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# SOCIAL AND POPULATION DYNAMICS OF YELLOW-BELLIED MARMOTS: Results from Long-Term Research

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## INTRODUCTION

Population dynamics is the consequence of the fitness strategies of individuals. Fitness is measured as reproductive success, i.e. the production of descendants. Individuals may forego short-term reproduction to increase survival (51), thereby increasing the incidence of iteroparity and lifetime reproductive success (LRS). Measured as production of offspring, LRS is not a panacea for answering evolutionary questions (64). However, the value of LRS is improved if the reproductive success of descendants is determined. Measuring LRS requires detailed, longitudinal studies of individuals. Such studies allow us to partition and evaluate the significance of various components of LRS, such as age of first reproduction, degree of iteroparity, production and survival of offspring, and recruitment (43).

A major component of the fitness strategy of an individual is its social behavior with conspecifics. Social behavior can affect various components of LRS. Aggressive behavior may reduce fecundity by inhibiting reproduction (112). Social behavior affects spacing behavior (82, reviewed in 45) that, in

turn, may limit immigration and group size and cause some individuals to disperse (35, 61, 70, 83). Dispersal may be density-independent (62) and is related to mating systems (65, 93). Among mammals in general, juvenile males are the predominant dispersers, especially in those species with promiscuous or polygynous mating systems (48). Generally, male mammals compete for mates, and females compete for resources for rearing young (e.g. 34). Hence, both males and females play key roles in the processes of dispersal and recruitment, especially with individuals of the same sex. Although dispersal should be viewed as a process to increase an individual's fitness (4, 52, 90), dispersal has demographic consequences (84, 102). Finally, social dynamics may be kin-biased (19); therefore, the population consequences of social behavior may depend on the relatedness of the individuals involved.

The information needed to assess the factors governing LRS is that needed to describe population dynamics and the mechanisms of population regulation. One advantage of focusing on individual fitness and deriving population dynamics from the activities of individuals is that we are freed from focusing on density as the most important agent acting on populations (45). Furthermore, life-history traits of individuals of a behavioral phenotype (41, 47) or of members of a kin group may be combined so that the demographic characteristics of alternative phenotypes or of kin groups of different sizes may be compared. Because survival is an exercise in probability (113), individuals should act to increase the probability of survival of their offspring and/or to reduce the probability of survival of the offspring of conspecifics (e.g. 33, 38, 75). Thus, the behavior of individuals can provide insights into population processes (68).

Detailed, longitudinal studies of individuals are readily conducted on relatively large, diurnal mammals. We initiated research on the yellow-bellied marmot (*Marmota flaviventris*) at the Rocky Mountain Biological Laboratory, Gothic, Gunnison County, Colorado, in 1962, at 2900 m. Additional work occurred in North Pole Basin at 3400 m. The semi-fossorial rodent is a member of the subfamily Marmotinae of the family Sciuridae (squirrels) and is closely allied to the prairie dogs and spermophiles (58, 67). This species occurs at high elevations, usually above 2000 m, in western United States, southcentral British Columbia, and southern Alberta (58).

In the Gothic area, the distribution of marmots is clumped and conforms closely to the mosaic formed by meadow and forest vegetation (103). Marmots occupy the open area relatively free of trees and shrubs, but which contains talus, rock outcrops, or scattered boulders under which burrows are constructed. Grasses (*Festuca*, *Bromus*, *Poa*) and large showy perennials characterize the meadows. The grasses contribute 9% to 41% of the total dry biomass; the variation occurs among sites and seasonally within a site (57, 80).

Marmot habitat patches are classified as colonial or satellite (= isolate; 49). A colony consists of one or more males, resident females, usually yearlings (animals one year old), and young (animals <4 months old) (5, 25). Satellite sites rarely have more than one female, a male may not be present, yearlings rarely are present, but young usually are present (25). Colonial sites have larger openings ( $\bar{x} = 58$  ha vs 6.6 ha), more residents ( $\bar{x} = 3.2$  vs 1.4), more resident females ( $\bar{x} = 2.1$  vs 1.0), and more burrows in use ( $\bar{x} = 14$  vs 2.3). Vegetative characteristics do not differ between the two types of sites (103). In effect, satellites are minihabitat patches, and there is a continuum of habitat sizes ranging from about 0.01 ha to 70 ha or more (15, 20). Area is correlated with the mean number of resident females ( $r = 0.86$ ) and with the total number of resident adults ( $r = 0.83$ ) (103).

## ACTIVITY PATTERNS

Density-independent weather factors may affect survival and reproduction. Animals may adjust their activity patterns to minimize their exposure to environmental stress. The alpine and subalpine environments where marmots live are characterized by large diurnal fluctuations in temperature, intense sunshine during the summer, and low temperatures and several months of snow cover during the winter (42, 63).

### *Annual Cycle of Reproduction and Hibernation*

**PATTERN AND TIMING** The annual cycle is a circannual rhythm (46, 110) with two phases—heterothermal and homeothermal (89). Immergence, hibernation, emergence, reproduction, and growth and preparation for immerge are sequentially linked. Emergence and immerge patterns follow an age-sex sequence (6, 78, 81). Adult males emerge first in late April or early May and are soon followed by adult females, yearling males, and yearling females. The same sequence occurs during immerge except that females that produced litters immerge later than males and nonreproductive females, and young immerge last, with female young immerging before males (24). Immergence begins in late August and usually is completed by mid September.

**PHYSIOLOGICAL CHARACTERISTICS** The physiology of the heterothermal phase is characteristic of hibernators (53, 59, 60, 71). Adults spontaneously terminate hibernation, but young do not terminate hibernation until fed or emaciated (60). Spontaneous termination of hibernation apparently is related to energy resources. The larger adults can withstand a prolonged fast, whereas the young cannot (59), and emerge when vegetation is available (78, 103). Also, adults must reproduce as early as possible; survival of young weaned late in the homeothermal phase is less than 10% (26).

All age classes gain mass at the rate of about 12 to 14 g/day, in the Gothic area, but young grow at a significantly greater rate at 3400 m (2, 26). Reproductive females initiate mass gain about three weeks later than yearlings, adult males, and nonreproductive females. The larger the young are at immersgence the more likely they are to survive (26); the critical factor may be the amount of fat accumulated because young that fail to fatten do not survive hibernation (87). In the laboratory, metabolic rate, change in body mass, and food consumption follow a circannual rhythm with the maximum and minimum values of metabolic rate preceding the maximum and minimum value of food consumption by at least one month and those of body mass by at least two months. The rhythm may be a critical mechanism that shifts energy expenditures from maintenance to production in preparation for immersgence (29, 115). Adult marmots decrease the time spent foraging in late summer (55, 78, 80). One intuitively expects an increase in foraging time as marmots fatten for hibernation; however, foraging time may be adjusted to an individual's energy balance, which is affected by the phase of the annual cycle. Thus, ground squirrels deprived of food for several weeks and returned to ad libitum feeding increase consumption sufficiently to return body mass to the level expected for that phase of the annual cycle (46). The relationship between the annual cycle of metabolism and change in mass and foraging needs further investigation in free-ranging marmots and other ground-dwelling sciurids.

