

MARMOTS ON THE MOVE? DISPERSAL IN A DECLINING MONTANE MAMMAL

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Olympic marmots (*Marmota olympus*) are large, burrowing rodents inhabiting scattered subalpine meadows on the Olympic Peninsula, Washington. Recently, the population has declined and become increasingly fragmented. The ability of Olympic marmots to recolonize abandoned habitat and to maintain gene flow among extant populations will depend on the number and success of dispersers and the distances that they travel. We monitored 84 radiotagged Olympic marmots to determine dispersal rates, distances, and success. Contrary to previous observations, 3-year-olds were most likely to disperse, although some 2-year-olds and even some older animals, particularly males, moved as well. Of marmots known to be still on their natal home range in the spring of a given year, 16% of 2-year-old males, 50% of 3-year-old males, 17% of 2-year-old females, and 29% of 3-year-old females subsequently dispersed. Dispersal rates for 3-year-olds were slightly lower when all animals were included in the analysis regardless of whether their dispersal history was known. Males dispersed farther than females (median = 984 m, $n = 14$ versus median = 267 m, $n = 13$) and 69% of females settled within 500 m of their original home range. If the observed dispersal patterns are representative of range-wide patterns and if Olympic marmot densities remain low, successful dispersal may be too infrequent to sustain reliable recolonization of vacant habitats or even genetic or demographic rescue of isolated marmot groups.

Key words: dispersal, Kaplan–Meier, *Marmota olympus*, metapopulation, Olympic marmot, radiotelemetry, translocations

Dispersal is a fundamental determinant of population persistence (Fahrig and Merriam 1985, 1994; Stacey et al. 1997; Stacey and Taper 1992). In particular, declines of metapopulations may be exacerbated by a breakdown in interpopulation movement. As local populations become smaller and more isolated, fewer potential dispersers are available even as the distances dispersers must travel to be successful become greater. More dispersers may die without locating suitable habitat and mates, and in the absence of sufficient demographic supplementation (e.g., Brown and Kodric-Brown 1977) and regular genetic exchange (e.g., Mills and Allendorf 1996), local populations may become increasingly small and inbred. Habitat patches that become vacant may not be recolonized. The greater that the distances between occupied habitat patches are, relative to the dispersal ability of

the organism, the greater the risk of this breakdown in connectivity (Fahrig and Merriam 1985; Smith and Peacock 1990). Thus, management plans for any patchily distributed, rare or declining species must consider whether between-population movements are likely to be sufficient to maintain essential population processes.

The Olympic marmot (*Marmota olympus*) is a large, ground-dwelling squirrel inhabiting patchily distributed subalpine and alpine meadows within a matrix of dense forest, rock, snowfields, and deep river valleys. Local populations of Olympic marmots have declined or become extinct in recent years, apparently without regard to marmot group or patch size (Griffin et al. 2008). These declines, apparently driven by high mortality of adult females (Griffin et al. 2008), have increased the natural fragmentation of the population. Entire clusters, or networks (sensu Ozgul et al. 2006), of interacting sites, such as those on Blue Mountain, have become extinct (Fig. 1; Griffin et al. 2008). In other cases, networks now contain only 1 or 2 occupied sites (e.g., Western Network; Fig. 1). Changes in treeline dynamics due to climate change also may be adding to

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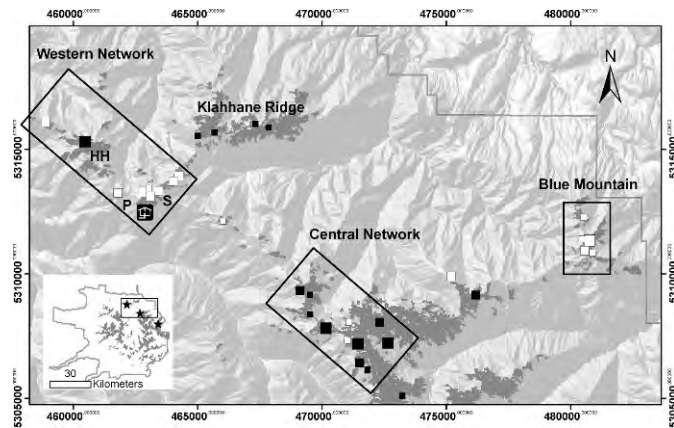


FIG. 1.—The northwestern portion of the range of the Olympic marmot (*Marmota olympus*) in Olympic National Park, Washington. Dark-gray patches overlaid on the shaded relief indicate open (meadow, rock, or bare ground) habitat >1,400 m in elevation. Black-filled squares indicate sites known to be occupied during most or all of 2002–2008 (not all sites were surveyed in all years) and white-filled squares indicate sites that were vacant or functionally vacant (i.e., only a single marmot present) in most years. The 3 symbol sizes correspond to the categories of number of breeding-age females on average supported by the site (≤ 1 , $>1-2$, >2). Number of breeding age females was based on data presented by Griffin et al. (2008) or by Barash (1973). Where no data are available, we estimated the potential number of females based on meadow size and burrow density. Site networks (sensu Ozgul et al. 2006) are indicated with black rectangles with names above. Hurricane Hill (HH), Picnic (P), and Sunrise Basin (S) are indicated by initials at the lower right corner of the appropriate square. The building symbol represents Hurricane Ridge Visitor Center. Axes are labeled in Universal Transverse Mercator coordinates (in m), with 5,000 m between tick-marks. Adapted from Griffin et al. (2008: figure 6). The inset (lower left) shows Olympic National Park (except the coastal strip) with the 3 groups of study sites (left to right: Western, Central, and Royal Basin) indicated with stars. The area shown in the detailed figure is indicated by a rectangle.

the fragmentation of Olympic marmot habitat: aerial photos taken in 1939 and 2001 show a considerable increase in tree cover in the area of the Hurricane Ridge Visitor Center (Fig. 2) and 20th century tree encroachment into subalpine meadows has been documented elsewhere in the marmots' range (Woodward et al. 1995).

