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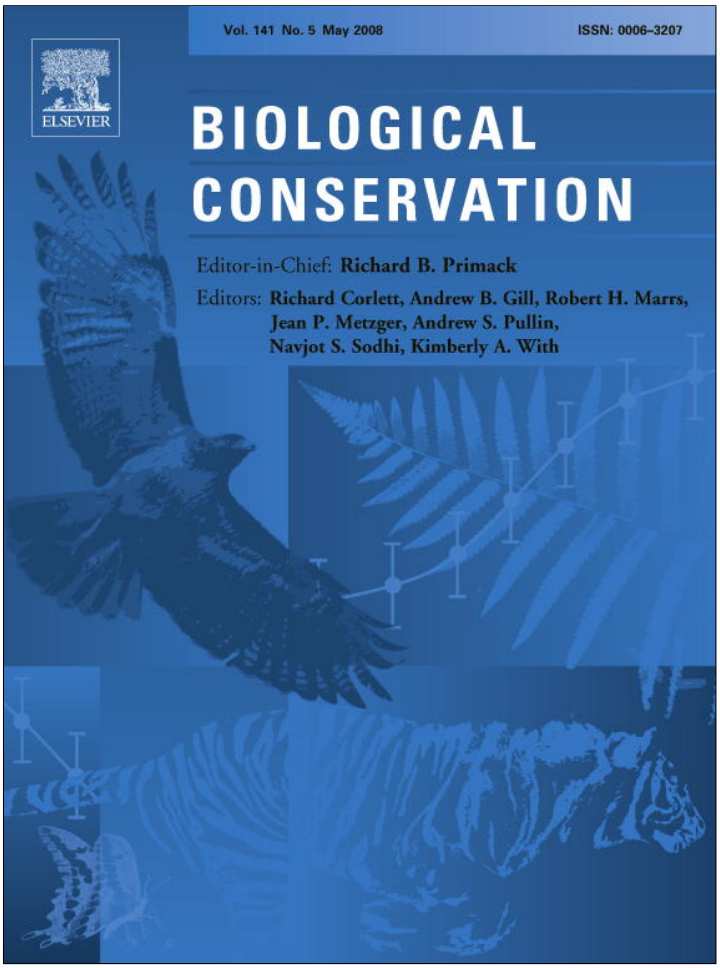

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The case of the missing marmots: Are metapopulation dynamics or range-wide declines responsible?

Suzanne C. Griffin[a,b,*], *Mark L. Taper*[b], *Roger Hoffman*[c], *L. Scott Mills*[a]

[a]*Wildlife Biology Program, Department of Ecosystem Conservation, College of Forestry and Conservation, University of Montana, Missoula, MT 59812-0004, USA*
[b]*Department of Ecology, Lewis Hall, Montana State University, Bozeman, MT 59717-5065, USA*
[c]*Olympic National Park, Division of Natural Resources, 600 Park Avenue, Port Angeles, WA 99362, USA*

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ABSTRACT

In the mid-1990s, anecdotal reports of Olympic marmot (*Marmota olympus*) disappearances from historically occupied locations suggested that the species might be declining. Concern was heightened by the precipitous decline of the Vancouver Island marmot (*Marmota vancouverensis*), coupled with reports that climate change was affecting other high-elevation species. However, it was unclear whether the Olympic marmot was declining or undergoing natural extinctions and recolonizations; distinguishing between normal metapopulation processes and population declines in naturally fragmented species can be difficult. From 2002–2006, we used multiple approaches to evaluate the population status of the Olympic marmot. We surveyed sites for which there were records indicating regular occupancy in the later half of the 20th century and we conducted range-wide surveys of open high-elevation habitat to establish current and recent distribution. We used these targeted and general habitat surveys to identify locations and regions that have undergone extinctions or colonizations in the past 1–4 decades. Simultaneously, we conducted detailed demographic studies, using marked and radio-tagged marmots, to estimate the observed and projected current population growth rate at nine locations. The habitat surveys indicate that local extinctions have been wide-spread, while no recolonizations were detected. Abundance at most intensive study sites declined from 2002–2006 and the demographic data indicate that these local declines are ongoing. Adult female survival in particular is considerably lower than it was historically. The spatial pattern of the extinctions is inconsistent with observed metapopulation dynamics in other marmot species and, together with very low observed dispersal rates, indicates that population is not at equilibrium.

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1. Introduction

The Olympic marmot (*Marmota olympus*) is a large ground-dwelling squirrel endemic to the Olympic Peninsula, in northwest Washington State, USA. Most Olympic marmot habitat (>90%) is protected within Olympic National Park. In the mid-1990s park staff observed that the Olympic marmot had disappeared from several well-known colonies, such as those in the

* *Corresponding author:* Address: Wildlife Biology Program, Department of Ecosystem Conservation, College of Forestry and Conservation, University of Montana, Missoula, MT 59812-0004, USA. Tel.: +1 360 457 6067.
E-mail addresses: olympicmarmots@aol.com (S.C. Griffin), markltaper@msn.com (M.L. Taper), roger_hoffman@nps.gov (R. Hoffman), scott.mills@cfc.umt.edu (L.S. Mills).
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meadows surrounding the popular Hurricane Ridge Visitors' Center. These observations, combined with anecdotal reports from visitors that marmots were absent from some less prominent locations and the dramatic, highly publicized declines of the Vancouver Island marmot (*M. vancouverensis*; Bryant and Janz, 1996), raised concern about the Olympic marmot. Reports that climate change has affected other high-elevation species, including the yellow-bellied marmot (*Marmota flaviventris*) (Inouye et al., 2000), added to the concern. However, Olympic marmot habitat is naturally fragmented and it remained possible that the extinctions were part of natural metapopulation process. In 1999, park biologists identified investigation of the Olympic marmot population as a priority project in their Resource Management Plan.

Logical first steps in any conservation effort are to determine if the species in question is actually declining, and if so, throughout what portion of its range. Due to data limitations, many species status evaluations are based on either apparent changes in occupancy patterns, or analyses of local population trends or demography. While considerable insight can be gained from these approaches, single metrics of status can be open to the criticism that the apparent declines are idiosyncratic to the particular study sites or that normal population processes, such as extinction and colonization within a metapopulation (Hanski, 1998), are responsible for perceived declines. Alternatively, declines might be missed or their detection delayed if the monitored metric is not sensitive to overall population performance (Taper et al., 2008). For example, occupancy rates may remain stable for several generations after a population decrease (Conrad et al., 2001). By evaluating multiple lines of evidence, it may be possible to arrive at a robust conclusion about a population's status when no one metric is irrefutable.

In this paper, we use several types of data collected at multiple spatial scales to evaluate the status of the Olympic marmot. Beginning in 2002, we collected these distribution and detailed demographic data as part of an unrelated study. We now use these data to allow us to consider four different lines of evidence for recent range-wide declines and for ongoing declines at a smaller number of sites. Specifically: we (1) resurveyed sites for which there was reliable evidence of long-term occupancy (>40 years) to determine if they were still occupied; (2) we surveyed habitat throughout the marmots' range to determine both recent and current distribution; (3) we examined 4–5 years abundance trends in three geographically discrete site groups; and (4) we used survival and reproductive data and female-based matrix models to determine if demographic rates are consistent with an ongoing decline at these sites. Our overall goal was to synthesize these four measures and, in doing so, to evaluate qualitatively the alternative hypotheses that the patterns we documented reflect real declines or that the patterns were manifestations of natural metapopulation processes. Where possible, we placed our results in the context of demographic and occupancy patterns in other marmot species.

2. Study area and study species

Olympic marmots are restricted to the upper slopes (>1400 m) of the Olympic Mountains, on the Olympic Peninsula in northwest Washington State (Fig. 1). Small groups of 3–20 marmots dig extensive burrow systems in alpine and subalpine meadows. These meadows range in size from <5 ha to >100 ha and are embedded in a matrix of forest, rock and snow. Like the closely-related hoary (*M. caligata*) and Vancouver Island marmots, Olympic marmots hibernate for 6–8 months a year, delay any dispersal until after the second hibernation, and only attain reproductive maturity at age 3 or 4 (Barash, 1973, 1974; Bryant, 1998, 2005; Bryant and McAdie, 2003). All three species typically breed biennially, but can occasionally breed annually (Bryant, 2005; Griffin et al., 2007a; Kyle et al., 2007). In any case all show unusually low-reproductive rates for a rodent.

Much of the Olympic Peninsula, including most of the higher elevations, is protected within Olympic National Park. Our study was restricted to park lands. There is a steep precipitation gradient from southwest to northeast across the peninsula: annual precipitation averages 600 cm of precipitation on *Mt. Olympus* while as little as 50 cm falls on the northeast corner. Eighty percent of this precipitation falls between October and March, mostly as snow above 750 m (Houston and Schreiner, 1994b). Even in the relatively dry northeast, snowpack lingers well into summer in the high-country. Several large rivers drain the central Olympic Mountains and have carved deep, steep-sided valleys that appear to act as barriers to marmot movement (S.C. Griffin et al., unpublished genetic data). The peninsula is surrounded by water on three sides and extensive lowland forest on the fourth – as a result, there are numerous endemic plant and animal species and subspecies on the peninsula, and the mammalian fauna in particular is impoverished relative to the mainland (Houston and Schreiner, 1994a).