**VARIATION IN WEATHER PATTERNS** Survivorship and reproduction could be affected by the length of the active season, which varies from year to year as a consequence of variation in the onset and/or termination of snow cover. When data from all colonies are lumped, reproductive females survive better the later the onset of winter, and young survive better the earlier winter terminates (25). Both mean litter size and percent total survival are positively correlated with the length of the growing season (99). The length of the growing season varies among marmot localities over a distance of 4.8 km in the East River Valley where the greatest difference in elevation between colonies is 165 m. Mean date of 50% snow cover differs among localities by as much as 21 days; the latest date was May 30. The number of litters per female and mean litter size are negatively correlated with time of 50% snow cover (109). This relationship probably is a phenotypically plastic response to environmental variation and not a heritable trait. The East River populations lie within the distances readily transversed by dispersers (108), and considerable gene flow occurs among these populations (97). The significance of the length of the growing season for reproduction is dramatically emphasized by the pattern in North Pole Basin where the mean date of 50% snow cover is June 30. About one fourth of the females weaned a litter each year, compared

to one half in the East River Valley (15), and no female produced litters in consecutive years during six years of study (78). Annual reproductive success of females is related to food resources (2). Females lost mass early in the active season and probably relied on body fat as a major source of energy. The failure to breed in successive years also appears to be phenotypic; about one fourth of the females each year initiated reproduction (including some that weaned litters the previous year) but failed to wean a litter, which suggests that their energy reserves were insufficient to sustain both maintenance and reproduction.

The annual cycle is a major constraint on population dynamics. The need to satisfy the energy requirements for hibernation limits reproduction to a single annual event occurring immediately after emergence. The short active season combined with large body size delays reproductive maturity until two years of age. Post-natal reproductive investment is extended into the second summer of a juvenile's life and probably is the major factor leading to sociality in marmots and other ground-dwelling sciurids (12). The need to mobilize energy for reproduction and then prepare for hibernation in a short time period undoubtedly accounts for the energy conservative physiology of this species and probably of other hibernating sciurids (29, 80, 81, 87, 88).

### *Daily Cycles*

**SEASONAL PATTERN** During the first two weeks after emergence the daily activity cycle is unimodal with peak activity in the early afternoon. As daily temperatures increase, the activity cycle becomes bimodal with peaks at 1000 and 1700 hrs (6). As temperatures continue to warm, the peak morning activity shifts to 0800 hrs and the afternoon peak to 1800 hrs, with some variation due to the direction of the slope on which a colony is located (5, 80, 87, 88, 106). As temperatures and photoperiod decrease in late summer, peak activity shifts to a later time in the morning and an earlier time in the afternoon and becomes unimodal just before immurement (80, 86).

**TIME BUDGET** On average, yellow-bellied marmots spend 72 to 84% of a 24-hr day in their burrows, 8 to 12% sitting above ground, and 7 to 16% in moderate activity and foraging (81, 87, 106). During lactation, females spend an average of 29% of their above ground time foraging. Foraging time decreases to 22% ( $0.1 > p > 0.05$ ) during the first four weeks post-emergence of the litter and to 18% in late summer about when the molt is completed (55). The seasonal change in the time budget of yearling females is similar except the decrease in foraging time occurs during the first four weeks post-emergence of the young and coincides with the completion of the molt. Oxygen consumption decreases markedly after the annual molt (96). The pattern of seasonal change in foraging is similar to the pattern of change in

metabolism and food consumption of laboratory animals. This similarity suggests that foraging is adjusted to current metabolic needs. The precise nature of the metabolic needs (e.g. lactation, growth, mate seeking) and its relationship to metabolic rate and the time budget remains to be determined.

**PHYSIOLOGICAL CONSTRAINTS** The thermoneutral zone extends approximately from 15 to 20°C for adults and 20 to 25°C for young (29, 86). Adult activity decreases when ambient temperature exceeds 20°C (5), and foraging occurs five times as frequently on cloudy as on sunny days (106). Air temperatures usually are lower than the lower critical temperature during the morning activity period. However, marmot activity is affected primarily by the standard operative temperature ( $T_{es}$ ), a measure that integrates all factors affecting thermal energy exchange (88). Foraging time decreases hyperbolically when  $T_{es}$  exceeds 25°C, frequently between 0900 and 1000 hrs. Marmots extend foraging time by becoming hyperthermic, but they cease foraging when body temperature approaches 40°C (88). The high  $T_{es}$  persists until late afternoon; marmots must either forage at  $T_{es}$ 's below the thermoneutral zone or engage in short foraging bouts during midday. Marmots do the former primarily but pay a cost of increased metabolic rate. This cost is reduced by minimizing activity at stressful  $T_{es}$ 's and by metabolic rates and thermal conductances that are much lower than predicted for a mammal of this body size (29, 80). Thus, thermoregulatory costs constitute only 1% to 6% of daily energy expenditure (87).

The activity pattern of marmots suggests that they are lazy (69). If, as suggested, foraging time is adjusted to metabolic rates, marmot foraging may be an example of Herber's case 2. At least part of the effect of being lazy is that it conserves energy (87), but it is unclear why much of the lazy time is spent sitting and sunning instead of in the burrow. Sunning does not affect body temperature but could possibly affect metabolic rate (106), especially when  $T_{es}$  is below the lower critical temperature. High  $T_{es}$  limits adult foraging time such that a marmot attempting to escape aggression by shifting its activity period to midday would probably reduce its effective foraging time by one half and would encounter a considerable energy deficit because it could fill its gut once a day instead of twice (88). Young can forage more extensively during midday because the  $T_{es}$  of young is lower; thus young encounter less heat stress and avoid much of the cold stress by foraging at higher  $T_{es}$ 's than adults (88).

**Water balance** Although marmots shift foraging areas away from water-stressed plants (57) and reject dried leaves in feeding trials (11), water metabolism only slightly affects diet choice. Water turnover rates in field animals may be up to five times those of laboratory animals provided water ad

libitum (87, 111). However, several features of water balance indicate that yellow-bellied marmots conserve water and that this conservation is related to metabolic rate and hibernation. The rate of evaporative water loss ( $\text{mg H}_2\text{O} \cdot \text{ml O}_2^{-1}$ ) is similar to that of desert dwellers and at the lower end of the range of other sciurids (32). Marmots on a restricted water regimen concentrate urine more than similarly stressed ground-dwelling sciurids (32, 111) and significantly reduce food consumption and metabolic rate (29, 111). The inability of marmots to mobilize water for evaporative cooling may be related to meeting water requirements during hibernation; at low temperatures characteristic of hibernation only about one half of metabolic water production is lost through evaporation, thereby providing water for urine formation (29). Marmots probably have no other water input during hibernation. Although low metabolic rates and low conductances (including low evaporative water loss) are essential for conserving energy, yellow-bellied marmots living in lowland, semixeric areas have higher metabolic rates at low temperatures associated with higher conductances and a greater ability to dissipate heat evaporatively (29).

