Biological Conservation 142 (2009) 2181–2190

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Reintroducing endangered Vancouver Island marmots: Survival and cause-specific mortality rates of captive-born versus wild-born individuals

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ARTICLE INFO

Article history:
Received 20 February 2009
Received in revised form 18 April 2009
Accepted 26 April 2009
Available online 21 May 2009

Keywords:
Age-at-release
Captive-breeding
Capture-mark-recapture
Cause-specific mortality
Demography
Endangered species management
Marmota vancouverensis
Population dynamics
Radio-telemetry
Reintroduction
Survival
Vancouver Island marmot

ABSTRACT

Recovery of the endangered Vancouver Island marmot (*Marmota vancouverensis*) is contingent upon releases of captive-born marmots into natural habitats. Success of such re-introduction programs largely depends on the ability of released animals to survive in the wild. However, whether and to what extent survival and cause-specific mortality rates of captive-born marmots differ from those of their wild-born counterparts remains unknown. We used radio-telemetry (1992–2007) and mark-resighting (1987–2007) data to estimate seasonal and annual survival rates of the Vancouver Island marmot, to compare survival and cause-specific mortality rates of captive-born marmots that have been released into the natural habitat with those of wild-born marmots, and to test for the effect of age-at-release on survival of the released marmots. Analysis of radio-telemetry data suggested no difference in survival of males versus females. However, annual survival of captive-born marmots released into the wild was low ($S = 0.605$; 95% CI = 0.507–0.696) compared to wild-born marmots ($S = 0.854$; 95% CI = 0.760–0.915). Marmots released as 2-year-old or older survived more successfully than those released as yearlings. Additional forensic evidence reinforced the idea that predation was the most important cause of mortality. Causes of death differed significantly between captive-born and wild-born marmots. Predation by golden eagles (*Aquila chrysaetus*) was the most important cause of mortality for captive-born marmots, whereas predation by wolves (*Canis lupus*) and cougars (*Felis concolor*) was more important for wild-born marmots. Age-specific apparent annual survival rate, estimated using the combined mark-resighting and radio-telemetry data, was lowest for pups ($S = 0.500$; 95% CI = 0.375–0.616) and highest for yearlings and adults ($S = 0.656$; 95% CI = 0.604–0.705); and apparent survival of 2-year-old was similar to that of yearlings and adults ($S = 0.649$; 95% CI = 0.527–0.754). Our results, based on the analysis of radio-telemetry data, suggest that delaying release of captive-born marmots until 2 years of age may enhance their probability of survival in the wild, and will likely improve the success of the release program.

1. Introduction

Understanding causes of population decline is an important first step towards recovery of endangered species (Caughley, 1994; Caughley and Gunn, 1996). Change in population size is the consequence of changes in one or more vital demographic rates (Caswell, 2001; Mills, 2007; Oli and Armitage, 2004); effects of the environment and management actions on the dynamics of populations are mediated through their influences on demographic variables. Furthermore, reduction in survival can lead to decline of wildlife populations whose growth rate is very sensitive to changes in survival rates (Heppell et al., 2000; Oli and Dobson, 2003; Stahl and Oli, 2006). Therefore, rigorous estimates of survival and knowledge about how various factors influence this key demographic rate are necessary for formulation of recovery plans and conservation of species at risk (Le Gouar et al., 2008).

The Vancouver Island marmot (*Marmota vancouverensis*) is endemic to Vancouver Island, British Columbia, Canada. Concern brought on by the restricted geographic distribution and low numbers, led to *M. vancouverensis* being listed as endangered in 1978 (Bryant and Page, 2005; Shank, 1999). Systematic field surveys suggest that the marmot population increased during the early 1980s to a peak of 300–350 individuals during the mid 1980s (Bryant and Janz, 1996). However, by 2004 the population had declined to approximately 35 individuals in the wild (Bryant, 2005). Landscape changes due to clearcut logging and increases in predation-related mortality are thought to have contributed to the population decline (Bryant and Page, 2005).

