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Chapter 17

Recruitment in Yellow-bellied Marmot Populations: Kinship, Philopatry, and Individual Variability

Abstract. Recruitment of females forms matrilines, most of which become extinct and are replaced by immigrants. Mother/daughter or sister/sister kin groups share space. Philopatry characterizes matrilines but is not essential for their persistence. Matrilineal bifurcation is associated with the partitioning of a single space into two or more spaces, each of which is shared by individuals who are related by 0.5. Although the number of residents may not change, the total space used increases when matrilines bifurcate. Recruiters differ from nonrecruiters primarily in the number of female yearlings produced. Social females recruit a greater proportion of their yearling daughters than do asocial animals. Male turnover and the presence of unrelated adult females do not significantly affect recruitment, whereas an immigrant adult female nearly always prevents recruitment. Recruitment of yearlings is more likely if they are philopatric; yearlings that wander widely disperse from their natal home ranges. Immigration generally is associated with occupying an empty area. There is no evidence of sex ratio adjustment by successful recruiters.

Introduction

A central problem of population biology is Why does no population increase without limit? Four schools of population regulation are the biotic, climatic, comprehensive, and self-regulation (Krebs, 1978*a;* Lidicker, 1978). The self-regulation school focuses on how members of a species may affect the dispersal, recruitment, and mortality of conspecifics. Central to the self-regulation school

is the hypothesis that social interactions influence population dynamics by affecting spacing patterns (Krebs, 1978*b;* Wynne-Edwards, 1962). Spacing is postulated to lead to dispersal, which may be the key to population regulation (Gaines and McClenaghan, 1980; Krebs et al., 1973; Lidicker, 1975). However, dispersal is density-independent (Gaines and McClenaghan, 1980), and much dispersal may be a function of mating strategies (Armitage 1981; Greenwood, 1980).

Dispersal as a mating strategy suggests that population dynamics may be a consequence of the reproductive strategies of individuals rather than a process of population regulation per se. Fairbairn (1978), for example, suggested that benefits at the population level were probably by-products of selection for dispersal at the level of the individual. Individual survival is an exercise in probability (White, 1978). The significant relation between body size and reproductive effort among ground squirrels suggests that reproductive effort is maximal to increase the probability of producing surviving offspring (Armitage, 1981). If selection has maximized reproductive effort, then social mechanisms may evolve to produce a competitive edge. For example, an animal may attempt to exclude other individuals from resources, or kin groups could act cooperatively. If resources are abundant, whether patchy or widely dispersed, an animal increases its direct fitness (Brown, 1980) by sharing resources with its descendants and may increase its indirect fitness by sharing resources with collateral kin. However, sharing resources with collateral kin should be limited because greater return can be expected from investing in offspring rather than in other kin (Rubenstein and Wrangham, 1980).

This individual selection model requires that individuals be variable; individual variability is central to the hypothesis of self-regulation (Bekoff, 1977; Krebs, 1978*b;* Lømnicki, 1978). Although it is unclear whether individual variability has high heritability (Krebs, 1978*b,* 1978*c*) or is developmental (Bekoff, 1977; vom Saal, 1981), the important issue, as emphasized by White (1978), is to determine who survives. Determining the mechanisms that dictate survivorship is also important.

Although dispersal is central to any analysis of individual fitness, the fate of dispersers is rarely known (Gaines and McClenaghan, 1980). Therefore an alternative is to study the process of recruitment. I use recruitment to indicate the retention of individuals in their natal population. By contrast, immigration is the addition to a population of animals that were born elsewhere. The obvious advantage of studying recruitment rather than dispersal is that recruitment can be observed and measured, known individuals can be followed, and the conditions

under which recruitment occurs can be analyzed for significant relations with demography, philopatry, and social dynamics.

Certain predictions about recruitment may be derived from the individual selection model and the different reproductive strategies of males and females. Because natal dispersal in mammals is predominantly by males (Greenwood, 1980), recruitment should establish matrilines, that is, groups of closely related females — for example, mother/daughters or sisters. Thus I define a matriline as consisting of all female descendants of a female who remain in their natal population to the end of their second summer of life. Because a greater return can be expected from investing in offspring rather than in the offspring of daughters or sisters, matrilines should bifurcate into potentially competing groups. For example, sisters or halfsisters, who are in a matriline that includes their mother, should initiate their own matrilines. This bifurcation should be characterized by spatial separation of the bifurcating matrilines. These predictions are tested for the yellow-bellied marmot (*Marmota flaviventris*).

Methods

Since 1962, demographic and behavioral data were obtained for six populations of marmots living in the East River Valley near Gothic, Colorado, at an elevation of 2,900 m. Marmots had a clumped distribution that conformed closely to the mosaic of meadow and forest vegetation (Svendsen, 1974). The characteristics of River-Bench, Picnic, North Picnic, and Marmot Meadow localities where marmots were intensively studied were described previously (Armitage, 1974; Svendsen, 1974). Each year all animals in the study sites were trapped, permanently labeled with numbered self-piercing metal ear tags, and marked in distinctive patterns with fur dye for visual identification. Because females with litters usually occupied a burrow distant from any other reproductive female, infants could be assigned to a specific mother. The few instances in which maternity could not be determined will be described later. Sex was recorded for each animal. Age was known for all animals first trapped as young. Age also could be determined for all animals first trapped as yearlings (animals 1 year old) or 2-year olds on the basis of body weight (Armitage et al., 1976). All marmots first trapped with body weights larger than those of 2-year-olds were assumed to be at least 3 years old.

Each summer marmots were observed for several hundred hours. Observations were concentrated in the morning and afternoon when marmots are most active (Armitage, 1962). Each population was censused regularly at intervals

varying from 5 to 20 min depending on the number of animals and the time required to locate each animal. The location of each animal was recorded as a pair of grid coordinates from a photographic map of each locality. All grid coordinates for each animal were used to plot a perspective block diagram of space use (Sampson, 1975). The individual behavioral profile was determined for 29 adults by mirror-image stimulation (Svendsen, 1974; Svendsen and Armitage, 1973). This profile was used as a measure of individual variability. Statistical analysis included multiple discriminant analysis (Cooley and Lohnes, 1971), chi-square, and ANOVA (Sokal and Rohlf, 1969). Hypotheses for chi-square testing were generated following the procedures described by Slade (1976).