## RESOURCE UTILIZATION

The two major resources of marmots are food and burrows. Young are weaned (emerge from the natal burrow) in late June to mid July when the standing crop of vegetation reaches 75% to 100% of its maximum (57, 81). All age classes gain mass; food does not appear to limit growth and preparation for hibernation (2, 26, 81).

### *Annual Energy Budget*

Marmots consume 0.8 to 3.1% of the aboveground primary production. Although the assimilation efficiency of 71% to 75% falls in the range of mammalian herbivores (66), the production efficiency of 22.8% is about seven times greater than that of other mammals (76, 81). The consequent high production/maintenance ratio of yellow-bellied marmots seems to be a consequence of the energy-conserving physiology.

Marmots are generalist herbivores (57), but their choice of plants is restricted by plant secondary compounds (11). Food selectivity is based primarily on relative abundance, phenology, nutritional quality, and energy requirements (57). Unfortunately plant epidermal cells do not survive digestive processes equally well, thus precluding the use of fecal analysis to assess diet. Diet choice requires more study; e.g. there is some indication that plants may be selected on the basis of their lipid composition (54). Access to foraging areas is strongly influenced by kinship; only closely related adult females share foraging patches (56). Mothers and juveniles and littermates (both young and yearlings) have nearly identical foraging areas.

### *Burrows*

Burrows are of three types: home or nest, flight, and hibernating. These are not mutually exclusive; the same burrow may be used for all three functions. When alarmed, marmots run to the nearest flight burrow; if possible, they return to the nest burrow (5). Burrows are widely distributed in marmot habitats; a marmot seldom is far from this place of refuge, typically less than 20 m (5, 56, 103). Flight burrows often have only one entrance whereas a nest burrow typically has several entrances. Most nest burrows and hibernacula occur in rocks or are dug in soil under rocks, logs, or bushes. Rocks and tree roots support the structure (104). In contrast to the alpine (*M. marmota*) and steppe (*M. bobac*) marmots, yellow-bellied marmots almost never construct a nest burrow in open meadow because of their vulnerability to badgers (*Taxidea taxus*) (3).

Quality burrows, especially those that function as a hibernaculum, may be the critical resource that determines breeding ratios (73), but the presence of several hibernacula in the territory of *M. marmota* (31) suggests other factors are also important. Group hibernation may be critical for survival and lifetime reproductive success where low temperatures increase the use of fat reserves (30, 31). At North Pole Basin, group hibernation was common and we knew of no instance in which less than two animals occupied a hibernaculum (78). We do not know the extent of group hibernation in the East River Valley. Dispersers fitted with radiotransmitters hibernated singly and about 12% died during hibernation, a figure not statistically different from the 10% hibernation mortality of residents (108). Much more needs to be learned about the energetics of hibernation of field marmots and its relationship to social structure and lifetime reproductive success.

## MATING SYSTEMS AND SOCIAL DYNAMICS

### *Male Reproductive Tactics*

**SEX RATIOS** Although sex ratios at weaning are 1:1 (18, 25), adult sex ratios are biased toward females (5, 6, 25, 78, 92). The female bias, readily apparent at colonial sites (Figures 1, 2), is a consequence of differential mortality; more males, especially at two years of age when they move around seeking females, fall to predators (108). Males may be monogamous in small habitat patches or may defend several females, each living alone, over an area twice the size of the territory of a colonial male (8, 108). Polygyny characterizes the mating system where females are clumped on colonial sites (5, 6, 8, 49); the average breeding sex ratio at these sites is 1:2.3 (15).

**TERRITORIALITY** Adult males are territorial and defend their territory against incursions by peripheral or transient males (8, 25). Living peripherally to clumped females may represent a waiting tactic; 30 of 52 colonial males

lived peripherally for one or more years before succeeding to the territory (15). Adult males generally behave agonistically to yearling males, including their sons (8). Rates of amicable behavior among males of all age groups are lower and rates of agonistic behavior are higher than expected based on the class composition of the population (27). Although rates of social behavior are highly variable, they are independent of the density of yearling and adult males (8). One source of the variability stems from the individual behavioral phenotypes that characterize marmots (105), but the precise contribution of individual variability has not been quantified. The consequence of adult male agonism to yearling males is that most yearling males disperse (8, 25). Dispersal may be delayed until age two where habitat structure and the dispersion of adult males results in local refugia where the yearlings can avoid the adults (8). Because all males disperse, virtually all males associated with females were born elsewhere and immigrated into their breeding population (8, 14, 25, 97). Fights among males are rare and we never observed a territorial male displaced by an intruder. Male turnover seems to occur when a resident male dies overwinter and a new male becomes resident after spring emergence (15).

**REPRODUCTIVE SUCCESS** The most important factor determining reproductive success is the ability to associate with adult females. Residence with females typically occurs at age three or older. The probability that a young male will survive to become a yearling is 0.47 (25) and the probability that a yearling male will live to age three is 0.36 (108). Thus, only about 17% of the males born reach an age that makes reproduction likely, but we have yet to determine what proportion do so. The second critical factor is the number of females that comprise the male's harem. Although the number of young or yearlings per female decreases as harem size increases, the number of young or yearlings per male increases (15). For each additional harem female, a male gains about 1.5 young and 0.6 yearlings. The number of females in a harem is determined by adult females; there is no evidence that adult males recruit females or exclude potential female immigrants (7, 9, 13, 25). The third factor affecting male reproductive success is length of residency. Mean length of residency is 2.24 years (15), but some males are resident for from 4 to 6 years (Figure 1; 14, 18). Considerable variance in the reproductive success of males is indicated, but this variance has not been calculated. The average male can expect a lifetime reproductive success of 11.1 young; polygyny is an evolutionarily stable strategy (15, 85).