Significant conservation accomplishments towards recovery of *M. vancouverensis* have been made through planned captive-breeding and release programs (Janz et al., 2000). Captive-breeding

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doi:10.1016/j.biocon.2009.04.019

facilities were established both on and off the island beginning in 1997, and captive-bred marmots have been released into their natural habitat since 2003 (Bryant, 2007). There have been both reintroductions of marmots into empty but historically occupied sites and re-enforcement of existing colonies with additional marmots. During 2003–2007, 96 marmots were released and monitored using radio-telemetry. Arguably, the most important conservation measure currently in place is the release of captive-bred marmots into their natural habitat. Although re-introduction programs have been successful in some cases, limitations of captive-breeding and re-introduction programs for species conservation are well documented (e.g., Caughley and Gunn, 1996; Snyder et al., 1996; Moorhouse et al., 2009). Success of such programs depends to a large extent on the ability of released animals to survive and reproduce in their natural habitats.

Often, released animals have a lower probability of survival in the wild than their wild-born counterparts, reflecting some cost associated with being raised or held in captivity (Beck et al., 1994; Mathews et al., 2005; Sarrazin and Legendre, 2000; Snyder et al., 1996). Any additional mortality may only apply for a period immediately post-release after which survival of released individuals increases to a rate near that of wild-born individuals (Bar-David et al., 2005; Sarrazin et al., 1994; Maran et al., 2009). Age at which animals are released can also influence their subsequent survival and the success of a reintroduction program (Green et al., 2005; Le Gouar et al., 2008; Sarrazin and Legendre, 2000). Understanding differences between captive-born and wild-born marmots in survival and causes of death can provide information to potentially improve success of the recovery program. However, whether and to what extent survival and causes of mortality of captive-born marmots differs from those of wild-born marmots, or if age at release influences survival of captive-born marmots, remained unknown until this study.

To provide demographic information needed for effective recovery of *M. vancouverensis*, Bryant and Page (2005) analyzed radio-telemetry data collected through 2004. These authors provided estimates of survival and also examined causes of mortality and seasonal variations in survival. Field study has continued since this work was completed, and many more marmots have been monitored via radio-telemetry. Consequently, sample sizes and our ability to test hypotheses regarding factors influencing survival of marmots have increased substantially in recent years.

Our goals were to build upon previous work, provide more rigorous estimates of survival, and test hypotheses about factors influencing survival of marmots using radio-telemetry data. Using a subset of radio-telemetry data collected since the first releases of captive-born marmots in 2003, we also tested the hypotheses that wild-born marmots would have a higher probability of survival than their captive-born counterparts, and that captive-born marmots released at an older age would survive better than those released as yearlings.

Predation is the most important cause of mortality of wild Vancouver Island marmots (Bryant and Page, 2005). Given that captive-born marmots are not exposed to predators during early, possibly important developmental stages as wild-born marmots are, their behavioral responses to the risk of predation may differ (Blumstein et al., 2001). Alternatively, their ability to escape various predators may differ due to disparities in experience or body condition. Thus, we also estimated cause-specific mortality rates, and tested for differences in mortality rates between captive-born and wild-born marmots for each cause.

Pups were seldom implanted with radio-transmitters. Consequently, radio-telemetry data were sparse and it was not possible to estimate survival rates for this age-class. We combined the radio-telemetry and long-term capture-mark-resighting (CMR) data and analyzed the combined dataset within a multi-state CMR modeling framework (Williams et al., 2002). Combining the data from two sources allowed us to estimate age-specific survival rates, and to test hypotheses regarding the influence of age, sex, habitat type, and geographic location on survival of marmots.

2. Methods

2.1. Study species

The distribution of *M. vancouverensis* is restricted to the interior mountainous zones of Vancouver Island (Nagorsen, 1987). Marmots live in open, subalpine meadows characterized by colluvial soils, diverse vegetation, and lookout spots (Heard, 1977; Milko and Bell, 1986). These small patches of suitable habitat were historically interspersed within much larger areas of dense old-growth forest, creating a pronounced metapopulation structure (Bryant, 1998).

Vancouver Island marmots are generalist herbivores (Martell and Milko, 1986) living in social colonies consisting of one or more family groups (Bryant, 1998). They exhibit slow maturation, delayed dispersal, and large body size relative to most marmots, but similar to other members of the *Marmota caligata* group (Armitage, 1999; Barash, 1989; Griffin et al., 2008). The annual cycle of Vancouver Island marmots consists of an active season (approximately, early May through early October) and hibernation during the winter in underground burrows for an average of 210 days (SE ± 7.6 days, Bryant and McAdie, 2003).

