Dynamics of immigration into Yellow-Bellied Marmot colonies

K. B. ARMITAGE

Ecology and Evolutionary Biology Department, The University of Kansas, Lawrence, KS 66045-7534 USA, e-mail: marmots@ku.edu

Abstract. Immigration and recruitment were examined in six colonies of Yellow-bellied Marmots (*Marmota flaviventris*) for 220 colony-years. Recruitment occurred significantly more often than immigration. Rates of immigration and recruitment were not significantly correlated among colonies nor were either significantly related to the area of the colony. The rates of immigration and recruitment did not differ when the population density of resident females was below the mean, but recruitment was significantly more likely when the population density was above the mean. Immigration was more likely to occur when population density was below the mean, but recruitment did not significantly vary with population density. Recruits were two-years-old whereas immigrants averaged 2.82-years-old. Of 32 yearling females who were potential immigrants to a site, only three became resident and the remaining were transients or peripherals. Two peripheral yearlings and six of 29 peripheral adults eventually became immigrants. Yearlings were more likely to be immigrants if the adult resident females were non-reproductive and if there were no philopatric yearlings present. Immigration and recruitment occurred in the same colony in the same year only eight times. Fitness of adult females is enhanced by recruiting daughters into matrilines consisting of mother:daughter:sister groups. Immigration occurs when empty space is available and there are insufficient recruits to occupy all available space.

Key words: immigration, recruitment, yellow-bellied marmots, density, yearling females, adult females

Introduction

The long term stability of a population requires that deceased adults be replaced. Replacement may occur by immigration, the movement of an animal that was born elsewhere into a habitat patch, or by recruitment, the retention of individuals on their natal habitat patch. The relative importance of immigration and recruitment is related to the social system of a species. For example, most females of ground-dwelling sciurids settle near kin whereas most males disperse (Armitage 1981). By contrast, in Fox (*Sciurus niger*), Gray (*S. carolinensis*), and Red (*S. vulgaris*) Squirrels, both sexes disperse from their natal home ranges, but some, especially females, may remain in their natal area (Wauters and Dhondt 1993, Edwards *et al.* 2003). Hence, in more social species, males may be the major immigrants whereas in more solitary species, both males and females are major immigrants.

A demographic study of Yellow-bellied Marmots (*Marmota flaviventris*) occupying six colony sites and 22 smaller habitat patches reported that both recruits and immigrants were sources of residents (Schwartz *et al.* 1998). The percentage of recruits and immigrants in the population varied with age class. For example, virtually all young were recruits; few adult males were recruits, but were immigrants. By contrast, most age classes of females consisted mainly of recruits.

Because virtually all resident, territorial males are immigrants and become resident when a territory becomes vacant (Armitage 1974), immigration of males will not be reported in this paper. This paper focuses on the role of immigration in maintaining adult yellow-bellied marmot populations (Schwartz and Armitage 2003), whose numerical fluctuation primarily results from changes in the number of female residents (Armitage 1991, 2003). Because immigration may be affected by recruitment (Armitage 1988), recruitment will also be considered.

Methods

Yellow-bellied Marmots were studied in the Upper East River Valley, Gunnison County, Colorado. Marmots are located on patches consisting of rocky outcrops or talus with adjacent meadows in a mosaic of spruce-aspen forest (Svendsen 1974). The sites ranged in elevation from 2,867m to 3,008m over a linear range of about 12km. The average number of resident adult females on a site varied from 1.63 to 6.35 among sites. In addition to the adult females, a typical social group consisted of an adult male, yearlings, and young (Armitage 1991).

The dynamics of immigration were analyzed in six colonies ranging in area from 0.2 to 7.24ha. These sites were monitored for 26 to 40 years beginning in 1962. Each year a site was studied, all marmots were trapped, aged, sexed, weighed, and provided with uniquely numbered ear tags at the time of first capture. Young, yearlings (marmots one-year-old), and two-year-old adults were easily aged by body mass (Armitage *et al.* 1976). Thus the age of animals first trapped at these ages was known throughout their life span. Marmots too large to age at first capture were recorded as adults three-years-old or

| Name of Colony | Number of Years Observed | Number of Years | | Rate per Year | | Total Number | |
		Event R	Occurred I	R	I	Recruits	Immigrants
Boulder	39	6	8	0.231	0.308	9	12
Cliff	26	5	4	0.385	0.154	10	4
Marmot Meadow	38	12	4	0.473	0.105	18	4
River	40	17	6	0.925	0.175	37	7
Picnic	40	23	8	1.25	0.275	50	11
North Picnic	37	6	17	0.297	0.568	11	21

Table 1. Characteristics of recruitment and immigration in six colonies of Yellow-bellied Marmots. The colonies are listed in the order of smallest to largest. R = recruitment, I = immigration.

older. Marmots were fur-dyed in a pattern of stripes and blotches for individual recognition during behavioral observations. Whenever an unmarked marmot was detected, attempts were made to trap and mark it. Not all attempts were successful; some individuals disappeared before they could be trapped.