### *Female Reproductive Tactics*

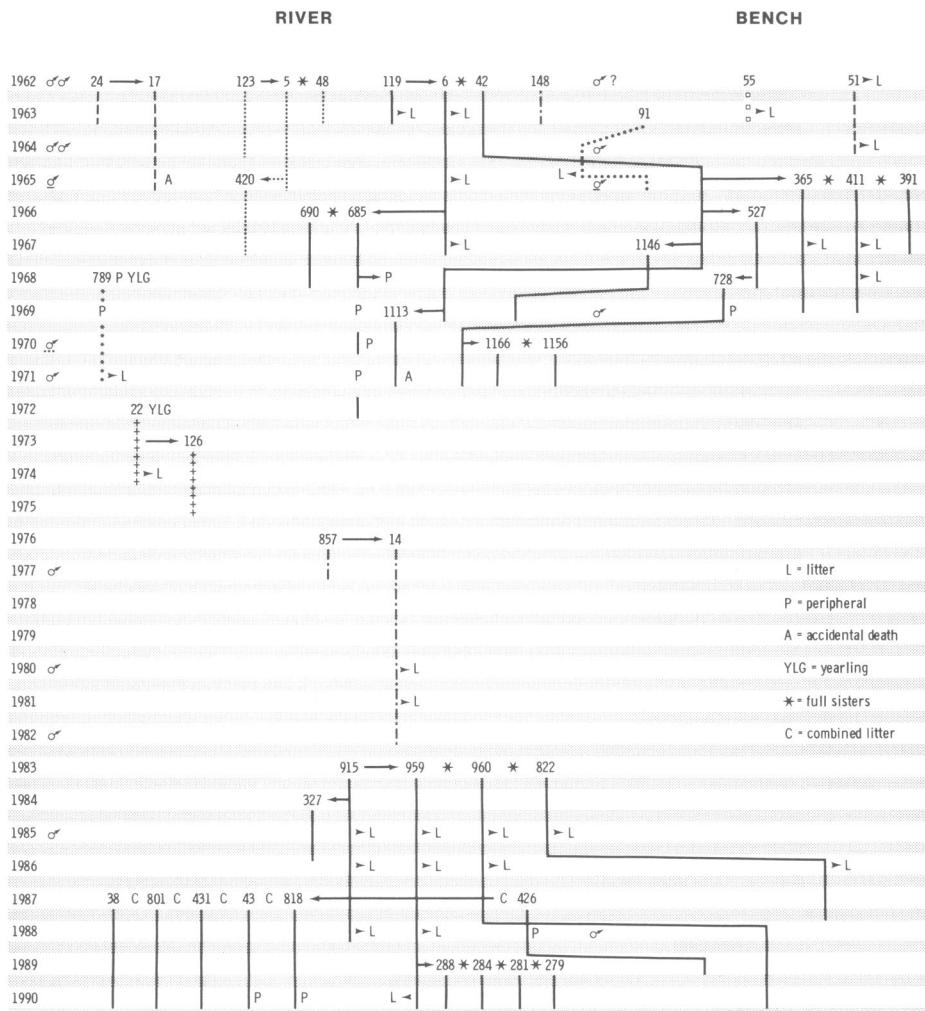
**NATURE OF GROUPS** The size of groups of adult females ranges from 1 to 5; mean size varies among colonies and ranges from 1.05 to 1.92; the grand mean is 1.47 (15, 20). Initially harems were treated as female social groups

(49), but now the harem ( $\bar{x}$  size 2.27 adult females) is considered to be a male reproductive unit that consists of one or more female groups (15, 20). A female group may also include young of the year and yearlings from reproduction the previous year (Figures 1, 2).

Female groups consist of closely related kin, primarily mother:daughter or sister:sister pairs (14, 15, 20). Groups continue through time as matrilines that may increase in size through the recruitment of daughters (Figure 1). Recruitment may decrease average relatedness as aunt:niece, grandmother:granddaughter, and other kin relationships develop. Thus, matrilines divide to form independent groups. For example, when average relatedness of four females within a matriline decreased to 0.25, the matriline divided to form two groups of two sisters each; each matriline had an average relatedness of 0.5 (14). Another group of five female kin had an average  $r$  of 0.0625, but the females were organized into two kin groups, each with an average  $r$  of 0.5. Matrilines are readily identified by patterns of space-use; members of a matriline share common home ranges and often live in the same burrow system, whereas members of different matrilines never share burrows and their home ranges overlap little or not at all (14, 21, 56). The mean size of matrilines is negatively related ( $p = 0.1$ ) with habitat area, but the mean number of matrilines is positively correlated ( $p < 0.05$ ) with habitat area (20). Thus, the increase in the number of resident females that is positively correlated with habitat area ( $p < 0.05$ ) does not increase the size of matrilines but increases the number of matrilines. The failure to form larger matrilines is the consequence of females forming stable associations only with individuals related by 0.5.

**MATRILINE RECRUITMENT** Replacement, that is, the addition of an adult female aged two or older to a population, is significantly correlated with recruitment ( $R_s = 0.94$ ,  $p = 0.01$ ). Recruitment is defined as either the retention of yearling daughters (14, 16) or of two-year-old daughters (20) in their natal colonies. The latter definition discounts mortality during hibernation following the yearling summer and is a more realistic index of reproductive success. Percent recruitment (the percentage of replacement that is recruitment) is unrelated to replacement ( $p > 0.1$ ) but is significantly related with the mean number of females ( $p = 0.1$ ) (20). Hence, replacement is more likely to be recruitment when more adult females are present. This relationship is interpreted to mean that a matrilineal group can exclude potential immigrants (an animal born elsewhere) and increase the probability that replacement involves a related recruit. Thus, population replacement is strongly affected by the social system.

About 53% of the yearling females become recruits; about one third of the recruitment events involve two or more yearlings from the same litter.



**Figure 1** Patterns of residency, recruitment, and immigration. Each animal is identified by ear-tag number in the year of immigration or birth. Vertical lines show years of residency. Matrilines are represented by vertical lines of the same pattern. Recruits are indicated by a short arrow in the year of birth; litters from which there were no recruits are indicated by an L. A male symbol indicates the year in which a given male became resident; male symbols with the same underlining indicate that the same male defended both River and Bench. The resident male of 1970 was born to female 6 in 1965. Bench colony was trapped out in 1969, and only a few animals have resided in that area since. A horizontal line crossing vertical lines indicates that young intermingled and maternity could not be determined. Updated from (14).