2.2. Study area

This study was conducted on Vancouver Island, British Columbia, Canada. The regional vegetation is dominated by western hemlock and mountain hemlock, with interspersed meadows. The landscape of Vancouver Island has undergone extensive change since the late 1950s when forestry companies began harvesting at progressively higher elevations. Clearcuts created open habitats resembling meadows, and marmots began to colonize them extensively during the 1980s. By the mid-1980s, more than half of the marmot population was living in clearcut habitats; however, few marmots have inhabited clearcut habitats since 2000.

The present distribution of marmots on Vancouver Island consists of two main populations (Bryant, 1998). The larger metapopulation, Nanaimo Lakes, is on the southern part of the island, and is characterized by mountains of lower elevation and less rugged terrain than the central and northern regions. All colonies within the Nanaimo Lakes metapopulation are concentrated in an area encompassing 840 km^2 within five adjacent watersheds (Bryant, 1998).

The smaller population on Mt. Washington is in central Vancouver Island, 80–95 km north of Nanaimo (Fig. 1). Based on DNA evidence, dispersal between the two metapopulations is unlikely (Kruckenhauser et al., 2009).

Releases of captive-born individuals have taken place at both Nanaimo Lakes and Mt. Washington. Within the past 2 years, there have also been re-introductions to Strathcona Provincial Park and Mt. Cain, to the west and north of Mt. Washington, respectively.

2.3. Field methods

Marmots were captured using single door Havahart traps baited with peanut butter; transferred to a tapered handling bag to restrict the marmot's movement, and sedated using procedures described in Bryant (1996). Each marmot received a pair of numbered metal ear tags. Individuals were classified into one of 4-age-classes: pup (0–1 years); yearling (1–2 years); 2-year-old (2–3 years old); or adult ($\geqslant$3 years old). Age was accurately known

