200 marmots, 161 of them yearlings that averaged 1.3 kg (range = 0.8-2.2 kg) when implanted. The remainder were adults weighing up to 4.3 kg. Replacement of failed or expired transmitters required one or more additional surgeries for 97 animals; 32 animals underwent three or more surgeries, and one animal was operated on seven times during four summers. In all, 355 surgeries were performed.

The time required for surgery, from injection of ketamine hydrochloride until the animal was returned to its cage, averaged 28 minutes (range = 16-64 minutes). Most surgeries, particularly those on animals receiving transmitters for the first time, required 20-25 minutes.

Marmots usually became fully immobilized 2-3 minutes after injection and remained so for 30-45 minutes. Some animals, notably those implanted with transmitters after midsummer, required one or more additional injections of ketamine hydrochloride (up to 210 mg/kg aggregate dosage) to effect complete immobilization. Addition of an equal volume of sterile physiological saline to the injection of ketamine hydrochloride (G. L. Florant, Temple Univ., pers. comm.) improved late-summer effectiveness.

Besides the increased dosage requirements for some animals, problems associated with the use of ketamine hydrochloride were limited to induction of torpor in one animal that underwent two surgeries on consecutive days. The day after the second surgery, the animal was discovered in torpor (body temp = 18.5°C; heart rate = 36 beats/min; 8 respirations/min). The animal recovered after being placed in an environmental chamber set hourly at 2°C above body temperature, underwent two more surgeries within the next two months, then was killed by a predator the following year.

Marmots appeared fully recovered from anesthesia by about one hour after surgery, and subsequent recaptures indicated healing was completed in about one week. Marmots never chewed or scratched sutures; indeed, marmots in the lab and in the field seemed oblivious to the incision.

Surgery to replace transmitters often revealed a thick, fibrous, sometimes highly vascularized membrane encasing the transmitter. Such transmitters were successfully recovered by making a scalpel incision in the membrane at one end of the transmitter.

Fates of all but 12 animals were known 30 days after surgery: five were killed by predators, seven died of accidents unrelated to surgery, two died of uncertain causes that may have been surgery-related, and the remainder were alive and behaving normally. Among the two animals that died of uncertain causes, one weakened soon after surgery and died in the laboratory three days later after failing to respond to antibiotics. A necropsy found no sign of infection or of physical obstruction by the transmitter, but did reveal a dense infestation of ectoparasites. The animal probably was somewhat debilitated before implantation, and the added stress of surgery may have led to pneumonia. The other animal died of unknown causes in its burrow 1-3 weeks following surgery. Excluding animals whose fates were unknown or who died of known causes unrelated to surgery, survival rates were 99% on the basis of number of surgeries (n = 330), 99% on the basis of number of animals (n = 178), and 100% for animals implanted more than one time (n = 85).

Growth rates of 73 implanted yearlings averaged 21 g/day, identical to the 21 g/day mean growth rate of 54 yearlings without implants. Fifty-four adult females carried transmitters 1-5 years each, for a total of 81 possible pregnancies. Thirty-seven litters emerged aboveground; the pregnancy rate of implanted females (0.46) was similar to the 22-year mean (0.48) for nonimplanted females in the study area (Armitage 1986). Litters produced by implanted females averaged 4.2 young, identical to the 22-year mean of 4.2 young for nonimplanted females in the study area (Armitage 1986).

DISCUSSION

Surgical procedures used in this study were simple, effective, and largely trouble-free. Although achieving full immobilization occasionally was a problem and torpor was induced once, ketamine hydrochloride proved to be a safe and effective anesthetic, despite dosages much greater than those typical for other mammals (Wright 1983). Infection was never a problem; the few mild inflammations that appeared around the incision were treated successfully by holding the animals an extra day and administering additional antibiotic by injection and by topical ointment. Individual sutures occasionally failed shortly after surgery, but the use of a simple interrupted pattern maintained closure until failed sutures were discovered and replaced the following day. Marmots never disturbed sutures, a response found in some species (Koehler et al. 1987) but not others (Smith 1980, Eagle et al. 1984, Koehler et al. 1987). Phylogenetic patterns in suture disturbance are obscure; within the family Sciuridae, this problem occurred in Franklin's ground squirrel (Spermophilus franklinii) (Eagle et al. 1984) but not in Townsend's ground squirrel (S. townsendii) (Koehler et al. 1987) or yellow-bellied marmots (this study).

Encapsulation of transmitters in tissue occurred in marmots and in other species (Eagle et al. 1984, Green et al. 1985, Guynn et al. 1987), but posed no discernable difficulties to the marmot or during transmitter removal. Transmitter adhesion to internal organs, which probably caused the death of an implanted beaver (Castor canadensis) (Guynn et al. 1987) and prevented transmitter recovery in an implanted Franklin's ground squirrel (Eagle et al. 1984), was never observed in marmots.

High survival of implanted marmots is consistent with results from other mammals; a few animals may be lost initially (Eagle et al. 1984, Koehler et al. 1987), but once procedures are refined, survival of implanted animals is very high (Koehler et al. 1987) or indistinguishable from that of nonimplanted animals (Smith and Whitney 1977, Smith 1980, Eagle et al. 1984). Replacement or recovery of transmitters has been attempted in several species (Eagle et al. 1984, Green et al. 1985, Koehler et al. 1987). Serial implants may not be suitable for some species (Green et al. 1985), but results for yellow-bellied marmots and for three other mammals (Koehler et al. 1987) indicate there is no effect on survival. Green et al. (1985) found that the necessity of cutting through scar tissue impeded surgery only slightly in serial implants; similarly, among 24 yellow-bellied marmots implanted three or more times, cutting through scar tissue increased surgery duration somewhat and produced minor bleeding, but posed no serious difficulties.

Previous reports have shown that reproduction can occur in implanted females, but quantitative evaluation of implant effects was lacking in most cases (Garshelis and Siniff 1983, Eagle et al. 1984, Green et al. 1985, Reid et al. 1986, Guynn et al. 1987). Two studies, however, that did determine effects on pregnancy rate and litter size (Smith 1980, Madison et al. 1985) reported findings that agree with my results; implants did not affect pregnancy rate or litter size. Similarly, the absence of any effect of implants on subsequent growth rates of marmots is in agreement with all other studies that have compared growth rates of implanted and nonimplanted animals (Smith 1980, Eagle et al. 1984, Madison et al. 1985).

Intraperitoneal implantation of transmitters was first introduced as a possible alternative for those species in which radio collars were infeasible. Early reports of efficacy were largely qualitative and established that implanted animals did survive surgery and that some of them subsequently bore young. My results and those of other recent studies establish quantitatively that intraperitoneal implants do not discernably affect survival, growth, or reproduction.

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CHAPTER TWO

DISPERSAL OF YELLOW-BELLIED MARMOTS

Dispersal may be viewed as the process by which an animal leaves its home range and moves to a different locality where it establishes a new home range. Descriptive data on dispersal are important in elucidating the causes and consequences of dispersal (Dobson 1982, Brody and Armitage 1985, Voigt et al. 1985, Waser 1985, Chepko-Sade and Halpin 1987), but few unbiased descriptions of dispersal exist.

Because almost all definitions of dispersal involve a one-way move between old and new home ranges that do not overlap, the locations of both home ranges, or at least the location and subsequent abandonment of the old home range, must be established before dispersal can be confirmed. Data from trapping and observation, the approaches most commonly used to describe dispersal in mammals, almost always are biased. Resolution of the time of dispersal is limited to the interval at which trapping or observations are conducted. Unless an individual is detected after dispersal, animals that die without dispersing cannot be distinguished from dispersers. Measures of dispersal distance and direction pertain only to those individuals that disperse within the range of trapping or observation and subsequently are detected; animals dispersing beyond that range are excluded.

The yellow-bellied marmot (Marmota flaviventris) is a large ground-dwelling squirrel that is widely distributed in western United States (Frase and Hoffmann 1980). Previously, dispersal of yellow-bellied marmots was described on the basis of trapping and observation; thus, data on age and month of disperal were based on disappearance (Armitage 1974, Armitage and Downhower 1974, Johns and Armitage 1979, Downhower and Armitage 1981, Webb 1981, Brody and Armitage 1985), and measures of dispersal distance were constrained by the size of the study area (Svendsen 1974, Schwartz 1979).

I used radio-telemetry to track the movements of individual dispersing yellow-bellied marmots in order to assess the age, month, direction, and distance of dispersal and to characterize the process of leaving.

METHODS

The study was conducted in the upper East River valley near Rocky Mountain Biological Laboratory (RMBL), Gunnison County, Colorado. Topography is typical of a glaciated, high-altitude valley; slopes are gentle on the valley floor, elevation 2850-2930 m, but rise abruptly to ca. 3900 m elevation on adjacent peaks. Vegetation is an interspersion of subalpine meadows rich in forbs, extensive stands of aspen (Populus tremuloides), and conifer groves. Areas above timberline support alpine meadows and shrubs, or are nearly devoid of vegetation.

Yellow-bellied marmots in the upper East River valley live in discrete patches of habitat that provide their two most important resources, rocks for burrow sites and herbaceous vegetation for food

(Svendsen 1974, Armitage 1986). Thus, marmot distribution is highly disjunct and irregular. Larger habitat patches support colonies that consist of one adult male, one or more adult females, yearlings, and young of the year. Noncolonial marmots live at smaller habitat patches that typically support one adult female, her young of the year, and sometimes an adult male (Armitage 1974, Armitage and Downhower 1974, Svendsen 1974). Fecundity is similar for colonial and noncolonial females, but survival of young to yearling age may be lower at noncolonial sites, and few yearlings born at noncolonial sites remain to become residents (Armitage and Downhower 1974, Van Vuren 1990). The mating system is facultatively polygynous; males establish territories that include females and exclude all other adult males (Downhower and Armitage 1971, Armitage 1974, 1986).

Marmots in the study area emerge from hibernation in early May; mating occurs within a few days after emergence (Armitage 1965). Most young of the year emerge aboveground during the first two weeks of July. All colonial young of the year apparently hibernate close to their natal burrow and do not disperse until at least their yearling summer; some noncolonial young disappear (Armitage and Downhower 1974), possibly because they dispersed, but dispersal of young has not been confirmed (Van Vuren 1990). Virtually all males (Armitage and Downhower 1974) and about one-half of females (Armitage 1984) disappear before two years old, presumably because they dispersed. Marmots can breed at two years of age, but most females and virtually all males do not do so until at least three years old

(Armitage 1986).

Marmots in the upper East River valley have been studied intensively since 1962 (Armitage 1986 and references cited therein). Each year, all young born in the study area were trapped shortly after emergence from the natal burrow and identified permanently with numbered ear tags. Adjacent litters sometimes intermingled before initial trapping, but for most young the mother was known.

From 1984 through 1989, 77% of male yearlings and 88% of female yearlings were instrumented with radio transmitters shortly after emergence from hibernation. Not all yearlings received transmitters because not enough transmitters were available; there was no evidence that excluded yearlings were a biased subset. Transmitters, which had a range of about 5 km and a life of up to two years, were surgically implanted into the peritoneal cavity. Surgery and the implanted transmitter had no discernable effect on subsequent survival, growth, or reproduction (Van Vuren 1989). Instrumented marmots were located every 1-3 days until they dispersed, whereupon they were located as often as practical. Failed transmitters were replaced whenever possible. A few marmots with failed transmitters disappeared before their transmitters could be replaced; these marmots were excluded from analysis.

I defined dispersal as the process of leaving the natal home range before breeding and establishing a new home range that does not overlap with the natal home range. Dispersers were those marmots that established a non-overlapping home range or that abandoned their natal home range but died before establishing a new home range. Because marmots lived in discrete habitat patches and because almost all dispersals were interlocality translocations, identifying dispersal was unambiguous in virtually all cases. Breeding dispersal (Greenwood 1980), detected only three times during the study, was excluded from analysis; thus, I describe natal dispersal (Greenwood 1980).

Time of dispersal was defined as the midpoint of the interval (usually 1-3 days) bounded by the last day the marmot was located in its natal home range and the first day it was either located elsewhere or confirmed to have left its natal home range. Dispersal direction was the azimuth from the natal burrow to the burrow in which the marmot first hibernated after dispersal, or to the site of death if the disperser died before hibernation. Dispersal distance was calculated only for those marmots that succeeded in establishing residency in a new home range; residency was defined as regular use of the same burrow for 14 days (Michener 1979). Dispersal distance was the straight-line distance from the natal burrow to the first hibernation burrow used after dispersal, or to the home burrow if the disperser established residency but died before hibernating.

The *G* statistic was used for tests of independence; because sample sizes were relatively small, Williams' correction was used (Sokal and Rohlf 1981). The Rayleigh test (Durand and Greenwood 1958) was used to test whether dispersal direction was random.

RESULTS

Ninety-two dispersers, 60 males and 32 females, were tracked until they established residency or until death if they died during transience. Some dispersers moved rapidly beyond the range of the receiver and were missing for up to 10 months; all, however, ultimately were found, except for three marmots (one male, two females) whose transmitters failed during transience. Thus, results for the 92 marmots probably are an unbiased description of dispersal in yellow-bellied marmots.

Dispersers of both sexes emigrated primarily as yearlings, although some marmots delayed dispersal until two or three years old (Table 1). I detected no difference between sexes in age at dispersal (two- and three-year-olds pooled; $\underline{G}_{adj} = 0.64$, $\underline{P} > 0.10$).

For both males and females, almost all dispersal occurred in May, June, or July (Fig. 1). I detected no difference between sexes in month of dispersal (August and September pooled; $\underline{G}_{adj} = 4.38$, $\underline{P} > 0.10$).

Marmots dispersed in all octants of the compass (Fig. 2), but dispersal direction was not random ($\underline{P} = 0.03$). Dispersal direction seemed only weakly related to topography; many dispersers moved either up or down the upper East River valley, but they seldom followed the river itself. Rather, they often followed igneous scarps along the sides of the valley that paralleled the river. Contrary to the suggestion of Shirer and Downhower (1968), the East River and other streams apparently posed no barrier to dispersers.

Instrumented marmots readily, and sometimes frequently, swam across the East River, which was up to 15 m wide, 1.5 m deep, and flowed at up to 2-3 m/sec. Many dispersers followed routes that corresponded to no discernable topographic feature and crossed large expanses of forest or open meadow that contained neither burrows for temporary safety nor habitat suitable for residency.

Males (median = 1825 m) dispersed farther (Mann-Whitney U-test, $P = 0.03$) than females (median = 350 m); although statistically significant, this test must be interpreted with caution because the requisite assumption of similar distributions possibly is violated. Maximum dispersal distances were 15.5 km for males and 6.4 km for females; marmots of both sexes, however, usually dispersed 4 km or less (Fig. 3). The distance distribution for females was highly skewed and leptokurtic; 52% of female dispersers established residency within 0.5 km of their natal burrow. The distance distribution for males also was skewed, but the mode was far less pronounced than for females. Excluding the first interval (0-0.5 km), distributions for both sexes seemed approximately uniform.

Studies based on trapping or observation usually reduce dispersal to a discrete classification: the animal is either recorded in its natal area, in which case it is a resident, or it is recorded somewhere else or vanishes, in which case it is a disperser. Radio-tracking allows greater resolution in describing the process of emigration. I identified three different patterns of emigration by marmots (Table 2). Forty-one percent emigrated abruptly; they abandoned their natal home range in a single, one-way move and made no recorded exploratory excursions outside their home range before dispersing. Thirty-three percent emigrated by a gradual process that included exploratory excursions before dispersing, incremental home range extension until a new, non-overlapping home range was established, or both. Exploratory excursions were defined as brief, two-way trips outside the natal home range to previously unvisited localities; recorded excursions were to localities 200-1500 m distant, and sometimes included the locality at which the disperser eventually established residency.

Twenty-seven percent of dispersers emigrated in two stages. In the first stage, dispersers left their natal area permanently but established a new, temporary home range only a short distance away ($\bar{x}$ = 265 m, range = 125-675 m). These home ranges were usually within view but beyond the home ranges of adults in the natal area, and apparently lacked suitable hibernacula. After a mean of 41 days (range = 14-67), the marmots dispersed a second time, always abruptly. Emigration pattern used differed between the sexes (G_{adj} = 7.12, $P < 0.05$); males dispersed more often than females in two stages (Table 2).

Abrupt dispersal and the second stage of two-stage dispersal were always rapid and directional. No disperser followed a route that resembled the spiral path suggested by Waser (1985). Some dispersers tracked when in transit covered several kilometers in one day; many departed the entire upper East River valley (width, ca. 5

km) within the 1-3 day relocation interval. Yearlings sometimes associated temporarily with one or more other yearlings before dispersing; members of such groups were observed playing together, sometimes were radio-located in the same burrow, and occasionally were caught in the same trap. Some of these associations were formed by two-stage dispersers at the temporary home range established after the first stage. Dispersal, however, was strictly solitary; dispersers were never known to travel in the company of any other marmot. Littermates occasionally dispersed within a few days of each other, but they always dispersed separately and to different localities.

DISCUSSION

Most dispersers emigrated during their yearling summer; emigration the year before reproductive maturity is typical of ground-dwelling squirrels (Armitage 1981). Few, if any, marmots emigrated during their natal summer, probably because body size was insufficient for successful dispersal (Barash 1974, Armitage 1981). Young first emerged at the midpoint of the relatively short growing season, leaving little time for accumulation of fat reserves for overwinter survival. Storing sufficient fat apparently is critical for young; only about one-half survive to yearling age (Armitage and Downhower 1974, Van Vuren 1990), and late-emerging litters suffer high overwinter mortality (Armitage et al. 1976). If dispersal is energetically expensive (Holekamp 1984a, Johnson 1988, Goldizen and Terborgh 1989), then higher fitness accrues to individuals that do not disperse until their yearling summer (Armitage 1981).

A substantial proportion (26%) of dispersers did not emigrate until after the yearling summer. The reasons for delayed dispersal are unclear; because some individuals of both sexes that dispersed as yearlings succeeded in breeding as two-year-olds (Van Vuren 1990), yearling dispersal to capitalize on possible reproductive opportunities the following year would seem advantageous. Two-year-olds weighed significantly more than yearlings for both sexes (Armitage et al. 1976); thus, larger size may have improved survival. Analysis of survival did not support this expectation (Van Vuren 1990). I suspect that delayed dispersal of some females was induced by reproductive inhibition; several females established residency in their natal area but subsequently dispersed after failing to breed, apparently because of reproductive inhibition (Armitage 1986).