3. Methods

3.1. *Surveys of historically recorded colonies*

As a first step in assessing Olympic marmot population status, we resurveyed historically recorded colonies. These sites were all in readily accessible areas of the northeast region of the park and have been periodically studied since the 1950s. Although marmot presence had been recorded in $\geqslant 1$ year at 31 colonies, we restricted our inference to the 25 sites that we were able to relocate confidently and where presence had been recorded $\geqslant 2$ times between 1950 and 1996 ($\bar{x} = 3.84$, SD = 1.86; Table 1). We were assisted in relocating colonies by J. Burger, who had conducted a presence–absence survey in 1989 (Houston and Schreiner, 1994a) and at that time had received guidance from two previous researchers (W. Wood and D. Barash).

In early 2002, we visited each of the 25 sites. Field workers typically watched sites for about 30 min from a good vantage point prior to 1100 h or after 1600 h, and then traversed the area on foot looking for active or abandoned burrows. Our extensive experience at occupied sites indicated that marmots are rarely below ground for >30 min during these hours. Burrows are always visible, often from >100 m, and regularly used burrows often have signs of occupancy, including evidence of recent excavation (fresh dirt and rocks in the entrance) or marmot scat in or near the mouth of the burrow.

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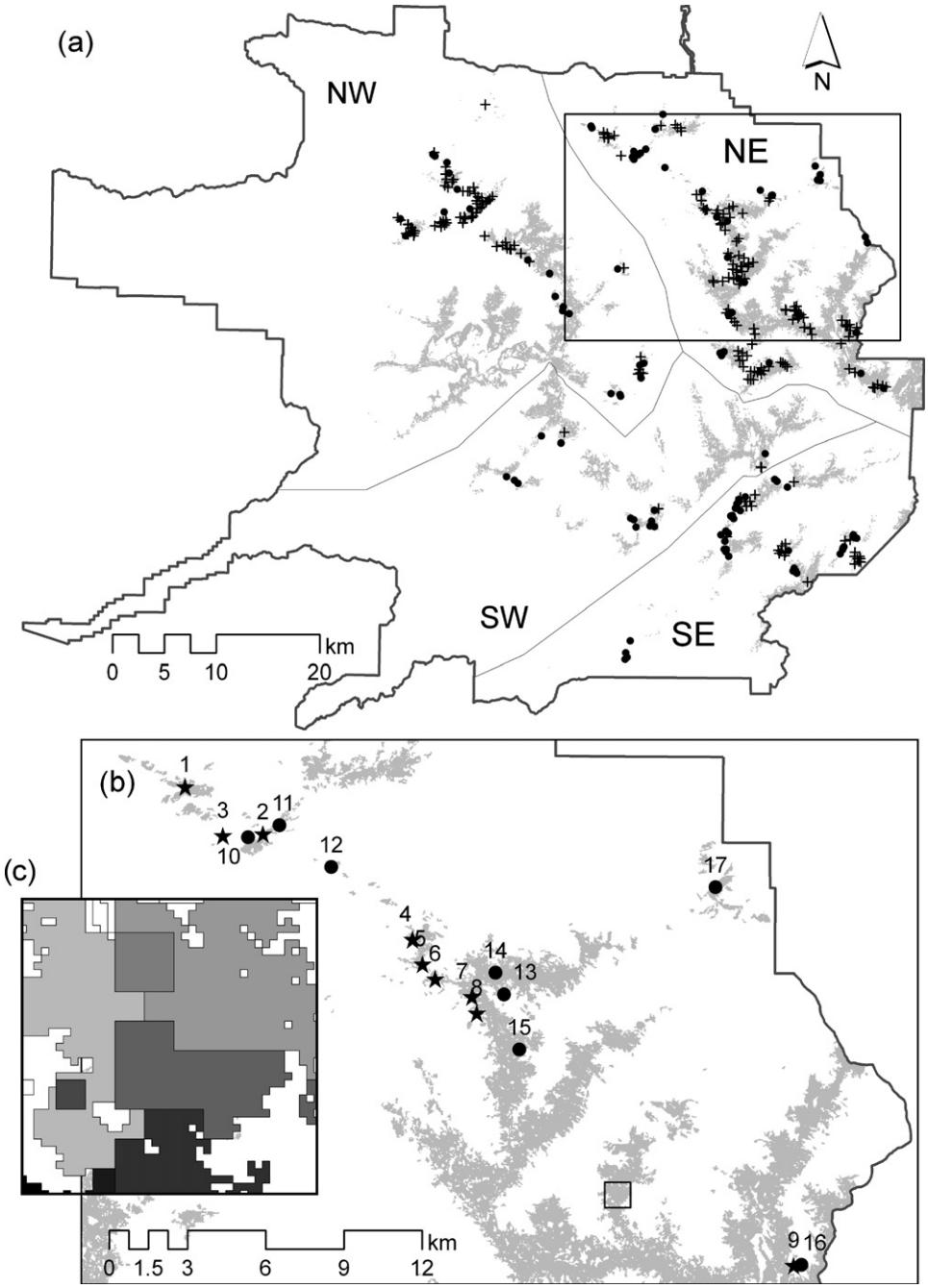

Fig. 1 – Locations where Olympic marmots (*Marmota olympus*) were studied within Olympic National Park in 2002–2006. (a) Locations of survey polygons marmots were detected (crosses) and those polygons that appeared to have been occupied by marmots in the recent past but were currently unoccupied (circles). Gray shading indicates those areas predicted to be suitable habitat. The four geographic regions delineated for stratification purposes are indicated by solid lines and labeled NW (northwest), etc. The inset, shown in detail in (b), encompasses the area where demographic studies were conducted (stars). The locations of historic colonies that were resurveyed but where demographic studies did not occur are indicated with circles. Labels correspond to site numbers presented in the text (Section 3.3. and Table 1). Inset (c) is an example of the polygons (each in a unique shade of gray) in a 1-km^2 area shown in (b). White represents areas that were not identified as potential habitat.

At occupied sites in the Hurricane Hill and Obstruction Point areas, we then initiated demographic studies (see below), negating the need for further presence–absence surveys. Sites where we did not find marmots were visited ⩾1 additional time in 2002, with additional visits in subsequent years through 2006. Many sites were also visible from roads that we regularly traveled (Table 1) – these sites were scanned for marmots at least weekly. Park ranger, education, and

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Table 1 – Occupancy data for 25 colonies of Olympic marmots (*Marmota olympus*) in Olympic National Park 1957–2006

No.	Colony	Access	1957[a]	1966[b]	1967[c]	1968[c]	1969[c]	1972[d]	1975[e]	1989[f]	1996[g]	2002[h]	2003[i]	2004[h]	2005[h]	2006[h]
Hurricane Ridge Visitors Center area																
2	Bartholomew (Sunrise Basin)	d, r		P	P	P	P			P		P	A	A	A	A
2	Widow (Sunrise Basin)	d, r			P	P	P	P		P	P	P	A	A	A	A
10	Meander	t			P	P	P			P		A	A	A	A	A
10	Marigold	t			P	P	P	P	P	P		A	A	A	A	A
11	Henderson	vc		P	P	P	P			P		A	A	A	A	A
11	Henderson Annex	vc			A	P	P			P		A	A	A	A	A
11	Lodge	vc		P	P	P	P			P		A	A	A	A	A
3	Picnic	d, t	P	P	P	P	P	P		P	P	P	P	P	P	P→A[†]
Hurricane Hill area																
1	Agean/Hurricane Hill Elwha	d, t				P	P					P	P	P	P	P
1	Cornus	d	P			P	P	P		P		P	P	P	P	P
1	Ridgely	d	P			P	P	P		P	P	P	P	P	P	P
1	Allee	d					P	P		P	P	A	A	A	A	A
1	Zenith	d, t					P				P	P	P	P	P	P
Obstruction Point road and vicinity																
4	Aureus (Eagle Point)	d, r	P	P	P	P	P	P		P		P	P	P	P	P
4	Aureus Annex	r			A	A	P			P		A	A	A	A	A
12	Steeple	r	P		P	P	A			P		A	A	A	A	A
13	Badger Valley	t	P					P		P		P	P	P	P	P
14	Elk Mountain	t						P		P		P	P	P	P	P
15	Swimming Hole		P					P				P	P	P		P
Royal Basin																
9	Royal Basin	d						P		P		P	P	P	P	P
16	Royal Basin East	t						P		P		P	P	P	P	P
Blue Mountain																
17	Large basin east of Blue Mountain summit	ol	P							P		A	A	A	A	A
17	Thistle	t	P	P	P	P				P		A	A	A	A	A
17	Rocky ridge south of east most switchback above campground	t	P							P		A	A	A	A	A
17	Slope north of rocky ridge and south of basin	t	P							P		A	A	A	A	A
	Blue Mountain – unspecified			1951[i], 1955[i], 1963[i], 1964[i], 1983[j]								A	A	A	A	A

'P' indicates that marmots were determined to be present in a given year, 'A' indicates that they were absent, and blanks indicate that no data are available. Number (No.) refers to locations are shown in Fig. 1. Sources are indicated in footnotes below the table. The codes in the access column refer to the location and study intensity of the site (d, demographic study site; vc, located adjacent to Hurricane Ridge Visitor Center and surrounding paved walking paths; t, adjacent to popular hiking trail; r, adjacent to road; ol, visible from popular overlook).

a Meagher (1957).
b Barash (1968).
c Barash (1973).
d Wood (1973).
e Watson (1976).
f Houston and Schreiner (1994a).
g Blumstein (personal communication).
h This study.
i Voucher specimens collected by M.L. Johnson, housed at the University of Puget Sound, Slater Museum, 1500 North Warner Street, Tacoma, WA 98416.
j J. Burger, Olympic National Park Education Division, personal communication.
† This colony became extinct during summer 2006.