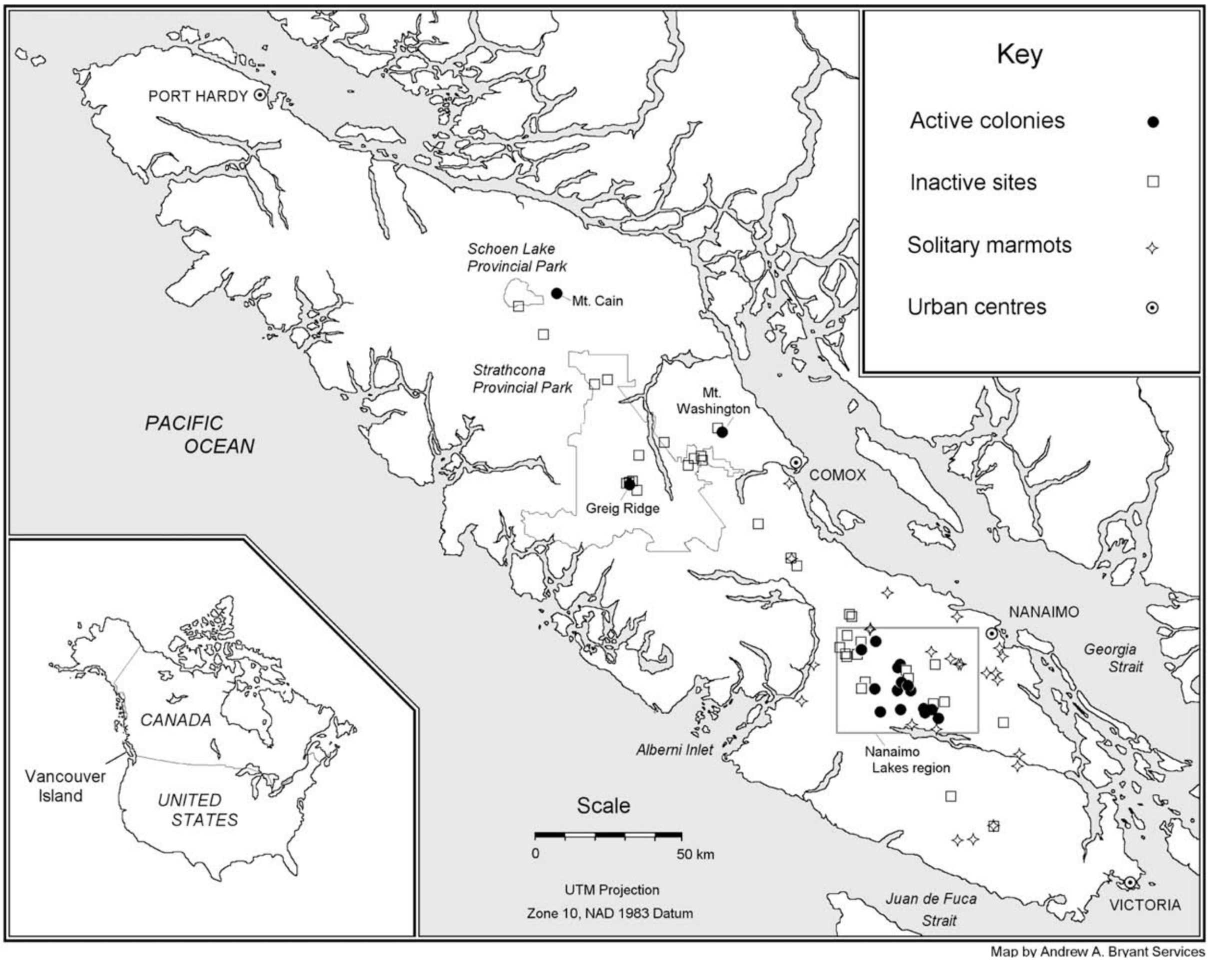

Fig. 1. Historically occupied (squares) and recently occupied (circles) sites for *M. vancouverensis*. The rectangle encompasses recently-active colonies within the Nanaimo Lakes region, from which the majority of survival data were obtained. Locations of the isolated Mt. Washington sub-population, and recent reintroductions at Mt. Cain and Greig Ridge are also shown.

for marmots captured for the first time as pups or yearlings; it was estimated for marmots captured for the first time as 2-year-old or adults (Bryant, 1998). The majority of trapping occurred during the months of July and August. Marmot resightings were made throughout the active season using 60× spotting scopes, usually before 1100 h when marmots were most active. Resightings were considered visual recaptures, and were included in CMR analysis.

Radio-telemetry of marmots began in 1992, with an increasing proportion of the marmot population radio-tagged since (Fig. 2). Types of transmitters and methods used for surgical implant of transmitters are described in detail by Bryant and Page (2005). Radio-tagged marmots were tracked from the ground or from a helicopter. Non-dispersing marmots typically remained close (100–1000 m) to home burrows in most cases, and thus could be tracked from the ground. However, helicopter flights were necessary to reach remote colonies and to track dispersing marmots. The frequency of tracking varied depending on funding, weather, road access problems, and research priorities in various years of the study (Bryant and Page, 2005).

2.4. Data analysis

2.4.1. Analysis of radio-telemetry data

We used known-fate models implemented in Program MARK (White and Burnham, 1999; Williams et al., 2002) to estimate and model survival of marmots. Based on radio-telemetry data, we constructed encounter histories for each marmot for each year with 13 time intervals: 12 active season intervals, each 2 weeks long; and one winter season (hibernation) interval, approximately 28 weeks long (Bryant and Page, 2005). The differences in time interval length between the active and the winter seasons were accounted for during data analysis. A marmot can survive and be radio-tracked for more than 1 year, each of which was considered a separate encounter history; therefore, sample sizes are reported as ‘‘marmot-years”.

We developed and tested an *a priori* set of candidate models investigating the effects of several factors on survival. First, we tested for the additive and interactive effects of sex and age on survival. For age effect, we considered a 2-age-class model (yearlings versus all older animals) and a 3-age-class model (yearlings, 2-year-old, and adults). Limited sample sizes did not permit consideration of pup survival or additional adult classes. Using the most parsimonious model from the preceding analyses, we tested for seasonal variation in survival using 2-season (active season, early May-early October; and winter, hibernation), 3-season (spring/early summer, emergence-31 July; August/fall, 1 August-immergence, and winter) and 4-season models (spring/early summer, emergence-31 July August, 1 August-28 August; fall, 29 August-immergence; and winter). Finally, we tested for the additive and interactive effects of habitat type (natural versus clearcut) and location (Nanaimo versus Washington) using the most parsimonious seasonal model as the base model.