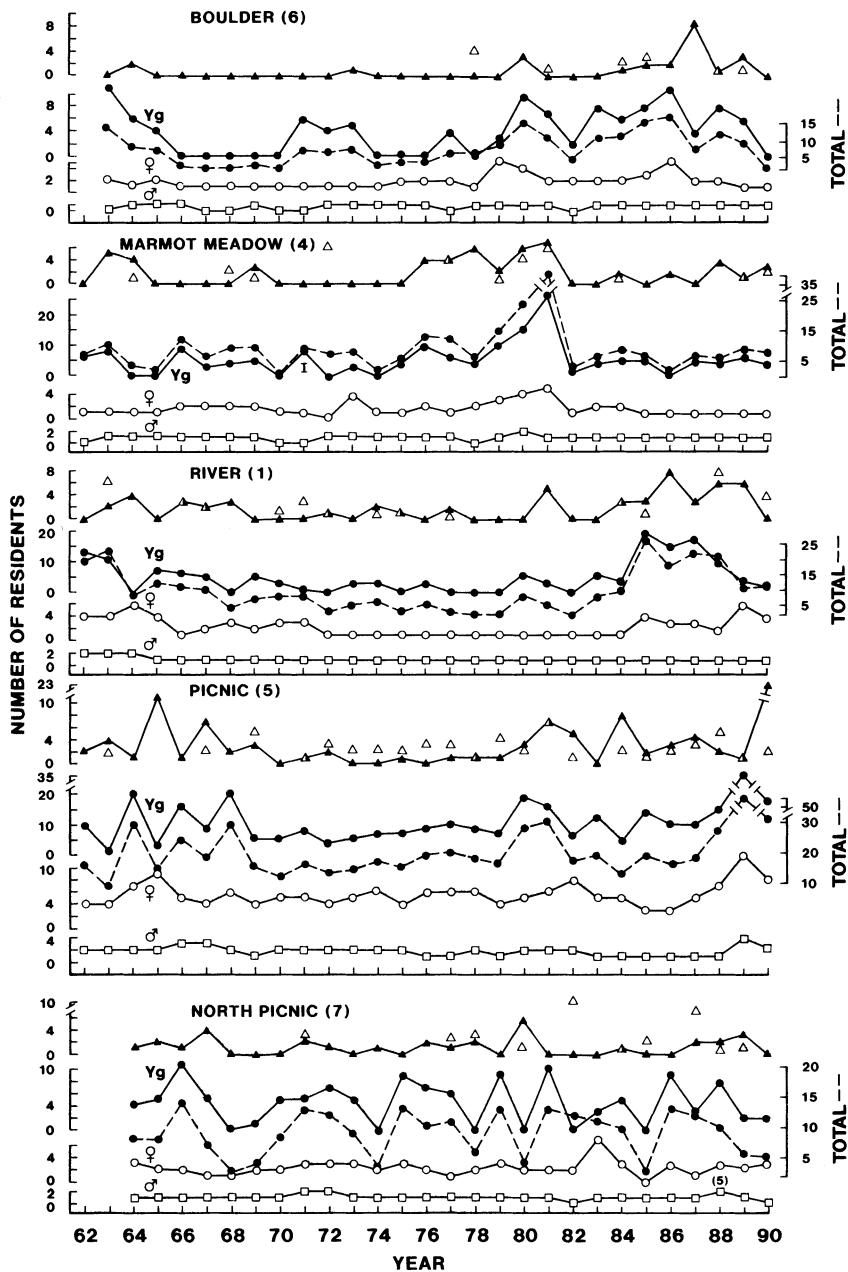


Figure 2 Population levels at five marmot colonies arranged in sequence with the smallest habitat area at the top and the largest habitat area at the bottom. The numbers in parentheses are the locality designations (8); number 1 is furthest down valley and number 7, furthest up valley. Male and female symbols refer to male and female adults, respectively. Yg = young. Solid triangles are yearlings that disappeared during the summer, and open triangles are yearlings that remained throughout the summer. Modified and updated from (25).

Recruitment is twice as likely to occur when the recruit's mother is present; the mother's reproductive status does not significantly affect recruitment (14). Recruitment occurs significantly more often than not when another adult female is present and when she is reproductive. Whether recruitment occurs is not affected by the kinship of the other females resident in the colony (14). We continue to build up sample sizes that will permit a more detailed analysis of recruitment. The structure of matrilines strongly implicates relatedness as critical to the recruitment process (14, 20, 21). For example, when immigration occurs, recruitment is highly unlikely; immigrants and potential recruits are unrelated. Recruitment is unaffected by males; newly resident males do not inhibit recruitment, and males are as likely to tolerate their daughters as not (14).

Of the adult females 40% successfully recruit one or more daughters. In comparison to nonrecruiters, recruiters are resident for a longer time (4.4 vs 2.6 years) and produce more litters (2.3 vs 0.7), more total young (9.8 vs 2.8), more female young (4.9 vs 1.4), and more female yearlings (2.9 vs 0.3). Mean litter size does not differ between the two groups (14). Three variables entered a stepwise discriminant analysis model of recruitment: number of female yearlings, number of female young, and number of litters. The number of female yearlings was the most important variable by far. The model correctly classified 89.6% of the 77 females used in the analysis. The significance of the number of yearlings agrees with life table analysis; the life expectancy of a young one is 1.7 years whereas that of a yearling is 2.0 years. An adult female that produces infants that grow into yearlings has a much greater probability of leaving reproductive descendants (14, 25).

**SEX RATIO MANIPULATION** Although the population sex ratio is 1:1, several lines of evidence suggest that sex-ratio is manipulated. The number of females per litter is higher for recruiters than for nonrecruiters (14). Sociable females over their lifetime produce more female young than other behavioral phenotypes whereas females classified as submissive-avoider produce more male young (16). Sex ratio does not vary with litter size, measurements of stress, density of adult females, or social environment, but does vary with age; young females produce significantly more daughters than sons (18). Social structure interacts with age; young females living with at least one additional female in the only matriline present on a habitat patch produce almost twice as many daughters as sons. Solitary young females, young females living alone or in a matriline when another matriline is present, and old females in all social organizations do not produce sex-biased litters. The young females living in a matriline with no other matriline present recruit more daughters per litter and more daughters per female young weaned than expected. By contrast, old females living alone with or without another

matriline present recruit significantly fewer daughters per litter or per female young weaned (18). These results do not support local resource competition (40) or female condition (107) models. Rather the results are consistent with the hypothesis that females produce the sex conveying the greater fitness gain. Female-biased litters are produced by those yellow-bellied marmots with a high probability of recruiting their daughters into the local population (18).

**REPRODUCTIVE SUCCESS: GROUP EFFECTS** Living in groups entails benefits and costs (1). A major benefit of matrilineal organization in yellow-bellied marmots is that a dominant group can exclude competing conspecifics from resources (15, 21). For example, immigration almost never occurs into an established group (Figure 1, also Figure 1 in 19). Also, a dominant matrilineal group may acquire the best burrow sites and foraging areas by causing a subordinate matriline to move to an area of lower quality (56). Additionally, a dominant group may suppress reproduction of a female from a different matriline (15).

The major cost of living in a matrilineal group is reproductive inhibition. Note that none of five females born at River in 1987 (thus recruited as yearlings in 1988) weaned litters in the presence of the older female 959, who recruited her four daughters in 1990 (Figure 1). Two-year-old females reproduce less often than expected when adult females, including their mothers, are present (21); the likelihood that three-year-old or older pregnant females successfully wean a litter is significantly less for females living in proximity to other adult females than for females living solitarily (15).

Per capita reproductive output decreases as group size increases in yellow-bellied marmots (49), black-tailed prairie dogs (74), and red deer (44). This relationship could be the result of the reproductive inhibition described above. Reanalysis of the marmot data disclosed that group effects on reproduction depend on the nature of the group. The production of young and yearlings increases as the size of the matriline increases, but per capita production of young and yearlings does not decrease. Although the number of young and yearlings produced increases with increased size of harems, the per capita production of both young and yearlings significantly decreases with increased harem size (15). The reduced per capita reproductive output of harems occurs because the number of litters per female decreases significantly as harem size increases, but mean litter size is unaffected. The difference between the effects of group size on the per capita reproductive output of matrilines and harems is attributed to competition that occurs between matrilines when harems consist of two or more matrilines. For example, if two matrilines each consist of one female, reproduction is unaffected. But if one matriline consists of two or more females and the other matriline one female, the female living singly produces significantly fewer young and yearlings (15). The group

effect may occur because only closely related females share foraging patches; the female living singly may be forced to forage in inferior patches during critical times, such as early post-emergence when little vegetation is available (2, 56, 104).

**REPRODUCTIVE SUCCESS: HABITAT EFFECTS** Habitat differences clearly exist. For example, at North Picnic, the largest habitat, the number of resident adult females consistently is lower than the number at Picnic, the second largest habitat (Figure 2). At Picnic, yearlings were recruited in 23 of 29 years, but only in 10 of 27 years at North Picnic. A critical question is whether any difference in habitat affects the reproductive output of individual females. One test for possible differences in habitat quality analyzes the variation in the reproductive output of individual females per year and in the reproductive output per female per matriline per year. The first analysis considers the lifetime reproductive output of individual females, expressed as average output per year. The second analysis examines the yearly per capita production of matrilines. In these analyses, variance is partitioned among colonies, matrilines, and individuals.