Results

Patterns of Recruitment

Although River-Bench previously was treated as two localities (Armitage 1973, 1974), the exchange of animals between the two suggests that it contained one population. The Bench portion of this site was terminated in 1969 when the remaining animals were removed. One male, son of female 6, was recruited in 1970 at age five (Fig. 17.1). Although he probably fathered the young born that year, the matriline died out. Several matrilines were established in 1962, but all died out by 1973 (Fig. 17.1). The line of female 119 persisted for 10 years, possibly because individuals shifted between the River and Bench sites (Fig. 17.1). A matriline established by female 42 (Armitage, 1973) split into three groups. One group remained at Bench, female 42 returned to River in 1968 and evicted the residents, and female 728 lived as a peripheral animal for a year before moving into River in 1970 when female 42 did not return. Extinct matrilines were replaced by immigrants. Two of these immigrants were first trapped as yearlings. However, to date no immigrant has successfully established a matriline that persisted beyond one generation.

The mosaic of vegetation and rocky outcrops at North Picnic (Armitage, 1974) provides numerous burrow sites where residents may be spatially separated. Many of these sites are peripheral to the main area of meadow, and marmots occupying these sites were designated peripheral animals. The population was maintained almost entirely by immigrants (Fig. 17.2). No matriline has produced a granddaughter.

Closely related female kin groups were introduced twice into North Picnic. In 1969 the introduction coincided with the immigration of highly aggressive female 755. The introduced females disappeared within 3 days. In 1974 two
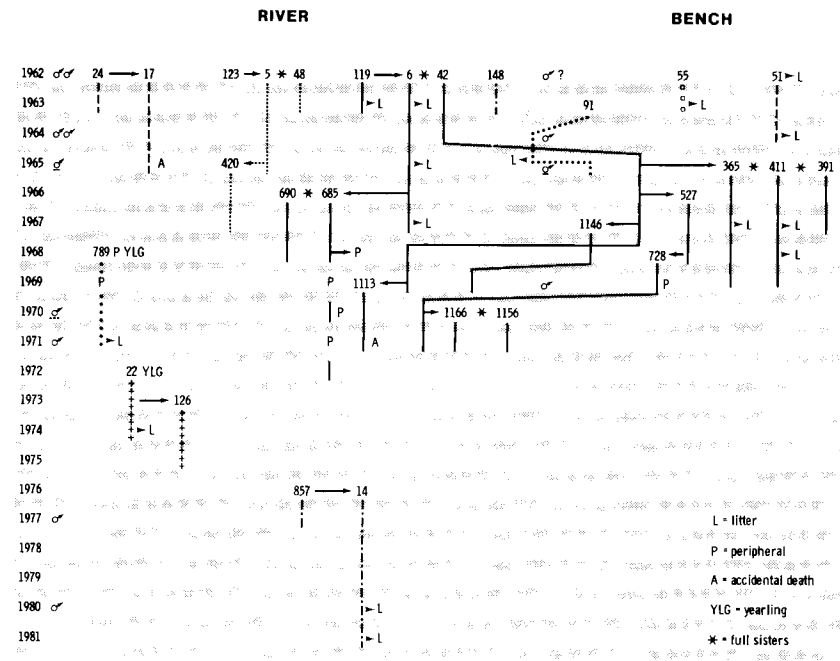
FIGURE 17.1. Patterns of residency, recruitment, and immigration at River-Bench. Each animal is identified by ear-tag number in the year of birth or immigration. Vertical lines show years of residency. Matrilines are represented by vertical lines of the same pattern. Recruits to a matriline are indicated by a short horizontal arrow in the year of birth. Litters from which there was no recruitment are indicated by an arrowhead pointing to L. Resident males are indicated by the male symbol in the first year of residency. The column of male symbols on the right represents males who were resident at Bench and separates Bench residents from River residents. Male symbols that have the same underline indicate that the same individual defended both River and Bench. The resident male of 1970 was born to female 6 in 1965.

females and their weaned young were introduced. Their introduction coincided with the immigration of aggressive female 324, who caused the introduced females to move to peripheral locations. Neither of the introduced females returned in 1975; only one of their young established residency (peripherally), and she failed to reproduce.

A second harem (see Downhower and Armitage 1971 for definition of harem) was established in 1970 when female 1047 immigrated into the locality to a burrow site that was in the territory of a second male and distant from the main burrow area. Although this female and her daughter 1076 collectively produced five litters, the matriline did not persist past 1975.

The failure of matrilines to persist at North Picnic is associated with the res-
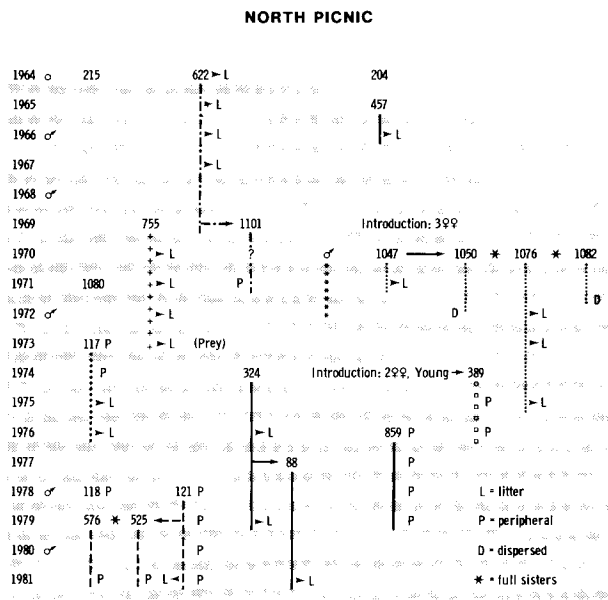
NORTH PICNIC

FIGURE 17.2. Patterns of residency, recruitment, and immigration at North Picnic. Numbers and symbols as in Fig. 17.1.

idency or immigration of highly aggressive animals. In 1982, aggressive females 121 and 88 were removed. Within a few days, peripheral females 576 and 525 moved into the main meadow area.

Usually only one adult female occupied Marmot Meadow. She lived at the major burrow site on the north side of an extensive meadow. In some years a second female occupied a secondary burrow site on the south side (Armitage, 1974). Matrilines died out after a few years (Fig. 17.3).

Because resident adult females at this locality generally acted aggressively, it was postulated that aggressiveness, coupled with chance events acting on a small population, prevented matrilines from persisting. For example, female 646 was shot by a tourist in 1967, and 1145 apparently died before she could reproduce. Therefore eight female young were introduced into this locality in 1971. By 1974 only one female remained, but this female established a matriline that persisted into 1982. Interestingly, three females occupying the main burrow area had litters in 1980 that lived in such close proximity that maternity could not be established. The entire group lived together as one social unit. In 1981 the same situation was repeated; in addition, four yearling females lived in the same burrow throughout the summer.