Most dispersal of yellow-bellied marmots occurred during a restricted portion of the active season, a pattern reported for other mammals (Michener 1979, Holekamp 1984a, Knowles 1985, Garrett and Franklin 1988, Wiggett and Boag 1989). Previous authors suggested that the time of dispersal was affected by attainment of a threshold age (Michener 1979), a threshold body mass (Downhower and Armitage 1981, Holekamp 1984a), or reproductive maturity (Boyce and Boyce 1988); by emergence of young of the year (Armitage and Downhower 1974, Knowles 1985, Garrett and Franklin 1988, Wiggett and Boag 1989); or by the presence of adults (Brody and Armitage 1985) or frequency of adult aggression (Downhower and Armitage 1981).

For yellow-bellied marmots, adult removal (Brody and Armitage 1985) and emergence of young (Downhower and Armitage 1981) were not related to time of dispersal. Relationships between time of dispersal and adult aggression or body mass were inconclusive; high rates of adult aggression were correlated with early dispersal of females but not males, and larger size was correlated with early dispersal of males but not females (Downhower and Armitage 1981). Further, significant correlations were relatively weak (Downhower and Armitage 1981).

My results do not support any one factor as a cause of timing of dispersal; instead, the particular day on which an individual chose to emigrate apparently resulted from complex factors that are poorly understood. Some dispersers emigrated in the absence of any observed adult aggression; others delayed emigration despite intense and sometimes injurious aggression. Survival was similar whether dispersers emigrated as yearlings or as adults (Van Vuren 1990), indicating that after reaching yearling age, increased growth did not improve chances of surviving dispersal. There was no clear relationship between time of dispersal and emergence of young; most dispersers had emigrated by early July, but many had not (Fig. 1).

Dispersal direction was random for red foxes (Vulpes vulpes) (Harris and Trewhella 1988) and for deer (Odocoileus hemionus) that moved less than 5 km (Bunnell and Harestad 1983). For deer moving more than 5 km, however, dispersal direction was nonrandom, probably because of the barrier posed by a seacoast (Bunnell and Harestad 1983). Topography also influenced dispersal of black-tailed prairie dogs (Cynomys ludovicianus) and Columbian ground squirrels (Spermophilus columbianus); dispersing prairie dogs usually followed roads (Knowles 1985), and dispersing ground squirrels followed topographic features, resulting in nonrandom dispersal direction (Wiggett and Boag 1989, Wiggett et al. 1989).

Topography did not appear to influence dispersal direction of yellow-bellied marmots by posing barriers to transit, because marmots could and did negotiate almost any terrain in the upper East River valley. Rather, topographic influence probably derived from linear geologic features, such as igneous scarps or beds of exposed slate, that provided suitable burrow sites at frequent intervals. Dispersers often followed these features, presumably moving from burrow to burrow. Dispersing marmots sometimes followed routes used by dispersers in previous years; likewise, some dispersing Columbian ground squirrels followed the same path as did previous dispersers (Wiggett and Boag 1989).

Distributions of dispersal distances for several mammal species were fitted to the Poisson (French et al. 1968) or normal (Dice and Howard 1951, Bunnell and Harestad 1983) distributions, with poor success. More recently a geometric model, first proposed by Murray (1967) and elaborated by others (Waser 1985, Buechner 1987, Miller and Carroll 1989), provided a good fit to data from some mammals. The geometric model converts dispersal distances to home range diameters and expresses distance moved as number of home ranges traversed until a vacancy is discovered or until the disperser stops because of residency or death. The probability of stopping is constant for each home range encountered.

Application of a general model to mammalian dispersal distances is hampered by the incongruent ways that distance is operationally determined. Some studies used settlement distance, the distance between the natal area and the location of eventual residency (Clout and Efford 1984, Murie and Harris 1984, Caley 1987, Boonstra et al. 1987, Jones 1987); this measure includes both philopatric and dispersing individuals and may be constrained by the size of the study area. Other studies determined dispersal distance from recovery by hunters or trappers of identification tags of marked animals (Storm et al. 1976, Harris and Trewhella 1988, Bunnell and Harestad 1983); human predation may be biased, and whether the animal was a resident when killed or was still a transient was rarely known. Distances moved by individuals between nest boxes (Nicholson 1941, Howard 1949, Dice and Howard 1951) may be biased by size of the study area and the spatial distribution of nest boxes. Few studies of mammals (Boyce and Boyce 1988, this study) reported apparently unbiased measures of dispersal distance between old and new home ranges.

Moreover, the effect of predation in shaping dispersal distance distributions is unknown and largely ignored. Yellow-bellied marmots that dispersed over 500 m suffered higher predation than dispersers that moved 500 m or less (Van Vuren 1990); the absense of predation would increase the mean and median dispersal distance and undoubtedly would affect the shape of the distribution as well. Because predation pressure may vary from year to year (Van Vuren 1990), dispersal distances measured in different years in the same population may differ solely because of predation. Buechner (1987) incorporated predation into a variant of the geometric model by assuming a constant probability that a disperser will stop because of either residency or death. This assumption promotes mathematical simplicity, but biological relevance seems obscure. Miller and Carroll (1989) extended the geometric model to allow probability of stopping to vary, but the added complexity may detract from interpretability.

Although the skewed nature of dispersal distances of yellow-bellied marmots is consistent with the geometric model, the geometric distribution is inapplicable to marmots because several assumptions (Murray 1967, Waser 1985) are violated, including random dispersal direction, contiguous home ranges, and homogeneous habitat. Yet the concept underlying the geometric model may explain sex differences in dispersal distances of marmots. I suggest that males dispersed farther than females because males had more restrictive requirements for successful dispersal. Females need only find an unoccupied locality with a suitable hibernaculum and adequate food resources. Because of the polygynous mating system of marmots, reproductive success usually is assured; a sexually receptive female almost always breeds. Males, in contrast, must locate a suitable, unoccupied burrow to survive, but for reproductive success they face an additional requirement: their home range must include undefended females.

Fitting any continuous distribution to marmot dispersal distances may be inappropriate because marmot dispersal distances appear to be disjunctly distributed. Many females and some males settled within 500 m of their natal burrow, but beyond that the distributions appear uniform. One possible explanation is the nonrandom direction of dispersal; as dispersal direction becomes increasingly nonrandom, the skewed distribution of the geometric model changes to a uniform distribution. Because stopping probability is constant, dispersers following the same path will be evenly distributed along the common route. Accurate prediction (or even explanation) of marmot dispersal distance may prove elusive. Which direction a marmot chooses at emigration and at what distance it establishes residency may be influenced by a complex and obscure array of factors. Some dispersers briefly investigated, then inexplicably abandoned, vacant habitat that recently had supported marmots, an observation also reported for Belding's ground squirrels (*S. beldingi*) (Holekamp 1986).

Abrupt departure by dispersing mammals was described previously (Storm et al. 1976, Fritts and Mech 1981, Holekamp 1984*b*, Peterson et al. 1984, Zimen 1984, Johnson 1986), but two-stage dispersal was not. I suspect that the first stage of two-stage dispersal involved the disperser escaping the social environment of the natal area without a major movement into completely unfamiliar habitat, and the second stage involved seeking suitable, unoccupied habitat. Between the first and second stages marmots grew substantially, often doubling in body mass, leading to the expectation that susceptibility to predation during dispersal would be lower and that subsequent overwinter survival would be higher. Analysis of survival of dispersers did not support this expectation (Van Vuren 1990).

The greater probability of males dispersing in two-stages may reflect intrasexual competition in the polygynous mating system characteristic of yellow-bellied marmots. Because males can breed when two years old, a yearling male that enters hibernation in its natal area may compete with the territorial male for mates the following spring. Thus, yearling males are subjected to aggression from the territorial male (Armitage 1974), and many disperse in two stages perhaps to escape that aggression.

Exploratory behavior in mammals was reported previously (Evans and Holdenried 1943, Madison 1980, Boutin et al. 1985, Holekamp 1986, Garrett and Franklin 1988, Jones 1989), but a connection between exploratory excursions and subsequent dispersal was described for only a few species; e.g., red foxes (Zimen 1984, Voigt et al. 1985), Columbian ground squirrels (Wiggett and Boag 1989, Wiggett et al. 1989), and gray wolves (Canis lupus) (Van Ballenberghe 1983, Peterson et al. 1984, Fuller 1989). The process of dispersal through incremental home range extension was described graphically by Madison

(1980) and Holekamp (1984b), and verbally by Voigt et al. (1985) and Jones (1989).

I subsumed exploratory excursions before dispersal, and dispersal through incremental home range extension, into one pattern because gradual dispersers, unlike abrupt or two-stage dispersers, gained knowledge of areas outside their home range before dispersing. Wiggett et al. (1989) ventured that the function of exploratory excursions was for indentification of a dispersal route. I suggest a different explanation for gradual dispersal in yellow-bellied marmots. Dispersal is not obligate in females because about one-half remain as residents; assessing opportunities outside the natal area may aid a female in deciding whether to disperse. For dispersers of both sexes, exploratory excursions may uncover promising localities to which to emigrate. Also for both sexes, gaining some knowledge of the outside world before dispersal should improve survival during dispersal (Jones 1989). Survival during the summer of dispersal was somewhat higher for gradual dispersers than for abrupt or two-stage dispersers, although the difference was not statistically significant (Van Vuren 1990).

Similarity in time of dispersal among littermates was used to infer the heritability of dispersal (Hilborn 1975, Beacham 1979, Boonstra and Craine 1988). In all three studies, however, methods for evaluating relatedness and time of dispersal were questionable. Further, presumed littermates shared a common social and physical environment as well as a common genetic background; similarity in presumed dispersal times within presumed litters may have resulted from their common environment rather than genetic similarity.

If dispersal tendency is heritable, then dispersal direction and distance, in addition to dispersal time, might be similar among littermates. The available evidence is inconclusive. Some studies reported no evidence of similarity in dispersal direction or distance among littermates or between littermates and their mother (Goundie and Vessey 1986, Holekamp 1986, Waser and Jones 1989). Rogers (1987:417) concluded that individuals "often" disperse in the company of relatives, but cited published data only for primates. Harris and Trewhella (1988) reported that littermates among urban red foxes tended to disperse in the same general direction, but local environment may have influenced dispersal direction. The few instances of similarity in dispersal times of yellow-bellied marmot littermates probably resulted from the influence of a common environment; for almost all dispersering marmots, dispersal was a strictly individual behavior.

My description of dispersal of yellow-bellied marmots raises new questions. Most dispersers emigrated as yearlings, but some delayed dispersal until two or even three years old, for uncertain reasons. Most dispersal occurred during the first half of the active season, but reasons are obscure. Some dispersers seemed to follow topographic features, but others crossed large expanses of seemingly inhospitable terrain. Sex differences in median dispersal distance are explicable in terms of differing requirements between males and females for successful dispersal, but the causes of dispersal distance distributions for each sex remain uncertain. Chance may play a role in dispersal distance; because of the highly irregular dispersion of marmot habitat, the particular direction taken by a disperser may result in prolonged travel before suitable habitat is reached. Some advantages seem to accrue to gradual and two-stage dispersers, but many dispersers nevertheless emigrated abruptly. Dispersal is a complex, individual behavior that remains poorly understood.

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Table 1. Frequency distribution (in percentages) of age at dispersal for male (n = 60) and female (n = 25) yellow-bellied marmots near RMBL, Colorado, 1984 through 1989.

	Age (years)		
	1	2	3
Males	72	27	2
Females	80	16	4

Table 2. Emigration patterns of dispersing male (_n_ = 58) and female (_n_ = 25) yellow-bellied marmots near RMBL, Colorado, 1984 through 1989. Numbers are percentages.

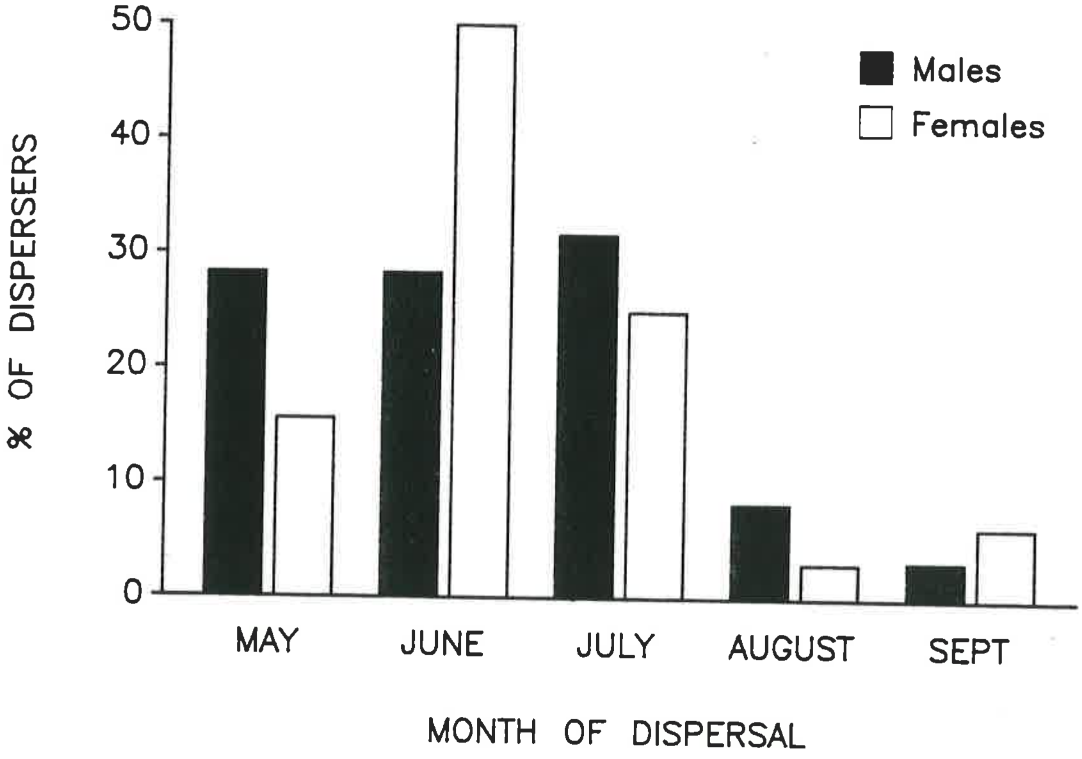
	Pattern		
	Abrupt	Gradual	Two-stage
Males	36	29	34
Females	52	40	8

FIGURE LEGENDS

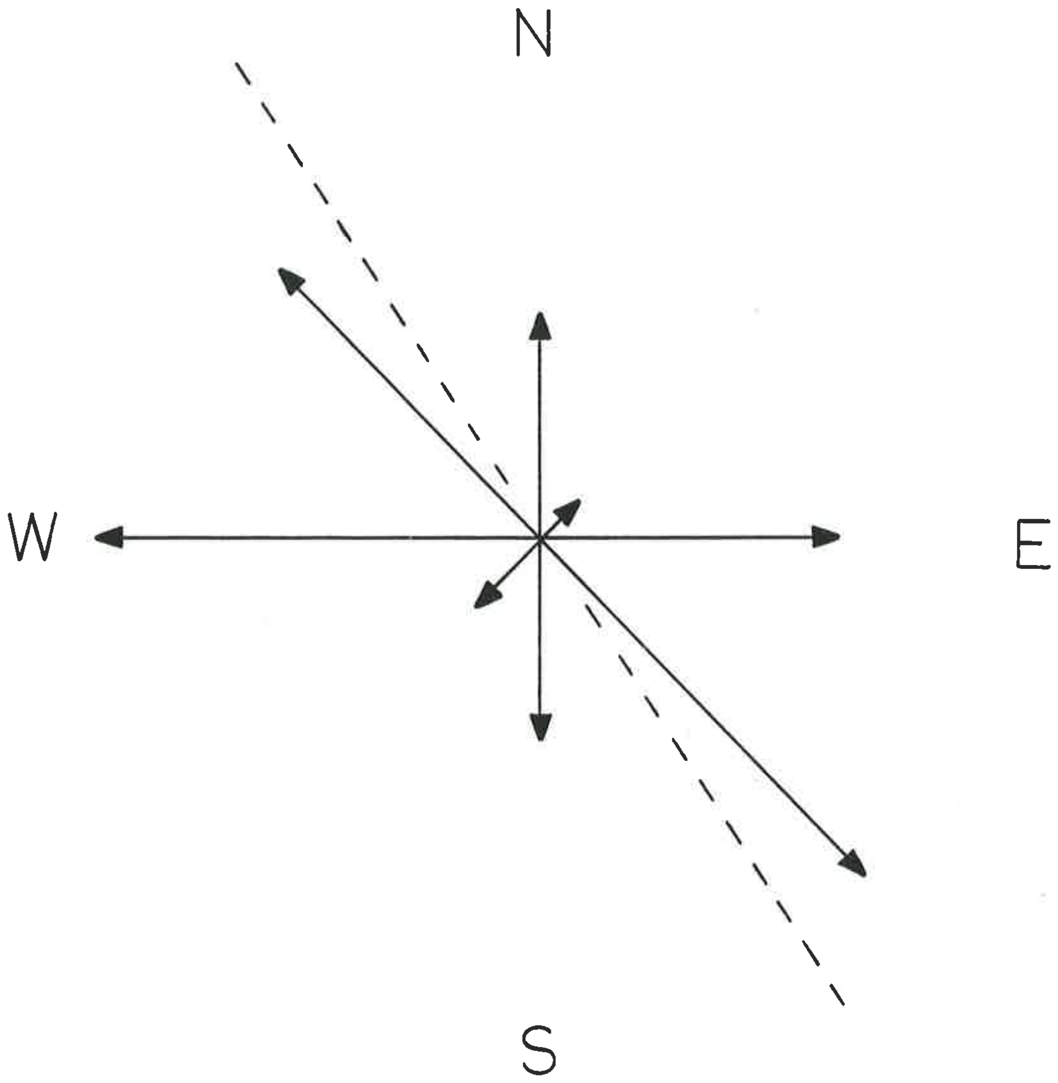
Fig. 1. Month of dispersal for male (n = 60) and female (n = 32) yellow-bellied marmots near RMBL, Colorado, 1984 through 1989.