The production of young per female per year differs significantly among colonies, but not among matrilines. However, only 5% of the variance is explained by differences among colonies; 95% of the variance occurs among individual females. Similarly, the yearly per capita production of young does not differ among colonies nor among matrilines; 99% of the variance is attributable to differences among years (15). The production of yearlings per reproductive female and per matriline differ significantly among colonies but not among matrilines. Again, most of the variance is explained by differences among individuals (60%) or differences among years (93%). The difference among years is best interpreted as differences among females. These differences are expressed by either weaning or not weaning a litter; mean litter size is independent of the size of matrilines and of colonies. I conclude that variation in reproductive success is primarily a consequence of differences among individuals that are essentially independent of habitat quality and size of matrilines.

This is not to say that habitat quality is unimportant; it could affect either annual or lifetime reproductive success by its effect on survivorship. Juvenile survivorship was calculated as the ratio of the number of yearlings captured to the number of young weaned. Juvenile survivorship differs among colonies ( $0.1 > p > 0.05$ ); lowest juvenile survivorship occurred in the smallest habitat and second lowest in the largest habitat (20). Adult survivorship was calculated as the ratio of the number of adult females present to the number of resident adult females the previous year. Adult survivorship does not differ among habitats, nor are adult survivorship and juvenile survivorship corre-

lated among habitats. Adult survivorship was significantly correlated ( $p = 0.05$ ) with juvenile survivorship only within one habitat and nearly so within two others ( $p = 0.1$ ) (20). Furthermore, survivorship of adult females is unrelated to mean harem size in which each female lived (15).

The lack of any significant habitat effect on adult survivorship suggests that females settle where resources are at least adequate for survival, but where reproductive success may be uncertain. The low contribution of habitat differences to reproductive success measured as production of young indicates that most females have resources adequate for reproduction. The high percentage of variance (40%) in the per capita production of yearlings that is explained by differences among colonies (15) and the significant effect of colony on juvenile survivorship suggest that the key to understanding variation in success of reproductive females is to determine the factors affecting juvenile growth and survival. Although some of the year-to-year variation within a colony can sometimes be attributed to predation (25), unexplained mass mortality (but probably predation, 15), or inadequate preparation for hibernation in late-weaned litters (25, 87), there is no evidence that any of these accounts for differences among colonies. Furthermore, the differences in juvenile survivorship cannot be accounted for by differences in the density of adult females, although density probably has minor effects (20).

One of the costs of living in poor quality habitat is that a trade-off between survivorship and per capita production of young may exist. These two characters are negatively related ( $r_s = -0.71$ ,  $p \approx 0.1$ ) among colonies. For the two colonies with the highest mean rates of juvenile survivorship, adult survivorship is significantly positively correlated with the per capita production of young. Thus, good habitat supports both reproduction and survivorship (20).

Although reproductive success and survivorship are partially attributable to habitat differences and population density, much of the variation remains unexplained. The demonstration of reproductive inhibition suggests that this variation could be a consequence of social behavior.

**SOCIAL DYNAMICS** Rates of amicable and agonistic behavior are related to population density, the age-sex structure of the population, individual behavioral phenotypes, and length of shared residency. Year-to-year changes in amicable and agonistic behavior are not correlated within or between colonies (10).

Within matrilines, amicable behavior predominates among adult females (14, 16, 21, 27, 78) because females related by 0.5 engage in more amicable behaviors than would be expected by their relative abundance in the population (15, 21). When relatedness is 0.25 or less, amicable behavior may be much less than expected. Thus aunt:niece behaviors are characterized as

either much less amicable or much more agonistic than expected based on the frequency of aunt:niece dyads in the population and their degree of sharing space (15, 21). When behavior among matrilineal females is primarily agonistic, relatedness is low (27).

Behavior among nonburrowmates living within a male's territory is predominantly agonistic but may be slightly biased toward amicable if the nonburrowmates are related by 0.25 or more. Behavior among marmots living in different harems is nearly always agonistic (27, 78). Behavior between yearlings and adults is highly variable; in general, female yearlings interact amicably with both parents, but agonistically with other females, whereas male yearlings interact agonistically with adult males and females but may behave amicably with their mothers (8, 27). Adult females may be highly agonistic to yearlings that are nonlittermate full sibs and to nieces; some females are agonistic toward their daughters (15).

Despite the complexity of individual variability, social relationships are strongly kin related. Virtually all of the significant differences in the frequency analysis of social behaviors among age-sex classes can be interpreted in terms of kinship (27). The kin-biased behavior suggests that marmots can discriminate kin from nonkin. Such discrimination has not been demonstrated, but kin discrimination based on familiarity is likely. For example, when two or three adult females wean their litters in the same or adjacent burrows so that young intermingle, there is no behavioral evidence for kin discrimination among the young or between adults and young (21). Young marmots interact only amicably with members of the matriline and share space with their mothers; space-use overlap between young and unrelated adult females is rare and slight (94). Also, young rarely share space with nonlittermates. Thus, young animals normally associate only with close kin, and this association may suffice as a basis for kin-biased behaviors.

**INDIVIDUAL DIFFERENCES** Much of the variability in social behaviors is related to individual behavioral phenotypes (105). Several factor analyses of behavior measured during mirror image stimulation (MIS) indicated that marmots could be classified as social or asocial; the asocial animals were either aggressive or submissive-avoiders (14, 105). These behavioral phenotypes apparently are stable among adults (103, 105) but may change during ontogeny (17). The social interactions among eight female young were significantly and inversely related to their ranking on the sociability factor determined from MIS and not to kinship (13). Six of the females were tested as yearlings. Social behaviors were positively correlated with rankings on the avoidance factor (17). When rankings on the MIS factors were compared between the young and yearlings, there was no significant correlation. Some animals had the same ranking each year; only a minority changed their

behavioral phenotype. It is not surprising that ontogenetic experiences affect the development of behavioral phenotypes. Social play occurs among young and yearlings but declines to very low levels about midsummer of the yearling year and is not a part of adult behavior (77, 91). Social play was postulated to facilitate social dominance and the coordination of agonistic behavior; this interpretation is consistent with ontogenetic influences on the expression of behavioral phenotypes. The manner and the degree by which experience molds the expression of behavioral phenotypes is unknown.

Behavioral phenotype affects the expression of social behavior which, in turn, influences reproductive success. Over a two-year period, submissive females produced few young whereas social females produced about one third of the young (103). When females were classified as either social or asocial, social females recruited more yearling daughters (14). The relationship between behavioral phenotype and lifetime reproductive success was examined for 19 females. Lifetime reproductive success was unrelated to the rank order of the females on the three MIS factors; this fact indicates that individual differences are not continuous. When females were placed in one of three groups according to the MIS factor on which each had her highest score, rankings for number of female yearlings, number of recruits, and number of two-year-old daughters varied significantly among groups. Mean values of the measures were highest for females classified as sociable (16). Social behaviors were not correlated with the three MIS groups; however, several measures of lifetime amicable behavior were correlated with recruitment.