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campground staff also visited most abandoned colonies weekly or even daily in the course of their usual activities and reported to us any unusual activity, marmot or otherwise. Given the high visibility of marmots and their burrows (Fig. 2), and the regular observation of these sites, we consider it almost impossible that marmots were present and not detected.

3.2. *Range-wide habitat surveys*

To determine the current and recent distribution of Olympic marmots, we systematically surveyed potential marmot habitat throughout the park. At the start of the study we had limited knowledge of the requirements of Olympic marmots, so we used very broad criteria to select potential habitat. Based on details from Barash (1973) and Wood (1973), and personal observations from 2001 (SCG) we assumed that marmots use high-elevation meadows with or without rock. Specifically, we used a Geographic Information System (GIS) to designated as potential habitat every 25 m × 25 m pixel of meadow, bare ground, or rock 1400–2157 m elevation. The upper elevation limit represents the upper limit of meadow, and thus food for the marmots, in the Olympic Mountains. We subdivided the resulting habitat patches by aspect – patches were split at 45°, 135°, 225°, and 315° – and eliminated any patch <9 pixels (0.56 ha; approximately the minimum Olympic marmot home range; Griffin, 2007). The resulting 3516 irregularly shaped polygons each encompassed 0.56–>200 ha. (median polygon area: 2.25 ha; 95% < 36 ha.) of contiguous, open, high-elevation habitat (Fig. 1). We used 1:24,000 topographic maps to subjectively classify the 3516 polygons as inaccessible ($n = 1845$), difficult to access ($n = 880$), and readily accessible ($n = 791$) based on distance to a trail, the steepness of the polygon, and the apparent ruggedness of the surrounding terrain. Polygons deemed inaccessible were removed from the selection process.

We stratified the remaining polygons according to slope (2 classes: <30%, ⩾30%), aspect (4 classes described above), area (3 classes: <25,000 m^2, 25,000–90,000 m^2, >90,000 m^2) and region (4 classes: Fig. 1). We used random numbers to select "primary" polygons for survey from each of these 96 slope-aspect-area-region combinations (hereafter, stratification cells); six readily accessible polygons were chosen for each difficult to access polygon. We selected four primary polygons per stratification cell in the northwest and northeast, three per cell in the southwest, and two per cell in the southeast, a ratio roughly proportional to the total number of polygons in each region. A few stratification cells contained fewer than the desired number of primary polygons, with the result that 302 primary polygons were selected for survey. Our assessment of access difficulty was not perfect; when a primary polygon proved inaccessible in the field, we substituted another by moving down the list of ordered random numbers.

In addition to the primary polygons, we also surveyed up to four "secondary" polygons in the vicinity of each primary polygon. Many primary polygons required multiple days of travel time to reach so these surveys of secondary polygons greatly increased our efficiency. In many cases, there were fewer than four secondary polygons available within a reasonable radius of the primary polygon ("reasonable" was terrain dependent but generally <1 km), or the density of primary polygons in an area was such that there were insufficient numbers of secondary polygons available. We also surveyed areas inside and outside the polygons where marmots or burrows had been reported in the past and additional polygons (including 46 classified as inaccessible) on an opportunistic basis. A few of these (collectively, "opportunistic") surveys took place in 2001 and 2006.

Selected polygons were visited on foot to determine occupancy status (occupied, abandoned, no sign). Field crew used maps and satellite images to visually identify the boundaries of the selected polygons and then walked rough transects across the polygon at approximately 20 m spacing, searching for marmots or burrows. Marmot burrows are often located beneath large rocks or are surrounded by large, diagnostic dirt mounds, which can be >1 m high and >3 m across (S.C. Griffin et al., unpublished data, Fig. 2). These mounds typically have a compacted, bare porch surrounded by dark green sedge (*Carex spectabilis*), making them visible from a considerable distance. The mountain beaver (*Aplodontia rufa*), which is abundant in the Olympic Mountains and makes slightly smaller diameter burrows, occupies wetter habitats than marmots do, leaves the excavated dirt in pyramid shaped piles, and typically digs numerous entrances in various stages of collapse which honeycomb small sections of hillside. Given even minimal experience, it is easy to accurately distinguish these two types of burrows.

Current occupation of marmot burrows was confirmed by the presence of: scat in the entrance; recent digging activity; characteristic flies or strong marmot odor in the entrance; marmot tracks, compacted and clipped grass on the mound; or trails of compressed vegetation between burrows. Abandoned marmot burrows could often be similarly diagnosed, although eventually the vegetation reverts to forbs, heather, or grass and the burrow entrances collapse. The rate of these changes appears to vary according to site conditions so precise dating of the last use is not possible; most abandoned burrows are probably undetectable after 7–15 years. When marmots were found, locations of representative marmots or burrows were usually taken with a handheld GPS unit (generally accurate to ±10 m) and the search of that polygon was terminated.

We conducted a χ^2 test for overall differences in the proportions of occupied, abandoned, and no sign polygons among the four regions. We followed this with pairwise tests for differences in the proportions of polygons that showed some sign of marmot activity (occupied and abandoned pooled) and those that showed no sign of marmot activity between each pair of regions, and pairwise tests for differences in the proportion of occupied and abandoned polygons between each pair of regions. We Bonferroni adjusted our alpha-level to $P = 0.004$ to control for Type 1 errors among these 12 pairwise tests (Sokal and Rohlf, 1995).

While we assumed that if marmots or active burrows were found, a polygon was unequivocally occupied, it is possible that we failed to detect marmots or abandoned burrows in some occupied or abandoned polygons. These errors, if common, could lead to an underestimate of currently occupied habitat and an overestimate of the severity of a decline (MacKenzie et al., 2006). Although Witczuk (2007) estimated a >90%

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Fig. 2 – Entrance mound outside a typical Olympic marmot burrow. These mounds are formed from excavated dirt and are either directly downslope from or surrounding the entrance hole. Large mounds can often be detected at a distance due the bright green sedge (*Carex spectabilis*) surrounding the compacted dirt porch.

detection rate for Olympic marmots, we independently investigated the potential effect of misclassification of occupied polygons in our data set. We had two independent observers visit 55 polygons in the same year, and then used adjusted Lincoln–Peterson models (Chapman, 1951) to estimate the single visit detection probability for an occupied polygon and the single visit detection probability for an abandoned polygon. We used these detection probabilities to explore how much we may have underestimated the proportion of occupied and abandoned polygons.

3.3. *Demographic study sites*

We used data from intensively-studied, marked animals at three geographically distinct groups of sites to estimate birth, death, and movement rates and population trends over 4–5 years. The Western site group consisted of (1) (numbers correspond to sites with stars in Fig. 1b) Hurricane Hill, where there was a cluster of several adjacent, often interacting colonies (elevation ~1600–1750 m; all aspects), (2) a single colony in Sunrise Basin (~1600 m, east-facing), and (3) a single colony "Picnic" at the Wolf Creek picnic area (~1520 m, south-facing). Earlier studies (Barash, 1973; Griffin et al., 2007b), including the historical colony inventories (Table 1), have considered individual family groups on Hurricane Hill and in Sunrise Basin; our demographic analyses would not have differed as a result of this subdivision and the fluidity of some family groups would have complicated study site definition, so we considered each of these contiguous areas as a single site. Hurricane Hill, Picnic, and Sunrise Basin were all within 3.3 km of each other in the vicinity of the Hurricane Ridge Visitors Center and all were studied beginning in spring 2002. With the exception of one or two marmots in a basin adjacent to Hurricane Hill, there are no other known marmot colonies <3.5 km of this group. Demographic data were available from earlier studies of these colonies (Barash, 1973; Wood, 1973).

The Central group was >10 km southeast of the Western group and consisted of five sites located along or near the Obstruction Point Road. These were (No. 4 in Fig. 1) Eagle Point (~1760 m, southwest-facing), (5) Pull-out (~1760 m, east-facing), (6) Marmot Flats (1750 m, northeast- to northwest-facing, relatively flat), (7) Obstruction Point (1830–1900 m, south- to west-facing), and (8) Pumpkin Seed Lake (1750–1820 m, west-facing basin). Eagle Point and Pull-out were occupied by single family groups, Pumpkin Seed Lake by 1–2 family groups depending on the year, and Obstruction Point and Marmot Flats were both occupied by several family groups in most years. The maximum straight-line distance between any two Central sites was 3.9 km, and no site was >1200 m from another. Studies began at these sites in late-spring 2002, with the exception of Pumpkin Seed Lake and Pull-out, which we first studied in summer 2003. There are other marmot colonies in the area, although we never detected any immigrants into our study colonies. These sites were chosen for study primarily out of convenience – they were the only currently occupied colonies near a road (although the road is closed until July due to snow).