Many other ground-dwelling sciurid species (e.g., other marmot species, ground squirrels, and prairie dogs) also inhabit similarly fragmented habitat, and the importance of regular dispersal in maintaining functioning metapopulations of these species is well established. Both empirical observations and simulation models based on long-term studies of the yellow-bellied marmot (*M. flaviventris*) have demonstrated the importance of regular movement of marmots among disjunct meadows (Armitage 2003; Ozgul et al. 2006). In particular, the regional persistence of these marmots depends on the dispersal of individuals from larger sites into smaller patches of habitat that occasionally become vacant. Examination of genetic data indicates that movement of black-tailed prairie dogs (*Cynomys ludovicianus*) among local habitat patches is

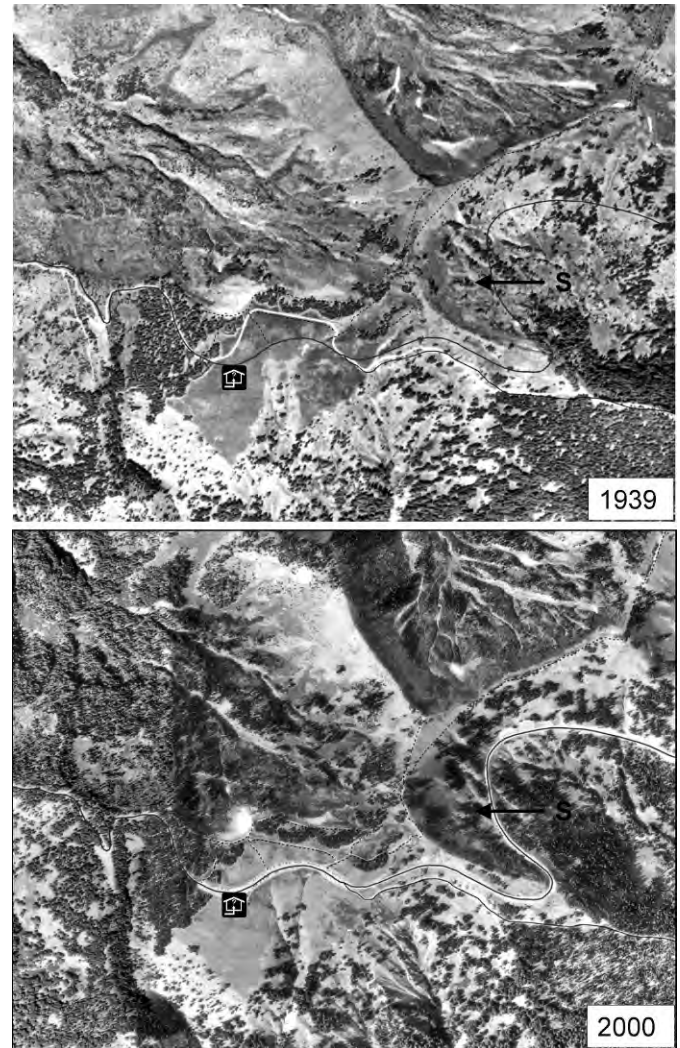


FIG. 2.—Aerial views of the area surrounding the Hurricane Ridge Visitors' Center from 1939 (upper pane) and 2000 (lower pane) show considerable tree encroachment in the 20th century. The current locations of roads (solid lines) and trails (dotted lines) are shown on both photos. The Hurricane Ridge Visitor Center (building symbol) and Sunrise Basin (S) are shown and correspond to the same symbols in Fig. 1. Other sites are not shown so as to avoid obscuring the changes in tree cover.

common, serving to recolonize habitat after sylvatic plague had caused local extinction and to maintain genetic diversity in extant populations (Roach et al. 2001). Sherman and Runge (2002) postulated that the loss of dispersal routes between local populations of northern Idaho ground squirrels (*Spermophilus brunneus brunneus*), as a result of fire suppression, contributed to the local collapse of that species. A similarly severe decline of the Vancouver Island marmot (*M. vancouverensis*) has been attributed, in part, to dispersers settling in newly created, poor-quality habitat (clear-cuts) when they might otherwise have recolonized patches or augmented small groups in higher-quality but more distant natural habitats (Bryant 1996).

The ability of Olympic marmots to recolonize abandoned habitat and to maintain gene flow among extant populations

clearly depends on the number and success of dispersers, both in reaching suitable habitat and subsequently finding mates, and the dispersal range of the marmots relative to the spatial distribution of habitat. If the probability of marmots effectively moving among disjunct habitats is too low to maintain metapopulation processes, biologists might want to consider reintroductions or translocations. It is relatively well established that dispersal in ground-dwelling sciurids is male-biased (Devillard et al. 2004), that males of some species disperse farther than females (Byrom and Krebs 1999; Van Vuren 1990), and that dispersal most commonly occurs before the attainment of reproductive maturity (Armitage 1981). However, there is limited information about rates of dispersal in Olympic marmots (Barash 1973) and effectively nothing is known about how far these animals travel.