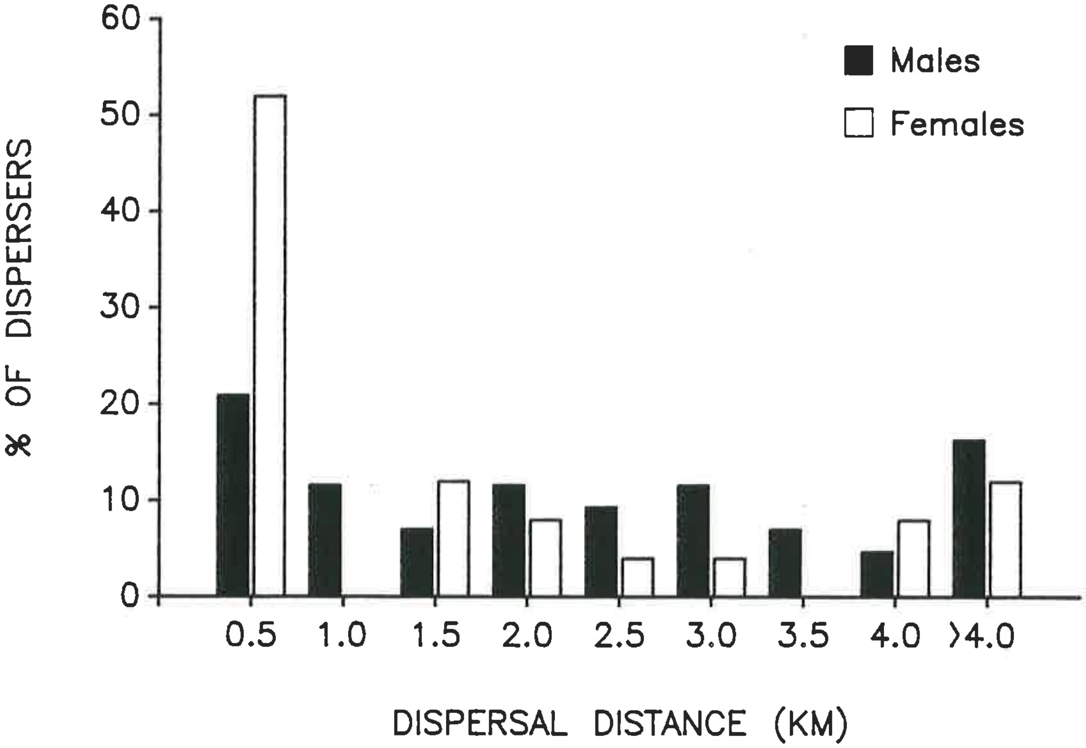
Fig. 2. Direction of dispersal for 87 dispersing yellow-bellied marmots near RMBL, Colorado, 1984 through 1989. The length of each arrow is proportional to the number of marmots dispersing in that direction. The dashed line indicates the orientation of the upper East River valley.

Fig. 3. Dispersal distances of male (n = 43) and female (n = 25) yellow-bellied marmots near RMBL, Colorado, 1984 through 1989. Distances were grouped into intervals of 0.5 km; the abscissa indicates the upper limit of each interval.



50
40
30
20
10
0
% OF DISPERSERS
■ Males
☐ Females
MAY
JUNE
JULY
AUGUST
SEPT
MONTH OF DISPERSAL


N
W
E
S


60
50
40
30
20
10
0
% OF DISPERSERS
■ Males
☐ Females
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
>4.0
DISPERSAL DISTANCE (KM)

CHAPTER THREE

SURVIVAL AND REPRODUCTION OF DISPERSING YELLOW-BELLIED MARMOTS

Dispersal has long been an enigma for mammalian ecologists. Dispersers are presumed to experience high predation when crossing unfamilar terrain and have difficulty locating suitable, unoccupied habitat. Thus, the belief that dispersal is costly is widely accepted (Gaines and McClenaghan 1980, Michener 1983, Clutton-Brock and Albon 1985, Lidicker 1985, Anderson 1989:10-11, Jones 1989) to the point of becoming dogma (Gadgil 1971, Danielson et al. 1986, Krohne and Burgin 1987, Johnson 1988). But, if dispersal is so costly, why do individuals disperse? The apparent difficulty of explaining dispersal in terms of individual fitness has led to models based on group selection (Van Valen 1971) and parental fitness (Hamilton and May 1977, Anderson 1989).

The risks of dispersal can be decomposed into two phases, transience and colonization (Johnson and Gaines 1985). The first phase incorporates the possible danger of travel through unfamiliar, potentially inhospitable habitat; the disperser might die from predation, exposure, accident, or stress (Gaines and McClenaghan 1980, Anderson 1989:11-12). The second is the uncertainty that the disperser's new home range will provide resources sufficient for survival and reproduction (Gaines and McClenaghan 1980, Michener 1983, Danielson and Gaines 1987). That dispersers might survive the transient phase but settle in poor habitat, with poor prospects for survival and reproduction, is implicit in the concept of a marginal-habitat dispersal sink (Lidicker 1975, Krohne et al. 1984, Tamarin et al. 1984).

Survival of dispersing mammals during the transient phase was assessed only by Boyce and Boyce (1988) and Garrett and Franklin (1988). Metzgar (1967) and Ambrose (1972) reported that familiarity of small mammals with an experimental arena reduced the risk of predation by owls. These results, widely cited as evidence that dispersers suffer relatively high predation during transience (e.g., Johnson and Gaines 1985, Krohne and Burgin 1987, Danielson et al. 1986, Anderson 1989:11, Jones 1989), elucidate the predatory behavior of owls but have no established relevance to dispersal. Experimentally translocated banner-tailed kangaroo rats (*Dipodomys spectabilis*) suffered higher mortality than did unmanipulated residents (Waser 1988), but the relevance of artifical translocation to natural dispersal by choice is unknown.

Some studies evaluated the colonizing success of dispersing mammals by comparing immigrants with philopatric individuals on predetermined study areas (Murie and Harris 1984, Jones 1986, 1988, Krohne and Burgin 1987); these studies, however, excluded dispersers that settled outside the study area. Other studies either were unable to identify dispersers unambiguously (Dueser et al. 1981, Danielson et al. 1986) or measured success only in habitats that were known, a priori, to be either low (Krohne and Burgin 1987) or high

(Johnson and Gaines 1985, 1987) in quality. I know of no study that determined the colonizing success of an unbiased sample of dispersing mammals monitored since emigration.

I report survival and reproductive success of dispersing yellow-bellied marmots (Marmota flaviventris) from emigration through colonization. I tested five hypotheses: 1) survival of philopatric and dispersing marmots did not differ, 2) age at dispersal did not affect survival; 3) distance dispersed did not affect survival; 4) the emigration pattern employed during dispersal did not affect survival; and 5) reproductive success did not differ between philopatric and dispersing marmots.

METHODS

The study was conducted in the upper East River valley near Rocky Mountain Biological Laboratory (RMBL), Gunnison County, Colorado. Elevation ranged from 2850 m to 3900 m; habitats were typical of subalpine and alpine environs of the Rocky Mountains.

The yellow-bellied marmot, a hibernating, ground-dwelling squirrel, is common in the upper East River valley and has been studied intensively since 1962 (Armitage 1986 and references cited therein). Most marmots inhabit discrete habitat patches in social groups called colonies, but some marmots live relatively asocially at smaller, noncolonial localities (Armitage and Downhower 1974, Svendsen 1974). The mating system is polygynous; males defend territories that include one or more females and exclude all other adult males (Downhower and Armitage 1971, Armitage 1974, 1986). Each year, all young of the year were trapped shortly after initial emergence from their natal burrow and marked permanently with ear tags. Thus, age and birthsite were known. Young of the year usually hibernate close to their natal burrow and do not disperse until one year or older (Armitage and Downhower 1974, Van Vuren 1990).

Field work was conducted early May through late September, 1984 through 1989. I surgically implanted radio transmitters (Van Vuren 1989) into 77% of male yearlings and 88% of female yearlings shortly after they emerged from hibernation in May. Failure to implant all yearlings resulted solely from shortage of transmitters; there was no evidence that excluded yearlings were a biased subset. Transmitters had a range of 5 km or more under excellent conditions and a life of up to two years. Surgery and the implanted transmitter had no discernable effect on subsequent survival, growth or reproduction (Van Vuren 1989). Instrumented marmots were located every 1-3 days until dispersal and as often as practical thereafter. Failed transmitters were replaced whenever possible.

A marmot was recorded as a disperser if it abandoned its natal home range before first reproduction (Van Vuren 1990); philopatric residents were those marmots that did not disperse. Three instances of breeding dispersal (Greenwood 1980) were excluded from analysis. Survival was indicated by variability in signal location or intensity and usually was confirmed by observation of the marmot. Mortality during summer was indicated by recovery of the transmitter or by constancy in signal location and intensity of an underground transmitter (Van Vuren 1990). Overwinter mortality was indicated by failure of the marmot to emerge from its hibernaculum. Because some tranmsitters failed during winter, overwinter mortality occasionally 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. Reproduction of females was suggested by swollen nipples in May and confirmed by subsequent emergence of a litter at the female's burrow. Reproductive success was assigned to those males that had exclusive access in May, as indicated by radio-telemetry, trapping, and observation, to a female that subsequently weaned a litter.

Marmots were tracked, when possible, until two years after dispersal (dispersers) or until three years old (philopatric residents). Annual survival of dispersers was decomposed into two intervals that corresponded to the two hypothesized risks of dispersal, transience and colonization. "First summer" was from the moment of dispersal until entry into the next hibernation. First-summer survival represented the probability of surviving transience and establishing a new home range. "First winter" was from entry into hibernation after dispersal until emergence from hibernation the following spring. First-winter survival reflected whether the disperser's new home range provided sufficient resources (food and hibernaculum) for year-round survival. Some marmots were tracked for a second year after dispersal; "second summer" was emergence from hibernation the spring after dispersal until entry into the next hibernation, and "second winter" was entry into hibernation the year after dispersal until emergence two years after dispersal. For each interval, survival was calculated by dividing the number alive at the beginning of the interval into the number alive at the end of the interval.

Most dispersers emigrated early in their yearling summer (Van Vuren 1990); to compare survival of dispersers and philopatric residents, I began the first-summer interval for residents when they emerged from hibernation as yearlings. The end of the first-summer interval (entry into the next hibernation), and all subsequent intervals (first winter, second summer, second winter), were defined as sequential immergence and emergence, the same as for dispersers. Because only one male failed to disperse, survival of philopatric residents was calculated for females only.

Transmitters of some marmots failed before dispersal or during transience and could not be replaced; these marmots were excluded from analysis. I could find no evidence that transmitters failed nonrandomly among marmots. Transmitters of other marmots failed after they survived the first-summer interval but before the end of the second-winter interval; these marmots were excluded from analysis beginning the interval during which the transmitter failed. Marmots that died because of human activities, such as trapping and handling, also were excluded.

Because sample sizes were small, the $\underline{G}$ statistic was adjusted with Williams' correction (Sokal and Rohlf 1981) for tests of independence. The G-test was not applied if expected frequences fell below five for more than 20% of cells, except where noted. Tests are two-tailed unless indicated otherwise; one-tailed hypotheses were tested whenever a priori justification existed.

RESULTS

Survival of philopatric female marmots was about 90% for each time interval, regardless of season (summer or winter) or age (yearling or two-year-old) (Table 1). First-summmer survival, the time of transience, was lower among females for dispersers than for philopatric residents (one-tailed test, $G_{adj} = 3.28$, $P < 0.05$); thereafter, survival of dispersers and residents was generally similar.

First-summer survival of male and female dispersers was nearly identical (Table 1); pooling the sexes, 73% of dispersers ($n = 84$) survived transience and hibernated. Likewise, no differences between sexes were evident in first-winter or second-winter survival. Second-summer survival, however, was lower for males, although the difference was not statistically significant ($G_{adj} = 2.23$, $P > 0.10$).

Delaying dispersal until two years old or older conferred no survival advantage to dispersers (Table 2). There was no detectable difference according to age in first-summer survival (one-tailed test, $G_{adj} = 0.01$, $P > 0.40$) or first-winter survival (one-tailed test, $G_{adj} = 2.23$, $P > 0.05$; expected frequencies are inadequate but inflate the G statistic, thus the interpretation is conservative).

The distance that a disperser moved, measured as the distance to the post-dispersal hibernaculum or to the site of death for dispersers killed before hibernation, affected survival. Ninety-one percent of those dispersers that moved 500 m or less ($\underline{n}$ = 22) survived, compared with 67% survival of dispersers that moved more than 500 m ($\underline{n}$ = 60); the difference is statistically significant (one-tailed test, $\underline{G}_{adj} = 5.41$, $\underline{P} = 0.01$).

Some marmots dispersed by a gradual process of incremental home range extension, exploratory excursions before dispersal, or both. Others dispersed abruptly or in two stages (Van Vuren 1990). First-summer survival of gradual dispersers was higher than that of abrupt and two-stage dispersers (Table 3); the difference approached statistical significance (one-tailed test, abrupt and two-stage pooled, $\underline{G}_{adj} = 2.45$, $0.10 > \underline{P} > 0.05$).

Age at first reproduction apparently was not affected by dispersal; 38% of females that dispersed as yearlings ($\underline{n}$ = 8) first bred as two-year-olds, compared with 42% of philopatric females ($\underline{n}$ = 26) ($\underline{G}_{adj} = 0.06$, $\underline{P} > 0.80$; expected frequencies are inadequate but inflate the $\underline{G}$ statistic, thus the interpretation is conservative). Frequency of reproduction after the first litter was 0.30 for dispersers (possible litters, $\underline{n}$ = 10) and 0.43 for philopatric residents ($\underline{n}$ = 30); lack of independence among observations precluded statistical analysis. Among dispersing males for whom reproductive success was known, six of nine that lived to three years fathered at least one litter.

DISCUSSION

The appropriate measure of the cost of dispersal is not a comparison of fitnesses of dispersers and philopatric residents, but rather is a comparison of the fitness of a disperser with the fitness of that same individual if it had not dispersed (Gaines and McClenaghan 1980). There are two potential biases in comparing dispersers with philopatric residents. First, philopatric residents may include mostly those individuals whose prospects of success at home were good to begin with. Second, by emigrating a disperser may alter the environment that prompted its emigration. To illustrate, consider a yellow-bellied marmot colony that has resources for three adult females but currently supports only one. She bears a litter of four female young. Two of these perceive the overcrowding and disperse; the remaining two now perceive adequate resources and remain. In this hypothetical example, comparing dispersers with residents is misleading; the appropriate comparison is between dispersal versus residency in an overcrowded colony. Doing so, however, obviously presents a formidable obstacle, and the best approximation remains a comparison of dispersers versus philopatric residents.

Female dispersers suffered higher mortality during transience than did females of approximately the same age that did not disperse; thus, the transient phase of dispersal entailed a cost. All first-summer mortality was attributable to predation (Van Vuren 1990); there was no evidence that any instrumented marmot died from exposure, accident, or stress. Subsequent overwinter survival was similar for philopatric females and both male and female dispersers, indicating that dispersers were successful at locating and colonizing habitat with sufficient resources for survival.

Dispersal might affect female fecundity in two ways. First, if dispersal is energetically expensive (Holekamp 1984, Johnson 1988, Goldizen and Terborgh 1989), the growth of female dispersers might be retarded sufficiently to delay age at first reproduction. Second, resources in the new home range might be adequate for little more than survival, resulting in a delay at age of first reproduction, lower frequency of subsequent reproduction, or both. Although sample sizes are small, there was no evidence that dispersers suffered a delay in age at first reproduction; thus, energetic costs of dispersal appear to be inconsequential for marmots. There was weak evidence, however, that frequency of reproduction was somewhat lower among dispersers, providing some support for the hypothesis that colonization of relatively poor habitat is a risk of dispersal.

Almost all male marmots disperse (Armitage and Downhower 1974); because of the polygynous mating sytsem in which a territorial male appropriates several females and excludes all other males (Armitage 1974, 1986), reproductive success of dispersing males should be low, or at least delayed several years. A majority of male dispersers bred within one year after reproductive maturity, a few of them at reproductive maturity, a surprising result that probably derives from the high turnover of territorial males (Armitage 1986).

The apparently low survival of males during the summer after dispersal resulted entirely from predation and was unexpected. The probable cause was the differing requirements between the sexes for successful dispersal and resultant effects on behavior of males and females. Females need only locate unoccupied habitat with adequate food resources and a suitable hibernaculum; because of the polygynous mating system, an estrous female probably is located and bred by a male. Thus, home ranges of most female dispersers remained relatively stable after termination of transience. Males also must locate suitable, unoccupied habitat, but they face an additional requirement for successful dispersal; their new home range must include unappropriated females. Most males dispersed as yearlings (Van Vuren 1990), and yearlings probably lacked the size necessary to defend a territory containing females. No yearling male acquired females the summer of dispersal. Instead, male dispersers apparently sought a locality, almost always isolated, that was adequate for overwinter survival. Those that survived usually moved again the following summer. Some dispersed a second time and others moved about a greatly enlarged home range, but all apparently were seeking undefended females; many were killed by predators. Unexpectedly high predation on males the summer after dispersal apparently constitutes a third, previously undescribed risk of dispersal. Not only must males survive transience and locate habitat suitable for overwinter survival, but they also must face the risk of predation the following summer, presumably when seeking undefended females.

No consistent pattern is evident among previous reports that compared the success of dispersers and philopatric residents in mammals. Survival was relatively low among dispersing black-tailed prairie dogs (*Cynomys ludovicianus*) that were captured during transience and radio-tracked until residency or death; only 44% (*n* = 27) survived, a significantly lower rate than among residents (Garrett and Franklin 1988). Survival of black-tailed prairie dogs possibly was overestimated because some dispersers may have died in transit before being captured and instrumented. In contrast, survival was high (98%, *n* = 42) among dispersing common voles (*Microtus arvalis*) during transience (Boyce and Boyce 1988), although it was not clear that all dispersers were tracked until residency or death. In one population of African lions (*Panthera leo*) dispersing females bred later than philopatric residents, whereas in another population dispersing females had lower survival than philopatric residents (Pusey and Packer 1987).

