

The effects of adult removal on dispersal of yearling yellow-bellied marmots

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The relative importance of adult–yearling interaction and individual behavioral phenotypes on dispersal of yearling yellow-bellied marmots was investigated. Two marmot colonies near Gothic, Colorado, were studied; one was treated as an experimental colony from which all adults were removed, while the second was left undisturbed. Analysis of dispersal patterns and behavioral observations indicated that agonistic behavior between adults and yearlings is not necessary for dispersal to occur. Dispersal of male yearlings appears to be independent of adult–yearling interactions, although dispersal of female yearlings probably is mediated by social interactions. Individual behavioral phenotypes could not be used to predict which animals dispersed nor the relative timing of their departure. Dispersal can be viewed as an important mating strategy; for yearling males it is likely to be the only option available for reproductive success.

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L'influence des interactions entre les jeunes de 1 an et les adultes, de même que celle des types de comportements individuels sur la dispersion des marmottes à ventre jaune de 1 an a fait l'objet d'une étude chez deux colonies des environs de Gothic, Colorado. Chez l'une des colonies, tous les adultes ont été retirés; l'autre colonie est demeurée intacte. L'analyse des routes de dispersion et l'observation du comportement des marmottes a démontré que les interactions antagonistes adultes – jeunes de 1 an ne sont pas essentielles à la dispersion. La dispersion des jeunes mâles semble indépendante des interactions adultes–jeunes, mais la dispersion des jeunes femelles semble fonction d'interactions sociales. Le type de comportement chez les individus ne permettait pas de prédire quels animaux allaient se disperser, ni à quel moment. La dispersion constitue peut-être une importante stratégie reproductive; pour les jeunes mâles, il s'agit probablement de la seule stratégie qui leur permette de se reproduire avec succès.

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Introduction

Dispersal of a particular age-class occurs in most social ground-dwelling sciurids (Armitage 1974; Downhower and Armitage 1981; Garrett et al. 1982; Holekamp 1984; McLean 1982; Pfeifer 1982; Svendsen 1974), but the proximate cause or mechanism that determines which individuals disperse remains unclear.

Yellow-bellied marmots (*Marmota flaviventris*) live in social groups composed of matrilineal units with an associated territorial male (Armitage 1984). Yearlings, animals 1 year old, may be present; juveniles emerge in mid- to late July and remain in the colony throughout their first summer. Virtually all male yearlings and approximately 60% of female yearlings disperse. The timing of departure varies; 57% of males and 40% of females disperse by mid-July, while 81% of males and 61% of females disperse by the 1st week of August (Downhower and Armitage 1981).

Behavioral interactions among individuals were cited as a cause of dispersal in a variety of small mammals (see Gaines and McClenaghan 1980 for review). Agonistic interactions between adults and young, or between dominant and subordinate individuals, may cause dispersal (Armitage 1974; Carl 1971; Downhower and Armitage 1981; Fairbairn 1978). However, such a relationship has not been supported by other studies (Armitage 1973; Pfeifer 1982). The ontogeny of social interactions, rather than aggression just before dispersal, may predict which animals leave the natal group and the relative timing of their departure (Bekoff 1977). Individuals that are asocial do not initiate interactions, or avoid interactions, with other colony members and will disperse first, whereas those that interact more will most likely delay dispersal (Bekoff 1977).

The timing of dispersal in yearling yellow-bellied marmots

indirectly supports the predictions made by Bekoff's social cohesion hypothesis outlined above. High levels of amicable behavior between adults and yearlings were associated with delayed dispersal. Male dispersal was not related to levels of aggression; however, agonism was associated with earlier dispersal of females (Downhower and Armitage 1981).