The final study area was in Royal Basin (No. 9 in Fig. 1), >15 km to the southeast of the nearest Central group site and 13 km from the nearest (remote) trailhead. Marmots were found throughout this large basin but our study area was a steep, east-facing meadow (1630–1770 m) where marmot densities were particularly high. We began work here in 2003 after it became obvious that the Western and Central sites did not

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encompass the full range of Olympic marmot densities and habitat types.

3.4. *Trapping, marking, and implantation of radio-transmitters*

We attempted to eartag all marmots at the demographic sites, and we implanted a subset with radio-transmitters. We generally followed trapping and handling procedures outlined in Bryant (1996), with exceptions described in Griffin et al. (2007b). At initial capture, marmots were sexed, aged, and marked with uniquely numbered metal eartags, which usually could be read with binoculars. We also attached one or two 1 cm pieces of colored wire to each tag to facilitate recognition when the tags were dirty or turned, or when a marmot would not permit field crew to approach close enough to read the numbers. The park did not permit us to fur-dye the marmots.

We classified marmots as juvenile, 1 year-old, 2 year-old, or adult, indicating that they had completed 0, 1, 2, or ⩾3 hibernations, respectively. Field aging at first capture for non-juveniles was verified with an algorithm developed from morphometric data collected on known aged animals. We collectively refer to 1 and 2 years-old as subadults – these age-classes do not depend on parental care but are not yet reproductively active. The sex of non-juveniles was easily determined by the morphology of the genitals, particularly the ano-genital length. However, the sexes of several unsedated juveniles were later proven to have been incorrectly assigned so we relied on data from the sedated animals for sex-ratio at birth. Juveniles were sedated when the veterinarian was present or when the attending field personnel had been trained by the veterinarian to administer injections. There was no reason to suspect that the sedated animals were non-random with respect to sex.

We surgically implanted 40-g radio transmitters in the peritoneal cavity of 102 marmots ⩾1 year-old, following published surgical methods (Van Vuren, 1989; Bryant and Page, 2005). These transmitters have not been found to influence marmot survival or reproduction (Van Vuren, 1989; Bryant and Page, 2005, S.C. Griffin et al., unpublished data). The signal from transmitter of one marmot was never detected following surgery; we removed this animal from the data set, leaving 101 marmots. Eighteen marmots received second surgeries to replace aging or failed transmitters.

3.5. *Survival and reproduction*

We confirmed the status (alive or dead) of marmots with radio implants at least twice per month during the active season, except during September 2002 and May 2003, when status was checked only once per month. We found three transmitters beneath the snow outside burrows in May 2003 – these animals were presumed to have died prior to initiating hibernation in September 2002.

We used the known-fate module of program Mark (White and Burnham, 1999) to rank 23 potential logit-linked models in which survival was estimated in ten 0.5-month active season intervals (1 May – 1 October) and the winter period. The model with the smallest AIC_c value (adjusted Akaike information criterion) was used to derive annual survival rates for adult males, adult females, and subadults. In formulating the candidate model set (Table 2), we considered patterns observed in marmots and other species. Various models included parameters for possible effects on survival of: spatial autocorrelation in environmental conditions or predator abundance among site groups; effects of age and sex class (adult females, adult males, and subadults); and seasonal differences for one or more age/sex classes (Bryant and Page, 2005; Hoogland et al., 2006; Griffin et al., 2007b). Because a

Table 2 – Known-fate models compared in program MARK (White and Burnham, 1999) for survival analysis of Olympic marmot (*Marmota olympus*)

Model	ΔAIC_c	w_i	k	Deviance	R^2_{KL}
t[a]*AF[b] + site2[c] + winter	**0.00**	**0.41**	**9**	**349.68**	**0.21**
t*AF + winter	1.21	0.22	8	352.90	0.20
t*AF + site3[d] + winter	1.94	0.15	10	349.59	0.21
t*class3[e,f] + site2 + winter	3.64	0.07	21	328.85	0.25
June*AF[g] + sept[h] + site2 + winter	4.59	0.04	4	364.35	0.17
t*class3 + winter	5.27	0.03	20	332.54	0.25
June*AF + sept + winter	5.34	0.03	3	367.12	0.17
t*class3 + site3 + winter	5.60	0.02	22	328.76	0.25
June*AF + sept + site3 + winter	6.50	0.02	5	364.25	0.17
class2[i] + winter	10.31	0.00	2	374.09	0.15
site2 + winter	10.61	0.00	2	374.39	0.15
class3 + winter	11.51	0.00	3	373.28	0.15
site3 + winter	12.60	0.00	3	374.37	0.15
winter	12.65	0.00	2	376.43	0.15
t*class2[j] + site2 + winter	13.77	0.00	18	345.13	0.22
t*class2 + winter	14.91	0.00	17	348.31	0.21
t*class2 + site3 + winter	15.72	0.00	19	345.03	0.22
t + class2 + winter	15.76	0.00	11	361.38	0.18
t + site2	15.88	0.00	11	361.50	0.18
t + class3 + winter	17.25	0.00	12	360.85	0.18
t	17.82	0.00	11	363.44	0.18
t + site3	17.85	0.00	12	361.45	0.18
constant	74.80	0.00	1	440.59	0.00

Radio-telemetry data were collected from 2002–2006 in Olympic National Park, Washington, USA. ΔAIC_c (the difference in the adjusted Akaike information criterion between each model and the top-ranked model), w_i (the weight of evidence in favor of each model), k (the number of parameters), model deviance, and the Kullback–Leibler R^2 (R^2_{KL}) value in each model are shown. The R^2_{KL} is a measure of goodness-of-fit suitable for logit and other non-linear models (Cameron and Windmeijer, 1997). We derived survival rates from the model indicated in bold font.

a Sampling intervals were ten 0.5-month periods (May 1 to September 30) and winter. t indicates that survival varied by interval, either for all animals or as indicated by interaction terms.

b t*AF: survival of adult females varies by interval.

c Site2: Western and Central site groups differ from Royal Basin.

d Site3: Western, Central, and Royal Basin site groups all differ.

e Class3: adult females, adult males, and subadults all differ.

f t*class3: survival varies by interval differently for adult females, adult males, and subadults.

g June*AF: adult female survival differs only in June.

h September: survival of all animals differs in September from the rest of the active season.

i Class2: adult females differ from adult males and subadults.

j t*class2: survival varies by interval differently for adult females and other animals.

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model that included separate parameters for September survival of all marmots and June survival of adult females had previously performed well on a subset of these data (Griffin et al., 2007b), we included three models with these parameters in our candidate model set. No radio-implanted marmot died during hibernation, so a single parameter for over-winter survival was applied to all sites and all three age/sex classes in every model.

We used two measures of reproductive success: weaning success (the proportion of females present in late-June that weaned litters) and litter size (for details see, Griffin et al., 2007a). In cases where logistics prevented checking females at <10 day intervals, if the mobility of infants when we discovered them suggested that they had been above ground for $\geqslant 10$ days, we excluded the litters ($n = 8$) from the analysis of litter size as some infants might have already been lost to predation. We assumed that the sex-ratio of marmots captured as juveniles was representative of the population at birth.

We determined apparent survival for each juvenile from initial tagging in the year of its birth until the following spring, based on whether the animal was trapped or resighted, either opportunistically or in a resighting session (see *Estimating abundance* below) in May or June. No tagged yearling that we failed to detect prior to 1 July was later trapped or resighted. Because some juveniles may have died prior to tagging, we also estimated survival based on the number of juveniles appearing above ground and the number seen the following spring, omitting litters for which we were not confident that we had fully counted the litter.

Reproductive rates and juvenile survival rates were determined for each site group and for the entire population. We used Chi-Square tests for association (χ^2 tests) or one-way analysis of variance (ANOVA), as appropriate, to test for differences among site groups.

3.6. Estimating abundance

We used two approaches to estimate abundance of non-juveniles for each site/season/year combination. First, we used data from mark-recapture type "resighting" sessions in robust design models (Pollock, 1982) to estimate abundance ($\hat{N}$). Following initial marking of the population, resightings were conducted in June and August of all years at all sites except Royal Basin, where dangerous snow conditions prohibited extensive work in June 2006. Each "encounter session" was 2–4 h-long. In each encounter session 1–3 people attempted to positively identify all marmots present by reading their eartags with binoculars or a spotting scope. Three encounter sessions were conducted at each site per secondary session. Second, we combined records from all sources (trapping, telemetry, opportunistic sightings, and resightings) to arrive at a minimum number alive (MNA) for each site in spring (prior to July 1) and fall (August 1 to initiation of hibernation) of each year. These 2-month periods cannot be considered entirely closed (i.e., deaths could occur) so if detection rates were high, MNA could exceed $\hat{N}$ without indicating that $\hat{N}$ was biased.

We analyzed the closed population portion of the resighting data with Huggins full heterogeneity models in program Mark (White and Burnham, 1999). The Huggins models allow detection probability to vary among and within secondary sessions; initial capture probabilities to differ from recapture probabilities; and a mixture of two groups with different capture probabilities. The open population parameters in these models estimate survival and migration. Estimated abundance $\hat{N}_i$ within each secondary session i, is a derived parameter.