Philopatric residents were compared with dispersers after they achieved residency. Relative survival of dispersers and philopatric residents varied according to the population density of banner-tailed kangaroo rats; philopatric residents survived better in years of high density, whereas dispersers survived better in years of low density (Jones 1986, 1988). There were no differences in survival among white-footed mice (*Peromyscus leucopus*) (Krohne and Burgin 1987) nor in fecundity among Columbian ground squirrels (*Spermophilus columbianus*) (Murie and Harris 1984). The relative effects of dispersal and philopatry on fitness deserves further study.

Some marmots delayed dispersal until they were two years or older; one explanation is that the larger body size of two-year-olds in comparison with yearlings (Armitage et al. 1976) improved prospects for survival (Van Vuren 1990). This expectation was not supported (Table 2); indeed, yearlings and adults appeared equally susceptible to capture by a variety of predators (Van Vuren 1990).

Gaines and McClenaghan (1980) suggested that chances of survival were inversely related to the amount of time a disperser spent in transit, and Svendsen (1974) and Miller and Carroll (1989) proposed that mortality of dispersers increased with dispersal distance. Assuming that velocity is consistent among dispersers, these predictions are equivalent. For yellow-bellied marmots, the distance (and, presumably, duration) of dispersal was inversely related to survival.

Further experiments based on the results of Metzgar (1967) and Ambrose (1972) revealed that susceptibility to predation resulted not from lack of habitat familiarity but from movement in general (Snyder et al. 1976). I suggest that marmots dispersing long distances suffered higher mortality because of movement, not because they were in unfamiliar habitat. Some dispersing males that died the summer after dispersal (Table 1) were killed near localities they had visited previously. Moreover, some noncolonial adult males moved regularly about large home ranges; these males suffered relatively high mortality, but in home ranges with which they were familiar (Van

Vuren unpubl. data). Boyce and Boyce (1988) concluded that high survival of dispersing common voles resulted from the short duration ($\underline{\bar{x}}$ = 39 minutes), and presumably distance, of transience. Dispersal of marmots was characterized by rapid, directional movement (Van Vuren 1990). Thus, an evaluation of the risks of transience for dispersers should incorporate a measure of the time or distance of transience.

Gradual dispersers (Van Vuren 1990) acquired knowledge of localities outside their home ranges through brief exploratory excursions, dispersal through incremental home range extension, or both; thus, survival of gradual dispersers should be relatively high (Jones 1989, Van Vuren 1990). The data indicated a trend in that direction (Table 3), although the difference was not statistically significant. Exploratory excursions may have been relatively safe because they were so brief (Van Vuren 1990); also, survival of dispersers that moved 500 m or less was similar to that of philopatric residents, indicating that home range extension by a series of short out-and-back moves incurred a low cost to survival.

One benefit of two-stage dispersal, besides escaping the social environment of the natal home range, might have been the gain in body mass between the first and second stages and its effect on subsequent survival (Van Vuren 1990). This expectation was not realized; there was no evidence that either first-summer or first-winter survival was higher for two-stage dispersers than for abrupt dispersers (Table 3).

The cost of dispersal was not measured previously for any mammal. For female yellow-bellied marmots, the cost of dispersal derives mostly from an increase in mortality during transience; except for the possibility of a reduced frequency of reproduction, fitness of dispersers after transience appeared similiar to that of philopatric residents. Thus, an estimate of the fitness of dispersing females relative to philopatric residents is 0.80, the ratio of first-summmer survival rates.

The presumed high cost of dispersal has been a problem in elucidating the causes of dispersal in mammals (Van Valen 1971, Waser et al. 1986, Anderson 1989). Among yellow-bellied marmots, however, the cost of dispersal was unexpectedly low; nearly three of four dispersers survived transience, and although first-summer survival was significantly lower for dispersing females than for philopatric females, the difference was relatively small.

The costs of philopatry for some yellow-bellied marmots may be substantial. For females, philopatry could mean a delay in onset of breeding because of reproductive inhibition (Armitage 1986). I suspect that dispersal of several females was induced by reproductive inibition; these females survived until two years of age in their natal area but failed to breed, probably because of the presence of a dominant female; all bred after dispersing. Thus, prospects for survival in the natal area may be high, but chances for reproduction could be zero. Additionally, many philopatric females that were killed by predators lived toward the periphery of colonies (Van Vuren unpubl. data); thus, for some females philopatry could entail a relatively high risk of predation. The cost of inbreeding depression, possibly substantial, remains to be established.

For males, one cost of philopatry probably is aggression, potentially injurious, from the territorial male. One male that failed to disperse as a yearling suffered a near-fatal injury, probably from the territorial male; the injured male recovered, then dispersed. Perhaps the greatest cost of philopatry for males is their poor prospects of competing for mates with the territorial male.

Dispersal may be the consequence of an assessment by an individual of the prospects of success in its natal area; if prospects are sufficiently low, the individual disperses (Grant 1978, Armitage 1988). In some situations for yellow-bellied marmots, the costs of philopatry probably exceed the costs of dispersal. Thus, dispersal of marmots is explicable in terms of improving individual fitness.

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Table 1. Survival of dispersing and philopatric-resident yellow-bellied marmots near RMBL, Colorado, 1984 through 1989. Survival rates were calculated for four sequential time intervals that began at emigration for dispersers and at emergence from hibernation as yearlings for residents. See text for further explanation.

	First summer	First winter	Second summer	Second winter
Male dispersers				
% surviving	73	90	55	100
_n_	55	29	20	7
Female dispersers				
% surviving	72	92	82	88
_n_	29	13	11	8
Female residents				
% surviving	90	91	89	92
_n_	39	32	28	13

Table 2. Survival of dispersing yellow-bellied marmots according to age at dispersal, near RMBL, Colorado, 1984 through 1989. Survival rates were calculated for two sequential time intervals that began at emigration. See text for further explanation.

Age at dispersal	First summer	First winter
One year		
% surviving	72	88
n	65	33
Two years or older		
% surviving	74	100
n	19	9

Table 3. Survival of dispersing yellow-bellied marmots, according to pattern of emigration, near RMBL, Colorado, 1984 through 1989. Survival rates were calculated for two sequential time intervals that began at emigration. See text for further explanation.

	First summer	First winter
Abrupt dispersal		
% survival	69	100
n	32	15
Two-stage dispersal		
% survival	65	83
n	20	6
Gradual dispersal		
% survival	84	81
n	25	16

CHAPTER FOUR

PREDATORS OF YELLOW-BELLIED MARMOTS

Predator-prey interactions are an important area of study in mammalian ecology, yet little is known about the relative importance of various potential predators to a given prey population. The act of a predator capturing prey is seldom witnessed, and the evidence is usually transient. Most of what we know about predation derives from analysis of predator diets, usually based on examination of stomach or scat contents, or occasionally based on focal animal observations of predator or prey. Diet analysis reveals much about the prey a given predator eats, but little about the predators of a given prey and their relative importance.

Diet analyses, along with anecdotal observations of individual captures, indicate that yellow-bellied marmots (*Marmota flaviventris*) are eaten by a variety of predators. Marmot remains were identified in diets of coyotes (*Canis latrans*) (Van Vuren 1990), mountain lions (*Felis concolor*) (Ackerman et al. 1984), badgers (*Taxidea taxus*) (Messick and Hornocker 1981), martens (*Martes americana*) (Hargis and McCullough 1984), and golden eagles (*Aguila chrysaetos*) (Marr and Knight 1983). Anecdotal observations demonstrated that wolves (*Canis lupus*) (Fryxell 1926), coyotes (Thompson 1979, Armitage 1982), and badgers (Bailey 1936, Verbeek 1965, Andersen and Johns 1977, Thompson 1979) prey on marmots. But, which of these predators consumes marmots on a regular basis, and when do they do so?

Yellow-bellied marmots in the upper East River valley, near Rocky Mountain Biological Laboratory (RMBL), Gunnison County, Colorado, coexist with several potential predators. Published information about predation on marmots in the area is limited to two observations of coyotes capturing marmots (Armitage 1982) and recovery of marmot remains from a golden eagle nest (Armitage and Downhower 1974). I report the use of radio-telemetry to describe predation on yellow-bellied marmots in the upper East River valley.

METHODS

A list of potential predators was compiled based on my observations and those of the year-round staff of RMBL (2-4 people) and summer residents (ca. 100-150 people). Coyotes seem particularly numerous in the valley; howling, usually by several individuals simultaneously, is heard frequently throughout the year, and fresh scats are encountered routinely (Van Vuren 1990). Individual coyotes are often observed. Black bears (*Ursus americanus*) are seen in the valley most summers, but sightings are few (usually ≤ 3 per summer), irregular, and localized. Badgers or their excavations are seen irregularly; some summers none are observed, other summers several sightings are reported and extensive excavations discovered. Martens are seen almost every summer, but low frequency of sightings suggests they are not particularly abundant. Longtail weasels (*Mustela frenata*) are exceedingly abundant in some years, virtually absent in others. Red foxes (*Vulpes fulva*) were seen only once in recent years, and no felids were ever observed.

Potential avian predators are golden eagles, red-tailed hawks (*Buteo jamaicensis*), Swainson's hawks (*Buteo swainsoni*), and goshawks (*Accipter gentilis*), all of which nest in the East River valley.

From 1983 through 1989, 200 marmots living near RMBL were instrumented with radio-transmitters that were surgically implanted into the peritoneal cavity (Van Vuren 1989). Transmitters were constructed as sealed cylinders 16-21 mm in diameter and 88-90 mm long, with a mass of 31-35 g. Most transmitters were coated with a 2-mm-thick layer of surgical-grade beeswax that rendered the transmitter physiologically inert and also received tooth impressions when bitten by a predator. Most implanted marmots were yearlings of both sexes, but some were adult (≥2 years old) males. Instrumented marmots were radio-located usually every 1-3 days throughout the summer active season (May-September). Transmitters in some marmots failed after implantation, whereas in others transmitters expired normally and were replaced, sometimes repeatedly. The time a given marmot carried a transmitter varied from a few weeks to five years.

Mortality was suggested by a constant signal that did not vary in location or intensity, then confirmed by walking to the location of the transmitter. In almost all recorded mortalities, the transmitter was recovered. Predator identity was assigned on the basis of tooth impressions in the beeswax coating of most transmitters, the nature of marmot remains in the immediate vicinity, or evidence of predator identity such as badger excavations, golden eagle feathers, and coyote fur or footprints. Tooth impressions were identified by comparison with coyote, black bear, badger, marten, and weasel skulls housed in the mammal collection at RMBL.

Predator identity was assigned to each instance of mortality based on the following criteria:

Coyote.--The transmitter was found on the surface of the ground, tooth impressions in the transmitter matched coyote teeth, no evidence of badger activity was found in the vicinity, and fur remaining from the marmot was limited to a few scraps.

Badger.--The transmitter was recovered at the entrance to, or inside of, a marmot burrow that recently and abruptly was greatly enlarged in what appeared to be a highly destructive fashion.

There were some exceptions to criteria for badgers. In two mortalities assigned to badgers the transmitter could not be recovered because the necessary digging would cause unacceptable damage to the burrow. I determined that both transmitters lay 1.0-1.5 m from the burrow entrance by extending an antenna lead into each burrow, without an antenna and supported by a flexible copper wire, until an abrupt signal change indicated the transmitter was within ca. 10 cm of the lead. Because marmot nest chambers average 2.9 m (range = 2.1-5.0) from the closest burrow entrance (Svendsen 1976), probably neither marmot died in its nest chamber.

Also in two mortalities assigned to badgers, the burrow was not visibly excavated. Both burrows, however, were rather large, and badgers have been seen entering, without digging, larger burrows of marmots. Transmitters in both cases lay within 1.5 m of the burrow entrance. In all exceptions to the initial criteria, a conclusion of badger predation was supported by known activity of badgers in the immediate vicinity at the time of death.

Raptor.--The transmitter was found on the surface of the ground, had no tooth impressions, and was accompanied by large quantities of marmot fur, including pieces of skin with fur intact. Raptors pluck the fur from large mammalian prey before eating (B. Haak pers. comm., R. T. Reynolds pers. comm.).

One mortality assigned to raptors did not meet the initial criteria for raptors. During dispersal, the marmot abruptly moved from the valley floor, 2875 m elevation, to 3475 m elevation on a ledge near the top of a vertical cliff overlooking the valley. I often observed golden eagles soaring along this cliff, and an inactive nest was located a few hundred meters away. The ledge was so inaccessible that a technical rock climber, reputed to be world-class in ability, flatly refused to recover the transmitter despite a substantial monetary offer. I frequently observed marmots negotiate precipitous terrain; though exceptionally agile, they are also cautious and carefully avoid routes that are too steep. Access to the transmitter required negotiating a route that almost certainly exceeded the climbing abilities even of marmots. I concluded that the marmot was killed by a large raptor, probably a golden eagle, and carried to the cliff to be eaten. The transmitter was not recovered.

Black bear.--The transmitter was found on the surface of the ground, and tooth impressions in the transmitter matched bear teeth.

Marten.--The transmitter was found on the surface of the ground, and tooth impressions in the transmitter matched marten teeth.

The analysis of predation and predator identity was based on three assumptions. First, I assumed that a recovered transmitter meant a dead marmot. In most cases the marmot remains found with each transmitter were insufficient to conclude, beyond any doubt, that the marmot was dead. Because the transmitter was inserted into the peritoneal cavity, it seems unlikely that the marmot could somehow expel the transmitter and live. Surprisingly, such nonfatal expulsion was documented for channel catfish (*Ictalurus punctatus*) (Summerfelt and Mosier 1984, Marty and Summerfelt 1986), but the evidence indicates that marmots have no such capacity. The first step in expulsion from catfish is adhesion of the transmitter to the intestine or the abdominal wall, yet during 155 surgeries to replace expired transmitters in marmots no adhesion to any internal structure was observed (Van Vuren 1990). No instrumented marmot was ever recaptured without its transmitter. No animal was ever recaptured after being classified as dead based on recovery of its transmitter.

Second, I assumed that a recovered transmitter meant that the marmot died from predation. The alternative, that some marmots died aboveground of other causes and subsequently were scavenged, is possible but unlikely. Because marmots always seek refuge in their burrows, nonpredation mortality would have to be sudden. Throughout 28 years of intensive field work on marmots near RMBL, only one sick individual was observed (Armitage and Downhower 1974, K. B. Armitage pers. comm.); a male at least eight years old was found dying within his home range, with no evidence of injury. Thirteen marmots were found dead aboveground near RMBL (Armitage and Downhower 1974, Van Vuren pers. observ.). Twelve were young of the year; one died apparently from a fall, and the other 11 died during sudden thunderstorms, presumably from hypothermia. Only one marmot one year or older was found dead aboveground, an eight-year-old female; her carcass was intact, and there was no evidence of cause of death. She was seen alive and behaving normally the day before.

Third, I assumed that evidence (tooth impressions, fur, badger excavations, footprints) associated with a recovered transmitter indicated the predator responsible for the mortality. Possibly, one predator killed the marmot, then a predator of another species visited the site and left evidence of its visit, such as tooth marks in the transmitter. I witnessed none of the predations reported here, so this assumption is difficult to evaluate. However, no transmitter had tooth impressions that indicated bites from two different species of predator.

RESULTS AND DISCUSSION

Predators of Marmots

Of 56 mortalities recorded during the study, 22 were assigned to coyotes. Coyote fur was found entangled on shrubs at the sites of some of these mortalities. Coyote tooth impressions in transmitters included canines, incisors, and premolars. Incisors and premolars, because of size and spacing, were diagnostic, but canines were not. The diameter of the tip of coyote canines (1-2 mm) differed from that of marten (0.5-1.0 mm) or black bear (3-5 mm) canines, but was similar to that of badger canines. Transmitters whose only tooth impressions were canines 1-2 mm in diameter could not be assigned reliably to coyote or badger based on tooth identity alone. I considered such transmitters evidence of coyote predation for three reasons. First, no tooth impressions were found in transmitters of confirmed badger kills. Second, no transmitter in question was found associated with any evidence of badger activity, such as excavation. Third, although badgers sometimes hunt marmots (Thompson 1979) and other prey (Sawyer 1925) in a cursorial fashion, they concentrate on young marmots, which are slow and clumsy; yearlings and adults, the subjects of my study, easily outrun badgers (Thompson 1979).

Transmitters of coyote kills were found in almost every conceivable situation, but always on the ground surface and never in or near a coyote den. Elevations ranged from 2800 m, on the valley floor beside the East River, to 3810 m, well above timberline. Habitats in which transmitters were found included conifer forest, aspen woodland, subalpine meadow, willow thicket, alpine tundra, and even expanses of unvegetated soil and rock far above timberline.

Remains of marmots found at sites of coyote kills were limited to a few hairs, often including the tip of the tail, and sometimes portions of the digestive tract. Virtually all of the marmot was missing in all cases. I suggest that the coyote, after killing the marmot, began feeding on the viscera, bit into the transmitter, then discarded it as inedible. Small marmots (e.g, yearlings) may have been consumed entirely on the spot; larger marmots evidently were partially consumed, then the remainder of the carcass carried off.

Seven mortalities were assigned to badgers. None of the recovered transmitters had any tooth impressions. Three of the mortalities occurred when a badger dug a marmot out of a "flight" burrow, a shallow burrow occupied temporarily when the marmot is threatened (Armitage 1988). The entrances of the three burrows lacked the encirclement of rocks thought to offer protection from badgers (Andersen and Johns 1977, Thompson 1979). Four marmots, however, were killed inside burrows whose entrances were at least partially armored with rocks; badgers ripped two apart, and the other two were sufficiently large for the badger to enter without digging. Burrows used continuously by marmots year after year, even those well protected by rock entrances, tend to become somewhat enlarged by the frequent activity. Thus, an armored burrow-entrance may not be enough; the rock armor must be immovable and just the right size to admit a large male marmot but not a badger, two animals that do not differ much in size. Unpredictability may play a role in badger predation; badger activity in the study area was highly irregular and infrequent, and perhaps badger avoidance has a learned component.