A second matriline was established at the secondary burrow site by female 110, who appeared in 1976. However, this line was virtually eliminated in 1981 when a badger dug into the burrow and destroyed female 458 and two litters of seven young. This incident illustrates further how a rare event impinging on a small population can cause extinction of a matriline. This instance of badger predation is the only one known at this locality in 21 years.

Recruitment at Picnic locality contrasts markedly with that at other sites. By 1980 all resident females were descended from female 67, who was a resident when the study began in 1962 (Fig. 17.4). Of eight immigrant females who became resident, only 880 established a matriline that persisted for any length of time, primarily because her daughter 843 lived to be 11 years old.

No immigrant entered Lower Picnic after 1967. By contrast, Upper Picnic was populated by successive immigrants. Some of the residents at Upper Picnic moved there from Lower Picnic. For example, immigrant 880 and her 2-year-old daughters moved there in 1970 when the resident females of the previous year
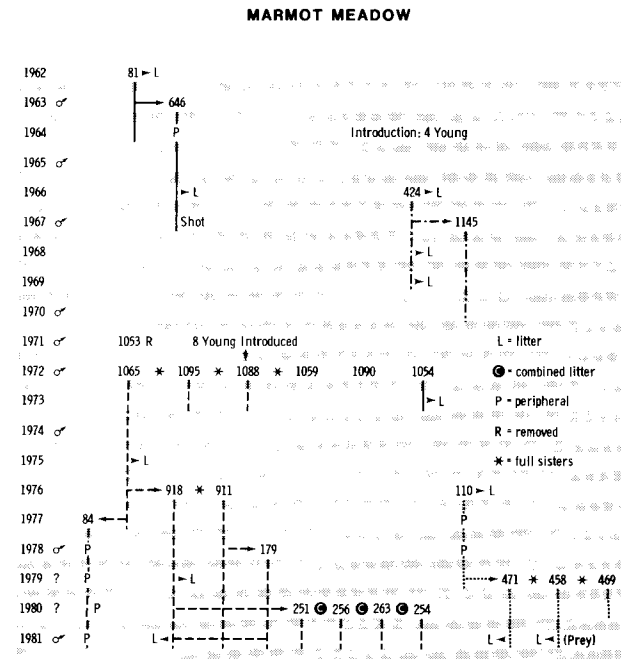
MARMOT MEADOW

FIGURE 17.3. Patterns of residency, recruitment, and immigration at Marmot Meadow. Numbers and symbols as in Fig. 17.1. A horizontal arrow that crosses two or more vertical lines indicates that young were of uncertain maternity because adult females shared the same burrow system and young emerged as a single social group (1980).

failed to return. Likewise, females 167 and 174 moved to Upper Picnic as 2-year-olds when females 843 and 1082 failed to return (Fig. 17.4).

A few animals resided at Middle Picnic, an area between and slightly south of Lower and Upper (Armitage, 1974). In 1966 and 1967, a male living at Middle Picnic established a third harem. No recruit came from this harem.

In 1976 and 1978, litters occurred in a common burrow system, so maternity could not be determined. As in the instances at Marmot Meadow, the young of the litters mingled and the adult females and young formed one social group.

One male, born to 834 at Upper Picnic, became resident in 1975. Although he fathered several litters, none of his descendants persisted.

The major matriline repeatedly split into independent matrilines. For example, the descendants of female 785 formed a matriline distinct from that of females 301 and 349. These animals behaved amicably with animals within the matriline but behaved agonistically with females of the other matriline (Armitage
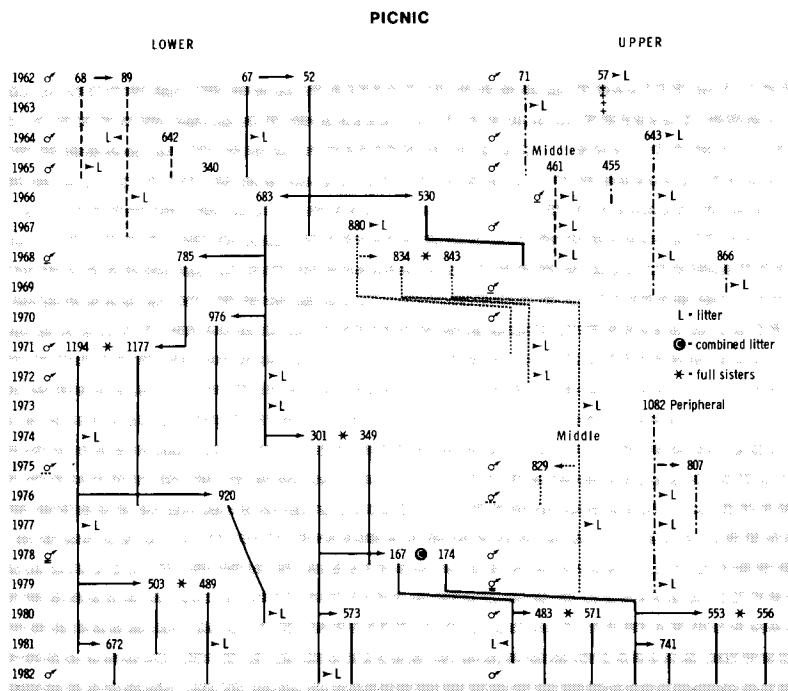

FIGURE 17.4. Patterns of residency, recruitment, and immigration at Picnic. The resident male at Lower Picnic in 1975 was born to female 834 at Upper Picnic in 1971. Note the combined litters in 1976 and 1978. Numbers and symbols as in Fig. 17.1.

and Johns, 1982). As in the other populations, most matrilines eventually became extinct, including the two established by immigrants.

Population Structure and Recruitment

Natal dispersal in yellow-bellied marmots occurs primarily in yearlings (Armitage and Downhower, 1974). Therefore recruitment is defined to have occurred if one or more female yearlings from the same litter remain in their natal locality throughout their second summer of life. In most instances, recruitment was verified by capture of the marmot as a 2-year-old. Of 135 female marmots who emerged as yearlings in their natal locality, 72 were recruited. Recruitment occurred 48 times; two or more yearlings from the same litter were recruited 18 times. In the data analysis, the recruitment of two or more yearlings from the same litter is treated as a single recruitment event.