During observations, the activity and location of a marmot within the site were recorded. Marking and observations made possible classifying individuals into residents (members of a social group whose activity is centered on the habitat site), transients (marmots that move through a site and do not remain for more than a few days), and peripherals (live near a colony, have no or few social contacts, home range lies outside that of the territorial male and the resident females) (Armitage and Downhower 1974). Adult or yearling marmots not previously trapped at a site were considered to be immigrants.

Results

The rates of immigration and recruitment, measured as the number of events per year (an event refers to immigration or recruitment occurring regardless of the number of recruits or immigrants), varied among colonies (Table 1). The smallest (Boulder) and largest (North Picnic) sites had rates of immigration higher than those of recruitment; at the other three sites, rate of recruitment was greater. Rates of immigration and recruitment among sites were not correlated (Spearman r_s = -0.54, p > 0.05). Area of the sites was not correlated with either immigration (r_s = -0.26, p > 0.05) or recruitment (r_s = -0.43, p > 0.05).

One reason for a lack of a relationship between area and immigration or recruitment is that the density of adult females may be more critical than area. Although there is a tendency for larger areas to have a higher mean density of adult females, the relationship is not significant (r_s = 0.66, p > 0.05). Therefore, I examined the relationship between density and recruitment and immigration by recording for each year in which recruitment and/or immigration occurred when the density of females was above or below the mean density for that site (Table 2).

When the density of adult females was below the mean, there was no difference in the number of recruitment or immigration events (38 vs. 41, G = 0.29, p > 0.5). However, when the density of adult females was above the mean, recruitment events occurred significantly more often than immigration events (31 vs. 7, G = 20.3, p < 0.001).

| Colony | Number of Resident Females | | | | | |
| | Below the Mean | | | Above the Mean | | |
	No. Years	R	I	No. Years	R	I
Boulder	11	1	7	28	5	1
Cliff	11	0	2	15	5	2
Marmot Meadow	28	9	3	10	3	1
River	27	8	6	13	9	0
Picnic	25	17	6	15	6	2
North Picnic	35	3	17	12	3	1

Table 2. The relationship between the number of resident adult females and recruitment and immigration. Resident females are those returning from the previous year and does not include new recruits or immigrants. The numbers are the number of years in which the events occurred. R = recruitment, I = immigration.

These results suggest that the density of resident females acts differently on immigration and recruitment. Immigration was significantly more likely to occur when the density of females was below the mean (G = 21.4, p < 0.001) whereas recruitment was equally likely when the density of resident females was above or below the mean (G = 0.23, p > 0.5).

Clearly, immigration or recruitment did not occur in every colony-year (a colony-year is one colony/site in one year) (Tables 1, 2). Of 220 colony-years, recruitment occurred in 69 and immigration in 48. Recruitment was significantly more likely than immigration (G = 5.14, p = 0.025). Both immigration and recruitment occurred in the same colony-year eight times. Four of those occurred at Picnic Colony and three occurred at North Picnic Colony when the density of resident females was below the mean. The other instance occurred at Boulder when the density of resident females was at the mean. Recruitment and immigration did not occur in the same year in River, Cliff, and Marmot Meadow colonies.

The number of recruits per year of occurrence varied from 1.5 to 2.17, mean = 1.84 (1.54 to 2.15 95% CI). The mean number of immigrants (1.21) was significantly lower (range was 1.0 to 1.5, 95% CI = 1.00 to 1.43).

By definition, recruitment occurs when a two-year-old female remains in her natal colony. Thus all recruits are aged two years, but the age of immigrants is usually unknown because most of them are too large to age based on body mass (Armitage *et al.* 1976). We recorded 22 inter-colony movements of known-aged female yellow-bellied marmots. These

females were immigrants into their colony of residency. They ranged in age from two to four years, mean age was 2.82 years. Thus, on average, an immigrant is about one year older than a recruit.

Although by definition, recruits are considered such at age two years, recruits were present as yearlings. Because about 50% of the yearling females become recruits (Armitage 1991), the question is asked do female yearlings become successful immigrants? During the period of this study at the six colony/sites, 32 yearling females were trapped who had not been born at the site. Six of these became residents; the others were either transient or lived peripherally. There was no effect of population density (number of resident females above or below the mean) on whether a yearling female became a resident or a transient/peripheral ($G = 0.13$, $p > 0.9$). Two of the peripheral females became immigrants as adults.

Previously I suggested that population density interacted with social behavior to form a population-behavioral system in which population density and rates of social behavior were not necessarily correlated (Armitage 1975, 1977). Because rates of behavior were not available for all six colony/sites, the reproductive status of resident females was used as an indicator of behavior. Adult females tend to express agonistic behavior to non-kin, and reproductive females may be highly agonistic to yearling females (Armitage 1986a,b). Yearling females were significantly more likely to become immigrants rather than transient/peripherals when no resident adult female was reproductive ($G = 6.64$, $p = 0.01$).

Although this report focuses on the role of adults in immigration, potential yearling immigrants may be affected by yearling residents. When resident yearling females were present, immigration by yearling females did not occur but did occur when resident yearlings were absent. The difference was highly significant ($G = 10.7$, $p = 0.001$).