Much of the marmot was recovered from some badger kills, ranging from a large portion of the skin with attached fur, to the entire carcass. There was a negative relationship between amount of the marmot that remained and time elapsed between time of mortality and time of examination, suggesting that badgers cached their prey and returned repeatedly to feed. Prey-caching by badgers was reported by Snead and Hendrickson (1942). In all cases reported here, the remains were buried inside the burrow under at least 10 cm of loose dirt. In one instance I excavated a marmot that was killed by a badger seven days earlier. The carcass was intact and bore no external signs of injury; removal of the skin, however, revealed massive laceration of the right shoulder. Evidently, the badger seized the marmot by the shoulder and bit repeatedly until a vital organ was reached. The badger did not feed on the carcass, but instead buried it under loose dirt in a chamber 2.5 m from the burrow entrance and plugged the entire burrow with dirt. The badger had not returned after seven days; apparently it had cached the carcass.

Six mortalities were assigned to raptors. I concluded that all of these raptors were golden eagles, in part because I found golden eagle feathers at two of the kill sites. Also, I can locate no reference to buteos or accipiters feeding on yellow-bellied marmots, whereas marmots may comprise up to 73% of the diet of golden eagles (Marr and Knight 1983). All mortalities recorded as eagle kills were found at relatively high elevation (>3100 m) sites characterized by steep, open slopes with low vegetation and no marmot burrows anywhere in the area. Evidently, eagles fed on the carcass then carried the remainder off, except for plucked fur and everted skin.

Four mortalities were assigned to black bears, based solely on the massive canine impressions in transmitters that, seemingly, only bears could make. All bear kills occurred at sites where sightings indicated bears were active. No marmot remains other than a few hairs were found with the transmitter; the marmot evidently was eaten entirely on the spot or was partially consumed, then carried off.

Three mortalities were assigned to martens, based solely on tooth impressions. Two of the transmitters bore paired canine impressions 11-12 mm apart, matching the distance between marten canines. The third transmitter was classified by diameter of single canine impressions. All three mortalities were located in or adjacent to conifers, the preferred habitat of martens (Hargis and McCullough 1984). No marmot remains were found with any of the three transmitters. The marmot evidently was partially consumed, then the remainder of the carcass was carried off.

Fourteen mortalities could not be assigned reliably to any one predator. All 14 transmitters were found on the ground surface, none had any tooth impressions, none was accompanied by marmot remains other than a few hairs and occasionally a portion of the digestive tract, and none occurred in association with evidence of badger activity. Coyotes, black bears, and martens all fit this description, but badgers and raptors do not.

All confirmed bear kills were in areas where bears were observed at the time of the mortality, and all confirmed marten kills were in or adjacent to conifers. Using this information, as well as discovery of coyote fur and foot imprints at some of the 14 mortalities, I classified 11 of the 14 mortalities as probable coyote predations. This decision received independent support when eartags of one of the 11 marmots were subsequently discovered in a coyote scat. The remaining three mortalities were classified as caused by coyotes, black bears, or martens.

I found no evidence of weasel predation at any of the 56 mortalities. Tooth impressions on a few transmitters assigned to coyotes could have been caused by red foxes, but I excluded red foxes from consideration because of their rarity in the study area.

Temporal Variation

Distribution of mortalities among months (Table 1) should be interpreted with caution, because numbers of marmots carrying transmitters varied somewhat among months. Sample size was increased by new implants but decreased by mortality; an analysis using a staggered-entry design (Pollock et al. 1989) to account for varying sample size is planned for the future, but in the meantime some general patterns are evident.

Marmots were eaten in all summer months by coyotes but were most vulnerable to coyote predation in July, a pattern that agrees with results from analysis of coyote scats (Van Vuren 1990). A relatively high predation rate by coyotes on marmots in May, however, differs from results of scat analysis. The discrepancy may derive from individual variability in coyote foraging. Scat analysis gives the average diet of several coyotes, but results from transmitter recoveries may be influenced by the foraging behavior of one or two individuals. Six of the 10 coyote kills in May occurred in just one year of the study, 1989. Repeated observations of fresh tracks and of the coyotes themselves indicated that at least two coyotes hunted intensively in marmot colonies during May 1989, while scat analysis suggested that in May most coyotes were hunting elsewhere for other prey, primarily voles and gophers (Van Vuren 1990). Thus, although availability of other prey seems, in general, to render marmots relatively safe in May (Van Vuren 1990), marmots are vulnerable to capture if individual coyotes decide to hunt them.

Badger predations were scattered throughout the year, a result of the highly irregular, infrequent, and unpredictable activity of badgers at localities inhabited by marmots. One predation occurred after the marmot entered hibernation, probably in late fall. Because some marmot burrows are sufficiently large to permit entry of a badger without visible excavation, badger predation, in addition to starvation and hypothermia, may be an important but undetected cause of overwinter mortality in marmots.

Golden eagle predations were infrequent and scattered throughout the summer, and probably resulted from chance encounters with marmots on open slopes away from a burrow. All black bear and marten predations occurred during July and August.

Age Variation

Yearlings might be more susceptible to predation than adults because of presumed vulnerability of dispersers, most of which were yearlings (Van Vuren 1990), and because yearlings (ca. 1-2 kg) were smaller than adults (ca. 2-4 kg) and less experienced. More adults than yearlings, however, were killed by predators (Table 2), and the ratio of adults to yearlings among predator kills (1.33:1) did not differ (G-test for goodness of fit, $\underline{G} = 0.309$, $\underline{P} > 0.50$) from the mean ratio of adult to yearling marmots (1.55:1) trapped in the study area (Van Vuren 1990). Thus, vulnerability to predation was not age-related; instead, yearlings and adults were captured according to their relative numbers in the population.

Predators varied greatly in size (ca. 1 kg to >100 kg) and hunting method (fossorial, cursorial, or aerial), but there was no evidence of age-specific predation by any predator (Table 2). Instead, all five predators captured both yearling and adult marmots. Surprisingly, the two smallest predators, martens and eagles, each killed adult male marmots whose mass exceeded 3 kg.

In conclusion, during at least 7000 hours of observation of yellow-bellied marmots near RMBL over 28 years, only two instances of predation were witnessed (K. B. Armitage pers. comm.). Yet in just six years of radio-telemetry work on the same population, 56 marmot predations were recorded. Predation is difficult to detect partly because it happens so quickly and partly because most predators leave little evidence of the event. Coyotes were the most important predator of marmots, with badgers second in importance. I suspect that eagle, bear, and marten predations resulted from chance encounters with marmots away from burrows, whereas coyotes and badgers may have actively sought marmots. There was no evidence that yearling marmots were more vulnerable to predation than adults, nor was there evidence of age-specific predation by any predator species.

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Table 1. Numbers of yellow-bellied marmots killed by predators, according to month and species of predator, near RMBL, Colorado, 1983 through 1989. Marginal totals are also given in percentages.

	May	June	July	August	Sept	Oct-April	Total	%
Coyote	10	7	13	2	1		33	59
Badger		1	2	1	2	1	7	13
Eagle	2	1	2		1		6	11
Bear			3	1			4	7
Marten			2	1			3	5
Unknown				2	1		3	5
Total	12	9	22	7	5	1	56	
%	21	16	39	13	9	2		

Table 2. Age of yellow-bellied marmots killed by predators, according to species of predator, near RMBL, Colorado, 1983 through 1989.

	Yearling	Adult
Coyote	13	20
Badger	3	4
Eagle	3	3
Bear	2	2
Marten	2	1
Unknown	1	2
Total	24	32

CHAPTER FIVE

YELLOW-BELLIED MARMOTS AS PREY OF COYOTES

The risk of predation may influence many aspects of mammalian behavior, including sociality (Alexander 1974, Crook et al. 1976, Hoogland 1981), foraging (Holmes 1984, Carey and Moore 1986, Devenport 1989), mating system (Armitage 1986), habitat selection (Thompson 1979, Andersen and Johns 1977), and dispersal (Webb 1981). Predation risk, however, usually is assumed rather than demonstrated; quantitative evaluation, even on a relative basis, is seldom reported.

The behavior of the yellow-bellied marmot (Marmota flaviventris), a large, hibernating ground-dwelling squirrel, has been studied intensively since 1962 near Rocky Mountain Biological Laboratory (RMBL), Gunnison County, Colorado (Armitage 1986 and references cited therein). Several lines of evidence suggested that predation was not a major source of mortality for marmots near RMBL. During more than 5000 hours of observation over 20 years, only two instances of predation on marmots were witnessed, both involving coyotes (Canis latrans) (Armitage 1982). Marmots were observed to chase off small carnivores such as weasels (Mustela frenata) and martens (Martes americana) (Travis and Armitage 1972). Further, in other areas where coyotes and marmots co-occurred, marmots comprised less than 7% of seasonal diets of coyotes (Murie 1940, Ferrel et al.

1953, Hawthorne 1972, MacCracken and Hansen 1982, Van Vuren and Thompson 1982).

During the summer of 1972, however, remains of yellow-bellied marmots were identified in 25% of 106 fresh coyote scats collected near RMBL (R. Powell, unpubl. rep., RMBL). This discovery suggested that risk of predation, particularly by coyotes, may be more important to yellow-bellied marmots than previously thought.

I describe coyote diets near RMBL to address three questions about the role of coyotes as predators of yellow-bellied marmots. First, are Powell's 1972 results representative of the long-term importance of marmots as prey of coyotes? Second, are marmots more vulnerable to predation, as has been suggested, during dispersal (Svendsen 1974) or during the mating season (Armitage 1986)? Third, are marmots a focus of coyote foraging efforts or are they alternate prey actively sought only when other prey are scarce?

METHODS

Diets were evaluated by identifying the contents of 395 scats deposited by coyotes from 1984 through 1989 near RMBL, elevation 2900 m. Vegetation in the area was a mosaic of aspen (<u>Populus tremuloides</u>) woodlands, spruce (<u>Picea</u> spp.) and fir (<u>Abies</u> spp.) groves, and subalpine meadows rich in forbs. Scats were collected May through September, the active season of marmots, by searching all roads and trails within 3 km of RMBL at intervals of one month or less. Scats found at the beginning of May were assigned to the period October-April. Scats found thereafter were assigned to the month in which they were collected. Scats encountered away from roads or trails were included only if they could be assigned reliably to a given month based on freshness of appearance and odor. Scats deposited from May through September, but for which the month was uncertain, were excluded from monthly analyses.

Scats were secured in fine-mesh nylon bags, soaked at least 24 hours in mild detergent soap, then rinsed thoroughly in warm water. Residual material was air-dried, separated by hand, and identified by comparison with specimens collected from the vicinity and housed at RMBL or the Mammal Collection of the University of Kansas Museum of Natural History. Coyote diets were calculated as percent frequency of occurrence of prey items among scats during a given time period. All percentages were arcsine transformed for statistical analysis.

Marmot remains recovered from scats were assigned to age class (young, yearling, or adult; Downhower and Armitage 1971) whenever possible, according to characters such as degree of epiphysial fusion, size of the sagittal crest, size of the scapula, claw shape, and dentition. An index of annual variation in marmot numbers in the study area was obtained by totaling the number of individual yearling and adult marmots identified during intensive trapping at 16 localities near RMBL during each of the six years of the study.

RESULTS

Prey items identified in scats fell into three groups based on overall frequency of occurrence. Voles (chiefly _Microtus montanus_) and gophers (_Thomomys talpoides_), which occurred in 43-45% of all scats, were the most prominent prey in coyote scats during all months May through September, as well as the period October-April (Table 1). Snowshoe hares (*Lepus americanus*), yellow-bellied marmots, birds, jumping mice (*Zapus princeps*), mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*), and porcupines (*Erethizon dorsatum*) were seasonally important and occurred in 7-15% of scats overall (Table 1). Chipmunks (*Eutamias* spp.), golden-mantled ground squirrels (*Spermophilus lateralis*), deer mice (*Peromyscus maniculatus*), muskrats (*Ondatra zibethicus*), and garter snakes (*Thamnophis sirtalis*) were eaten irregularly and infrequently and occurred in 2% or less of all scats.

Although marmots trapped in the study area ranged annually from 61 to 92 individuals, numbers were relatively stable the last four years of the study when 88-92 individuals were identified. Armitage and Downhower (1974) also reported relative stability in marmot numbers near RMBL. If coyotes captured marmots only when encountered during routine foraging, marmot occurrence in scats should vary according to marmot abundance. However, I detected no positive correlation among years between summer (May-September) percentages of marmots in scats and marmot numbers in the study area ($\underline{r} = -0.65$, $\underline{P} > 0.50$, one-tailed test).

Status of marmots as alternate prey, actively sought only when other prey were scarce, would be suggested by a negative correlation with occurrence of other prey in scats. Summer percentages among years of marmots in scats were not correlated (one-tailed test) with summer percentages of voles ($r = 0.32$, $P > 0.50$), snowshoe hares ($r = -0.68$, $P > 0.05$), birds ($r = 0.22$, $P > 0.50$), or jumping mice ($r = -0.30$, $P > 0.20$), but were negatively correlated with summer percentages of gophers ($r = -0.83$, $P < 0.025$) (Fig. 1).

Remains of 32 marmots recovered from scats could be aged: 17 adults, 13 yearlings, and 2 young. The ratio of adults to yearlings identified in scats did not differ from the mean ratio of adult to yearling marmots (1.55:1) trapped in the study area (G-test for goodness of fit, $G = 0.199$, $P > 0.50$).

DISCUSSION

The high frequency of voles in coyote scats is consistent with other studies of coyote diets (Murie 1940, Gier 1957, Hawthorne 1972, Todd et al. 1981), but prevalence of gophers is not. The year-round percentage of gophers in scats near RMBL (43%) is the highest yet reported. Andersen and MacMahon (1981) suggested that inadequate food was the primary cause of death in subalpine populations of *T. talpoides*; my results, apparently the first on diets of subalpine coyotes, indicate that mortality from predation should not be discounted. Further, the high frequency of gophers in scats throughout the year indicated that gopher vulnerability was not restricted to dispersing juveniles.

Snowshoe hares appeared common near RMBL during most years of the study; hence, a 15% occurrence in coyote scats seemed low considering the primacy of lagomorphs in coyote diets reported for other localities (Gier 1957, MacCracken 1981, MacCracken and Hansen

1982, Pederson and Tuckfield 1983). Birds were particularly common in scats during July and August, probably as a result of vulnerability of newly fledged young (Van Vuren and Thompson 1982). Deer and elk occurred most frequently in scats during winter (October-April), possibly as carrion; another peak in occurrence, during July, probably derived from vulnerability of neonates (Salwasser 1974, Van Vuren and Thompson 1982). The low frequency of occurrence in scats of chipmunks, golden-mantled ground squirrels, and deer mice, all common near RMBL, is perplexing.

Yellow-bellied marmots occurred in 17% of summer (May-September) scats, with summer percentages ranging from 10 to 38 among years. Thus, Powell's findings from 1972 are supported; marmots were a regular and important prey of coyotes during summer. The frequencies of marmots in coyote scats reported herein, whether on a seasonal or annual basis, are the highest yet reported.

Marmots mate during the first half of May. Males in particular were active aboveground at this time (Van Vuren unpubl. data), and snowcover often was extensive (Van Vuren 1990), leading to the expectation that predation risk was high. This expectation was not supported; frequency of marmots in scats was lowest during May (Table 1). Perhaps coyotes were focusing on other prey that also were vulnerable to capture in May. The ground surface in meadows was exposed for several days after snow melted but before appreciable growth of herbaceous vegetation, probably increasing the vulnerability of species such as gophers and voles. Also, snowmelt saturated the soil with water and may have forced gophers to disperse over the surface to dryer soil (Ingles 1949, Hansen and Ward 1966). Gophers and especially voles occurred most frequently in scats during May (Table 1).

Most dispersing marmots were yearlings and emigrated May through July (Van Vuren 1990). If dispersers were particularly vulnerable to predation, there should be a high frequency occurrence of marmots in scats May through July and a yearling bias among marmot remains recovered from scats. These predictions were not realized. Marmots were relatively frequent in scats only in July (Table 1), and there was no bias toward yearlings among ageable marmot remains. Coyotes were not preying predominantly on dispersers.

Vulnerability of newly emerged young (Hawthorne 1972), which appear aboveground near RMBL during July, might account for the July peak in occurrence of marmots in scats. However, the scarcity of ageable remains of young marmots in scats (2 of 32 overall, 1 of 5 in July) suggests that young were not highly vulnerable to predation. Young marmots near RMBL typically remained close to the safety of their natal burrow for some time after emergence, probably reducing susceptibility to predation. The relatively high rate of predation on marmots in July remains unexplained; possibly, the cause lies not in marmot vulnerability but in an unidentified functional response by coyotes to changing prey availability.

Voles and gophers, the principal prey of coyotes, occurred primarily in subalpine meadows, suggesting that coyotes concentrated their foraging efforts there. A focus by coyotes on meadows may explain the unexpectedly low occurrence in scats of snowshow hares, which I never observed in meadows. Habitat use by coyotes elsewhere corresponded to availability of major prey (Litvaitis and Shaw 1980, Todd et al. 1981).

Snowshoe hares in Alberta, unlike near RMBL, were a major prey of coyotes (Todd et al. 1981). In Alberta, hare occurrence in coyote diets was positively correlated with hare density and negatively correlated with occurrence of several other prey in diets (Todd et al. 1981, Todd and Keith 1983), leading to the conclusion that coyotes shifted to alternate prey when hares were scarce (Todd and Keith 1983).

I propose a similar relationship between gophers and marmots near RMBL. Gophers, because of their larger size (ca. 150 g) in comparison with voles (ca. 50 g), could be the single most important prey of coyotes near RMBL. Estimates of gopher abundance were not available, but subalpine populations of _T. talpoides_ elsewhere varied markedly in density among years (Hansen and Ward 1966, Andersen and MacMahon 1981). If annual variation in summer occurrence of gophers in coyote diets (23-65%) resulted from variation in gopher abundance, then the inverse relationship between marmots and gophers in scats (Fig. 1) suggests that marmots were alternate prey, subject to increased predation pressure when gophers were scarce. Marmots probably are difficult to capture, but their proposed importance as alternate prey may derive from relative stability of numbers and predicability of location. Most marmots live in colonies distributed throughout the RMBL vicinity, and those colonies under study have been occupied continuously since at least 1962. Thus, a hungry coyote during summer always knows where to find marmots to stalk.