The formation of matrilines and the higher than expected rates of amicable behavior between mothers and daughters (Armitage and Johns, 1982) suggest that mothers may actively recruit daughters. Therefore, the first question asked is, Is recruitment likely when the mother is present? The answer is affirmative; recruitment was twice as likely to occur as nonrecruitment (Table 17.1, $\chi^2 = 7.5, P < 0.01$). The mother's reproductive status did not significantly affect recruitment (Table 17.1, $\chi^2 = 1.7, P > 0.1$). However, given that recruitment occurs, neither the mother's presence or absence nor her reproductive status significantly affected recruitment (Table 17.1).

Recruitment could fail because another adult female's behavior causes the yearling female to disperse or become more susceptible to predation. However, recruitment occurred significantly more often than no recruitment when an adult female other than the mother was present (Table 17.1, $\chi^2 = 11.6, P < 0.001$). Recruitment also was more likely to occur when the other female was reproductive ($\chi^2 = 8.0, P < 0.005$). However, given that recruitment may occur, neither the presence or absence of another adult female nor her reproductive status significantly affected recruitment (Table 17.1). One possible explanation for why the presence of another adult female has no significant effect on recruitment is that some of these females could be closely related to the mother. Closely related adult females might accept potential recruits, thereby increasing their inclusive fitness (Hamilton, 1964). For this analysis, close kin were aunts, sisters, or daughters. There was no significant relation between degree of kinship between mothers and other females and whether recruitment occurred (Table 17.1).

If an immigrant adult female was newly resident in the same summer that

TABLE 17.1. Number of times recruitment occurred or failed in relation to the mother's presence and reproductive status and to the presence, reproductive status, or kinship of adult females other than the mother. Recruitment was considered to occur once each time one or more female yearlings from the same litter remained in their natal locality throughout their second summer of life.

	Recruitment occurred	Recruitment failed	χ^2	P
Mother				
Present	40	19 }	1.7	>0.1
Absent	8	8		
Reproductive	18	11 }	0.86	>0.1
Nonreproductive	22	8		
Other female				
Present	35	16 }	0.002	>0.1
Absent	9	4		
Reproductive	24	8 }	2.68	≅0.1
Non-reproductive	10	9		
Nonkin	20	10 }	0.13	>0.1
Close kin	15	6		

potential yearling recruits occurred (n = 9), recruitment was significantly unlikely ($\chi^2 = 5.4, P < 0.025$). The only instance of recruitment and immigration in the same year occurred when the immigrant occupied a peripheral area at North Picnic (Fig. 17.2, ♀ 121, 1978).

Newly resident males establish dominance over females; females often react by fleeing (Armitage, 1974). Fleeing may lead to dispersal by yearling females (Armitage and Johns, 1982). Of the 27 possible instances of recruitment coinciding with male turnover, half led to recruitment. Thus, the presence of a new male had no significant effect on recruitment ($\chi^2 = 0.04, P > 0.5$). Similarly, when the resident adult male from the previous year returned, recruitment did not differ significantly from no recruitment ($\chi^2 = 1.3, P > 0.1$).

Characteristics of Recruiters

Ninety-nine adult female yellow-bellied marmots were resident in the study localities; 40 females successfully recruited one or more of their female offspring. The failure of more than half of the females to recruit direct descendants suggests that there may be demographic or behavioral differences between the two classes of female marmots. Recruiters were resident for a longer time and

produced more litters, more young, more female young, and more female yearlings than nonrecruiters (Table 17.2). However, there was no significant difference in mean litter size (F = 1.7, 0.25 > P > 0.1), nor did recruiters produce a higher proportion of female young than nonrecruiters (Table 17.2).

The demographic characteristics (Table 17.2) are likely highly correlated. For example, a female who is resident for a longer time would probably produce more litters. On average, more litters should produce more young, more female young, and eventually more female yearlings. Therefore, the demographic data were submitted to stepwise discriminant analysis using the BMDP program (Dixon, 1981).

Three variables entered the model: number of female yearlings, number of female young, and number of litters. The number of female yearlings was by far the most important variable. The model correctly classified 89.6% of the 77 females used in this analysis. Three of 44 nonrecruiters were misclassified as recruiters, and five of 33 recruiters were misclassified as nonrecruiters. Four of the five recruiters misclassified as nonrecruiters were females of short residency who produced only one litter, and one was a yearling female who was recruited into the natal population. The fifth female produced only two female yearlings from two litters, but both were recruited. Each of the three misclassified nonrecruiters produced two or more female yearlings from two or more litters, but none was recruited.

Individual Variability

Much of the variation in demographic parameters of recruiters and nonrecruiters, and the misclassification of some animals, could result from individual behavioral differences (Svendsen and Armitage, 1973). These differences are expressed

TABLE 17.2. Some demographic characteristics ($\bar{X} \pm SE$) of recruiters (n = 40) and nonrecruiters (n = 59). N for litter size: recruiters, 91; nonrecruiters, 42.

	Recruiters	Nonrecruiters
Number per female		
Years of residency	4.4 ± 0.32	2.6 ± 0.16
Litters	2.3 ± 0.20	0.7 ± 0.23
Total young	9.8 ± 0.87	2.8 ± 0.56
Female young	4.9 ± 0.45	1.4 ± 0.30
Female yearlings	2.9 ± 0.23	0.3 ± 0.10
Mean litter size	4.3 ± 0.15	3.9 ± 0.26
Mean sex ratio (♀ ♀ / litter)	0.52 ± 0.03	0.46 ± 0.05

demographically; for example, aggressive females produced more young than social or avoider females, but social females produced more young in polygamous situations (Svendsen, 1974).

Twenty-nine adult females were classified as either social or asocial based on their behaviors during mirror-image stimulation (MIS). Social animals were those that made nose contact and pawed and nuzzled the image, usually fed, explored the MIS arena, and generally carried the tail up or wagged the tail during interaction with the image. Asocial animals did not make contact with the image, rarely fed or explored, frequently remained in the rear of the arena, often chirped or stared at the image, and often oriented away from the image. The asocial category probably included both the avoider and aggressive categories of Svendsen (1974).

The demographic characteristics of these two groups were similar except that social animals produced slightly more offspring and recruited about twice as many yearlings as the asocial animals (Table 17.3). The high standard errors indicate that most of the demographic differences were not significant. There was no significant difference in litter size (F = 0.51, P ≅ 0.5). The mean sex ratios were virtually identical (Table 17.3).