Given the recent declines of Olympic marmots, the importance of regular among-site movement, and the paucity of information about dispersal in this species, we sought to quantify Olympic marmot dispersal rates and the distances that dispersers travel. Data on dispersal rates and distances, in conjunction with information on drivers of occupancy patterns and abundance, could provide insight into the conditions under which a given site is likely to be recolonized naturally and, thus, whether translocations may be a useful or necessary management tool in efforts to recover the species.

As part of a broader effort to understand metapopulation dynamics in the Olympic marmot, we collected data on dispersal rates and distances of radiotagged individuals during 6 active seasons, defined as the period between emergence from hibernation in the spring and initiation of hibernation the subsequent fall. Our objectives were: to estimate the simple proportion of all spring residents to disperse during the subsequent active season given the contemporary level of mortality; and to estimate the proportion of spring residents expected to disperse in the absence of active season mortality (e.g., if mortality rates were reduced in the future), computed using Kaplan–Meier methods.

We carried out both analyses on 2 data sets. In constructing the 1st data set, we neither distinguished between pre- and postbreeding dispersal nor considered the dispersal history of marmots, because this may not be known for a given site. By quantifying dispersal rates of all animals regardless of history, we intended to provide managers with a tool to predict the likely number of dispersers from a site based on limited demographic data from a single point in time. The 2nd data set consisted of the subset of animals that were known to have not previously dispersed, and was intended to facilitate comparison with reports on other species.

MATERIALS AND METHODS

Study species and study area.—Olympic marmots are highly social ground-dwelling squirrels found on the upper slopes (>1,400 m) of the Olympic Mountains, on the Olympic Peninsula in northwestern Washington State. Much of the Olympic Peninsula, including most of the higher elevations, is

protected within Olympic National Park. Olympic marmots are closely associated with alpine and subalpine meadows, where they forage and dig the burrows in which they shelter from predators and weather, give birth, care for young, and hibernate for 7–8 months each winter. Multiple family groups may inhabit a single meadow, which may range in size from <5 ha to >100 ha. A family group typically consists of an adult male (≥ 3 years old), 1 or more adult females, and assorted younger animals (Barash 1973). About 40% of females breed in a given year beginning at 3 years of age (Barash 1973; Griffin et al. 2008). The age of reproductive senescence is unknown, but over the course of our studies, 3 surviving females produced pups when they were ≥ 9 years old. In years when a female does breed, a litter of 1–6 juveniles 1st appears above ground in mid-July to mid-August. Details about recent demographic rates are given elsewhere (Griffin et al. 2007, 2008). Barash (1973) reported that approximately 30% of females and 50% of males disperse at 2 years of age. Several large rivers drain the central Olympic Mountains and have carved deep, steep-sided valleys that probably act as barriers to movement by marmots.

Our study sites were located in the northeastern portion of Olympic National Park. The Western group of study sites (Fig. 1) consisted of Hurricane Hill, where there was a persistent cluster of frequently interacting family groups inhabiting adjacent cirque basins, and the small sites Picnic and Sunrise Basin. Picnic and Sunrise Basin were vacant for most of the study, and between them contained ≤ 2 marmots at any one time from 2003 to 2008. Hurricane Hill, Picnic, and Sunrise Basin were ≤ 3.3 km of each other. With the exception of 1 or 2 marmots in a basin adjacent to the Hurricane Hill study population and the occasional marmot at Picnic or Sunrise Basin, the nearest occupied habitat patch to Hurricane Hill was >3.5 km away at Klahhane Ridge. The Central site group (Fig. 1) was >10 km southeast of the Western group and included 5 study sites, occupied by 1–4 family groups each, located along or near the Obstruction Point Road. The maximum straight-line distance between any 2 Central sites was 3.9 km, and no site was >1.2 km from at least 1 other. There are additional marmot groups in the area, which we visited occasionally. The final study site was a large meadow in Royal Basin, >15 km to the southeast of the nearest Central group site. The study meadow in Royal Basin was almost completely surrounded by additional, although more sparsely occupied, habitat. For additional details see Griffin et al. (2008).

Radiotelemetry, home ranges, and dispersal.—In 2003–2008, we recorded the dispersal behavior of Olympic marmots that were ≥ 2 years old and carried a working radiotransmitter at the beginning of a given active season. From 2002 to 2007, 106 marmots ≥ 1 year of age had 40-g radiotransmitters (IMP-300; Telonics, Inc., Mesa, Arizona) surgically implanted in the peritoneal cavity by a licensed and experienced veterinarian following published trapping and surgical methods (Bryant and Page 2005; Griffin 2007; Griffin et al. 2008; Van Vuren 1989). The transmitters had an expected battery life of