In conclusion, my results indicate that risk of predation by coyotes near RMBL was substantial and should be considered in interpretations of the behavior of yellow-bellied marmots. Predation by coyotes on marmots was unexpectedly low during May, the time of mating, possibly because coyotes focused on other prey. Predation was greatest during July, but the reason was unclear. There was no evidence that dispersers were especially vulnerable to predation. Marmots apparently served as alternate prey; predation risk was greatest during years of low gopher occurrence in scats, and presumably low gopher abundance in the study area as well.

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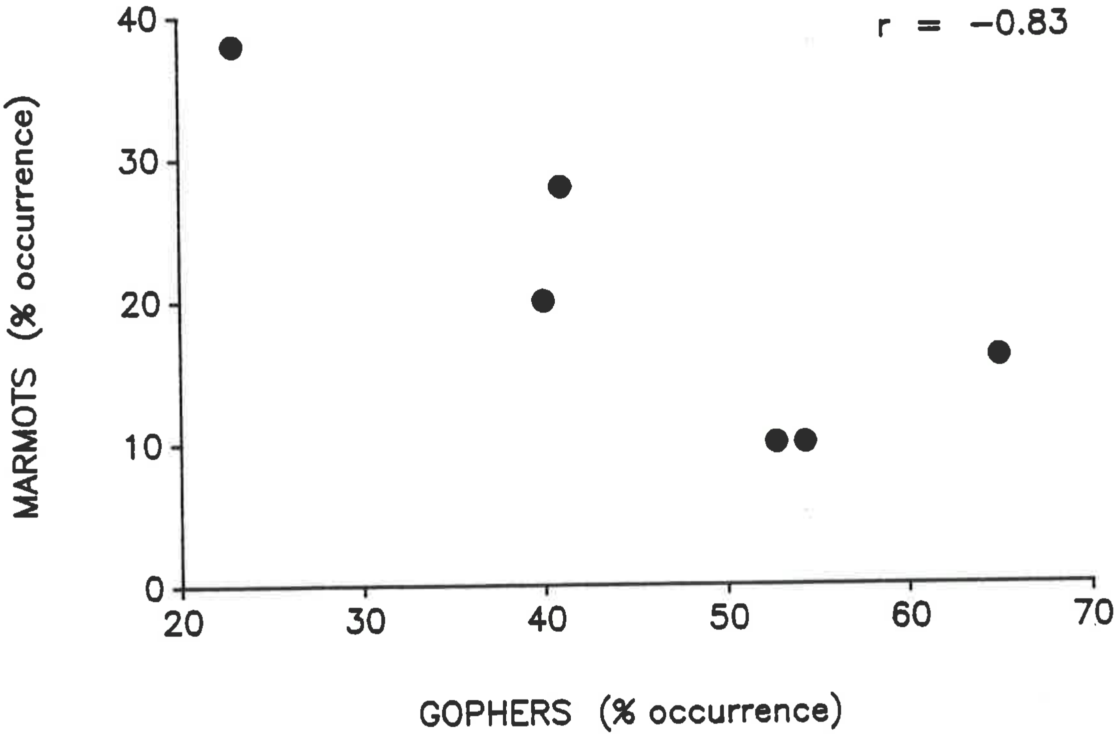
Table 1. Percent frequency of occurrence of prey items identified in coyote scats collected near RMBL, Colorado, 1984 through 1989. Prey that occurred in 2% or less of scats overall are not shown.

	May	June	July	August	Sept	Oct-April	Overall
n	116	78	20	31	15	121	395
Vole	55	42	35	35	60	37	45
Gopher	53	49	45	52	60	23	43
Snowshoe hare	11	17	5	29	13	18	15
Marmot	11	19	35	16	13		12
Bird	8	15	35	29		7	12
Jumping mouse	3	27	20	13	13	1	10
Deer and elk	3	3	15	10	13	17	9
Porcupine	9	1	5		7	11	7

FIGURE LEGENDS

Fig. 1. Relationship between percent occurrences of gophers and marmots in coyote scats collected near RMBL, Colorado, 1984 through 1989.


r = −0.83
MARMOTS (% occurrence)
GOPHERS (% occurrence)
0
10
20
30
40
20
30
40
50
60
70

CHAPTER SIX

SURVIVAL OF YELLOW-BELLIED MARMOTS

Survivorship estimates reported for small or medium-sized mammals may be biased in several ways. First, because mortality and emigration are difficult to distinguish, survivorship usually is calculated on the basis of "disappearance rate" (Sherman and Morton 1984); thus, the consequences of two distinct phenomena, survival and philopatry, are subsumed into one value. Second, estimates usually pertain only to philopatric individuals; emigrants are excluded because their fates are unknown, and ages of immigrants are unknown unless they are young enough to be aged on the basis of body mass. Third, because of male-biased dispersal among mammals (Greenwood 1980), survivorship data for males may not be available at all. Finally, studies based on trapping exclude animals that are present and alive but do not enter traps.

All four biases pertain to survivorship estimates calculated for yellow-bellied marmots (Marmota flaviventris) based on trapping (Armitage and Downhower 1974). The use of radio-telemetry reduces these biases. I report a new analysis of survival of male and female yellow-bellied marmots based on determination of survival largely through radio-telemetry.

METHODS

The analysis derives from six cohorts of marmots born 1983 through 1988 in subalpine habitats near Rocky Mountain Biological Laboratory (RMBL), Gunnison County, Colorado. Young of the year first began emerging from their natal burrows about 1 July and were trapped usually within two weeks, sexed, and permanently identified with numbered ear tags. Young of the year that survived overwinter emerged from hibernation the following May as yearlings; intensive trapping efforts, supplemented by visual observation to identify untrapped animals, were directed toward yearlings in May.

Radio-transmitters were surgically implanted (Van Vuren 1989) in 77% of male yearlings and 88% of female yearlings shortly after emergence from hibernation. Failure to implant all yearlings resulted solely from an insufficient number of transmitters; there was no evidence that non-implanted yearlings were a biased subsample. Implanted marmots were radio-located usually every 1-3 days throughout the summer (May-September) active season thereafter. Transmitters that expired were replaced whenever possible; some marmots carried transmitters continuously for five years.

Survival was indicated by variability in signal location and intensity and in most cases was confirmed by observation of the marmot. Mortality during summer was indicated by recovery of the transmitter or by constancy in signal location and intensity of an underground transmitter (Van Vuren 1990). Overwinter mortality was indicated by failure of the marmot to emerge from its burrow after hibernating. Transmitters of some animals failed overwinter, and overwinter mortality could not be distinguished from early-season dispersal. Such instances, and any others in which status (either alive or dead) could not be determined with a high degree of confidence, were excluded from analysis. Some marmots whose transmitters failed could not be recaptured promptly; these marmots were excluded from analysis for the time period during which failure occurred. The few marmots that died because of human activities, such as trapping and handling, also were excluded.

Survival for the first year was calculated as the proportion of young of the year that was retrapped as yearlings the following spring. These estimates may be biased slighty because some young may have dispersed outside the study area before their first hibernation, then survived overwinter. A few such early dispersals were suspected, but extensive searches the following spring failed to discover any of these young as yearlings.

Annual survival after the first year was partitioned into two periods: summer (emergence from hibernation until entry into hibernation) and winter (entry into hibernation until emergence from hibernation). Survival for each period was calculated as the proportion of animals alive at the beginning of the period that survived until the end of the period. Thus, a decline in sample sizes with age resulted both from mortality and from transmitter failure. A few marmots with failed transmitters were eventually recaptured and equipped with new transmitters; these animals were restored to calculations beginning the next time period. Transmitters were removed from seven females that achieved residency in their natal colony and that were trapped and observed readily. Survival of these females was determined by trapping and observation.

RESULTS

About half the young marmots survived their first year (Table 1); these results are consistent with reports from previous studies in the same area that focused on colonial marmots (summarized in Van Vuren 1990), and with results from a nearby alpine population (Johns and Armitage 1979). High first-year mortality probably resulted, in part, from overwinter death of young that failed to store sufficient fat to survive their first hibernation (Armitage et al. 1976).

All summer mortalities were attributable to predation (Van Vuren 1990); there was no evidence that any implanted animal died during summer from any other cause. Cause of death during winter was usually unknown, but probably was starvation, hyopthermia, or badger (_Taxidea_ _taxus_) predation (Van Vuren 1990).

Survival rates of males and females were indistinguishable until they reached their third summer at two years of age; marmots of both sexes become reproductively mature then. Females that hibernated as yearlings had consistently high survival, both summer and winter, thereafter until they were at least six years old. Males, in contrast, suffered high mortality during their third summer.

Sex and age-specific patterns of survival were illustrated graphically by constructing survivorship curves for male and female marmots. The product of summer and winter survival rates was used to estimate annual survival rates for each age class. Each cohort, beginning with 100 of each sex, was devalued by the proportion surviving that year to obtain an estimate of numbers the following year. The resultant survivorship curves (Fig. 1) should be interpreted with caution because of small sample sizes among older animals, particularly males. Nevertheless, the survivorship curves illustrate high mortality of both sexes until two years of age, after which survivorship curves diverge because of higher male mortality.

DISCUSSION

Survival of females from one to two years of age, based on trapping, was 0.458 (Armitage and Downhower 1974), far lower than the estimate of 0.761 obtained from the product of summer and winter survival as determined by radio-telemetry (Table 1). Most female dispersers emigrated as yearlings (Van Vuren 1990), and the disparity between estimates largely reflects the error that results from calculating survivorship on the basis of disappearance rather than known mortality. Nearly all dispersing marmots disappeared, but most of them survived (Van Vuren 1990).

Distinguishing between emigration and death is a recurring problem in estimating survivorship of mammals. Some authors attempted to resolve the problem indirectly; Sherman and Morton (1984) and Jones (1986) concluded that most individuals that disappeared from their study areas had died, because vigorous trapping efforts in adjacent areas recovered few missing individuals. Dispersing marmots often moved long distances abruptly and rapidly (Van Vuren 1990) and were virtually impossible to discover without radio-telemetry; thus, conclusions about the presumed death of dispersers based on disappearance, despite extensive trapping efforts, may be inappropriate.

A female-biased sex ratio among adults is typical for many ground squirrels (Verts and Costain 1988, Michener 1989), including yellow-bellied marmots (Armitage and Downhower 1974). The causes are poorly understood (Schmutz et al. 1979, Smith and Johnson 1985, Verts and Costain 1988, Michener 1989), but may be related to reproductive activity of males and its effect on male survival (Schmutz et al. 1979, Sherman and Morton 1984, Michener 1989). Among mammals in general, male-biased mortality in many species coincided with the onset of reproductive maturity (Clutton-Brock et al. 1982:278-279, Sherman and Morton 1984, Michener 1989, Van Vuren and Coblentz 1989). Clutton-Brock et al. (1982:279) suggested that high energy expenditure of males during the breeding season, resulting in poor condition at the onset of winter, left males susceptible to disease, starvation, or predation. This suggestion was confirmed for feral sheep (<u>Ovis</u> <u>aries</u>); reproductively active males searched for females and fought with males at the expense of eating, leading to starvation the following winter (Jewell 1986).

Among ground squirrels, proposed causes of male-biased mortality include differences between the sexes in dispersal, predation, intrasexual conflict, exposure, and overwinter mortality (Michener and Michener 1977, Schmutz et al. 1979, Sherman and Morton 1984, Michener 1989). Previous attempts to explain male-biased mortality succeeded only in excluding differential overwinter mortality as the cause (Schmutz et al. 1979, Sherman and Morton 1984).

In yellow-bellied marmots, survival of males and females did not differ during dispersal (Van Vuren 1990) or overwinter (Table 1), and no deaths from intrasexual conflict or exposure were detected. Instead, male-biased mortality derived solely from higher predation during summer on males, mostly two-year-olds (Table 1). The reason two-year-old males were so vulnerable is uncertain, but it probably involved the extensive movements, presumably in search of undefended females (Van Vuren unpubl. data), of males that had dispersed the previous summer (Van Vuren 1990).

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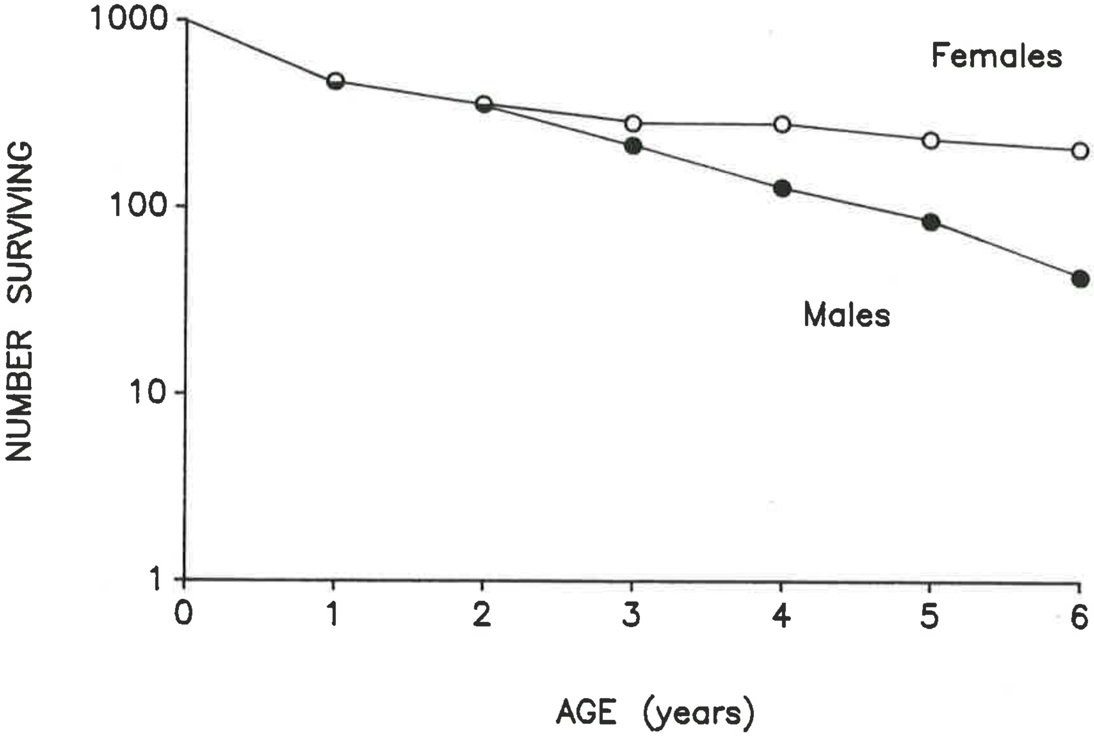
Table 1. Age-specific survival of male and female yellow-bellied marmots near RMBL, Colorado, 1983 through 1989. Statistical comparisons are not reported for survival after entry into hibernation at two years of age because of very low (<2) expected values.

		Males		Females			
Age	Period	_n_	survival	_n_	survival	_G_	_P_
0-1	Annual	203	0.468	181	0.475	0.020	>0.50
1-2	Summer	62	0.823	69	0.826	0.003	>0.90
	Winter	40	0.925	47	0.915	0.028	>0.50
2-3	Summer	33	0.606	41	0.875	7.154	<0.01
	Winter	14	1.000	21	0.905		
3-4	Summer	12	0.750	15	1.000		
	Winter	5	0.800	12	1.000		
4-5	Summer	3	0.667	12	0.917		
	Winter	1	1.000	10	0.900		
5-6	Summer	2	1.000	9	0.889		
	Winter	2	0.500	6	1.000		
6-7	Summer	1	1.000	6	1.000		

FIGURE LEGENDS

Fig. 1. Age-specific survival of male and female yellow-bellied marmots near RMBL, Colorado, 1983 through 1989.



1000
100
10
1
NUMBER SURVIVING
0
1
2
3
4
5
6
AGE (years)
Females
Males

SUMMARY

Surgical implantation of a transmitter into the peritoneal cavity was a fully workable alternative to radio-collars for yellow-bellied marmots. Surgery, which usually required 20-25 minutes, was simple, effective, and largely trouble-free. Transmitters were replaced in some marmots up to six times. Survival until 30 days after surgery was 99%, and neither growth rate nor frequency of reproduction differed between marmots that carried implanted transmitters and those that did not.

Marmots dispersed primarily as yearlings, although some delayed dispersal until two or occasionally three years old. Predominantly yearling dispersal may have resulted from two constraints: young of the year were too small to survive dispersal, and two-year-olds were old enough to be competitors of resident adults. Most dispersal occurred May through July, the first half of the active season, for uncertain reasons. Dispersers emigrated toward all octants of the compass, often crossing large expanses of terrain containing no marmot habitat. Dispersal direction, however, was nonrandom, probably because some dispersers followed linear topographic features that provided burrows for refuge. Dispersal distance distributions for both sexes were skewed; although marmots dispersed as far as 15.5 km, about half settled within 1.5 km. Males dispersed farther than females, probably because of more stringent requirements for successful dispersal. Both sexes must survive transience and locate

unoccupied habitat, but males also must secure undefended females.

Three patterns of dispersal were identified. Some marmots dispersed abruptly; others dispersed through a gradual process that included prior exploratory excursions, incremental home range extension, or both. Some marmots, mostly males, dispersed in two stages; the first stage was a short move to a temporary home range, followed by a second, longer move later in the summer. The first stage of two-stage dispersal may have resulted from the disperser escaping the social environment of the natal area, particularly aggression from the territorial male. Dispersers always emigrated alone.

Dispersing females suffered significantly higher mortality during transience, all due to predation, than did females that remained philopatric. Thereafter, survival of dispersers and philopatric residents was similar. Age at first reproduction among females was similar for dispersers and for philopatric residents, but frequency of reproduction apparently was lower for dispersers. Thus, the cost of dispersal was significant and primarily entailed the risk of predation during transience. Survival of male and female dispersers was similar except during summer the year after dispersal; males apparently suffered higher mortality than females because of extensive movement, presumably to locate undefended females for mates. Marmots that delayed dispersal until two or three years old gained no survival advantage over those that dispersed as yearlings. Dispersal distance affected survival during transience; survival was lower for marmots that dispersed more than 500 m than for those that dispersed shorter distances. Survival during transience was somewhat higher for marmots that dispersed gradually than for those that dispersed abruptly or in two stages. The cost of dispersal for marmots potentially was lower than proposed costs of philopatry; thus, dispersal of marmots is explicable in terms of improving individual fitness.