For these analyses, we subdivided the Central and Western site groups as follows: Central-A included the three Central sites where we began studies in 2002 (Eagle Point, Marmot Flats, and Obstruction Point), and Central-B included the two sites where we began work in 2003 (Pull-out and Pumpkin Seed Lake). Because Picnic and Sunrise Basin were extinct or functionally extinct for much of the study, we only conducted regular resightings at Hurricane Hill. Therefore, MNA is presented separately for each Western site and $\hat{N}$ is only presented for Hurricane Hill. We fit a slightly different suite of candidate models for each site group to account for differences in data structure and quantity (Supplementary Online Material [SOM]). For all models with $\Delta AIC_c \leqslant 2$, we examined the model structure, estimates of $\hat{N}$, and associated 95% confidence intervals for each site group to identify the model from which we ultimately derived estimates of $\hat{N}$. When these highly-ranked models differed by only a single parameter, we followed the recommendation of Burnham and Anderson (2002) and relied on estimates from the least parameterized of the models.

3.7. Estimation of population growth rates

We used a diffusion analysis approach (Dennis et al., 1991; Morris and Doak, 2002) to determine the average estimated intrinsic growth rate ($\hat{\bar{r}}$) and associated standard errors for each site group (or subgroup) separately based on each of spring MNA, fall MNA, spring $\hat{N}$, and fall $\hat{N}$. For the spring MNA estimates, we included a projected MNA for spring 2007. This number is MNA fall 2006 plus 2006 juveniles seen in September, minus any animals known to have died during the fall (Taper and Gogan, 2002). If marmots without radio-transmitters died, the MNA spring 2007 would be inflated. While it was possible that immigrants could increase local populations in spring 2007, this did not occur in previous years.

We also used deterministic matrix models to project population growth rate for each site group based on that group's observed demographic rates. The Central sites were modeled together. We used a pre-birth pulse census, female-based model, where the "birth pulse" is the emergence of juveniles from burrows beginning about July 15 and the census occurs immediately post-hibernation (May). As at that time there are no juveniles present in the population, we modeled spring to spring survival of three age-classes (1 year-old, 2 year-old, adult). Adult females present at the start of year t produced female 1 year-olds in year $t + 1$ at the following rate per adult female: *(survival adult females May 1–July 15) x (proportion of females reproducing) x (litter size) x (proportion of female pups) x (survival of juveniles from emergence to spring)*. We parameterized the model for each site based on the estimated survival and reproductive rates at each site group, regardless of whether these rates differed significantly among site group.

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We transformed the annual asymptotic discrete population growth rate λ to the continuous time growth rate ($\ln\lambda = r$). Age distribution on average at each site was close to the stable age distribution assumed by the asymptotic λ.

4. Results

4.1. Historically occupied sites

Of the 25 colonies where marmots had previously been recorded in multiple years, 12 were not occupied in 2002. All occupied colonies were confirmed to be occupied at the initial visit. Three additional colonies went extinct during the course of our study: marmots disappeared from two colonies in Sunrise Basin between fall 2002 and spring 2003, and the last marmot disappeared from "Picnic" in mid-summer 2006, although the absence of any male at that isolated site meant that the colony had been functionally extinct since 2002. Thus, in fall 2006, 60% (15/25) of the historically known colonies were not occupied. A 1989 survey had visited 22 of these 25 sites and found marmots at all of them (Houston and Schreiner, 1994a) – thus, the extinctions we observed are a recent phenomenon. Colonies tended to go extinct in clusters; disappearances from Blue Mountain and from the areas around the Hurricane Ridge Visitor's Center accounted for 12 of the 15 extinctions. No recolonizations have been detected and no new areas were known to be colonized as of fall 2006. The high visibility of many of the extinct sites and the intense interest shown by park staff, combined with the foot surveys, makes it extremely unlikely that marmots would not have been detected if they were present at, or recolonized, these sites during the course of the 5-year study.

4.2. Habitat surveys

We surveyed 282 primary, 379 secondary, and 148 opportunistic polygons. These represent 94% of all primary and 23% of the total predicted polygons. Of these 809 polygons, 244 (30%) were surveyed formally or opportunistically in multiple years ($\bar{x} = 1.45$ years, SD = 0.88). We ultimately classified 219 polygons (27%) as occupied, 111 (14%) as abandoned, and 484 (60%) as without sign of marmots. The proportions were very similar when based on the 282 primary polygons: 30% were classified as occupied, 16% as abandoned, and 55% as without sign of marmots. In both cases the ratio of abandoned to occupied polygons was slightly greater than 0.5:1.

There were large regional differences in both the proportion of polygons that showed some sign of marmots (i.e., occupied or abandoned vs. without sign) and the ratio of abandoned to occupied habitat ($X^2_6 = 179.89, P < 0.001$; Fig. 3). The proportion of polygons in the southwest with any sign of marmots was only 11%, compared to >42% in each of the other three regions (pairwise χ^2 tests, all P's < 0.001). Of the polygons with sign of marmots, a higher proportion appeared to be abandoned in the southwest and southeast regions (76% and 58%, respectively) than in the northwest and northeast regions (24% and 26%, respectively; all pairwise χ^2 tests, all P's < 0.001) (see Fig. 3).

Fifty-five polygons were visited twice in the same year by observers who had no prior knowledge of occupancy status. Sixteen of these were classified as occupied in the first visit, 17 in the second, with 15 classified as occupied in both visits. Based on the adjusted Lincoln–Peterson estimator (Chapman, 1951), the estimated number of these test sites that were occupied was 18.1 (SE 0.38) and the single visit detection probability was 0.92, very similar to an independent estimate in the same system of a 93% detection rate (Witczuk, 2007). Given a detection probability of 92%, we would expect to detect marmots in 99% of the occupied polygons visited at least twice and 92% of the occupied polygons visited once. We detected marmots at 118 single visit polygons and 101 multiple visit polygons; adjusting for detectability would lead to a minor adjustment resulting in an estimated 229 occupied polygons (i.e., 118/0.92 + 101) compared to the observed 219. This represents just a 5% increase over the unadjusted numbers – not a biologically important difference.

A similar analysis of polygons classified as abandoned in one or both of two within year surveys points to a lower single survey detection probability (0.63) for abandoned polygons but signs of prior occupancy still would be detected at >85% of abandoned polygons surveyed twice and at 95% of those polygons surveyed ⩾3 times. Adjusting for this detection rate produces a corrected estimate of 159 abandoned sites, an increase of 43% from the uncorrected count of 111. The adjusted proportions of occupied, abandoned, and no sign polygons would be 28%, 20%, and 52%, increasing the ratio

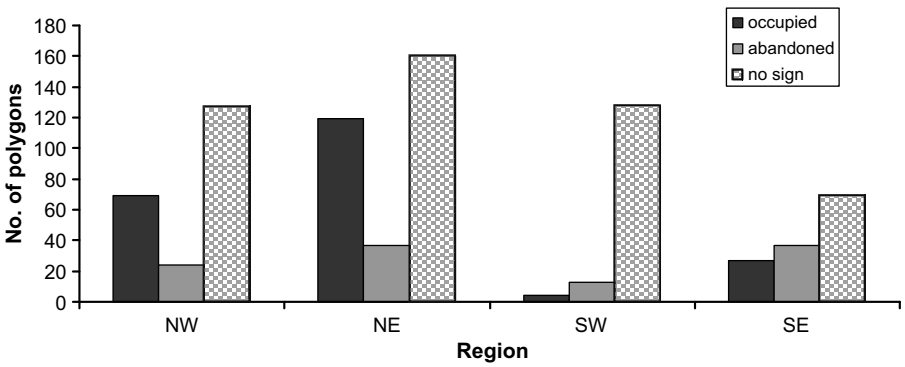

Fig. 3 – Proportion of occupied, abandoned, and no sign polygons in Olympic marmot habitat survey differed by geographic region. See Fig. 1 for delineation of regions.

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of abandoned to occupied to 0.7:1. While the adjusted number provides a useful upper bracket for the true number of abandoned polygons, it probably represents an overestimate, because in many cases, surveyors had prior knowledge about historical occupancy and so may have been predisposed to recognize old burrows, possibly increasing detection rates of abandoned burrows on sites that actually were abandoned; by contrast, the double surveys were intentionally conducted by observers with no knowledge of occupancy status.

4.3. *Survival and reproduction*

We monitored 101 subadult and adult marmots for a total of 1504 0.5-month active season intervals and 124 7-month over-winter intervals. Thirty-three marmots died during the study, the signal from 11 marmots disappeared along with the animal, and 4 marmots outlived their transmitters and were subsequently recaptured. No radio-implanted marmot died during hibernation.

Multiple lines of evidence suggested that the 11 missing animals were in fact dead. If the transmitters had failed and the animals remained alive, our high detection probability (see *Abundance trends*) means that we should have relocated most animals. The 11 missing marmots were not particularly cryptic – they were trapped an average of 1.5 times each and seen in 61% of possible resighting sessions in the year prior to their disappearance. Of the 4 transmitters known to have failed, three had exceeded their expected battery life, while of the 11 missing transmitters, only two were at or near the end of their expected battery life. The median age of the missing transmitters was less than half their expected lifespan. Alternatively, if animals had dispersed off the study area we would expect the 'missing' marmots to be disproportionately subadults and males. In fact, eight of the 11 missing animals were adult females; seven of these had weaned young in that year or previous year. We were not able to locate any missing animals from fixed-wing aerial telemetry flights. Finally, we have recovered seven badly damaged although still operable transmitters from predated marmots, suggesting that predators may bite and destroy transmitters. Given all this evidence, we treated missing marmots as having died in the interval in which they were first missing. If missing marmots did disperse from the study area, our survival rates would actually represent apparent survival, a distinction that is irrelevant to the local populations given the complete lack of immigration.