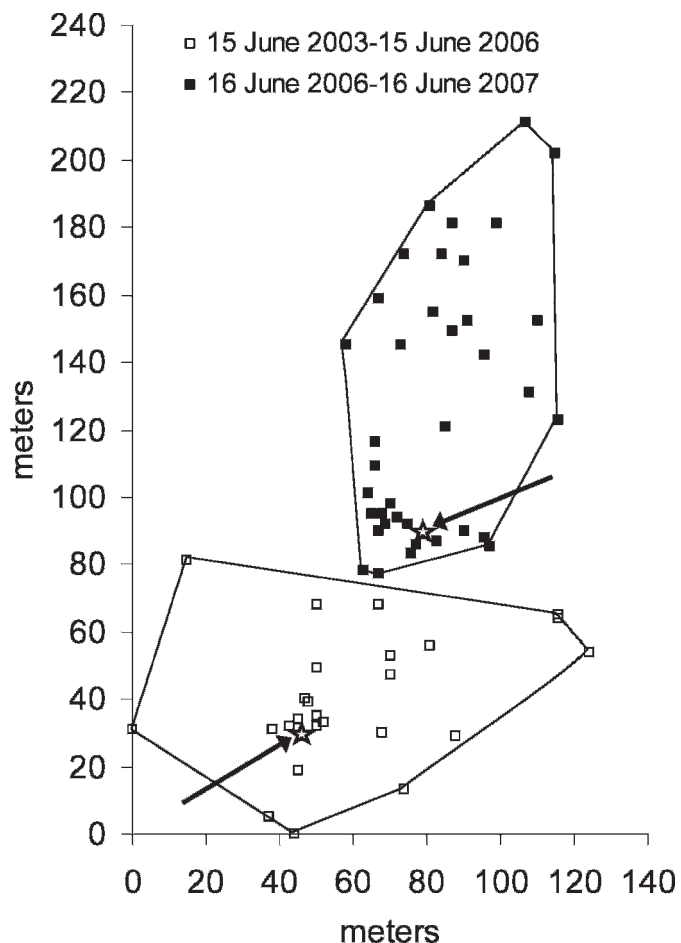


FIG. 3.—Example of location data used to identify short-distance dispersal by radiotagged Olympic marmots (*Marmota olympus*). For the individual whose locations are shown here (a 5-year-old female at Royal Basin), open squares represent the 29 locations recorded from 15 June 2003 to 15 June 2006 and the filled squares represent the 40 locations recorded from 16 July 2006 to 16 July 2007. Some locations may not be discernable because the marmots were often found repeatedly in the same burrow. The location of the 2006 and 2007 hibernacula are shown by hollow stars pointed to by the lower and upper arrows, respectively. Distances in meters demonstrate the scale of the marmot's movements along the north-south axis and east-west axis.

approximately 3 years, although in practice they often worked up to 4 years. With 3 exceptions, we did not implant juveniles (i.e., young-of-year) because there was no expectation that they would disperse as yearlings. The 3 juveniles that were implanted received a smaller transmitter (IMP-200; Telonics, Inc.). We replaced 17 transmitters before they failed and 6 after failure. Intraperitoneal transmitters have been widely used in studies of marmots with no detectable reduction in survival or reproduction (Bryant and Page 2005; Van Vuren 1989). All marmots at the study sites were ear-tagged and monitored beginning in 2002 (Western and 3 Central sites) or 2003 (Royal Basin and 2 Central sites—Griffin et al. 2008). Juveniles and spring yearlings (i.e., until approximately 1 July) are easily identified by their size and color (Karels et al. 2004). Marmots that were not initially trapped as juveniles or

yearlings were assigned to age classes (1, 2, or ≥ 3 years) using an algorithm based on mass, zygomatic arch width, and the Julian date on which they were measured. All trapping and handling procedures were approved by the University of Montana's Animal Care and Use Committee and followed the guidelines of the American Society of Mammalogists (Gannon et al. 2007).

Radiotagged marmots were located from the ground throughout the active season (approximately 1 May–1 September). We initiated regular tracking immediately after transmitter implantation to monitor survival and to inform us of the home-range location. We walked to the target marmot and recorded its location when 1st seen or the location of the burrow entrance if the animal was below ground, using a handheld global positioning system unit accurate to ≤ 10 m. In the event that we could not locate an animal in its usual home range, we increased telemetry effort (i.e., listening from multiple mountain peaks and ridgelines in and around all study areas) and we increased visual observation of the area to increase the probability that we would detect it if the radio had failed. Either one of us (PCG) or a park employee also searched from the air for missing animals at least once per year. However, the aerial searching was not particularly effective; only 1 missing marmot was found from the air and we were notified of its whereabouts by a ranger a few days later.

Marmots were considered available for the dispersal study only in years in which they were present with working radiotransmitters immediately posthibernation. Consequently, a marmot was not included in the analysis of dispersal behavior until the spring of the year after the implantation of its 1st radiotransmitter. Inclusion of animals in the summer in which they received implants could have biased the results by disproportionately sampling those marmots that failed to disperse or dispersed later in the season. After a dispersing animal appeared to have settled in a new home range, we continued to monitor it periodically until it died, until the apparent failure of its radiotransmitter, or through the end of data collection in late fall 2008. However, animals that dispersed off the study sites were not included in analysis of dispersal rates in subsequent years.

We considered a marmot to have dispersed when it made a 1-way movement away from its established predispersal minimum convex polygon home range, resulting in either the establishment of a new, nonoverlapping home range or death during a sustained period of movement (>7 days) away from the initial home range (Van Vuren and Armitage 1991). Under this definition, it was possible for a marmot to establish a new range adjacent to its original range (Fig. 3). Some authors have required the animal to move 1 or more nominal home-range radii between trapping events or between the initial trapping event and subsequent radiotelemetry-based locations (Gillis and Krebs 1999; Sandell et al. 1991), but the size of Olympic marmot home ranges can vary by an order of magnitude, making such an arbitrary definition difficult to apply. Although we relied primarily on the radiotracking data

to determine whether an animal had dispersed under our definition, for each animal we also examined plots that included all locations where the animal was trapped or resighted to confirm the assessment. Dispersal distances were determined based on the distance between the pre- and postdispersal hibernacula. When 1 or more hibernacula were unknown because a dispersing marmot died before hibernation ($n = 2$), the radio apparently failed ($n = 2$), or the predispersal hibernaculum was unknown ($n = 1$), we substituted the distance between the predispersal hibernaculum and the death location, the predispersal hibernaculum and the last known location, or initial trap location and postdispersal hibernaculum, respectively.

