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Survival of dispersing and philopatric yellow-bellied marmots: what is the cost of dispersal?

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Understanding the evolution of dispersal has been hindered by a lack of reliable measures of the cost of dispersal. We report that survival of dispersing yellow-bellied marmots (*Marmota flaviventris*) (0.73) was only 16% less than survival of philopatric marmots (0.87). A cost-benefit analysis reveals that the survival cost of dispersal may be less than some other costs of philopatry; thus, dispersal is explicable as a tactic to improve individual fitness.

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Dispersal, defined as the one-way movement of an animal away from its home area (Lidicker 1975), has long been an enigma. Dispersal seems inherently dangerous. Dispersers must move through unfamiliar terrain, and when doing so they become vulnerable to predation, aggression, stress, and malnutrition; further, all suitable habitat already may be occupied by conspecifics (Gaines and McClenaghan 1980). Philopatry, in contrast, entails remaining in familiar habitat known to be of adequate quality. Thus, the belief that dispersal is more costly than philopatry is widely accepted (Gaines and McClenaghan 1980, Michener 1983, Stenseth 1984, Lidicker 1985, Anderson 1989, Jones 1989).

But, if survival of dispersers is so low, how can dispersal be explained as a product of natural selection? This enigma has led to models of the evolution of dispersal through group selection or parental fitness, in addition to numerous models based on individual selection (Anderson 1989, Johnson and Gaines 1990). These models suffer from a lack of empirical tests (Johnson and Gaines 1990); determining the evolutionary basis of dispersal requires reliable measures of the cost of dispersal (Fairbairn 1978, Gaines and McClenaghan 1980, Waser et al. 1986, Armitage 1988, Johnson and Gaines 1990), yet

obtaining unbiased estimates of the probability of surviving dispersal is extraordinarily difficult (Gaines and McClenaghan 1980, Johnson and Gaines 1990). We determined the survival rates of dispersing and philopatric yellow-bellied marmots (*Marmota flaviventris*) for 1 year. Our purpose was to test the hypothesis that survival is lower for dispersing than for philopatric marmots, and to evaluate simple cost-benefit models for the evolution of dispersal.

Methods

The study was conducted 1983–1990 near Rocky Mountain Biological Laboratory, Gunnison County, Colorado, USA. The yellow-bellied marmot, a large, ground-dwelling squirrel, hibernates mid-September until early May and typically lives in colonies associated with discrete habitat patches. Marmots do not disperse until at least 1 year old; nearly all males and about one-half of females eventually disperse (Armitage and Downhower 1974, Armitage 1984).

Each spring, yearling marmots were trapped shortly

Table 1. Survival of dispersing and philopatric yellow-bellied marmots near Rocky Mountain Biological Laboratory, Gunnison County, Colorado.

	Active season	Overwinter
Dispersing males		
Survival	0.73	0.87
n	55	31
Dispersing females		
Survival	0.73	0.90
n	30	20
Philopatric females		
Survival	0.87	0.91
n	38	33

after emergence from hibernation in early May and were surgically implanted with radio-transmitters that functioned for at least 1 year (Van Vuren 1989). Instrumented marmots were radio-located every 1–3 d until 1 yr after they dispersed or until 2 yr old, whichever came later. A marmot was considered a disperser if it permanently abandoned its natal home range before first reproduction; philopatric marmots were those that did not disperse. The few marmots that dispersed after reproducing were excluded from analysis.

We calculated survival of marmots for one year, decomposed into two seasonal intervals that corresponded to the homeothermal and heterothermal phases of the annual cycle. The active season was from emergence from hibernation in spring until immergence into hibernation the following autumn, and overwinter was from immergence into hibernation until emergence the following spring.

The appropriate measure of the survival cost of dispersal is a comparison of the survival of dispersers with the survival of the same individuals if they had not dispersed; measuring both values, however, is impossible. Experimental manipulations, although conceptually desirable, are problematic because artificially-enforced translocation is not the same process as naturally-occurring dispersal. Thus, the best approximation of the cost of dispersal is a comparison of survival rates of dispersing and philopatric marmots of similar age.