There were three survival models for which $\Delta AIC_c \leqslant 2$, indicating roughly equivalent support in the data. All three allowed adult female survival to vary across the season, while adult males and subadults shared a constant survival rate. These models differed only in how survival rates were assumed to vary among the site groups – the top-ranked model provided for Royal Basin to have higher survival rates than the other two site groups (Fig. 4). Indeed, for all model structures, the model with a separate parameter for Royal Basin outranked the others. Royal Basin is geographically separate and topographically dissimilar from the other site groups. Perhaps because of these differences, marmot density is higher and reproductive performance is lower than at either the Western or Central sites, and it is therefore plausible that survival rates at Royal Basin could differ from the other site groups. Accordingly, we derived the survival estimates from this top-ranked model, which estimated annual survival of adult females to be considerably lower than that of adult males and subadults, and survival of all animals to be lower at the Western and Central site groups than at Royal Basin (Table 3).

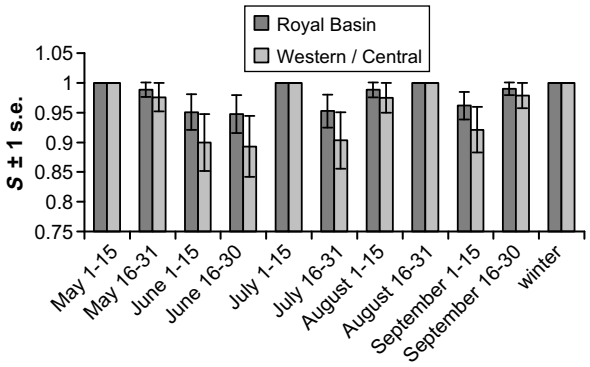

Fig. 4 – Interval specific estimates of adult female survival at Royal Basin and at the Western and Central site groups, derived from the top-ranked model (Table 2).

This model likely overestimated apparent survival rates in subadults at Royal Basin. Our sample of implanted subadults at that remote site was limited to four 2-year-olds implanted in June 2004 and 6 yearlings implanted in August 2006 (total 36 active season intervals). Although none of these died or dispersed prior to age three, only 11 of 21 subadults tagged in 2003 and 2004 at Royal were subsequently detected as adults. Many or all of the other 10 tagged marmots presumably died or dispersed.

Among the reproductive rates, only the proportion of females present in mid-July that successfully weaned litters differed significantly among site groups ($X_2^2 = 6.13; P < 0.05$; Table 3), with the best performance at the Central sites and very low reproduction at Royal Basin. Litter size averaged 3.31 ($n = 19$ litters), with little variation among site groups. The sex-ratio of the pups was somewhat skewed (0.58 female, $n = 59$), particularly at the Central sites where several litters were entirely female, but did not differ significantly from 1:1. Juvenile survival from emergence through hibernation appeared similar across sites as well (0.60, $n = 89$).

4.4. *Abundance trends*

All site groups except Central-B experienced declines from the first to last season of the study, as measured by both the mark-recapture estimates of $\hat{N}$ and MNA (Fig. 5). The increase at Central-B was driven by Pumpkin Seed Lake; the other colony in the group, Pull-out, declined from four to three marmots from fall 2003 to fall 2006. Two sites in the Western site group, Sunrise and Picnic, became extinct during the study. The structure of the mark-resight models used to estimate abundance differed across site groups (SOM), reflecting differences in the candidate models sets, resighting conditions, and variation in sample sizes at the different site groups. As expected, daily detection probabilities varied considerably across sites and across years but even the lowest of

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Table 3 – Reproductive and survival rates for Vancouver Island marmots, historic populations of Olympic marmots, and 2002–2006 Olympic marmots at three site groups

Demographic rate	Vancouver Island marmots[a]	Olympic marmots				
		Historic[b]	Hurricane Hill	Obstruction Point	Royal Basin	All colonies
Proportion of females weaning litters	0.41 (134; 0.33, 0.50)	0.41 (59; 0.28, 0.54)	0.38 (24; 0.19, 0.59)	0.48 (44; 0.32, 0.63)	0.21 (34; 0.09, 0.38)	0.36 (102; 0.27, 0.46)
Litter size	3.38 (58; 1.14)	4.04 (24; 1.20)	3.22 (9; 1.39)	3.33 (18; 1.08)	3.50 (2; 0.71)	3.31 (29; 1.14)
Sex-ratio (proportion female)	0.51 (108; 0.41, 0.61)		0.55 (11; 0.23, 0.83)	0.59 (44; 0.43, 0.74)	0.5 (4; 0.68, 0.93)	0.58 (59; 0.44, 0.70)
Juvenile survival (from emergence)	0.53 (75; 0.42, 0.65)	0.55 (64; 0.40, 0.66)	0.63 (24; 0.41, 0.81)	0.57 (58; 0.43, 0.70)	0.71 (7; 0.29, 0.96)	0.60 (89; 0.49, 0.70)
Juvenile survival (from tagging)			0.65 (20; 0.41, 0.85)	0.64 (53; 0.50, 0.77)	0.80 (15; 0.52, 0.96)	0.67 (88; 0.56, 0.77)
Adult female survival (annual)	0.76 (– [–]; 0.68, 0.83)	0.89	0.62 (11 [181]; 0.47, 0.75)	0.62 (18 [187]; 0.47, 0.75)	0.80 (11 [205]; 0.61, 0.91)	0.69 (40 [573]; 0.58, 0.78)
Adult female survival (to July 15)	0.96		0.78 (11 [99]; 0.66, 0.91)	0.78 (14 [83]; 0.66, 0.91)	0.89 (10 [91; 0.79, 0.99])	0.83 (35 [273]; 0.72, 0.93)
Adult male and subadult survival	0.76 (– [–]; 0.68, 0.83)		0.78 (24 [282]; 0.69, 0.85)	0.78 (40 [482]; 0.69, 0.85)	0.89 (18 [148]; 0.75, 0.96)	0.79 (82 [912]; 0.72, 0.85)
Projected r			−0.12	−0.08	−0.01	−0.07

For litter size, the mean, with sample size and SD in parentheses, is shown. For all other rates, the sample size, and upper and lower 95% confidence limits are given. For the adult and subadult survival rates, sample size – representing the number of radio-tagged individuals – is followed by the number of 0.5-month active season intervals in square brackets. Some females were monitored as both subadults and adults.

a Vancouver Island marmot reproductive rates reported for wild marmots in Bryant (2005), juvenile survival through 2004 from A.A. Bryant (personal communication). Adult survival rates from Bryant and Page (2005); it was not possible to determine sample sizes of the appropriate non-juvenile age and sex classes from this reference.

b Historic Olympic marmot rates from Barash (1973); Table 3. Data therein are insufficient to determine female survival to July 15.

the estimated rates would lead to >80% of marmots being detected in a 3-day sampling period.

There was generally high concordance between MNA and $\hat{N}$ ($r = 0.94$, $n = 32$, $P < 0.001$; Fig. 5), although the MNA estimate on average detected one marmot more than $\hat{N}$. This discrepancy often occurred when radio-tagged marmots died shortly before the resightings, particularly in the spring when the resighting was late in the ~2-month period used to determine MNA.

4.5. *Population growth rates*

Most (11 of 16) estimates of population growth rate based on the time-series, and all projections based on matrix models, indicated that the marmot populations in our three study areas are declining (Fig. 6). At the Western sites the matrix model, parameterized with five years of demographic rates, predicts a population declining at 12% per year. This rate of decline is greater than that of the estimates obtained from the trend data but within 1 SE of three of the four of those estimates. For the Central sites, the matrix model projects a population declining by 8% per year, a rate very close to that observed in the time-series at the large Central-A site group. For Royal Basin the projected annual decline of 2% is not as severe as that detected in the population trends but again falls within 1 SE of the observed trends. To determine the effect that the likely overestimate of subadult apparent survival might have had on the projected growth rate at Royal Basin, we decreased subadult survival from 0.89 to 0.75 in the matrix model. The decrease resulted in a projected 5% annual decline in population size, which although still less severe than the declines indicated by the trend data, represents a sharply declining population.

5. Discussion and conclusions

Multiple lines of evidence all indicate that Olympic marmots have undergone local and range-wide declines over the last 10–15 years. In the northeast, marmots have disappeared from several areas where there was evidence of continuous occupancy for >40 years, and current population trends and demographic rates indicate that the declines are ongoing in extant populations. While the strongest and most dramatic evidence comes from the northeast where the historical record is most complete, similar or higher ratios of abandoned to occupied habitat in other regions suggest that the declines are a widespread phenomenon. Few historical records of marmots exist in the southwest and there is sparse physical evidence of current or recent occupation, so it is plausible that habitat density or quality in that region is and has been too low to support a substantial marmot population. The southeast, where the ratio of abandoned to occupied habitat is even higher than in the northeast, may warrant particular concern.