Statistical analyses.—We used the radiotelemetry data to estimate dispersal rates for 2 data sets: all marmots that were present at the beginning of a year (i.e., immediately posthibernation), and for the subset of marmots that were known to have never dispersed before the year in question. A marmot was assumed to be on its natal home range if it was 1st tagged as a juvenile or yearling and the home range it occupied when it entered the study included the location where it was initially captured. In either data set, marmots could be included in different age classes in different years and in the oldest age class in multiple years.

From each data set, we estimated rates in 2 ways for each of 6 age and sex classes (2-year-old females, 3-year-old females, ≥ 4 -year-old females, 2-year-old males, 3-year-old males, and ≥ 4 -year-old males). The 1st method we used was to compute a simple binomial proportion of animals present in the spring that subsequently dispersed. Although this simple proportion does not account for early season deaths of animals that would otherwise have dispersed, it does provide an estimate of how many dispersers might be expected from a population of known spring abundance, given current mortality rates. However, if mortality rates during the period of interest are high, the simple proportion of dispersers may underestimate the underlying propensity for dispersal because animals are not available to disperse if they are killed before they have an opportunity to do so. During the years of this study, some age and sex classes of Olympic marmots experienced high active-season mortality (Griffin et al. 2008). Therefore, we also computed dispersal rates using the Kaplan–Meier approach (Pollock et al. 1989a, 1989b) in which the sample size for each sampling period (i.e., 0.5-month interval—Griffin et al. 2007, 2008) is adjusted by right-censoring dead animals and those whose radiotransmitters failed.

RESULTS

Radiotransmitters were implanted in 107 nonjuvenile marmots (46 yearlings, fifteen 2-year-olds, and 46 ≥ 3 -year-olds). Although we were unable to distinguish 3-year-olds from older animals at 1st capture, when marmots entered the dispersal study after their 1st postimplant hibernation almost all could be placed into the age classes of 2-year-olds, 3-year-olds, and ≥ 4 -year-olds. Thus, the age class of most marmots

included in the dispersal study was known with certainty: all 2- and 3-year-olds were initially tagged as juveniles or spring yearlings and most of the older animals had been observed for enough years that they were unequivocally ≥ 4 years old. It is possible that 1 or more of 4 marmots were initially misclassified as 3-year-olds when they were actually large 2-year-olds; if so, these animals would have been incorrectly placed in the ≥ 4 -year-old class for 1 year. Somewhat more females than males were sampled, particularly among the younger animals. This reflects a skewed sex ratio at birth (initially reported for Central sites in Griffin et al. [2008] and observed through 2007).

Of the 107 implanted marmots, 17 animals died and 1 radiotransmitter failed during the year of implant. An additional 4 marmots died and 1 disappeared before we could gather sufficient data to evaluate their movements the following year. Of the remaining 84 marmots included in the study for 1 or more years ($\bar{X} = 2.4$ years, $SD = 1.3$ years, maximum = 6 years), 50 were known to have not previously dispersed, 8 were known to have previously dispersed, and the dispersal history of the remaining 26 was unknown. Over the course of the resulting 202 marmot-radio years, 10 transmitters failed and 32 marmots were killed or believed to have been killed (Griffin et al. 2008). We monitored a majority of marmots in all age and sex classes known to be present on the study sites during the years of the study (Table 1). We located each marmot an average of 61 ($SD = 34$) times during the course of the study (excluding locations during hibernation); on additional occasions, we confirmed that the marmot was in its usual area without actually recording the location. Radiolocation effort varied among years but was higher in later years when more marmots carried radios. Effort was lowest in 2003, when the 9 marmots that survived the active season were located an average of 9.6 times or about 2 times per month. Effort peaked in 2006, when the 31 season-long survivors were each located an average of 38 times or about 2 times per week.

Dispersal rates.—A total of 27 radiotracked marmots dispersed during the course of the study. In each analysis, a greater proportion of males than females dispersed at all ages (Table 2), and rates were highest among 3-year-olds followed by 2-year-olds. All 2- and 3-year-olds that dispersed did so before 1st reproduction, as did the 2 older females. However, at least 3 (possibly 4) of the 5 males ≥ 4 years old moved after reproducing ≥ 1 years, with the dispersal typically following the death of their mate. Four of these 5 dispersing older males were ≥ 3 years old when 1st tagged, so we do not know if they had previously dispersed as 2- or 3-year-olds. In addition to the radiotagged marmots, we detected dispersal of 8 ear-tagged marmots (1 juvenile, one 2-year-old female, three 2-year-old males, and three 3-year-old males). Although yearlings were not specifically included in the study, we did not observe dispersal of any ear-tagged or radioimplanted yearling. A single tagged juvenile (out of $n = 140$ tagged) dispersed to another basin, where he remained for the duration of the study, hibernating 485 m from his parents' hibernac-

TABLE 1.—The total of Olympic marmots (*Marmota olympus*) of each age and sex class present at each site group and at all site groups combined during the years when dispersal of radiotagged marmots were studied (available), the number of marmot-radio years used in analyses that considered all marmots without regard to previous dispersal history (radiotagged (total)), and the number of marmot-radio years used in analyses that considered only marmots that were known to have never previously dispersed (radiotagged (never dispersed)). Numbers represent marmot-radio years; some individuals were monitored in multiple age classes or in the oldest age class in multiple years.