The purpose of this study was to test whether absence of adults would delay or prevent dispersal by yearlings, and to relate individual behavioral phenotypes to the timing of dispersal. Higher than expected rates of agonistic interactions occur between adults and yearlings (Downhower and Armitage 1981). If the hypothesis that dispersal is proximally mediated by agonistic interactions between adults and yearlings is correct, the removal of adults should significantly delay or prevent dispersal. In addition, if dispersal did occur, removal of adults (and consequent removal of adult–yearling interactions) allows examination of the relationship between the behavior of individual yearlings and the timing of dispersal.

Materials and methods

Marmots were studied from 15 June through 15 August in 1982, and from 17 June through 12 August in 1983. Data were collected from two localities during 1982: North Picnic Colony was the experimental colony and Picnic Colony was the control. In 1983, only data from North Picnic were gathered. The characteristics of the two localities are described elsewhere (Armitage 1974).

Each year, all animals were trapped. Upon capture, animals were transferred to a handling bag, weighed, sexed, permanently tagged with fingerling ear tags (if not done previously), and given distinct marks using Nyazol fur dye to facilitate subsequent recognition during field observations. Age was determined from previous years' trapping data and weight (Armitage et al. 1976). During 1982, all adult animals at North Picnic Colony were removed at first capture; when immigrants appeared in the study site, trapping was resumed until they were caught and removed.

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Marmots were observed between 0645 and 1100 (Mountain Day-light Time) each morning except in inclement weather. In 1982 and 1983, observations were conducted at North Picnic Colony from 17 June through 15 August, and from 19 June through 8 August, respectively. Picnic Colony was observed intensively only from 14 June through 15 July in 1982. Later observations at Picnic Colony were sufficient to determine the presence or absence of particular individuals, but were not extensive enough to include in the analysis of behavior among colony members.

Each colony was scanned continuously with a field model telescope or binoculars; the location of each individual was determined with a clear, numbered grid overlying a photograph of the area. Animals' positions were recorded at 10-min intervals. Interactions were noted and later classified as cohesive or agonistic and grouped accordingly. Greeting, allogrooming, and play were classified as cohesive behaviors; avoidance, chase, and flight as agonistic.

Results

Yearling disappearance, dispersal, and recruitment

Ten yearlings, 6 female and 4 male, were resident at North Picnic Colony at the onset of the study in 1982. Two resident adult females were removed before observations began. Following removal of the adult females, two 3-year-old females, who were born at North Picnic but had dispersed as yearlings, returned to the colony. Six adult males immigrated to the colony one at a time. All immigrants were captured and removed within 3 days of first sighting, except an animal (not one of the above) that arrived late in the season and could not be caught. One male and all six female yearlings remained at North Picnic at the end of the season in 1982. Three male yearlings dispersed; the male that had not dispersed by mid-August in 1982 dispersed after the study had ended, or before it began in 1983, as he was the territorial male at Picnic Colony in 1983. The six females were present as 2-year-olds in June 1983; two of them subsequently disappeared.

Picnic Colony usually supports two harems, Upper and Lower (Armitage 1974). In 1982, five adult females, one adult male, and four yearlings (three females and one male) resided at Upper Picnic; three adult females, one adult male, and one yearling female resided at Lower Picnic. All four yearlings from Upper Picnic dispersed; the yearling female at Lower Picnic was present when the study ended in 1982 but was not present in 1983.

The number of yearling dispersers versus nondispersers differed significantly between the two colonies (G -statistic, $P < 0.05$); however, the timing of dispersal did not differ significantly.

The most striking observation of this study was the large number of recruits at North Picnic Colony in 1982. An individual is classified as a recruit if it remains in its natal colony throughout its yearling year. Six yearling females in 1982 remained at North Picnic when the study ended in mid-August and were present as 2-year-olds in 1983. From 1964 through 1981, only 5 of 16 female yearlings born at North Picnic were recruits; of these, only two remained as 2-year-olds, and a third lived peripherally. These differences in the number of recruits ($\chi^2 = 8.3$, $P < 0.005$) and number of 2-year-old residents ($\chi^2 = 5.0$, $P < 0.05$) are highly significant.