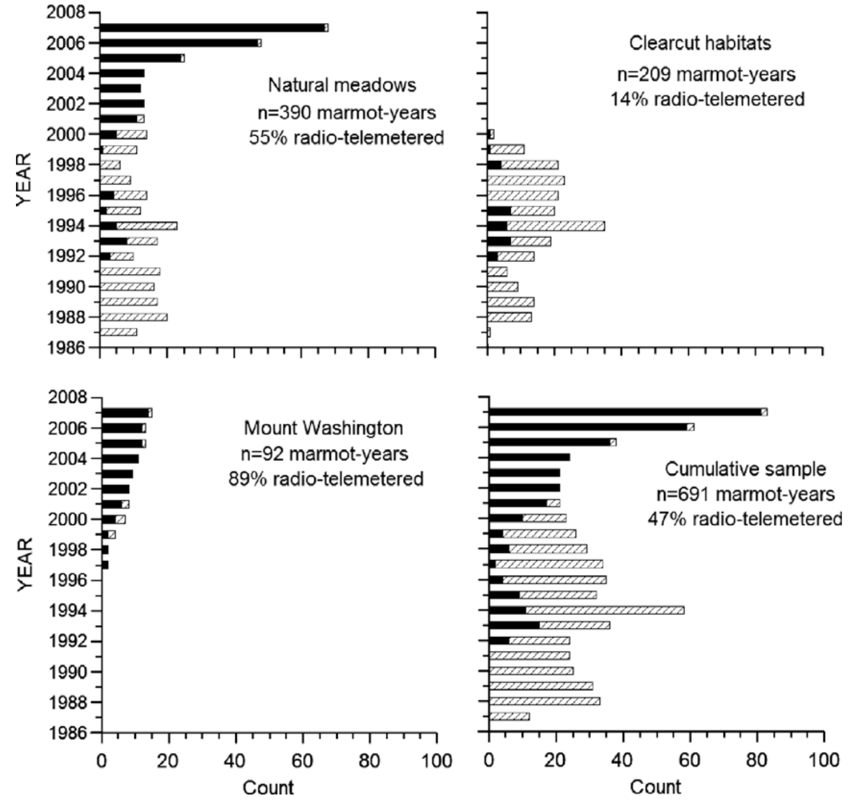

Fig. 2. Changes in numbers of ear-tagged (hatched bars) and radio-telemetered (solid bars) marmots for which annual survival data were available. Almost half of the sampled marmots were telemetered, with the Mt. Washington sub-population being particularly well-represented. The overall trend illustrates greatly increased reliance upon radio-telemetry in recent years, largely driven by growing numbers of reintroduced captive-born marmots.

A subset of radio-telemetry data collected from 2003–2007 contained both wild-born and captive-born individuals that were released into natural marmot habitat; these data were used to test for the effect of origin and "release cost" on survival. Analyses proceeded as described previously, except that we also tested for the effect of origin (captive-born versus wild-born) on survival. Additionally, we tested for the effect of "release cost", where survival of released individuals was allowed to differ from that of wild-born individuals for 1 year post-release but not thereafter (represented by the covariate, "first"). Small sample sizes precluded testing for the effect of year or influence of temporal covariates. To test if survival of released marmots was influenced by the age at which a marmot was released, we used a subset of data including captive-born individuals only.

When a radio-tagged marmot died, cause of mortality was determined based on clues left by predators on and around the recovered transmitter (Bryant and Page, 2005). Winter mortalities were occasionally confirmed by excavation of hibernacula, although the specific cause of winter mortality could not be determined. We attributed each mortality event to one of five causes: (1) eagle, (2) cougar, (3) wolf, (4) winter, and (5) unknown (includes unknown predator). We estimated cause-specific cumulative mortality rates from radio-telemetry data using the nonparametric cumulative incidence function estimator (NPCIFE; Heisey and Patterson, 2006). The NPCIFE is a generalization of the staggered-entry Kaplan–Meier method of survival estimation (Pollock et al., 1989), and uses information on the number and timing of deaths from each cause and the number of radio-collared animals at risk at the time to estimate cause-specific mortality rate. We tested for differences in cause-specific mortality rates between captive-born and wild marmots' using the Cox proportional hazard model stratified by cause of mortality (Heisey and Patterson, 2006).