The demographic data were submitted to stepwise discriminant analysis. One variable, number of recruits, entered the model. The model correctly classified 83.3% of the social animals and 56.3% of the asocial marmots. The two social animals classified as asocial failed to recruit; female 1050 never reproduced, and female 920 produced one litter with one daughter who was not recovered as a yearling.

The seven asocial animals misclassified as social were successful recruiters. Three resided at Picnic. Each one (349, 1177, 843) was recruited with a sister

TABLE 17.3. Some demographic characteristics ($\bar{X} \pm$ SE) of adult female marmots classified as social (n = 13) or asocial (n = 16). N for litter size: social, 27; asocial, 26.

	Social	Asocial
Number per female		
Years of residency	4.6 ± 0.71	4.3 ± 0.48
Litters	2.3 ± 0.38	1.6 ± 0.33
Total young	7.9 ± 1.6	6.8 ± 1.4
Female young	3.7 ± 0.84	3.2 ± 0.89
Female yearlings	2.3 ± 0.44	1.8 ± 0.57
Female recruits	1.5 ± 0.34	0.7 ± 0.23
Mean litter size	3.8 ± 0.34	4.1 ± 0.30
Mean sex ratio (♀♀ / litter)	0.45 ± 0.06	0.43 ± 0.06

(Fig. 17.4). Females 349 and 1177 produced joint litters with their sisters, and each failed to return the year after reproduction (Fig. 17.4). Thus their recruits were shared with their sisters, and it was the sisters who were present when recruitment actually occurred. Female 843 lived most of her adult years alone at Middle Picnic, where one yearling remained with her for one year. Females 622 and 324 were highly aggressive animals living at North Picnic. Although each produced several yearling females, only one daughter of each was recruited (Fig. 17.2). Female 1101 was born in the last year of her mother's life and was present only as a peripheral animal. Female 88 was born in the fourth year of her mother's residency (Fig. 17.2). She was highly aggressive; perhaps this aggressiveness enabled her to become a recruit. Females 110 and 911 lived at Marmot Meadow (Fig. 17.3). The three recruits of female 110 became residents after their mother's death. In effect, they populated a vacated site. Although female 911 was classified as asocial, her MIS profile placed her close to the social group. Her recruitment pattern is more nearly like that of the social animals, and she seems to be the only female misclassified as social whose recruitment pattern was not associated with special circumstances.

Patterns of Space Use

One possible explanation for the lack of significant effects on recruitment by nonmothers (Table 17.2) is that space may be shared by close relatives and that other animals are excluded from this space. Thus juveniles and yearlings would be protected from agonistic behavior that might otherwise be directed toward them by unrelated or distantly related animals. The possible importance of patterns of space use is supported by the observation that female yearlings that are eventual recruits have home ranges that overlap considerably with those of female adults, whereas those that disperse do not (Armitage, 1975). In this chapter I will focus on the relation between kinship and use of space.

Only a sampling of the nearly 300 perspective block diagrams generated from the field data can be presented. Because the dynamics of matriline formation, bifurcation, and extinction are best demonstrated at Picnic locality, selected space-use patterns from Picnic are presented to illustrate six major points associated with recruitment. Picnic locality consists of a meadow on a steep slope with a talus area of 0.85 ha containing about 78 burrows (Armitage, 1974; Svendsen, 1974). The upper side of the talus is bordered by a line of aspen. Lower Picnic includes the line of aspen and all the area below it (the first 18 grids on the vertical axis of the perspective block diagrams). All the area beyond grid 25 on the horizontal axis is meadow. Above the aspen an exposure of rocks on a steep slope
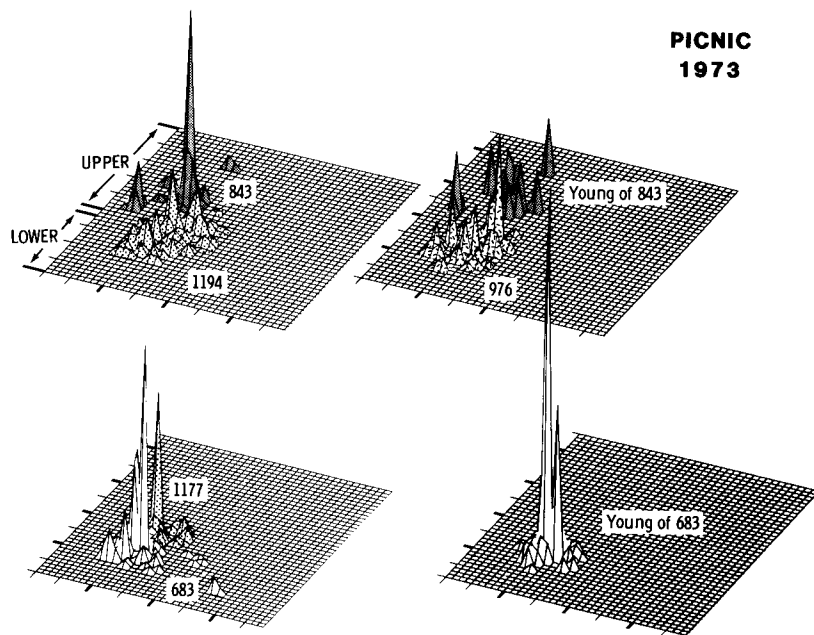
FIGURE 17.5. Perspective block diagram of space use at Picnic (8.7 ha) in 1973. The height of the peaks for each animal represents the frequency of occurrences. Each animal is identified by one ear-tag number. Closely related animals, such as mother and young or sister pairs, are indicated by the same pattern of shading. The grid lines on the horizontal axis (bottom and top of each diagram) that runs along the bottom and top of the mountain slope are 5 m apart. The grid lines on the vertical axis (left and right sides in the diagram), which runs up the mountain slope, are 9 m apart. Every fifth grid line is marked along the left (vertical) and bottom (horizontal) axes to facilitate comparison of space-use patterns. Every tenth grid line is accentuated. The talus area of Lower Picnic lies between grid lines 7 and 15 on the vertical axis and between lines 12 and 24 on the horizontal axis. All the remaining area of Lower Picnic is meadow with a few scattered clumps of trees. North is toward the bottom of the figure; east is to the left and west to the right.

forms the main burrow area of Upper Picnic. Above the burrow area is a gently sloping meadow studded with large boulders. Animals at Upper Picnic usually foraged from the burrow area up-slope or across-slope (line 20 and higher on the vertical axis of the perspective block diagrams).