These apparent declines are particularly troubling given the precarious status of the nearby and taxonomically similar Vancouver Island marmot population, which crashed to near extinction in the 1990s and would likely have gone extinct if not for an intensive captive breeding program. Changes in

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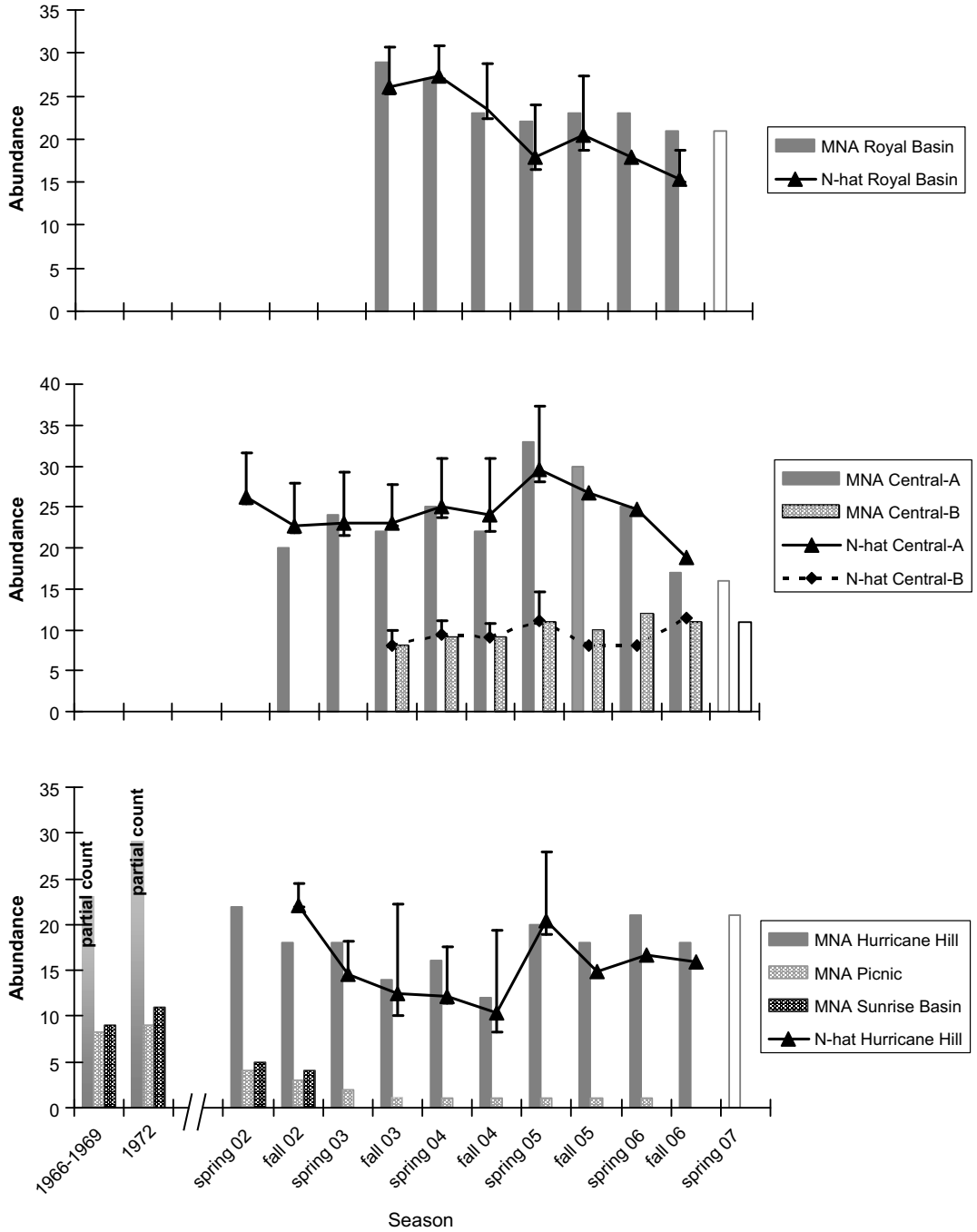

Fig. 5 – Abundance of Olympic marmots age ⩾1 year at intensive study sites 2002–2006 (by site group), with projected maximum abundances for spring 2007. MNA represents the number of animals detected by any means during the spring (May and June) or fall (August and September) of each year. N-hats, with 95% confidence intervals, are estimates from mark-resight data.

the abundance and distribution of predators resulting from industrial forestry appear to have played a considerable role in the decline of that species (Bryant, 1998). Although the mountain landscapes within Olympic National Park are relatively pristine, predator–prey dynamics across the peninsula were altered by the extirpation of the wolf (*Canis lupus*) in the early 20th century, the simultaneous arrival of the coyote (*C. latrans*), industrial forestry and residential development outside the park, and current and historic ungulate hunting practices. Currently, coyotes regularly prey on marmots throughout Olympic National Park (Griffin, 2007; Witczuk, 2007).

Both Olympic and Vancouver Island marmots evolved on actual or effective islands in the absence of many mainland predators and competitors, and both have probably never numbered more than a few thousand. Given this history, it is possible that both species are particularly vulnerable to novel predators, although Blumstein and colleagues (Blumstein,

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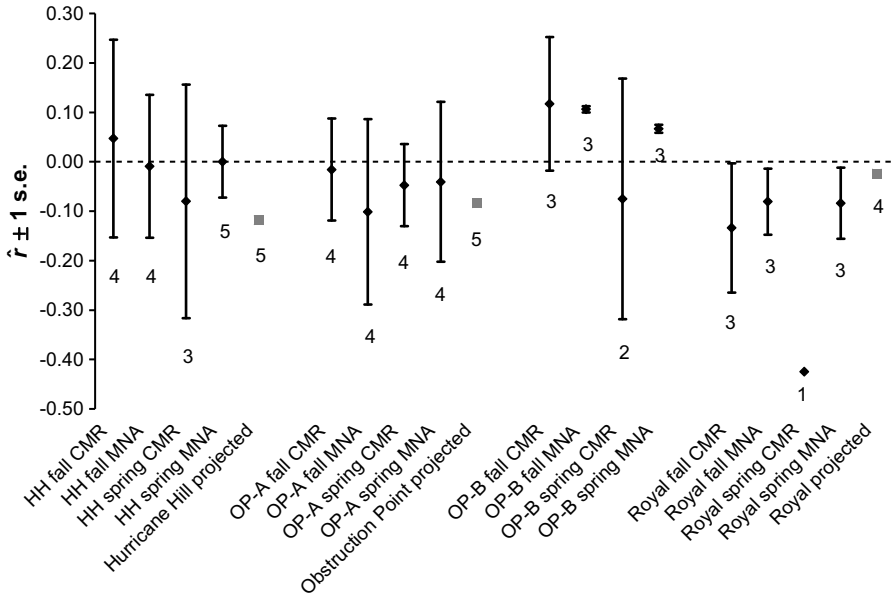

Fig. 6 – Estimates of the mean intrinsic growth rate (*r*) ± 1 SE for each site group for spring and fall based on mark-resight estimates (CMR) and minimum number alive (MNA) in each period, and based on a group specific deterministic matrix model (projected). Diffusion analysis (Dennis et al., 1991) was used to obtain the estimates, with 1–5 intervals per site/season/method combination. The number of sampling intervals (CMR and MNA) or the number of years of survival and reproduction data obtained (matrix projections) is shown below each data point. The last data point used in spring MNA regressions was the expected maximum value for spring 2007, based on marmots known alive in fall 2006. See Fig. 4 for specifics on sampling intervals and data points used.

1999; Blumstein et al., 2001) reported that Olympic and Vancouver Island marmots both have anti-predator behavior comparable to that of the mainland marmot species, findings consistent with the multi-predator hypotheses (Blumstein, 2006). Regardless of how well-developed the anti-predator behavior is in the Vancouver Island and Olympic marmots, their low-reproductive rates, low population density, and restricted range place them at significant risk of extinction (Purvis, 2000) and increases in total predator abundance or distribution within their respective systems could prove disastrous. Logging, species introductions, and other human activities have similarly jeopardized insular endemics all along the North Pacific Coast (Cook and MacDonald, 2001; Cook et al., 2006).

5.1. *Distinguishing declines from metapopulation processes*

Marmots have been postulated to exhibit classic metapopulation dynamics (Bryant and Janz, 1996; Ozgul et al., 2006) and any evaluation of status that relies on occupancy rates must consider whether the observed occupancy patterns represent equilibrium background extinction and colonization patterns. A qualitative analysis of the spatial and temporal distribution of the observed extinctions and recolonizations, dispersal patterns, and demographic rates in the context of other stable and declining populations of marmots all suggest that this is not the case.