Social measures of behavioral individuality converge on one key index of reproductive success: Sociable females are by far the most successful recruiters. The question remains: Why is there so much behavioral variability? Possibly fitness may be related to heterozygosity or to developmental processes that by their nature produce individuals of different fitnesses. Alternatively, phenotypic plasticity could be an evolutionarily stable strategy. Social and ecological environments of marmots vary; perhaps each behavioral phenotype is most fit under a particular set of conditions. Thus, a female that produces variable offspring is more fit than a female that produces only one behavioral phenotype (for a more extensive discussion, see 16). The significance and evolutionary maintenance of individuality; i.e. variable behavioral phenotypes, remain to be determined.

## POPULATION CONSEQUENCES OF REPRODUCTIVE TACTICS

### *Population Structure*

Analysis of population structure focused on clumped breeding units consisting of 1 to 3 males, 1 to 12 adult females, up to 8 resident yearlings (mostly females), and up to 36 young (Figures 1, 2). Peripheral animals, those living

adjacent to but not interacting with the resident population, may be present. Transients, those that move through a colony but do not remain for more than a few days, occur irregularly (25). These breeding populations are not isolated; nearly all resident males are born elsewhere and immigrate into the colonial habitat, and some female adults are immigrants (Figure 1; 14, 18, 20). Thus, the effective population size is larger but is unknown (100). The difficulties of measuring effective population size are discussed elsewhere (39). Given that marmot breeding units are clumped and that mating is nonrandom, one questions to what degree a calculation of effective population size is realistic. However, the subdivision of the marmot population into semi-isolated breeding units suggests that effective population size may be relatively small.

### *Population Dynamics*

**CHANGES IN DENSITY** Clearly, adult males have little effect on the density of marmot colonies (Figure 2). Except for North Picnic in 1988 when five two-year-old males remained for all or part of the summer, typically one or two males reside at each colony. In some years no resident male was observed or trapped, even though females produced litters. This situation occurred primarily at the two smallest colonies. Sometimes males at those areas are wide-ranging and live elsewhere during the summer. Some absence of males probably results from predation, but specific information is lacking. The major change in density results from the annual production of young; the curves for total number and number of young are very similar for all colonies (Figure 2). The influence of yearling residents on total number varies widely among colonies. In only 6 of 28 years do yearling residents affect the total residents at Boulder, whereas resident yearlings affect population density in 22 of 29 years at Picnic. The number of adult females varies among colonies, and its effect on population density also varies. Thus, the number of adult females varied: from 3 to 11 at Picnic, reached a maximum of 4 twice at Boulder, and exceeded 3 only once at North Picnic, three times at Marmot Meadow, and seven times at River. Changes in density are not correlated among colonies (9, 10, 25). Each colony has its density characteristics; although mean density is affected by the size of the colony's habitat, the factors that determine what the mean density is for each colony are not clearly understood.

**RECRUITMENT AND IMMIGRATION** An increase in the number of adult residents or replacement of deceased adults occurs through immigration or recruitment. Immigration plus recruitment equals replacement, the addition of an adult female to the population. Replacement was calculated as the number of new adults added divided by the number of residents the previous year (20). Replacement was related to survivorship in only one colony; replace-

ment decreased as survivorship increased. Because survivorship was calculated as a rate and the rate could be the same over a wide range of densities, survivorship was calculated as the number of adult females returning. The number of females returning was negatively correlated with replacement in three of the five colonies (20). However, the correlations explained only 12 to 22% of the variation in replacement; although density is a factor, other factors, especially social, are important. When rates of immigration and recruitment within colonies were analyzed separately, only two of ten correlations were significant. The lack of simple density-dependence was also supported by the low and insignificant correlations between survivorship and recruitment within colonies and recruitment and the mean number of adult females among colonies. Immigration varies from 0.15 to 0.46 females per year; by contrast recruitment varies from 0.23 to 1.07 females per year (22). Immigration or recruitment occurred in 73 of 141 colony-years (a colony-year is one colony studied for one year; a calendar year could have a maximum of six colony-years). In only five colony-years did immigration and recruitment occur in the same colony. Twice as many females became residents as recruits than did as immigrants (22).

Immigration occurs primarily when deceased residents are not replaced by recruits (Figure 1). For example, at Picnic Colony, only one female immigrant became a resident between 1974 and 1990. The immigrant occupied space that was vacant because two female residents died over winter (see Figure 1 in 18). During the same period, 27 females were recruited.

**DENSITY-DEPENDENCE** No simple density-dependence is evident in any marmot colony (Figures 1, 2). One reason for the lack of density-dependence is that virtually all male yearlings emigrate regardless of population density. Recruitment or immigration often does not occur at low densities; recruitment often occurs at high densities (Figure 1, also Armitage 14, 18). Demographic factors such as number of young per female, number of litters per female, number of female yearlings, and percentage of female yearlings becoming resident were not significantly related to number of female residents, number of female recruits, or percentage of female yearlings becoming resident, except that the recruitment of female yearlings was positively correlated with the number of litters per female (25). This relationship may mean simply that successful females both reproduce and recruit (see discussion of matriline recruitment) and that recruitment is a function of fitness strategies rather than of density-dependence (20, 21). Although social behavior may mediate replacement, mean interaction rate and mean number of residents were unrelated. Rates of amicable behavior were not related to population density in any colony; the rate of agonistic behavior was related to density in one colony (7, 9). Rates of amicable and of agonistic behavior between yearling females

and either adult males or adult females, and among adult females, were independent of measures of population density whether colonies were analyzed separately or lumped (9). An examination of possible stress effects failed to find any relationship between blood corticosteroid concentrations and two measures of population density (23). Social status and social behavior were the major factors affecting corticosteroid concentrations. A stress response seems to be more strongly related to behavioral phenotype than to population density. Stressed females, those ranking high on the MIS submissive-avoider factor, produced litters at about one fourth the rate of unstressed females (18). A different measure of stress indicated that stressed females produced litters at about one third the rate of unstressed females (18). Densities at which both stressed and unstressed females lived varied; thus there was no evidence that density was the direct cause of the stress.

### *Dispersal*

**AGE AND PATTERN** Dispersal occurs when a marmot moves away from its natal colony. Most dispersal occurs when marmots are yearlings, but some dispersal occurs as late as age three (25, 101, 108). Age of dispersal is unaffected by sex. Although dispersal occurs throughout the active season, it is concentrated from May to July. Males tend to disperse earlier in the season (May) than females (June). All males and slightly less than one half of the females disperse (8, 14). Dispersal occurs in all directions but is weakly correlated with topography, especially with the direction of the East River Valley (101, 108). Dispersal distance, measured as a straight line from the natal burrow to the first hibernaculum, is highly skewed; most dispersers moved 4 km or less, but distances were as great as 15.5 km for males and 6.4 km for females. Median dispersal distance was less than 400 m for females and greater than 1500 m for males (108). These differences may reflect different requirements for the two sexes; females need find only an unoccupied site with a suitable burrow and food whereas a male must locate both a suitable burrow and food and undefended females.