Philopatry. I define philopatry as the use by descendants of the same space as their immediate ancestors. Philopatry is best exemplified by the similarity of space use of juveniles and their mothers. Not only was the overall area used by juveniles nearly identical to that of their mothers, but the frequency of use of space within the home range was similar (Fig. 17.5, ♀ 683 and her young; ♀ 843

and her young; Fig. 17.6, ♀ 1177, ♀ 1194, and their combined litter). Yearling females may be philopatric. In 1976 the space-use patterns of yearlings 829 and 807 were similar to those of their mothers, 843 and 1082, respectively (Fig. 17.6). Similarly, the space-use patterns of 489 and 503 were more like that of their mother 1194 than that of their older maternal half-sister 920 or their distant kin 301 (Fig. 17.7). This comparison is best demonstrated by the similarities in the major peaks representing high frequency of space use; the position of the peaks of 489, 503, and 1194 are virtually identical; the peak of 920 is displaced to the right, and that of 301 is displaced upward and to the left (Fig. 17.7).

Yearling excursions. Although space-use patterns of yearlings were philopatric, they frequently traveled into space used by nonkin or by distantly related kin or spent some time in areas little frequented by their mothers. The latter situation is exemplified by yearlings 503 and 489, who frequently were active in areas to the west of the main activity of their mother, 1194 (Fig. 17.7). This pattern of space use overlapped low use areas of their half-sister 920, but none of the space they used overlapped that of their distant kin 167, 174, and 301.

Although yearling 167 was observed most frequently in her mother's home
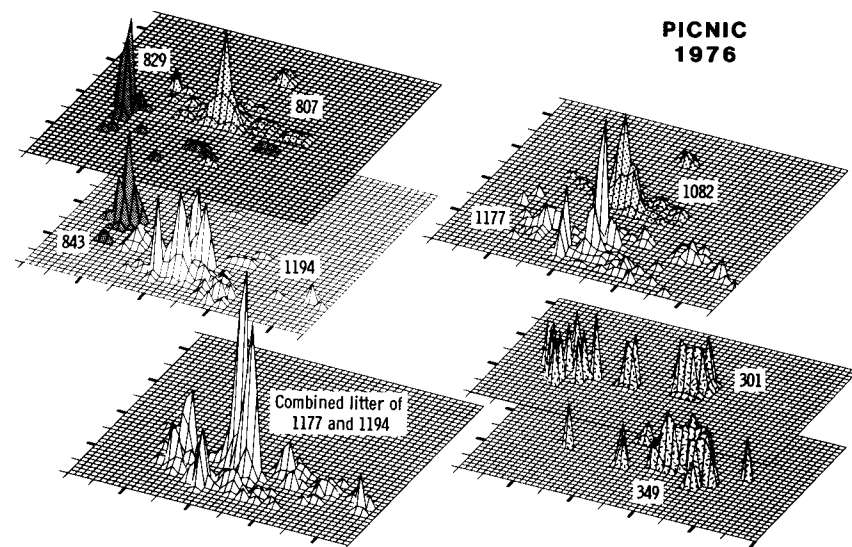
FIGURE 17.6. Perspective block diagram of space use at Picnic in 1976. Note that two sets of diagrams are overlapped to facilitate comparison and reduce the size of the figure. The horizontal base line of the overlapped diagram is accentuated to indicate separation of the two diagrams. The lower left corner is the common reference point for all diagrams.

area, she ranged into Upper Picnic or into areas of Lower Picnic inhabited by distant kin (Fig. 17.8). Such excursions were rare or nonexistent for the five resident adult females. Female 167 did not establish any area of prime use as evidenced by the lack of any major peak in her perspective block diagram. Her sister, 174, also wandered widely and was seen so rarely within the colony area that data were insufficient for analysis. Yearling 829 also ranged into Lower Picnic where unrelated animals lived (Fig. 17.6). These yearlings either did not return the next year or changed locations within the locality. By contrast, yearling 807 was completely philopatric, shared space with her mother, 1082, and returned to the same area the next year (Fig. 17.6).

In 1980, female 495 wandered widely and did not establish any area of primary use (Fig. 17.7). Her mother, 1082, failed to return from the previous year (Fig. 17.4). The space used by 1082 the previous year (Fig. 17.8) was occupied by adult females 167 and 174 (Fig. 17.7). Thus 495 was unable to occupy the space she had used as a juvenile. None of the residents was related to 495; she and a sister (not shown) dispersed by early summer.

The mother (981) of 1194 and 1177 was not present during their yearling year. However, these yearlings did not venture into adjoining home ranges but were
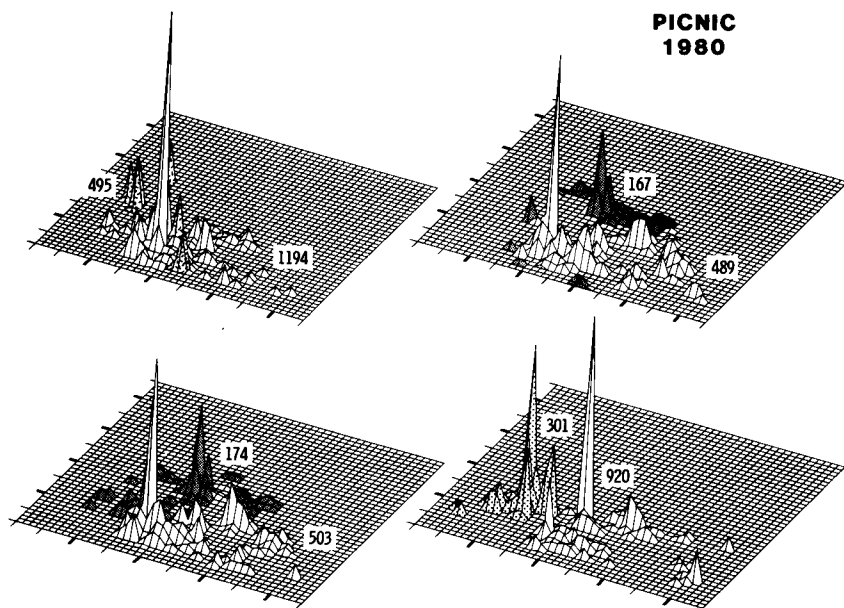