	2-year-olds		3-year-olds		≥4-year-olds	
	Male	Female	Male	Female	Male	Female
Western sites	12	11	4	11	24	35
Available						
Radiotagged (total)	7	7	2	7	14	18
Radiotagged (never dispersed)	6	7	1	6	0	3
Central sites						
Available	8	22	10	20	43	46
Radiotagged (total)	6	14	8	17	25	24
Radiotagged (never dispersed)	6	14	8	15	3	10
Royal Basin						
Available	7	5	6	5	22	37
Radiotagged (total)	4	2	3	3	15	26
Radiotagged (never dispersed)	4	2	3	3	4	5
All sites						
Available	27	38	20	36	89	118
Radiotagged (total)	17	23	13	27	54	68
Radiotagged (never dispersed)	16	23	12	24	7	18

ulum. Dispersal for all age and sex classes was concentrated in June and July, with 3 animals moving in May, 11 moving in June, 10 moving in July, and 3 moving in August.

As expected, most estimates of dispersal rates derived from the Kaplan–Meier approach were higher than the simple proportion of animals present in the spring that subsequently dispersed (Table 2). The sole exception to this pattern was 2-year-old females—the 1 death in this age and sex class occurred in late August, after dispersal generally would have occurred. Also, dispersal rates of 3-year-olds increased when we considered only animals that were known to have never dispersed (Table 2).

Dispersal distances.—The distribution of dispersal distances was right-skewed, especially for females. Thirty-six percent of males and 69% of females moved <500 m and only 2 females moved >1,500 m (Fig. 4). Although patch boundaries were not always easily delineated (e.g., at Royal Basin), with only 2 or 3 exceptions, marmots dispersing <500 m remained within

their starting habitat patch. Males moved farther than females, and younger animals moved farther than older animals (Fig. 4). Beyond 500 m, the distribution of distances appeared to be very flat, a pattern also noted in yellow-bellied marmots (Van Vuren 1990). The median distance traveled by 2- and 3-year-old males was 1,800 m ($n = 9$), whereas for comparably aged females, the median distance was only 305 m ($n = 11$). Among older animals, males also tended to move farther than females, although the distances traveled were generally shorter than for younger animals. Median distance for males >3 years old was 444 m ($n = 5$) and the 2 older females moved just 50 m and 115 m. Seven (54%) of the 13 dispersing females and 3 (17%) of the 14 dispersing males settled in home ranges adjacent or nearly adjacent to their original home range and within a contiguous habitat patch. The 2 marmots that dispersed and died before hibernating were both young males and each had already moved >4,000 m. Thus, although they might have moved farther if they survived, the additional

TABLE 2.—Dispersal rates of radiotagged Olympic marmots (*Marmota olympus*) by sex and age class, with standard errors shown in parentheses. Shown are rates for all radiotagged marmots, and the subset that was known to have not previously dispersed. For each data set, rates were computed as a simple proportion of marmots present in the spring that dispersed in a given year, and with the Kaplan–Meier method.

	2-year-olds		3-year-olds		≥4-year-olds	
	Male	Female	Male	Female	Male	Female
All marmots	$n = 17$	$n = 23$	$n = 14$	$n = 27$	$n = 53$	$n = 68$
Proportion	0.18 (0.10)	0.17 (0.08)	0.43 (0.14)	0.26 (0.09)	0.09 (0.04)	0.03 (0.02)
Kaplan–Meier	0.20 (0.10)	0.17 (0.08)	0.49 (0.14)	0.30 (0.10)	0.10 (0.04)	0.03 (0.02)
Nondispersers	$n = 16$	$n = 23$	$n = 12$	$n = 24$	$n = 12$	$n = 18$
Proportion	0.16 (0.10)	0.17 (0.08)	0.50 (0.15)	0.29 (0.09)	0.17 (0.08)	0 (0)
Kaplan–Meier	0.22 (0.11)	0.17 (0.08)	0.57 (0.15)	0.33 (0.10)	0.20 (0.18)	0 (0)

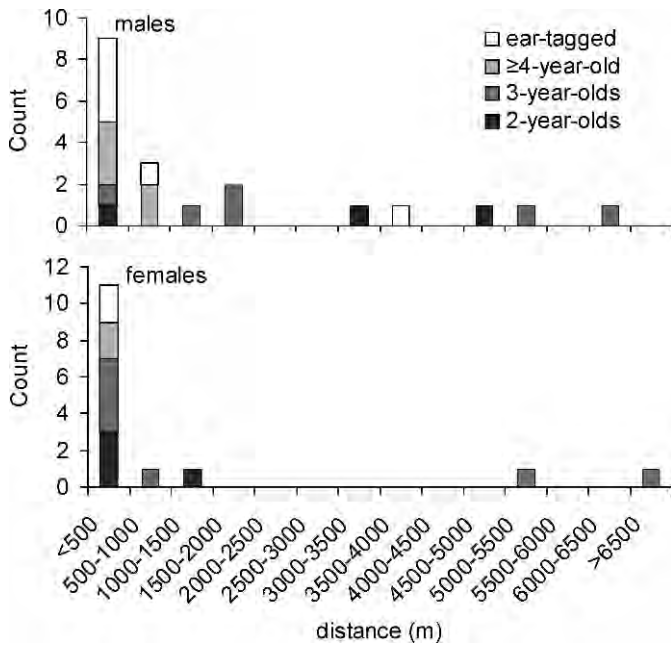


FIG. 4.—Dispersal distances of male and female Olympic marmots (*Marmota olympus*). Solid fill indicates data from radiotagged 2-year-old (black), 3-year-old (dark gray), and ≥ 4 -year-old (light gray) individuals. White fill represents opportunistic observations of 8 ear-tagged marmots.

distance would not have affected the median distance traveled by young males, nor any of the conclusions that follow. The distances moved by the 8 ear-tagged marmots were generally similar to those moved by the radiotagged marmots (Fig. 4). The longest movement (16.3 km) was made by a 3-year-old female.