In a different experiment at Marmot Meadow Colony (Armitage 1984; K. B. Armitage, unpublished data) all of nine yearling females were recruits when an adult male but no adult female was present. In 22 years when one or more adult females were present, 7 of 20 female yearlings were recruits. This difference in number of recruits is highly significant ($\chi^2 =$

10.6, $P < 0.005$), and suggests that the adult females but not the adult male have the critical role in determining whether female yearlings emigrate.

Observations and interactions

Each 10-min interval of observation was treated as a separate survey. The average frequency of observation for each animal was calculated by summing the number of surveys in which the individual was seen and dividing by the total number of surveys for that week. For 14 of 15 yearlings from both colonies, the frequency of observation was not significantly correlated with the number of surveys.

Although the frequency of observation varied among individuals and among weeks there was no significant seasonal trend at either colony. The frequency of sighting individuals did not differ between the two colonies in 1982; overall, each individual was sighted during 16–29% ($\bar{x} = 22.0$, $SD = 15.0$) of all surveys at North Picnic and during 17–26% ($\bar{x} = 22.0$, $SD = 14.0$) of all surveys at Picnic Colony.

To estimate the amount of time an animal spends in social activity in relation to other activities, the availability of the animal for interaction was incorporated into the calculations (methods in Michener 1980). The total number of interactions observed over a 1-week period for each animal was divided by the number of surveys in which the animal was observed (Table 1). The interaction rates at Picnic Colony include only those interactions involving yearlings as one or both participants. Adult–adult interactions were not germane to the study and were excluded.

The frequency of interaction for each individual was neither correlated with nor dependent upon the frequency of observation or the number of surveys at either colony. The interaction frequencies for yearlings ranged from 0.00 to 0.67 ($\bar{x} = 0.22$, $SD = 0.17$; Table 1) at North Picnic, and from 0.00 to 0.50 ($\bar{x} = 0.16$, $SD = 0.16$; Table 1) at Picnic. The individuals of the two colonies differed in their frequencies of interaction; Picnic Colony animals interacted less than North Picnic marmots (Fischer's exact probability, $P = 0.002$). Furthermore, if only data among yearlings are considered, yearlings at Picnic Colony interacted less than yearlings at North Picnic ($P = 0.01$; Table 1), and a significantly greater proportion of the time they spent interacting was devoted to agonistic behavior ($P = 0.01$; Table 1).

Behavior and dispersal

Although the yearlings from Picnic Colony were involved in more agonistic interactions than those from North Picnic, and 80% of them dispersed, the timing of dispersal and agonistic behavior were not significantly correlated at either colony. The frequency of interaction or the proportion of time spent interacting agonistically did not differ significantly between yearling dispersers and nondispersers at North Picnic. Analysis of the number of interactions initiated by yearlings at North Picnic revealed no significant difference (Fischer's exact test, $P = 0.50$) between dispersers and nondispersers in the tendency to initiate interactions.

Play behavior may substitute for aggression and provide the means by which dominance–subordination relationships are established (Armitage and Johns 1982). The frequency of play and the percentage of interactions that were classified as play were significantly greater for North Picnic yearlings than for those at Picnic (Wilcoxon two-sample test, $P < 0.05$; Table 1). At North Picnic, dispersers played significantly more than nondispersers ($P < 0.025$) and the percentage of inter-

TABLE 1. Interaction rates for yearling marmots at North Picnic and Picnic colonies during the first 4 weeks of study in 1982