Predators of marmots were identified by tooth impressions left in the beeswax coating of recovered transmitters, along with other evidence. Five predators were identified; in terms of number of marmots killed, coyotes (Canis latrans) were most important, followed by badgers (Taxidea taxus), golden eagles (Aguila chrysaetos), black bears (Ursus americanus), and martens (Martes americana). More marmots were killed by predators in July than in any other month, for unknown reasons. Large size did not reduce susceptibility to predation; yearling and adult marmots were killed in about the same ratio as they occurred in the population.

Analysis of scats of coyotes, the principal predator of marmots, indicated that marmots were a regular and substantial component of coyote diets. Unexpectedly, marmots were not especially vulnerable to predation during the mating season, possibly because coyotes focused on other prey. Marmots were most vulnerable to predation during July, a result consistent with that from analysis of transmitters recovered from predator-killed marmots; the cause was unknown. Marmots apparently served as alternate prey. Predation risk was greatest during years when gophers (Thomomys talpoides), probably a preferred prey of coyotes, were infrequent in scats.

Age-specific survivorship analysis indicated that survival rates of males and females were indistinguishable until two years of age, the age of reproductive maturity. During the third summer of life males suffered higher mortality than females, apparently because many males were moving extensively in search of undefended females. The female-biased sex ratio in marmots, typical among ground-dwelling squirrels, was caused solely by predation on males, primarily during the third summer of life.

APPENDIX ONE

INFLUENCE OF GROWING SEASON PHENOLOGY ON INTRAPOPULATION VARIATION IN LIFE HISTORY TRAITS OF YELLOW-BELLIED MARMOTS

Growing season phenology may influence life history traits of ground-dwelling sciurids in two ways. First, delay in the onset of the growth of vegetation during spring may force ground squirrels, newly emerged from hibernation, to subsist on stored fat during mating and gestation (Downhower and Armitage 1971, Knopf and Balph 1977, Murie and Harris 1982). Second, duration of the growing season may limit the time available for squirrels to acquire the food resources necessary for growth, reproduction, and accumulation of reserves for overwinter survival (Barash 1974, Andersen et al. 1976, Bronson 1980, Kiell and Millar 1980, Armitage 1981, Phillips 1984).

Previous studies of ground squirrels used snow cover or depth as an index of growing season phenology to explain life history variation (Downhower and Armitage 1971, Armitage et al. 1976, Knopf and Balph 1977, Morton and Sherman 1978, Bronson 1980, Murie and Harris 1982, Phillips 1984). Most of these studies investigated temporal variation among years in one or more populations. Qualitative observations of local geographic variation (Shaw 1925, Svendsen 1974, Andersen et al. 1976, Pfeifer 1982, Fagerstone 1988), however, suggest that the approach might be refined further to examine variation among localities within a single population.

The yellow-bellied marmot (Marmota flaviventris) is a large, hibernating, ground-dwelling squirrel that occupies a variety of habitats throughout much of western United States (Frase and Hoffmann 1980). The two most important resources required by yellow-bellied marmots are rocks for burrow sites and green herbaceous vegetation for food (Svendsen 1974, Andersen et al. 1976, Andersen and Johns 1977, Armitage 1986). In the upper East River valley, near Rocky Mountain Biological Laboratory (RMBL), Gunnison County, Colorado, marmots live in discrete habitat patches, typically subalpine meadows with rock outcrops or talus, where these two resources co-occur (Svendsen 1974).

Some life history traits of marmots near RMBL vary considerably among localities, suggesting that habitat quality varies as well (Armitage 1988). The cause of this variation, however, is uncertain. Overall forage production is an unlikely candidate because dense herbaceous vegetation is present throughout the East River valley for most of the summer; marmots consume less than 4% of aboveground primary production (Kilgore and Armitage 1978). Time of food availability, however, may be important. Marmots often emerge from hibernation by burrowing through the snow and must subsist on stored fat until vegetative growth begins (Downhower and Armitage 1971). Time of snowmelt during spring differs among localities and seems correlated with time of emergence of marmots from hibernation. Thus, variation in life history traits among localities may derive, in part, from variation in snowmelt patterns and its influence on growing season phenology. My objective was to determine if variation in time of snowmelt among localities within a single population of yellow-bellied marmots was a significant predictor of variation in reproduction and growth of marmots.

METHODS

The upper East River flows generally southward through a valley that exhibits the "U" shape characteristic of past glaciation. Elevation of the valley floor is ca. 2900 m and gradient is gentle, averaging 20 m/km. Eight localities were selected that were part of a long-term study of yellow-bellied marmots that began in 1962 (Armitage 1986 and references cited therein). The greatest distance between localities was 4.8 km, but the greatest difference in elevation was only 165 m. Localities were on either side of the valley or on the valley floor, so slope exposure varied.

Data on patterns of snowmelt were collected during May and June from 1983 through 1989. Field work began in early May when most of the upper East River valley remained covered with snow. At intervals of 1-5 days, each of the eight localities was surveyed and percentage snow cover within 75 m of the center of the locality was estimated visually. As snowmelt progressed and snow cover at a given locality approached 50%, surveys were increased in frequency to estimate as accurately as possible the date at which one-half of the locality was free of snow. The date of 50% snowcover was estimated for each locality by linear interpolation between estimates made immediately before and after. Estimates were averaged across the seven years of the study to give one mean date of 50% snow cover, expressed as number of days past 30 April, for each locality.

At each of the eight localities, intensive trapping for marmots was conducted annually for at least 12 years. Each trapped marmot was weighed and affixed with metal ear tags for permanent identification, if not already so marked. Successful reproduction of females was suggested by swollen nipples and subsequently confirmed by emergence of a litter at the female's burrow.

Frequency of reproduction at each locality was calculated by totaling the number of females at least three years old present each year, then summing over all years during which trapping was conducted; this sum was divided into the total number of litters observed. Some females first breed when two years old (Armitage and Downhower 1974), but only females three years or older were considered in order to reduce the confounding effects of socially-induced reproductive inhibition (Armitage 1986) on age of first reproduction. Also, because resources for reproduction derive, in part, from fat stored the previous summer (Andersen et al. 1976, Kiell and Millar 1980), females that were not resident at a given locality for at least one year were excluded.

Litter size was determined by trapping and observation. Body mass of young of the year on 1 August, at age ca. two months, was estimated for marmots born 1983 through 1989. All young that were weighed within seven days of 1 August were corrected to estimated mass on 1 August using a 25.6 g/day mean growth rate reported for 29 young in the same area (Svendsen 1974). Litter size and estimated mass of young on 1 August were averaged across years for each locality.

The effects of time of snowmelt on rate of reproduction (litters/female), mean litter size (young/litter), and mean body mass of young were evaluated with simple linear regression. The independent variable was transformed if the relationship appeared curvilinear. Values for rate of reproduction were arcsine transformed before analysis.

RESULTS

Mean date of 50% snowmelt differed among localities by as much as 21 days, from 9 May to 30 May. Annual variation in date of 50% snowmelt for any one locality ranged to 35 days.

Frequency of reproduction among localities ranged from 0.53 to 0.68 litters/female and was related to time of snowmelt by a negative curvilinear function (Fig. 1). A fourth-power transformation of time of snowmelt explained 78% of the variation in frequency of reproduction.

Accurate data on litter sizes could not be obtained from one locality. Among the other seven, mean litter size ranged from 3.64 to 5.13 young. Like frequency of reproduction, litter size was related to time of snowmelt by a negative curvilinear function; a fourth-power transformation of time of snowmelt explained 80% of the variation in litter size (Fig. 2).

Among localities, mean body mass of young ranged from 712 to

1048 g and was negatively related to time of snowmelt (Fig. 3). Time of snowmelt explained 77% of the variation in mass of young.

DISCUSSION

Some of the variation in time of snowmelt resulted from slope exposure, degree of shading by trees, and spring avalanches that redistributed snow. Most of the variation, however, resulted from asymmetrical snow deposition during winter; snowfall is consistently greater toward the head of the valley, apparently because of an interaction between storm path and local topography (B. Barr pers. comm.). Snowpack in early May was always 0.5-1.0 m deeper at the northernmost locality than at the southernmost locality.

Plant growth began as soon as the soil was exposed by snowmelt, a relationship typical of plants in subalpine (Svendsen 1974) and alpine (Billings and Bliss 1959) environments. Thus, time of snowmelt represented the onset of the growing season. Plant senescence appeared to be caused by cessation of the summer monsoon season, onset of hard freezes, or both. Both factors acted consistently over the entire study area, and plant senescence, as indicated by pronounced yellowing, occurred generally simultaneously throughout the valley. Thus, time of snowmelt was also an indicator of duration of the growing season.

The active season of high-elevation ground squirrels should be timed in some fashion to maximize growth and reproduction (Armitage et al. 1976, Morton and Sherman 1978, Michener 1979, Bronson 1980), but how this is accomplished is not well understood. Michener (1977) suggested that high-elevation populations, because of the risk of unpredictable late-winter storms (Morton and Sherman 1978), are relatively inflexible in adjusting time of emergence to spring conditions; this suggestion was not supported by subsequent research (Morton and Sherman 1978, Bronson 1980, Murie and Harris 1982, Phillips 1984).

Variability in weaning dates of marmot litters near RMBL (Armitage et al. 1976) suggests that onset of the active season may vary as well. Emergence times of marmots near RMBL were not quantified, but responsiveness of marmots to spring conditions can be inferred by evaluating two alternative scenarios. If marmots were flexible and delayed emergence in response to a late winter, reproduction that year would be little affected, although fat storage and perhaps reproduction the following year might suffer. Alternatively, lack of flexibility would place female energy requirements out of phase with resource availability if the growing season is delayed. Females would have to subsist on fat reserves, and reproduction would be depressed because some females might fail to breed and others might conceive, then later abort. The second alternative is supported by Downhower and Armitage (1971), who reported that reproduction was depressed during years when snowmelt was delayed. Thus, marmots near RMBL adjust their emergence times to spring conditions imperfectly. Perhaps marmots show elements of both alternatives; they may time their emergence to coincide with the long-term average of local conditions, but also may vary emergence times somewhat according to conditions in a given year.

Translocated yellow-bellied marmots in Oregon adjusted their active season to local phenology in just two years (Thompson 1979), indicating that marmots at localities with consistently late snowmelt could shift their active season accordingly; qualitative observations near RMBL suggest they do so. However, because the growing season ends more or less simultaneously throughout the upper East River valley, a consistently delayed active season means a shorter time of access to growing vegetation for food.

A lower frequency of reproduction at localities where snowcover persisted (Fig. 1) probably was a physiological response to reduced annual food intake. Individual female marmots near RMBL sometimes breed in consecutive years, demonstrating a capacity for annual breeding, but this capacity often is not realized. One explanation is reproductive inhibition (Armitage 1986), but I suggest the principal reason is that food resources are not available for a sufficient length of time during the short growing season to satisfy annual needs for both maintenance and reproduction. Females probably breed whenever they have accumulated fat reserves, in excess of those needed to survive hibernation, that are sufficient to initiate production of a litter. Thus, females breed on average two of every three years at localities where snow melts early, but only about every other year where snow persists.

The effects of late snowmelt on frequency of reproduction and on litter size were similar; consequently, these two variables covaried

(Fig. 4). Thus, females exposed to longer growing seasons responded both by breeding more often and by producing larger litters. Annual production of young, the product of frequency of reproduction and litter size, showed the expected negative curvilinear relationship to time of snowmelt (Fig. 5).

Young marmots that are born too late in the season fail to accumulate sufficient fat to survive hibernation (Armitage et al. 1976). Data on overwinter survival of young were not available for enough localities for analysis, but smaller sizes on 1 August of young at localities with delayed snowmelt suggests that, in addition to lower fecundity, females at these localities may also bear the cost of higher overwinter mortality of their young. Young with inadequate fat reserves might delay hibernation, but benefits of such a tactic are questionable because the nutritive quality of post-senescense vegetation may be low.

My results suggest that time of snowmelt, through its influence on growing season length, is a major determinant of habitat quality for yellow-bellied marmots near RMBL. Females would gain a reproductive advantage by seeking out burrow sites that melt out early, but few, if any, do so. Such a search requires movement that entails the risk of predation (Van Vuren 1990), and better quality habitat may already be occupied by other marmots (Armitage 1988).

The negative curvilinear relationships between time of snowmelt and both frequency of reproduction and litter size suggest effects may extend beyond habitat quality to habitat suitability. Snow may melt so late in some areas that the growing season is not long enough for a female to breed at all. Excessive persistence of snow may explain why some sites that otherwise seem to provide adequate resources are not regularly inhabited by marmots.

Whether variation in life history traits in ground squirrels represents genetic variation or phenotypic plasticity has been a topic of considerable interest (Bronson 1979, Dobson and Kjelgaard 1985, Barash 1989:315-316). Barash (1974) proposed that frequency of reproduction in yellow-bellied marmots was a heritable trait. My results indicate otherwise. The eight localities were separated by distances that were well within those typically traveled by dispersers (Van Vuren 1990); 10 marmots moved between localities during the study. Thus, opportunities for genetic differentiation were limited. Rather, the high degree of predictiveness of time of snowmelt in explaining frequency of reproduction and litter size suggests a phenotypically plastic response to environmental variation.

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FIGURE LEGENDS

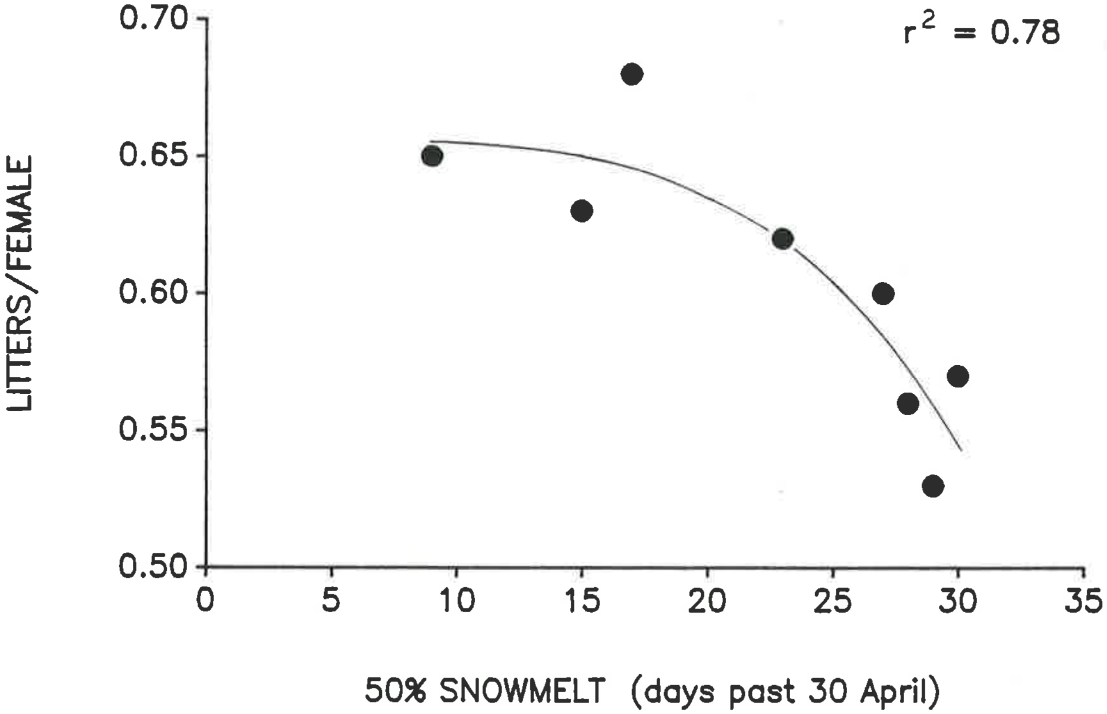
Fig. 1. Relationship between frequency of reproduction of female yellow-bellied marmots and mean date of 50% snowmelt among eight localities near RMBL, Colorado. The regression model is arcsine $\underline{Y}^{0.5} = 54.08 - 0.00000800\underline{X}^4$, $\underline{F}_{1,6} = 21.0$, $\underline{P} < 0.005$.

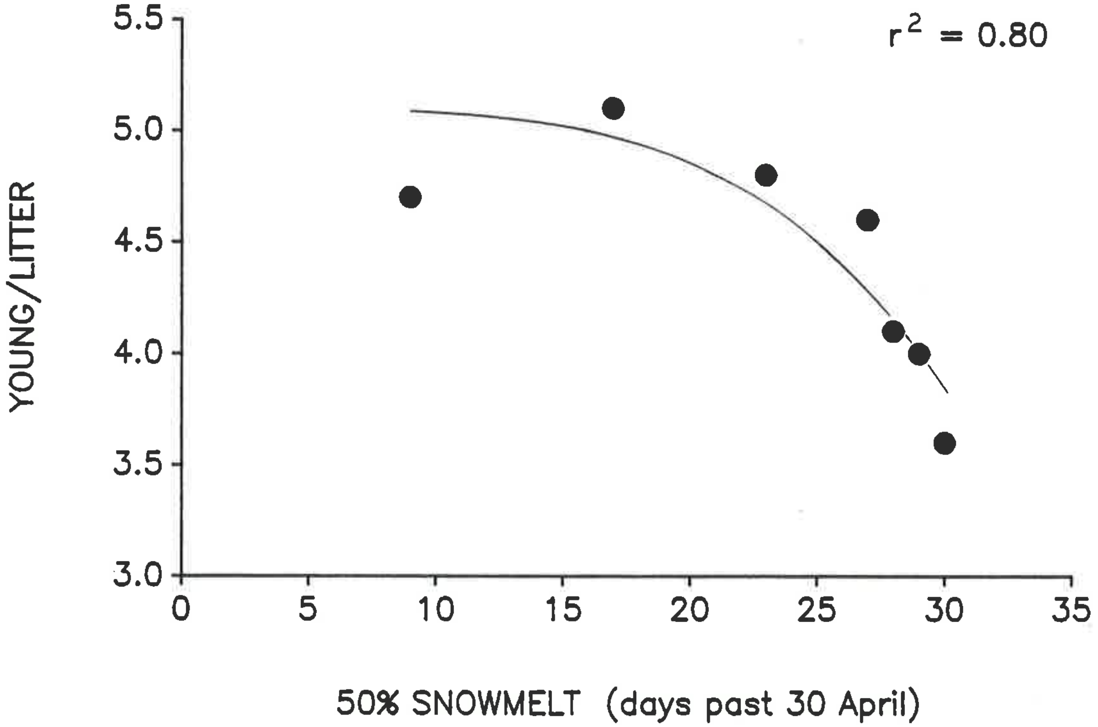
Fig. 2. Relationship between mean litter size of yellow-bellied marmots and mean date of 50% snowmelt among seven localities near RMBL, Colorado. The regression model is $\underline{Y} = 5.10 - 0.00000154\underline{X}^4$, $\underline{F}_{1,5} = 18.8$, $\underline{P} < 0.01$.