Direction and terrain covered.—Although marmots were not continuously tracked during dispersal, in general they appeared to follow ridgelines or other topographic features that maximized their chances of encountering suitable habitat and other marmots. Only 1 of the 27 dispersers was known to have abandoned the ridgelines, although the starting and ending locations of 3 others suggest that they might have as well. Only 2 dispersing animals were detected below 1,400 m and only 1 of these below 1,000 m. Although marmots remained in or near open habitat, they did not restrict their movements to occupied or even suitable habitat. One animal crossed >30 m of fast-moving water on her way to spending 2 months on an island in Lake Mills at <200 m elevation. Although marmots were rarely >100 m from open habitat, 3 dispersing animals were found in thick stands of small-diameter conifers and in rock outcrops in the forest. As has been reported for other sciurids (Holekamp 1986; Van Vuren 1990), dispersing Olympic marmots were found in previously occupied marmot habitat, which they occupied briefly before moving on. In fact, 2 animals were found in the same abandoned burrow in different years. Each subsequently left the area.

Two animals that did not encounter other marmots continued to travel in the spring after hibernation. One, a

female aged 3 years at time of dispersal, wintered at low elevation and subsequently moved to the Elwha Ranger Station, where she took up residence beneath a storage building for several weeks. She was eventually captured and translocated to occupied habitat at the request of park staff. This marmot traveled >22 km over the 2 summers. A 2nd marmot, a male aged 2 years at time of dispersal, wintered at the unoccupied Picnic site, and subsequently moved to the complex of meadows around the Hurricane Ridge Visitor Center. In Sunrise Basin, he encountered an untagged disperser, possibly from the Klahhane Ridge area. We are confident that this animal was not in Sunrise Basin before this time because within 48 h of the arrival of the radiotagged marmot, we began receiving reports from rangers and visitors. In the previous several years, we had never received such a report. The radiotagged male and the untagged marmot were seen together repeatedly through the summer.

Survival and reproductive success of dispersers.—Because of the limited number of radiotagged dispersers, information on survival and reproduction should be considered preliminary. Survival of dispersers during the 1st summer appeared to be high. Of the 27 radiotagged dispersers, 23 entered hibernation, 2 were killed before establishing a new home range, 1 transmitter was believed to have failed, and we lost the signal of 1 marmot. This last animal was in a very remote area and may still be alive, although we could not detect him from an airplane. Thus, $\geq 85\%$ of dispersers entered hibernation in the year of dispersal. Of the 1st-year survivors, 80% (12 of 15) survived to a 2nd hibernation.

Eight males and 8 females survived long enough that they could have bred the year after dispersal. Three of the females did breed that year, 4 did not produce litters, and the reproductive status of 1 was unknown. For males, these numbers were identical, although reproductive success was determined by observing females in the new home range. Two females, each of which moved <150 m, produced their 1st litters at age 6 in the year after their dispersal. All dispersers known or believed to be reproductively successful moved <500 m.

Immigration.—During the course of the study, few untagged marmots immigrated onto the study sites. The marmot that arrived in Sunrise Basin in 2008 was the only untagged immigrant at any Western site. Two untagged marmots appearing in 2008 were the only untagged animals to appear at a Central site. From 2003 to 2008, a total of 6 immigrants were recorded at Royal Basin. Unlike the Western and Central sites, there are untagged family groups adjacent to the Royal Basin study population, so these last immigrants could have arrived from as little as 100 m away.

DISCUSSION

We observed dispersal, a key component of population dynamics, in radiotagged Olympic marmots of all age and sex classes that we monitored. We found that although some marmots dispersed as 2-year-olds, most movements were

undertaken by 3-year-olds. Of marmots known to be still on their natal home range in the spring of a given year, 16% of 2-year-old males, 50% of 3-year-old males, 17% of 2-year-old females, and 29% of 3-year-old females subsequently dispersed. Unexpectedly, a small proportion of marmots ≥ 4 years old moved, in some cases after successful reproduction. However, most male and all female Olympic marmots that dispersed did so before their 1st reproduction. Dispersal distances were longer for males (median = 984 m, $n = 14$) than females (median = 267 m, $n = 13$), although most dispersers (36% of males [5 of 14], and 69% of females [9 of 13]) settled within 500 m of their original home range. The few marmots known to have survived and reproduced the year after the dispersal event all moved < 500 m. The underlying probability of dispersal in the absence of predation, as estimated with the Kaplan–Meier approach, was somewhat higher than the raw proportion of animals that dispersed (Fig. 4), but the differences appeared to be of little biological significance because mortality of the most-dispersive age classes was relatively low.