Discussion

Recruitment occurred in more colony/years, at a younger age, in greater numbers, and at higher rates than immigration. These results suggest that yellow-bellied marmots form closed social groups. This interpretation is supported by two additional lines of evidence. Seven adult females were introduced into three marmot colonies (Picnic, North Picnic, Marmot Meadow); none became resident. Similarly, seven yearling females were introduced into two colonies (Marmot Meadow and Picnic); none became resident. When all the adults were removed from one colony, all the yearling females remained and two three-years-old females immigrated (Brody and Armitage 1985).

However, it is possible that immigration rarely occurs because potential immigrants are not present. During this study, 41 adult females were recorded as peripherals or transients. This number is a minimal estimate as it is based on sighting a strange animal and then trapping it before it disappears. None of the 12 transients became immigrants and six of the 29 peripheral females became immigrants. These numbers indicate that it is the closed nature of the social system rather than the availability of potential immigrants that accounts for the low rates of immigration. However, when weather events cause a major population decline, recovery may be slow because of a lack of potential immigrants. Where extinction occurred, the sites were repopulated by immigrants. Major colonies (Picnic, River, Marmot Meadow) were repopulated by recruits (Armitage 2003).

The social system of yellow-bellied marmots consists of female kin groups consisting of mother:daughter:sister groups. These groups persist through time as matrilines (Armitage 1991, 2002). An immigrant, territorial male may defend one or more female groups. Fitness increases as matriline size increases (Armitage and Schwartz 2000) and then decreases in matrilines of four or larger. Females act to increase their direct fitness (Oli and Armitage 2003) and direct fitness is increased by recruiting daughters who occupy available space and reproduce, thus producing grand-offspring. Immigrants would compete for resources, reduce the number of reproductive descendents of residents, and lower their fitness. No immigrant female has ever joined a matriline; immigration occurs when empty space becomes available. The occupation of empty space explains why immigration is far more likely to occur when the density of resident females is below average. Recruitment of daughters to form matrilines explains why recruitment is independent of the density of resident females.

Immigration and exchange of individuals between social groups probably varies among ground-dwelling sciurids, but few species have been studied for sufficient time to quantify immigration. The minimum immigration rate of *Spermophilus beldingi* at Tioga Pass was 0.7% for females; the maximum rate was 6.0% (Sherman and Morton 1984). In the Uinta ground squirrel (*S. armatus*), emigration decreased when population numbers were reduced by removal, but data on individual movements and immigration into a local population were not recorded. One population was maintained by immigration (Slade and Balph 1974). These patterns suggest that immigration may be low when a population is self-sustaining, which could be a consequence of the behavioral rejection of strangers. Movements of female Columbian ground squirrels (*S. columbianus*) were concentrated within their patch; only one of 60 was trapped more than 200m from her center of activity (Weddell 1991). Resident adult females were highly aggressive towards immigrant females and no immigrant female successfully displaced a resident. Successful immigrants occupied vacant sites on the periphery of the colony (Wiggett and Boag 1992). The authors suggested that adult females gain fitness through philopatry and the retention of daughters on the natal site, a process similar to that of yellow-bellied marmots.

Among the highly social black-tailed prairie dogs, coterie members resist immigration; successful immigration is rare (Hoogland 1995). Immigrants arrived alone; only 24% of female immigrants reared at least one litter. Most reproductively unsuccessful immigrants disappeared.

Interfamily regrouping occurs during the second half of the active season in *M. bobac*, *M. menzbieri*, *M. caudata*, and *M. baibacina*. Female immigrants into new families successfully breed the next year (Mashkin 2003). However, the proportion of females participating in regrouping over several years was not stated, but may be high. In a high altitude population of *M. marmota*, immigration occurred into a family by adult

females born in other families on the site. Adult female immigration also occurred by females born outside the site (Lenti Boero 1999). Immigration by an adult female into a family characterized this population. Female Golden Marmots (*M. caudata aurea*) also moved between groups; most were to smaller groups (Blumstein and Arnold 1998). By contrast, no successful immigration occurred in three years of study of *M. olympus* colonies, but immigration established new colonies (Barash 1973).

Interfamily regrouping has not been observed in *M. flaviventris*; members of a matriline may split off to form a daughter matriline adjacent to the parental matriline (Armitage 2002). By contrast, Eurasian marmots demonstrate such regrouping, but the extent is not fully quantified, but probably occurs at low rates. The differences in the rates and patterns of immigration may be related to the likelihood that a disperser can find suitable habitat. In those species with delayed dispersal (Armitage 1999, Blumstein and Armitage 1999), individuals reach a size that makes them competitive with residents. These species lose reproductive output but gain survival (Blumstein and Armitage 1998). In small, more asocial species, survival decreases because dispersal occurs at a smaller, younger age, but reproductive output is enhanced. For all species, philopatry is more successful than immigration, but the role of immigration varies among species and should be further investigated.

Acknowledgements

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