FIGURE 17.7. Perspective block diagram of space use at Picnic in 1980.
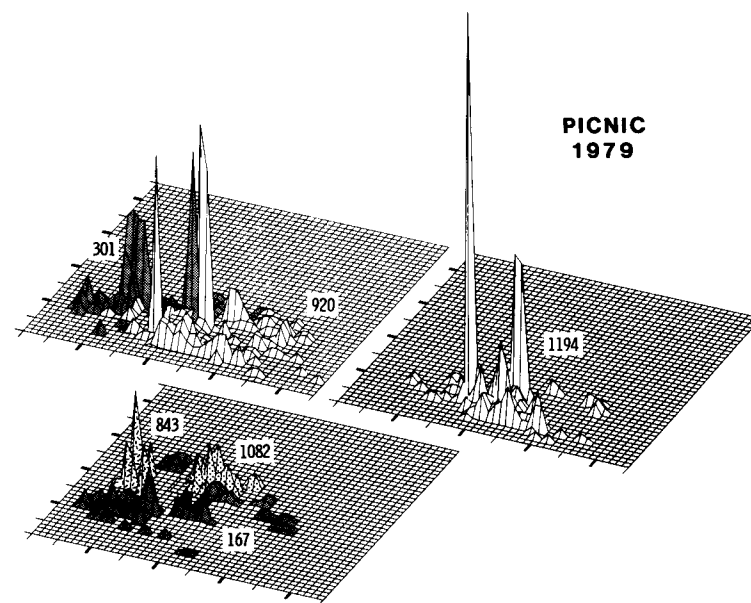
FIGURE 17.8. Perspective block diagram of space use at Picnic in 1979.

active as part of the kin group occupying Lower Picnic (Fig. 17.9). In contrast to 495, 1177 and 1194 were philopatric in their yearling year and were recruited into the population (Fig. 17.4).

Immigration. Successful immigration generally was associated with occupying an empty area or displacing a resident. The latter was rare, but it occurred when 4-year-old female 1082 immigrated into Upper Picnic in 1974. Female 843, who had ranged through much of that area (Fig. 17.9) moved to the east (Fig. 17.6). The space-use patterns of these two unrelated females remained separate during their subsequent residency (Fig. 17.8).

Twice females moved from Lower Picnic to Upper Picnic. Each time the residents of the previous year had not returned. In 1970 females 880, 843, and 834 formed a kin group unrelated to the kin group on Lower Picnic (Fig. 17.4). There was no overlap between the two kin groups in their space use (Fig. 17.9). By contrast, females 167 and 174 frequently returned to Lower Picnic but only into the area occupied by their mother, 301 (Fig. 17.7). In each case the immigrants usurped space that might otherwise have been used by potential female yearling recruits. This takeover of space probably accounts for the lack of recruitment when a new immigrant is present.
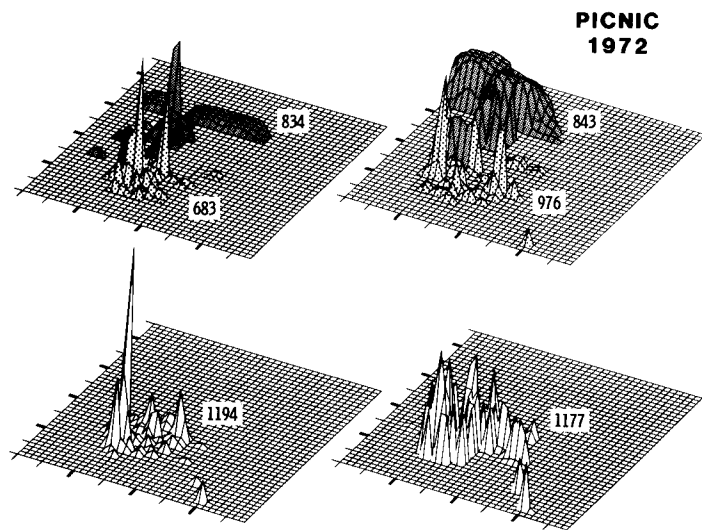
**PICNIC
1972**

FIGURE 17.9. Perspective block diagram of space use at Picnic in 1972. The kin group on Upper Picnic consists of sisters 834 and 843. On Lower Picnic, the kin group consists of 683, her daughter 976, and her granddaughters 1177 and 1194, who are half-nieces of 976.

Matrilines share space. In 1972 sisters 834 and 843 occupied Upper Picnic, and a kin group consisting of mother, daughter, and granddaughters, who were half-nieces of the daughter, occupied Lower Picnic (Fig. 17.4). The members of each kin group shared space with each other but not with members of the other kin group (Fig. 17.9). Although the members of each kin group had nearly 100% overlap in their home range areas, each individual had its own characteristic pattern of areas of high frequency of use (Fig. 17.9). This pattern of each individual developing its own area of high frequency of use was characteristic of matrilines occupying the same general area; for example, females 683, 976, 1177, and 1194 in 1973 (Fig. 17.5). However, sometimes two sisters used space almost identically; for example, females 489 and 503 in 1980 (Fig. 17.7). Such similarity in both the areal extent and frequency of use of areas within the home ranges occurred only between sisters (excluding the philopatry of mother and juveniles), although mother/daughter patterns were often similar (e.g., ♀ 1194 and her 3-year-old daughter, 920; Fig. 17.8).

Over time, individuals in a matriline were replaced. Of the animals resident at Lower Picnic in 1973, one remained in 1979 (Fig. 17.4). In 1979 the residents were active in the meadows to the west of the talus, where they rarely went in 1973 (compare use of area beyond horizontal grid 25, Figs. 17.5, 17.8). This

increase in the use of space at Lower Picnic occurred with no change in the density of residents and was evident by 1976, when a somewhat different cast of characters was present (Fig. 17.6). A possible explanation for the increased use of space by this matriline is given below.

Matrilines may continue without philopatry. Although the matriline on Lower Picnic demonstrates a strong association with philopatry, such an association is not essential for a matriline to continue. Females 843 and 834 continued a matriline at Upper Picnic (Fig. 17.9) that began at Lower Picnic with immigrant 880 (Fig. 17.4). Similarly, females 167 and 174 moved to Upper Picnic in 1980, where they continued a matriline initiated by female 301. Although they made incursions into their mother's space during this first year at Upper Picnic (Fig. 17.7), these incursions ceased in the following years.

Matrilines may continue when emigrants successfully establish residency in a new area. Female 1082, by immigrating into Upper Picnic (Fig. 17.4), continued a matriline begun by female 1047 at North Picnic (Fig. 17.2). The movement of females 42 and 728 from Bench to River (Fig. 17.1) also continued matrilines. The movement of female 42 is an example of breeding dispersal (Greenwood, 1980). Neither the frequency nor the causes of breeding dispersal are known, but it may continue matrilines in habitats distant from their origin.