Animal No.	Week 1			Week 2			Week 3			Week 4		
	A	B	C	A	B	C	A	B	C	A	B	C
North Picnic												
891 (MD)*	0.21	0.19	0.00	0.35	0.22	0.02	0.31	0.18	0.02	0.20	0.12	0.02
		0.90			0.62	0.06		0.56	0.06		0.60	0.10
876 (F)	0.29	0.24	0.00	0.30	0.23	0.00	0.26	0.14	0.00	0.14	0.11	0.00
		0.82			0.78			0.53			0.75	
894 (MD)	0.56	0.67	0.00	0.25	0.19	0.00	0.23	0.15	0.00	0.11	0.11	0.00
		0.78			0.75			0.67			0.75	
896 (MD)	0.67	0.56	0.05	0.50	0.45	0.00	0.42	0.26	0.00	0.07	0.00	0.00
		0.78	0.07		0.91			0.62				
878 (F)	0.19	0.19	0.00	0.19	0.06	0.00	0.31	0.28	0.00	0.50	0.50	0.00
		1.00			0.33			0.91			1.00	
882 (MD)	0.38	0.31	0.00	0.39	0.39	0.00	0.12	0.12	0.00	0.20	0.20	0.00
		0.83			1.00			1.00			1.00	
798 (F)	0.32	0.24	0.00	0.37	0.21	0.05	0.28	0.12	0.08	0.50	0.00	0.00
		0.75			0.57	0.14		0.43	0.28			
640 (F)	—	—	—	0.36	0.28	0.00	0.29	0.19	0.00	0.50	0.25	0.00
					0.80			0.67			0.50	
880 (F)	0.56	0.12	0.06	0.18	0.09	0.00	0.18	0.12	0.00	0.14	0.00	0.00
		0.22			0.50			0.67				
884 (F)	0.25	0.00	0.00	0.14	0.07	0.00	0.19	0.12	0.00	0.07	0.00	0.07
					0.50			0.67				1.00
Picnic												
672 (F)	0.16	0.00	0.00	0.13	0.06	0.00	0.12	0.00	0.04	0.16	0.02	0.05
					0.44				0.30		0.10	0.30
741 (FD)	0.47	0.07	0.27	0.14	0.00	0.10	0.13	0.03	0.03	0.15	0.00	0.15
		0.14	0.58			0.68		0.25	0.25			1.00
661 (FD)	0.27	0.09	0.09	0.28	0.07	0.14	0.18	0.18	0.00	0.00	0.00	0.00
		0.35	0.34		0.25	0.51		1.00				
646 (MD)	0.00	0.00	0.00	0.00	0.00	0.00	0.57	0.14	0.43	0.00	0.00	0.00
								0.25	0.75			
751 (FD)	0.50	0.25	0.25	0.15	0.08	0.08	0.45	0.18	0.18	0.00	0.00	0.00
								0.40	0.40			

NOTE: A, total interaction rate; B, rate of play; C, agonistic interaction rate. Second rows in columns B and C denote percentage of interactions that were classified accordingly.

*M, male; F, female; D, disperser.

actions that were classified as play was significantly greater for dispersers ($P < 0.025$) at North Picnic Colony. However, male yearlings play more than females (Armitage 1974; this study), and it is the male yearlings who dispersed. Therefore, the significant difference in play behavior could be interpreted as a sex difference, rather than a difference between dispersers and nondispersers.

Discussion

The results of this study indicate that the proximal causes of dispersal are not the same for males and females. Sex differences in dispersal are a consequence of the type of mating system (Greenwood 1980); female marmots are philopatric and males associate themselves with a colony of females (Armitage 1984). Adult males are territorial and exclude all other males from their home range. Thus, dispersal should be biased in favor of males (Greenwood 1980).

Four main hypotheses regarding the cause of dispersal may be applied to marmots: (i) there is a genetic basis for dispersal; (ii) individuals disperse to avoid inbreeding; (iii) dispersal is based upon behavioral phenotypes, either of the dispersing

animal or of the other members of the colony who in effect "force" individuals to emigrate; and (iv) dispersal is a result of an individual's assessment of its social status or mating potential in the colony that it inhabits. The four hypotheses are not mutually exclusive, and it is important to distinguish between the cause of dispersal and the effect.