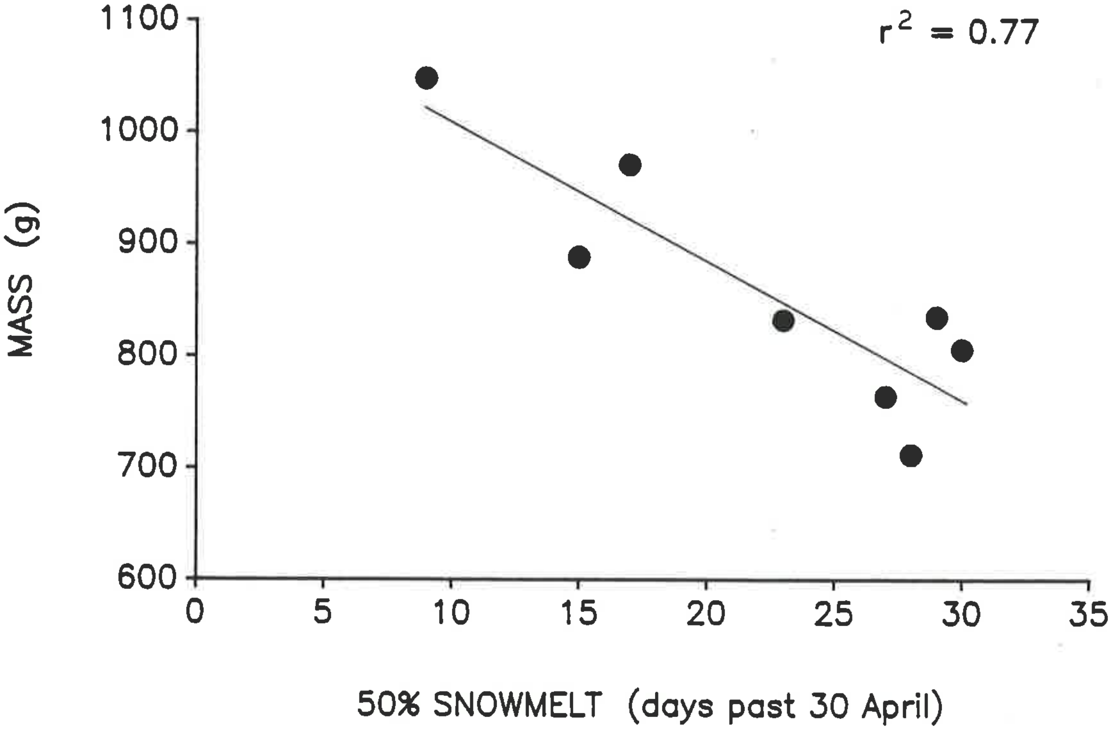
Fig. 3. Relationship between mean body mass of young yellow-bellied marmots on 1 August and mean date of 50% snowmelt among eight localities near RMBL, Colorado. The regression model is $\underline{Y} = 1133.7 - 12.44\underline{X}$, $\underline{F}_{1,6} = 20.1$, $\underline{P} < 0.005$.

Fig. 4. Relationship between mean litter size and frequency of reproduction of female yellow-bellied marmots among eight localities near RMBL, Colorado. The relationship is significant ($\underline{r} = 0.88$, $\underline{P} < 0.01$).

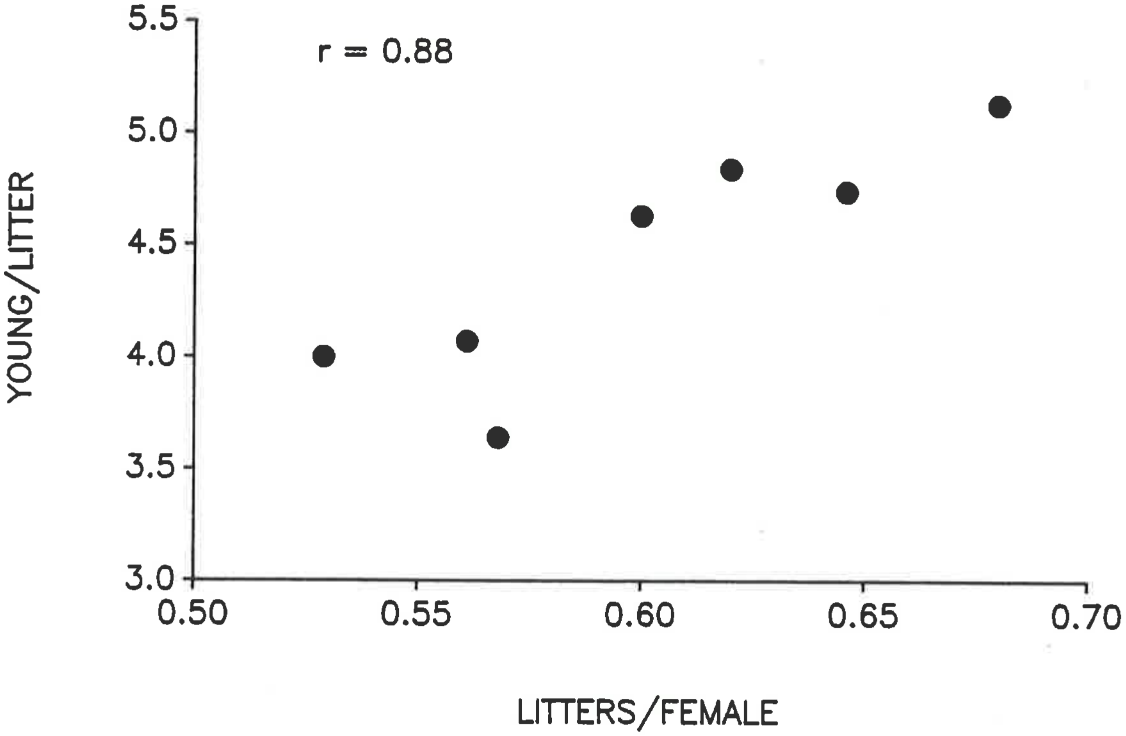
Fig. 5. Relationship between mean number of young produced per female yellow-bellied marmot and mean date of 50% snowmelt among seven localities near RMBL, Colorado. The regression model is $\underline{Y} = 3.38 - 0.00000160\underline{X}^4$, $\underline{F}_{1,5} = 29.0$, $\underline{P} < 0.005$.


r^2 = 0.78
LITTERS/FEMALE
0.70
0.65
0.60
0.55
0.50
0
5
10
15
20
25
30
35
50% SNOWMELT (days past 30 April)


r^2 = 0.80
YOUNG/LITTER
5.5
5.0
4.5
4.0
3.5
3.0
0
5
10
15
20
25
30
35
50% SNOWMELT (days past 30 April)



r^2 = 0.77
MASS (g)
1100
1000
900
800
700
600
0
5
10
15
20
25
30
35
50% SNOWMELT (days past 30 April)


r = 0.88
YOUNG/LITTER
LITTERS/FEMALE
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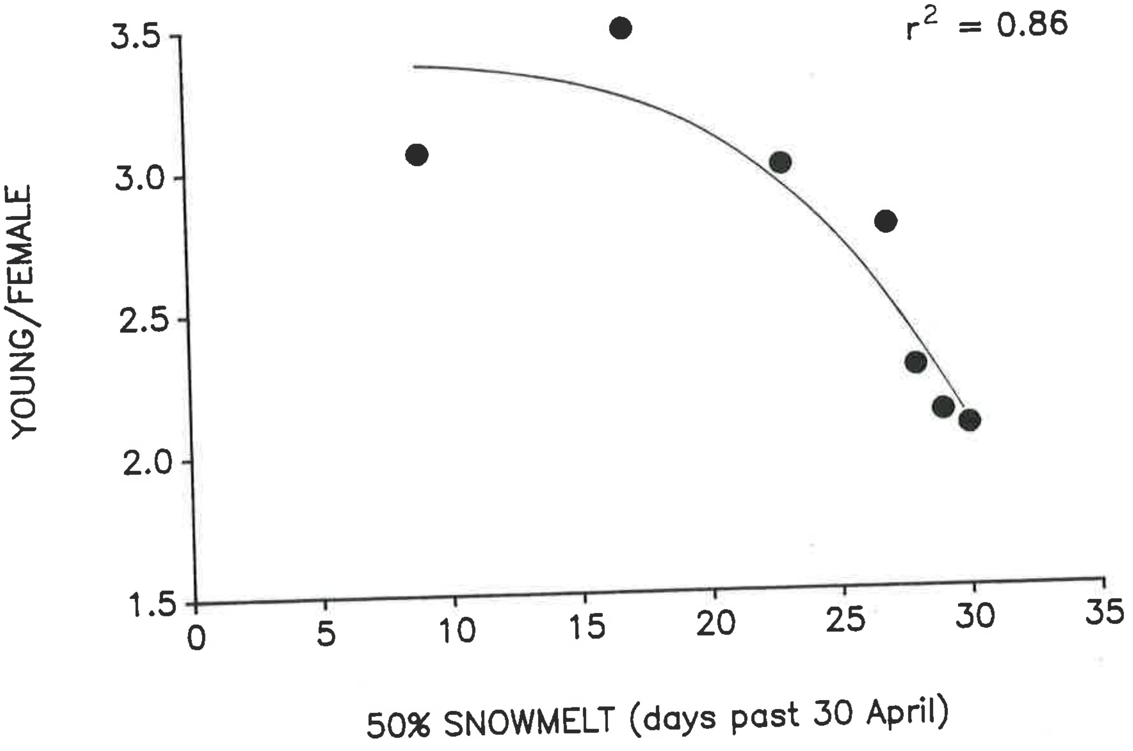
5.0
4.5
4.0
3.5
3.0
0.50
0.55
0.60
0.65
0.70


r^2 = 0.86
YOUNG/FEMALE
3.5
3.0
2.5
2.0
1.5
0
5
10
15
20
25
30
35
50% SNOWMELT (days past 30 April)

APPENDIX TWO

A COMPARISION OF REPRODUCTION AND SURVIVAL BETWEEN COLONIAL AND NONCOLONIAL YELLOW-BELLIED MARMOTS

Yellow-bellied marmots (Marmota flaviventris) usually live in colonies, defined as social groups that occupy a piece of circumscribed habitat (Svendsen 1974). Not all marmots are colonial; some lead a relatively asocial existence outside of colonies, variously described as transient, isolated, peripheral, or satellite (Downhower and Armitage 1971, Svendsen 1974). During seven years of radio-telemetry research on yellow-bellied marmots, I identified some marmots that lived for a season in burrows peripheral to colonies, but none that were transient more than a few days (Van Vuren unpubl. data). Few marmots, particularly females, were ever isolated from other marmots, and "satellite" implies a subordinate status that has not been demonstrated. In this report, all marmots living outside of colonies will be referred to as noncolonial.

A comparison of reproduction and survival between marmots living in colonies and those living elsewhere would help elucidate the costs and benefits of group-living. Further, because the harem-polygynous mating system of yellow-bellied marmots derives from the social structure, the range of sociality shown by marmots, from colonial to relatively asocial, suggests that the mating system may vary accordingly (Armitage 1986).

Three studies compared reproduction and survival between colonial and noncolonial localities near Rocky Mountain Biological Laboratory (RMBL), Gunnison County, Colorado (Table 1). Some measures of reproduction varied among studies, probably due to small sample sizes ($\underline{n} \leq 13$ for noncolonial localities), but all three studies agreed that about one-half of colonial young were recaptured as yearlings, whereas noncolonial young were rarely, if ever, recaptured. Downhower and Armitage (1971) proposed that low recapture rates at noncolonial localities resulted from mortality or early dispersal, and concluded that noncolonial females were reproductively less successful than colonial females. These data suggest that colonial females may have higher fitness than females living outside colonies, and that males that cannot acquire a harem within a colony have little chance for reproductive success.

Results of these three reports, however, may have been affected by a bias of sampling effort toward colonies, in three ways: 1) colonies were trapped more intensively than noncolonial localities; 2) colonies were trapped earlier in the season, before most yearlings dispersed; and 3) colonies were subject to more intensive visual observation, resulting in improved trapping efficiency.

From 1983 through 1989, my research on dispersal of yellow-bellied marmots (Van Vuren 1990) focused, in part, on noncolonial marmots. Here I re-evaluate reproduction and survival of colonial and noncolonial yellow-bellied marmots near RMBL to derive estimates more reliable than those reported previously (Downhower and Armitage

1971, Armitage and Downhower 1974, Svendsen 1974) because of improved sample size and because of greater effort directed toward noncolonial localities. Additionally, I will compare survival of dispersers from colonial and noncolonial localities.

METHODS

I defined a colony as a circumscribed locality that typically supported two or more adult (≥2 years old) females that interacted socially and had overlapping home ranges. Six colonies were included in this analysis (River, Marmot Meadow, Cliff, Picnic, Boulder, North Picnic). Noncolonial sites were those that typically supported at most one adult female (Lower Falls, Upper Falls, River Bend, West River Bend, River Annex, Bench Cabin, Gothic Townsite, Copper Bend, Billy's Cabin, Beaver Talus, White Log, Waterfall Talus, SOB, Rolling Rock). Three localities (Marmot Meadow Annex, Copper Creek, Gothic Talus) were excluded from analysis because of irregular sampling effort or uncertain classification.

Adult females resident at each locality were monitored by trapping, radio-telemetry, and observation. Successful reproduction, suggested by swollen nipples during gestation, was considered confirmed when a litter appeared aboveground. Reproductive rate was computed by dividing the total number of litters into the number of possible pregnancies (number of adult females present each year, summed over seven years). Litter size was determined by trapping and by observation. Litters whose size was not accurately known were excluded from analysis. Recapture of yearlings was facilitated by searching intensively for all yearlings, regardless of social origin, shortly after they emerged from hibernation in May. Survival of dispersers was determined by surgically implanting radio-transmitters (Van Vuren 1989) in yearlings shortly after they emerged from hibernation, then monitoring their fates (Van Vuren 1990). Survival was calculated according to Van Vuren (1990).

RESULTS

No differences in rate of reproduction ($G = 0.259$, $P > 0.50$) or litter size ($t = 0.065$, $P > 0.90$) between colonial and noncolonial females were detected (Table 1). Because some females were responsible for more than one litter or possible pregnancy during the seven years, the assumption of independence of observations is violated for both tests. I doubt, however, that this violation unduly influenced the results.

A higher proportion of young born in colonies were recaptured as yearlings than young born at noncolonial sites ($G = 13.678$, $P < 0.005$) (Table 1). Survival rates of dispersers, both during the summer of dispersal and through the following winter, were virtually indistinguishable between colonial and noncolonial sites (Table 2). Survival rates of yearlings that did not disperse, although of considerable interest, could not be compared meaningfully because few yearlings failed to disperse from noncolonial sites. Only four females and no males born at noncolonial sites became adult residents at their natal locality.

DISCUSSION

Colonial living conferred no advantage in reproduction to females, nor did it influence the probability that their offspring one year or older would survive dispersal. Rather, young of colonial females had a higher probability either of survival until yearling age or of remaining sufficiently close to their natal burrow to be detected and trapped the following spring. Also, yearling daughters of colonial females were more likely to become adult residents there (Armitage and Downhower 1974).

Svendsen (1974) reported that noncolonial sites occurred in smaller forest openings than did colonies. I suggest that the lower recapture rate of young at noncolonial sites may have occurred because resources, such as suitable hibernacula or space, were insufficient to support a female and her offspring on a longterm basis. Some young may have perceived this limitation and dispersed early; others may have remained and hibernated, only to suffer high overwinter mortality. Most of those that survived eventually dispersed. Dispersal during the first summer of life has been suspected on a few occasions but never confirmed; hence, the effects of early dispersal and overwinter mortality on recapture rates cannot be distinguished.

Whatever the cause, females at noncolonial sites seldom recruited their daughters; this failure to form matrilines, and the loss of direct fitness benefits that acrue from matriline formation, may be the real fitness cost of a noncolonial existence (Armitage

1988).

The demonstrated reproductive success of noncolonial females has implications for the mating system of yellow-bellied marmots. Because harem males rarely leave their territories (Armitage 1974), most litters born outside of colonies evidently 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 male territoriality, and noncolonial males may have difficulty defending territories that include more than one female.

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Table 1. Summary of results of four studies that compared mean litter size, rate of reproduction (litters per female per year), and percentage of young of the year recaptured as yearlings, between colonial (Col) and noncolonial (Non) localities occupied by yellow-bellied marmots near RMBL, Colorado. Noncolonial is synonymous with isolates (Downhower and Armitage 1971) and satellites (Armitage and Downhower 1974, Svendsen 1974).

	Litter size		Litters/female		% recaptured	
Study	Col	Non	Col	Non	Col	Non
Downhower and Armitage 1971	4.50	4.14	0.50	0.28	50	7
Armitage and Downhower 1974	4.15	4.46	0.48	0.26	47	2
Svendsen 1974	2.77	3.63	0.46	0.73	54	0
This study	4.20	4.18	0.64	0.60	55	35
n	49	33	105	70	233	139
SD	1.34	1.42				

Table 2. Survival of dispersing yellow-bellied marmots from colonial and noncolonial localities near RMBL, Colorado, 1983 through 1989. First summer: dispersal until onset of hibernation. First winter: onset of hibernation following dispersal until emergence the next spring.

	First summer		First winter	
	n	Survival rate	n	Survival rate
Colonial	60	0.73	33	0.91
Noncolonial	23	0.74	9	0.89