Three different dispersal patterns occur. Forty-one percent of dispersers abandoned their natal home range in a single, one-way, abrupt move to a new locality. Thirty-three percent emigrated by a gradual process of incremental home range extension until a new home range was established. Females dispersed by this process more than did males. This gradual process may enable females to find the closest adequate resources. Twenty-seven percent of dispersers emigrated in two stages. In the first stage, dispersers left their natal home range but established a new home range nearby, on average 265 m distant. After a mean of 41 days, the animals moved again. Males dispersed more often in two stages and often doubled body mass between the two

movements (108). Apparently, the first move enabled animals to escape social stress, and the second move involved finding unoccupied habitat with a suitable hibernaculum.

**SURVIVAL AND REPRODUCTION** The survival rate during the first summer was about 20% less for dispersers than for residents (only females). Survival during the first winter was about the same for both dispersers and residents. During the second summer, the survival of female residents was unchanged, but that of male and female dispersers decreased. Survival of dispersers and residents was similar during the second winter. Mortality during the summer was caused by predators; 60% of the kills were by coyotes (*Canis latrans*) (108).

About the same proportion of female residents and of female dispersers first bred at age two. Thus, any loss of reproduction by residents because of reproductive inhibition by resident adults appears not to be compensated by dispersal. Fecundity of female dispersers older than two years was lower than that of resident females. Sample sizes are small but suggest that dispersers may suffer a reduction in the frequency of reproduction (108).

**PROXIMAL CAUSES OF DISPERSAL** The causes of dispersal likely differ between the sexes. Yearling males cannot compete with adult males; adult males do not tolerate potential reproductive competition. The dispersal of males thus seems inevitable (8, 50). However, the timing of dispersal may be affected by social or physiological factors. In general, dispersal of ground-dwelling sciurids is not correlated with rates of social behavior, but evidence suggests that social mechanisms are important (72). Yearling male yellow-bellied marmots remain longer at their natal site when rates of amicable behavior are high or when June body mass is low (50).

Because half of the females become recruits, the factors determining if females disperse are likely more complex than those for males. Social tolerance by adults seems to be critical; yearlings are more likely to become recruits if their home ranges overlap those of adult females, especially those of their mothers, by more than 50% (9, 14). Recruitment may be stressful; yearling recruits had higher concentrations of corticosteroids than those that disappeared ( $p = 0.066$ ) (23). The timing of dispersal is independent of the number of yearling females or of adult females. Females disperse earlier when rates of aggression are high and remain longer when rates of amicable behavior are high (50). As discussed earlier, recruitment of yearling females is strongly associated with amicable behaviors between the yearlings and their mothers (16).

An alternative hypothesis is that dispersal is genetically determined (see 79

for discussion of genetic models). However, when adults were removed from North Picnic colony, none of six yearling females dispersed. The number of recruits in that year was greater than the total number for the previous 17 years (36). In another experimental population at Marmot Meadow, no yearling females dispersed when an adult male but not an adult female was present (17). These results and those described above suggest that dispersal is not genetically determined but is socially mediated by adults interacting with same-sex yearlings (50). Yearlings may assess the probability of future reproductive success in their natal home ranges and decide to remain or disperse. Amicable and/or agonistic behavior may be one but not the only cue to the decision-making process. Further research on this complex problem is necessary and must consider kinship, individual behavioral phenotypes, social behavior, population density, and patterns of space-use.

### *Genetic Structure*

Neither gene frequencies nor heterozygosity at eight loci was associated with altitude, habitat, age, sex, survivorship, litter size, or a suite of behavioral variables (98). The formation of matrilines through yearling recruitment in discrete colonies, the low exchange rate of individuals between groups, and the restriction of mate selection to those in the group promote genetic heterogeneity among social groups (97). The genotype frequencies drift among colonies but do not go to fixation because of the high rate of male immigration (e.g. Figure 1). The social system thus supports the theory of gradual evolution, not of accelerated evolution in closed societies.

## POPULATION DYNAMICS: THE ROLE OF DIRECT FITNESS

When this research began, the intent was to determine if social behavior played a critical role in a density-dependent population regulation (114). It soon became evident that density did not drive the system. In general, marmot biology is consistent with the model that self-regulation of population size may occur when resources are unequally partitioned among iteroparous individuals of different behavioral rank (84). Differential reproductive success coupled with either scramble or contest competition may initiate dispersal. An individual of low rank may not disperse because its reproductive success improves if others disperse, but it should disperse if its fitness as a resident is lower than its expected fitness as a disperser (84). This variability in the timing and incidence of dispersal is consistent with the frequent lack of density-dependence in dispersal and the lack of a consistent relationship between social behavior and dispersal (9, 14, 22, 25, 36, 45, 50, 62, 72, 82). In general, individual variation, spatial heterogeneity, behavioral interactions

among individuals, and dispersal behavior determine the dynamics and stability of ecological systems (84). To this general model should be added the role of kinship.

As information on kinship accumulated, I formulated the hypothesis that the population system is driven by direct fitness strategies. Major increases in resident adult females occur when daughters are recruited (Figure 1, Figure 2: River 1964, 1983–1990; Marmot Meadow 1977, 1981; Boulder 1979, 1986; Picnic 1974, 1982, 1989; also see 7, 14, 15, 20, 21). Whether a female chooses to disperse or remain in her natal colony affects both her fitness and the fitness of her mother. Because fitness depends on producing reproductive descendants, a female should act to increase the probability that her daughters will survive to reproduce. Survivorship, and probably reproductive success, of daughters is higher for recruits than dispersers. The daughter should decide whether to disperse based on how her fitness is affected. Thus, arguments about whether dispersal benefits residents or dispersers are misdirected (4); the fitness of both is affected. Although a female recruits daughters, her fitness is increased by producing more daughters rather than granddaughters. However, the daughter's fitness is enhanced by reproducing rather than helping her mother. Gains in indirect fitness do not offset losses in direct fitness (19, 20, 21, 95). Kin selection (= indirect fitness) is a minor component in this system. The major importance of direct fitness is supported by the following: preponderance of mother:daughter matrilines, small size of matrilines, space-sharing by close kin, fission of matrilines as average  $r$  decreases, amicable behavior directed primarily to kin related by 0.5, and agonistic behavior to all related by 0.25 or less; reproductive suppression of daughters, and lack of any linear relationship between fitness benefits and degree of relatedness (21).

Reproductive competition develops both within and between matrilines as expressed through infanticide (28, 37) and reproductive suppression. Recruitment declines or ceases; presumably yearling females decide that reproductive opportunities lie elsewhere and disperse. The population of adult females declines as older females die; eventually the process is repeated. Competition seems to be for reproductive success, not resources per se. Animals may disperse to escape reproductive inhibition and not because burrows and food are limited. However, the possibility that the quality of a key resource limits reproduction, if not density (2), and causes dispersal cannot be excluded. Thus, population density may be a consequence of access to one or more critical resources or of behavioral/physiological competition for reproductive success. These issues can be clarified by examining blood hormones for evidence of reproductive suppression and by a more critical assessment of resource availability and use.

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