Although few studies have addressed the issue, empirical (i.e., electrophoretic) data do not suggest that dispersal is controlled by a genetic polymorphism in ground squirrels (Michener and Michener 1977). However, male-biased dispersal displayed in all ground-dwelling sciurids (Holekamp 1984) and the independence of dispersal and aggression in this study suggest there may be a genetic basis for male dispersal.

Black-tailed prairie dogs may disperse to avoid inbreeding (Hoogland 1982). Sex differences in timing and distance of dispersal in most ground squirrels promotes outcrossing (Dobson 1979). In marmots, even with no dispersal, the demographic probability of incest is very low (Armitage 1974). Thus, inbreeding avoidance is likely a consequence of male dispersal rather than a cause.

Past studies suggest that the nature of interactions between

yearlings and adults determines whether yearlings are recruited or disperse (Armitage 1975, 1984; Armitage and Downhower 1974). While probably true for females, yearling male dispersal appears to be independent of adult-yearling interactions.

In this study, yearling males at North Picnic dispersed despite the absence of adults and a lack of agonistic interactions. We cannot conclude, with absolute certainty, that the immigration of the adult male in 1982 did not cause the dispersal of yearlings; however, it is unlikely that his presence was the cause for several reasons: at least one yearling male dispersed before the immigrant's appearance; there was no apparent antagonism between the immigrant and the remaining yearlings; other individuals had moved in previously and not caused dispersal of those present; and the new animal used an area not frequented at that time by the eventual dispersers.

Play, a common form of social interaction among yearling marmots, probably is important in the social development of individuals which may ultimately determine who disperses and when (Bekoff 1977). Although individuals at North Picnic engaged in frequent play bouts, and did not differ from non-dispersers in the overall frequency of their interactions, dispersal occurred despite the apparent social bonds that were established.

A number of lines of evidence suggest that social behavior between adult and yearling females mediates dispersal. This view is strongly supported by the failure of all 15 yearling females in two colonies to disperse when adult females were absent. Whether a female yearling disperses probably depends on a complex interaction of individual behavioral phenotypes (Svendsen and Armitage 1973) with the rates of agonistic and cohesive behaviors in which the yearlings participate. Female yearlings disperse early when rates of agonistic behavior are high (Downhower and Armitage 1981) and yet females may be recruited despite high rates of agonism if one (or more) adult female is sociable (Armitage 1977). Thus the ratio of amicable to agonistic interactions may be important in determining which yearling females will be recruited. The nondispersers at North Picnic Colony (all female) engaged only in amicable, cohesive interactions with siblings and other yearlings.

Females are most successful reproductively if they can exclude other matrilineages from the colony in which they live (Armitage 1984). Therefore, females should act aggressively towards other, unrelated individuals in an attempt to garner the available resources for their own direct descendents. Cohesive interactions prevail among closely related animals, while dispersive interactions predominate among distant relatives (Armitage and Johns 1982). At North Picnic, failure of matrilineages to persist and dispersal of introduced animals were associated with the residency or immigration of highly aggressive females (Armitage 1984). Although in this study the colony was not followed long enough to determine if matrilineages will persist, the large number of females recruited suggest that a lack of agonism allowed the females to remain.

Evidence from other ground squirrels (see Holekamp 1984 for review) supports our conclusion that male dispersal is not directly caused by aggression from conspecifics. Aggression does, however, stimulate dispersal of some female sciurids (Holekamp 1984). Competition for quality breeding sites probably causes female *Spermophilus elegans* to interact aggressively (Pfeifer 1982).

While broad generalizations regarding dispersal are difficult to make (Gaines and McClenaghan 1980), one theme appears

to underlie dispersal in social ground squirrels; dispersal is male biased and the proximal causes differ for males and females. The patterns of dispersal must ultimately be interpreted in light of the mating structure of the population and reproductive strategies available to individuals. Female marmots may, depending on the social composition of their natal colony, remain in the colony where they were born and reproduce successfully. The probability of a yearling male obtaining residency, and ultimately breeding, in its natal colony is so low that males must emigrate to have a chance at reproductive success.

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