For dispersers, the year of survival analysis began at the start of the active season during which the disperser emigrated. Most marmot dispersers emigrated early in the active season at 1 yr of age (Van Vuren 1990); therefore, to facilitate comparison of similar-aged marmots, the year of survival analysis for philopatric marmots began at the start of the active season at age 1 yr. For each seasonal interval, survival was calculated by dividing the number of marmots alive at the beginning of the interval into the number alive at the end of the interval.

Results

Although marmots dispersed up to 15.5 km from their natal burrow (Van Vuren 1990), equivalent to ca. 150 home range diameters (Armitage 1974), all instrumented marmots were monitored at least until the end of the active-season interval, except for three dispersers whose transmitters failed when the marmots were in transit. We have no evidence that transmitters failed nonrandomly among dispersers; thus, our results were not biased by a lack of information about long-distance dispersers, a shortcoming that has plagued previous studies (Sherman and Morton 1984, Zeng and Brown 1987, Jones 1988). Transmitters of 11 dispersers failed during hibernation, and status (either dead or alive) at spring emergence could not be determined with certainty and without bias; these marmots were excluded from analysis of overwinter survival.

We detected no differences in survival between male and female dispersers during the active season ($G = 0.004$, d.f. $= 1$, $P = 0.95$) or overwinter ($G = 0.150$, d.f. $= 1$, $P > 0.50$) (Table 1), therefore we pooled the sexes for comparison of dispersing and philopatric marmots. Dispersers suffered higher mortality during the active season than did philopatric marmots of comparable age (one-tailed test, $G = 3.11$, d.f. $= 1$, $P < 0.05$). All mortalities during the active season were attributable to predation, primarily by coyotes (Canis latrans) and badgers (Taxidea taxus) (Van Vuren 1990). We detected no difference in overwinter survival between dispersing and philopatric marmots (one-tailed test, $G = 0.153$, d.f. $= 1$, $P > 0.25$).

Discussion

Dispersers are thought to face several risks when in transit, as well as the uncertainty of locating suitable, unoccupied habitat (Gaines and McClenaghan 1980). Our results show that there is a survival cost to dispersal for marmots, but only during transience or shortly thereafter; almost all dispersers that survived transience and entered hibernation had succeeded in establishing home ranges that provided sufficient resources, particularly a suitable hibernaculum (Armitage and Downhower 1974), for overwinter survival. The fitness of dispersers relative to philopatric marmots, calculated as the ratio of active-season survival rates, was 0.84, surprisingly high considering the large cost previously assumed of dispersal.

The fitness cost of a lower probability of survival faced by dispersers (16%) may be less than several other costs of philopatry. Dispersal in marmots apparently is nearly obligate for males but facultative for females, suggesting that costs of philopatry differ between the sexes (Brody and Armitage 1985). For female marmots, philopatry may entail reproductive costs such as inbreeding depression (Johnson and Gaines 1990) and reproductive inhibition (Armitage 1988). Inbreeding depression has not

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been measured in marmots, but estimates of the loss of fitness due to close inbreeding in some other mammals and birds range as high as 15–42% (Hill 1974, Bengtsson 1978, Shepher 1983, Keane 1990, Ribble and Millar 1992). Reproductive maturity in marmots is reached when 2 yr old, but philopatric female marmots that live near older female relatives often fail to breed until 3 yr old (Armitage 1986). The fitness loss incurred by this delay in age at first reproduction is 20%, calculated from l_x and m_x series for marmots (Armitage and Downhower 1974) as the ratio of the reproductive values (v_1) of yearlings excluding (1.299) and including (1.632) the term for offspring production at age 2 yr.

The cost of philopatry for males evidently is severe. The mating system is polygynous (Armitage 1986), and young males that attempt to remain in their natal colony may be precluded from breeding by the adult male (Brody and Armitage 1985) or may be at risk of fatal aggression. Although unquantified, mortality from conspecific attack is a nontrivial risk of philopatry; 12 males that had not yet dispersed were bitten severely by conspecifics. One male that failed to disperse when 1 yr old suffered a near-fatal attack by another marmot upon emergence from hibernation the following spring. The male recovered, then dispersed.

Dispersal may be the consequence of an assessment by an individual of prospects of success in its natal area; if prospects are sufficiently low, the individual disperses (Grant 1978, Armitage 1988, Stenseth and Lidicker 1992). Our results establish that the cost of philopatry can exceed the cost of dispersal. Thus, dispersal is explicable as a tactic to improve individual fitness.

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