First, the spatial patterns of the Olympic marmot extinctions are unlike the long-term patterns in an apparently stable yellow-bellied marmot metapopulation (Ozgul et al., 2006), although both populations consist of groups of nearby sites (termed "networks" by Ozgul et al.) consisting of several large or high-quality patches and additional smaller or lesser quality patches (Fig. 7). Many of the larger yellow-bellied marmot colonies have been continuously occupied for >40 years (Blumstein et al., 2006), and the estimated annual local extinction probability drops off rapidly with local population size (Ozgul et al., 2006). These patterns are consistent with apparent Olympic marmot extinction and colonization processes from 1957 to 1989, a period in which occasional extinctions and colonizations of the smallest sites occurred but the larger colonies appear to have been persistent (Table 1). Simulations demonstrated that overall population persistence is sensitive to extinctions of colonies where the population size of adult females averages >1 and to the extinction of individual networks (Ozgul et al., 2006). These features highlight the importance of larger sites as a source of colonists and of inter-network movement for maintenance of the overall population.

In contrast to the pattern of persistent large patches maintaining networks of sites reported by Ozgul et al. (2006), all or most of the colonies within some individual networks of Olympic marmot sites have become extinct, with little regard to colony size (Figs. 1 and 7). This pattern of extinctions has predictably led to increased isolation of the remaining sites and presumably increased their extinction risk. For example, historically there were ⩾5 sites that averaged >1 adult female in the vicinity of the Hurricane Ridge Visitor Center (Barash, 1968,1973) – these would have fallen within our Western site group. With the extinction of these and the adjacent smaller sites, Hurricane Hill has become very isolated (>10 km from

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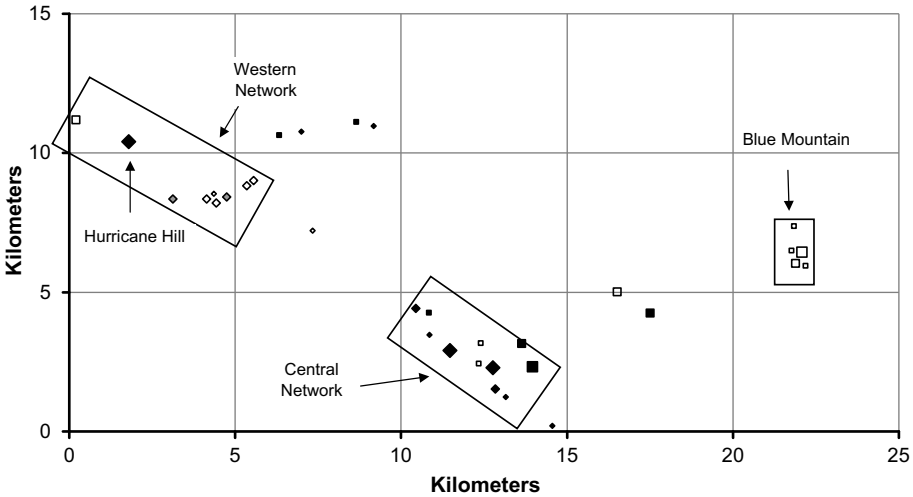

Fig. 7 – Distribution of current and known historic Olympic marmot colonies on the northern ridge system in Olympic National Park. The Central and Western Colonies occupied as of fall 2006 are shown with black symbols, historically occupied colonies that were abandoned by 2002 are shown with hollow symbols, and colonies (Picnic and Sunrise Basin) that became abandoned since 2002 are shown with gray fill. Symbol size corresponds to number of breeding age females typically supported by the site (⩽1, >1–2, >2). Number of breeding age females was determined from data collected in this study or by Barash (1973) or was estimated based on meadow size and burrow density at sites where no data are available. Sites where average number of females was known are with diamonds and those for which we estimated size are shown with squares.

any colony >5 marmots) and seems likely to succumb to stochastic events. Four tiny sites (2–4 marmots) on Mt. Angeles also seem unlikely to persist in the absence of support from the now-extinct sites. Similarly, the abandoned sites on Blue Mountain included at least two relatively large, persistent marmot colonies and several smaller ones. The nearest potential source of colonist (i.e., a site currently occupied by >5 marmots) is now >8 km from Blue Mountain. Numerous other examples of "network" extinctions appear to exist in other regions of the park and many of the remaining networks are becoming increasingly isolated.

A second reason why current occupancy patterns are not representative of equilibrium metapopulation dynamics is that Olympic marmot dispersal patterns appear to severely limit the probability of widespread recolonizations. While the majority of yellow-bellied marmots of both sexes disperse as yearlings (Van Vuren, 1990; Schwartz et al., 1998), and other marmot species are known to move long distances (Van Vuren and Armitage, 1994, A.A. Bryant, personal communication), movement of Olympic marmots appears to be more limited. We have no record of any untagged marmot migrating onto any of our study sites during the 4–5 years of study and dispersal >0.5 km was extremely rare among the 101 radio-tagged marmots. Two radio-tagged males traveled ~5 km before being depredated and two established new home ranges 0.5–1 km from their initial home range. Additionally, we recaptured two ear-tagged males that successfully dispersed distances of <0.8 km and 2.5 km. No female is known to have settled >0.4 km from her natal home range. Sherman and Runge (2002) reported a similar lack of movement among ground squirrel colonies during a severe population collapse.

Finally, current Olympic marmot mortality rates, particularly those of adult females at the Western and Central site groups, are more similar to (although slightly lower than) the endangered Vancouver Island marmot (Bryant and Page, 2005, A.A. Bryant and S.C. Griffin, unpublished data) than they are to rates recorded for Olympic marmots in the 1960s (Barash, 1973). Population growth rates for long-lived, late-maturing species are known to be sensitive to changes in the survival rates of adult females (Heppell et al., 2000; Oli and Dobson, 2005) – the low projected population growth rates are consistent with this. In addition, the slightly reduced reproductive rates in the current population may be a secondary effect of the high female mortality rates. The most parsimonious explanation for the consistently high mortality of adult females in June would be that they are more vulnerable to predation due to pregnancy or lactation (e.g., Hoogland et al., 2006), and several of the females that were killed in this period were known or suspected to be pregnant or lactating.

It is also important that both the proximate and ultimate causes of the declines be identified (Sherman and Runge, 2002). The widespread distribution of the abandoned sites supports earlier findings that direct human disturbance is probably not responsible (Griffin et al., 2007b). Similarly, we saw no indication of disease in the ⩾200 marmots we handled and ⩾100 examined by a veterinarian. Over-winter survival was high, reproductive rates were in the expected range, and body condition was good (data not shown), suggesting that neither forage quality nor over-winter conditions have been degraded by climate change, although they may be in the future. The high mortality of adult females at two of three site groups suggests that predation is the proximate cause of the immediate declines. It is possible, however, that the population may have become more vulnerable due to landscape level changes in meadow distribution, as has been proposed for the Idaho ground squirrel (Sherman and Runge, 2002). Aerial photos of the Hurricane Ridge area taken in 1939

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and 2000 show substantial increase in tree cover during that period, although the net change in high-elevation meadows across the park is unknown. If forest cover did increase over the last century due to climate change or fire suppression, the result would have been increasing isolation and decreasing size of suitable meadows, leading to a decreased frequency of successful dispersal events, improved cover for terrestrial predators, and possible Allee effects resulting from smaller groups of marmots.

5.2. *Management recommendations and research needs*

We recommend implementing a range-wide monitoring program that takes into consideration the role of local networks of sites in population persistence, as well as continuing to monitor abundance and demographic rates at a subset of sites. It should be possible to design an occupancy monitoring program that will allow the detection of collapse of local networks. Occupancy monitoring is also financially and logistically more feasible than demographic monitoring. However, continued demographic monitoring is recommended because age and sex biases in mortality rates could lead to a time lag between functional declines and numerical declines or site abandonment (e.g., Conrad et al., 2001; Balbontin et al., 2003; Ferrer et al., 2003). Furthermore, demographic monitoring, particularly with radio-transmitters, provides considerably more information about the causes of declines than occupancy monitoring can provide.

Because of the important role that connectivity plays in maintaining marmot populations (Ozgul et al., 2006), we also recommend more extensive research into Olympic marmot dispersal patterns. If Olympic marmot dispersal rates are too low to assure recolonization of high-value colonies (those that are relatively large or situated to serve as linkages between networks) or to allow at least occasional gene flow among isolated colonies, translocations should be considered. Finally, the likely effects of climate change on both the marmots and the high-elevation landscape should be investigated. If high-elevation meadows become more fragmented, active management of marmots may be required to prevent extinction. If the large, cold-adapted Olympic marmots are physiologically incapable of surviving in a warmer world, management actions may just forestall the inevitable.

5.3. *Conclusions*

Our research indicates that Olympic marmot populations are declining and the long-term persistence of the species may be at risk. An earlier estimate of 2000 Olympic marmots (Barash, 1989) appears to have originated in a 1918 Forest Service report (Sheffer, 1995). We believe the number of marmots is currently $\leqslant$1000, but this estimate is tenuous as well due to the wide range of marmot densities, which often appear to be unrelated to habitat characteristics, and the difficulties associated with assessing population size of unmarked animals at remotes sites. Assessments of the status of small, scattered, populations in remote landscapes will almost always involve some degree of uncertainty. Alone, none of the four lines of evidence that we presented would absolutely demonstrate that Olympic marmots are in a sustained decline across their range. However, each is consistent with such a decline, while the spatial pattern of the extinctions is inconsistent with metapopulation dynamics of a population at equilibrium. In effect, by considering multiple metrics of distribution and demography, as well as how the observed patterns compare to those seen in other species of marmots, we have reduced the uncertainty about the status of the marmot to a negligible level.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2008.03.001.

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