Our results are in concordance with previous observations on this and other species of marmots, suggesting that the patterns observed were generally representative of Olympic marmots despite the small sample sizes in some age and sex classes. Dispersal in yellow-bellied marmots (Armitage 1991) and, anecdotally, in Vancouver Island marmots (Bryant 1998; A. A. Bryant, pers. comm.) occurs primarily in the year before, or the year of, attainment of reproductive maturity. No Olympic marmot is known to have bred before age 3 years, and from data collected for the study by Griffin et al. (2008), we computed the average age of 1st reproduction of Olympic marmots to be at least 4.2 years ($SD = 1.37$ years, $n = 14$). The near absence of dispersal in Olympic marmots before age 2 years and the relatively high rates of movement at 3 years of age highlights the “slower” life history of the species relative to yellow-bellied marmots, which typically disperse as yearlings (Armitage 1991). Similarly, dispersal in all 3 species tends to be male-biased and males are more likely than females to undertake long-distance movements (Armitage 1991; Bryant 1998; Van Vuren 1990). From the observed dispersal rates of 2- and 3-year-old marmots that had not previously dispersed (Table 2), computed with the Kaplan–Meier method, we calculated that 66% of males and 45% of females will disperse as 2- or 3-year-olds if they survive long enough to do so. These rates are somewhat higher than those reported by Barash (1973), but because he was working without radiotransmitters, it is possible that mistook dispersal of 3-year-olds for mortality, that his threshold distance for identifying dispersal was higher, or that dispersal patterns differ according to current ecological conditions. Available evidence indicates that dispersal rates of Vancouver Island marmots are similar to those of Olympic marmots (Bryant 1998; A. A. Bryant, pers. comm.), although reported dispersal events among Vancouver Island marmots did not include the short-distance movements that were common among Olympic marmots. Almost all male

and $> 50\%$ of female yellow-bellied marmots disperse (Armitage 1991).

Olympic marmots undertook very-long-distance movements less often than either Vancouver Island marmots (Bryant 1998; A. A. Bryant, pers. comm.) or yellow-bellied marmots (Van Vuren 1990). However, most of the short-distance dispersal movements by Olympic marmots were made into home ranges that had recently become vacant or habitat patches where marmot density had recently declined. At least some of these animals might have moved farther if nearby habitat had been saturated or otherwise unavailable, although dispersal rates in rodents often decline when habitats are saturated (Nunes 2007). Because Olympic marmot populations were generally well below saturation during our study, we were not able to test for effects of density on dispersal rates or distances. Barash (1973), working at a time of much higher marmot densities, did report slightly lower natal dispersal rates than we detected, but as discussed above, this may have been the result of different methods and assumptions. Also, without radiotransmitters, he could not determine dispersal distances. Studies of genetic similarity among disjunct marmot groups might help clarify whether connectivity was higher in the past when densities were greater, as appears to be the case for Vancouver Island marmots (Kruckenhauser et al. 2008).

In recent years, high mortality of adult females has reduced the Olympic marmot population (Griffin et al. 2008) to a level where natural dispersal may be too low to ensure the functioning of the metapopulation. When Olympic marmot densities and distribution are at moderate to high levels, the dispersal rates and distances we observed should be sufficient to assure regular movement among occupied habitat patches and recolonization of the occasional vacant patch. Young males often move several kilometers, and the apparent propensity of marmots to locate occupied or previously occupied habitat suggests that a regular genetic connection would be maintained among even the most isolated colonies. When most habitat was occupied, the shorter movements made by young females would have facilitated recolonization of the occasional vacant patch. However, if the observed dispersal patterns are representative of range-wide patterns and if marmot densities remain low, successful dispersal may be too infrequent to allow reliable recolonization of vacant habitats or even genetic or demographic rescue of the most isolated marmot groups. As an example, as recently as 1989, all habitat patches in the Western Network group (Fig. 1) were occupied (Houston and Schreiner 1994), but by 2003 all except Hurricane Hill and Picnic, where a single female persisted, were vacant (Griffin et al. 2008). Hurricane Hill, with about 20 marmots, and Klahhane Ridge, with < 10 marmots, were the only potential sources of colonists for the vacant sites in the group (Griffin et al. 2008). Given recent demographic rates, abundances (Griffin et al. 2008), and observed dispersal patterns, approximately 0.9 female and 1.2 male marmots were expected to disperse from their current home ranges on Hurricane Hill each year. With 69% of

females and 36% of males settling within 500 m of their original home range, we can expect <0.3 female marmots and <0.8 male marmots to disperse away from Hurricane Hill in a given year. Thus, the chances of recolonization at the extinct sites seem quite small. Consistent with this, there has only been a single known instance of 2 marmots arriving simultaneously at a vacant site in 7 years. The situation is likely to be similar for many other portions of the Olympic marmot's range, particularly in the southeast where declines have been severe (Griffin et al. 2008).

The recovery and long-term persistence of Olympic marmots will require that the proximate cause of the decline, the high mortality rate of adult females (Griffin et al. 2008), be arrested. If this can be accomplished, the resulting increase in local densities should lead to a greater number of dispersers, increased recolonization and rescue, and, eventually, reduced intercolony distances. However, reducing mortality may take a number of years, if it can be accomplished, and in the meantime additional isolated populations may go extinct because of stochastic genetic and demographic processes. Therefore, we propose that concurrent with addressing the mortality issue, management consider translocations of marmots. Specifically, such actions could be targeted at reestablishing or supplementing strategically located patches (e.g., to restore connectivity within networks) and at maintaining gene flow to currently isolated populations. The potential benefits of such actions should be evaluated on a case-by-case basis, considering the distribution of habitat and the density of marmots within a several-kilometer radius. Finally, a warmer climate and increased CO₂ levels may increase tree encroachment into the subalpine meadows. The effects of this encroachment could include increased fragmentation of marmot habitat. Consequently, the ability of marmots to successfully disperse through the changing landscape should be reexamined periodically. Strategic translocations could be a useful tool to mitigate such effects, along with habitat maintenance measures such as controlled burns that reduce tree encroachment into marmot habitat.

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