Bifurcation of matrilines. The bifurcation of matrilines is associated with the partitioning of a single matrilineal space into two or more spaces, each of which is shared by individuals who are related by 0.5. This subdivision of matrilineal space occurred gradually over several years.

The members of the matriline occupying Lower Picnic in 1973 shared the space (Fig. 17.4) and had an average relatedness of 0.29. This group consisted of a female, her daughter, and her two granddaughters who were half-nieces of the daughter. By 1976 the average relatedness of the four residents was 0.25. Although the decrease in average relatedness was slight, the residents formed two groups consisting of two sisters each. Amicable behavior among the four females was significantly less than expected (Armitage and Johns, 1982), and the younger females 301 and 349 wandered widely and concentrated their activities in areas little frequented by females 1177 and 1194 (Fig. 17.6).

By 1979 average relatedness of the five residents had increased to 0.34, but they again formed two kin groups, female 1194 and her daughter 920, and female 301 and her daughters 167 and 174 (Fig. 17.4). The average relatedness within each kin group was 0.5, but relatedness was only 0.0625 between members of the different kin groups. The two kin groups clearly partitioned the available space,

1982 were descended from one female (Fig. 17.4). Of a population of 27 adult *Spermophilus tridecemlineatus,* 24 were derived from only four of 20 females resident four years earlier (McCarley, 1970). The average annual production of young was about 33% greater in the four successful reproducers than in the 16 unsuccessful reproducers. Chance may play a role as more female descendants may result from female-biased litters (Michener, 1980).

If more females may be recruited from female-biased litters, the question arises whether yellow-bellied marmots adaptively vary the sex ratio of their progeny (Clutton-Brock, 1982). This question focuses on whether reproductive success varies more widely among males and females when parental investment influences the success of offspring (Trivers and Willard, 1973). The reproductive success of individuals in the wild is related to mating strategy. In polygynous species such as yellow-bellied marmots, in which males predominate in dispersal, reproductive success is difficult to measure. Because for all practical purposes only female yellow-bellied marmots are recruited into their natal populations, sex-ratio manipulation by the best recruiters should favor females. If one examines small samples, evidence can be found to support this prediction. For example, two adult females produced all-female litters and recruited all their daughters. However, another recruiter produced only 27% female offspring, and seven of nine young of female 14 were males even though River was underpopulated (Fig. 17.1). When large sample sizes were considered, there was no evidence for sex-ratio manipulation (Table 17.2).

This relationship was explored further by comparing the eight best recruiters with the poor recruiters. The best recruiters recruited three or more daughters during their residency and produced 30 of the 72 recruits. The 20 poor recruiters produced one recruit each. The best recruiters produced more young ($\bar{X} = 14.1$ versus 8.6), more female young ($\bar{X} = 6.5$ versus 4.4), and more yearling daughters ($\bar{X} = 4.6$ versus 2.5). There was no difference in the proportion of female offspring (best: 0.46, poor: 0.52). The most striking difference was that the best recruiters recruited 81% and the poor recruiters recruited only 41% of their yearling daughters. This analysis supports the result of the stepwise discriminant analysis that producing yearling daughters is the critical factor determining successful recruitment. The analysis also indicates that some females simply are good recruiters. The behavioral profiles of seven of the best recruiters were known; five were classified as social. Thus individual variability in behavior is more important in determining recruitment than sex bias in litters.

One reason that sex-ratio bias does not occur in marmots is that dispersal may be a successful reproductive strategy. For males, dispersal is the only strategy,

and any female who produces sons has some expectation of reproductive success. For example, female 683 (Fig. 17.4), who recruited all of her yearling daughters, produced a son who became resident at Cliff, where he was the putative father of four young. A son of female 424, who recruited only one daughter while resident at Marmot Meadow (Fig. 17.3), became resident at North Picnic, where he was the putative father of nine young. Females also disperse and successfully reproduce. For example, female 1082 moved from North Picnic to Picnic. A number of immigrant females produced litters (Figs. 17.1–17.4). The number of immigrants plus the large number of transient marmots trapped at our study sites (Armitage and Downhower, 1974) indicate considerable movement. Many of these animals become satellites (Svendsen, 1974). Possibly, reproductive success among some of these animals is as high as that of some recruiters. As a consequence, there may be no net gain for producing sex-biased litters over the long term, and annual breeders, such as marmots, may be unable to manipulate the sex ratio profitably in the short term. More fitness may accrue from successful recruitment than from sex manipulation.

If marmots are maximizing their direct fitness, why is there so much variation in recruitment? Population density does not account for this variation; some females failed to recruit daughters even when populations were low (e.g., River, after 1971, Fig. 17.1; North Picnic, Fig. 17.2; Marmot Meadow, Fig. 17.3). The characteristics of the potential recruits doubtless are a factor, and their role will be the subject of a future paper. A possible dispersal strategy to balance a recruitment strategy seems inadequate to explain the variability. Possibly selection has favored phenotypic plasticity. There are many social (Armitage, 1977) and ecological environments (Svendsen, 1974), and they are not constant but change in space and time. The variability among yellow-bellied marmots enables this species to live as isolated individuals, as monogamous pairs, in harems (Downhower and Armitage, 1971), or in large colonies consisting of several contiguous harems (Johns and Armitage, 1979). In the same geographic area, they occur in grass/forb or sagebrush/grass/forb meadows, along riverbanks, under cabins, in a small talus patch in an aspen woodland, and even in trees (Garrott and Jenni, 1978). Some of the variability, especially behavioral, expressed in marmots may result from intrauterine influences during development (vom Saal, 1981) or may be a consequence of postnatal developmental experiences (Bekoff, 1977). Heterozygosity may increase fitness (Lidicker, 1981; Smith et al., 1975). Both developmental and heterotic models imply that the production of superior phenotypes will be associated with inferior phenotypes. Thus phenotypic plasticity as an adaptive strategy and/or the mechanisms involved in producing superior

phenotypes will continually be associated with the production of individuals whose fitness is relatively low and who do not contribute to subsequent generations. Our attempts to describe and explain individual fitness may be confounded by the presence of these evolutionarily expendable animals. An adaptive system that produces phenotypes of differing fitnesses makes understandable the high rate of extinction of most matrilines and the high level of individual variability. Social biology and population dynamics theories are in a state of flux. We are well advised "to concentrate on basic issues that bear on a variety of theoretical postures" (Arnold, 1981). The formation of matrilines, the sharing of space by close relatives, and the differences between recruiters and nonrecruiters suggest that kinship and individual variability are central to these issues.

Acknowledgments

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