2.4.2. Analysis of combined CMR and radio-telemetry data

From 1987–1992 the *M. vancouverensis* population was monitored by capture-mark-recapture (CMR) only. From 1992–1999 $\leqslant$ 10% of the known population was radio-telemetered; from 2000–2006, >60% of the known population was radio-telemetered, with an estimated maximum of 95% radio-tagged in 2006 (Fig. 2). Analyses of radio-telemetry data is the method of choice for the estimation and modeling of survival because they provide estimates of true survival rates and also allow determination of cause of death (Williams et al., 2002). However, radio-telemetry data were sparse or non-existent until about a decade ago. Also, only a few pups were radio-tagged, so survival of pups could not be estimated using the same methods. Thus, we merged radio-telemetry and CMR data because the combined dataset (a) spanned a longer period of time (1987–2007), (b) allowed estimation and modeling of survival of pups, and (c) had larger sample sizes which would increase the precision of estimates of survival.

To merge the two data sets, the radio-telemetry data were converted into capture histories with annual intervals between capture occasions. A marmot was considered detected if it was radio-tracked any time during July/August of a given year. A marmot was excluded from the dataset if it was only tracked for a portion of a year which did not overlap the trapping season (July/August); however, this was uncommon as most marmots were monitored during some portion of that 2 month interval. Merging the two datasets inevitably leads to a loss of temporal resolution and other information contained in the radio-telemetry data, but we gain a cohesive data set over the entire duration of the study (1987–2007).

We analyzed the combined dataset using multi-state Cormack–Jolly–Seber models implemented in Program MARK (White and Burnham, 1999; Williams et al., 2002). The states used were 4-age-classes chosen based on the biology of the species, as described previously. Vancouver Island marmots disperse as 2-year-old, and females reproduce for the first time as 3 or 4-year-old (average age of first reproduction = 3.6 years; Bryant, 2005). Probability of transition from younger to subsequent older age classes was fixed to 1.0, and probability of transition from older to younger age classes was fixed to zero because those transitions are impossible.

The dataset was divided into two groups, based on monitoring method (radio-telemetry and mark-resight). Recapture rate for the radio-telemetry group was fixed to one; this group, therefore, contributed to the estimate of survival rate, but not to recapture rate. Fixing the recapture rate to one in CMR analysis effectively results in a known-fate model. Marmots for which radio transmitters failed were censored. Marmots that were initially monitored by CMR and subsequently radio-tagged were censored from the CMR group and then entered in the radio-tagged group for the appropriate time intervals. Analysis of combined data proceeded as described for the radio-telemetry data; one main difference was that pups were also included as an age class using the combined data.

We used Akaike's Information Criterion, corrected for small sample size (AIC_c), for model comparison and for statistical inferences (Burnham and Anderson, 2002). Model comparison was based on the differences in AIC_c values (ΔAIC_c), and relative support for each model in a candidate model set was based on AIC_c weight.

3. Results

3.1. Analysis of radio-telemetry data

One hundred and thirty-two marmots were radio-tracked during 1992–2007 for a total of 367 marmot-years. The number of marmots radio-tracked varied over the study period at each site (Fig. 2). There were 92 marmot-years of radio-tracking recorded for yearlings, 89 marmot-years for 2-year-olds, and 186 marmot-years for adults (Table 1).

Although annual survival of females ($S = 0.750$; 95% CI = 0.654–0.826) was slightly higher than that of males ($S = 0.675$; 95% CI = 0.584–0.754), there was no evidence of a sex effect (Table 2a). There was also no evidence that survival was age-specific using 2-age-classes (yearlings and older marmots ⩾2 years) or 3-age-classes (yearlings, 2-year-old, and adults), nor was there any evidence for additive or interactive effects of sex and age. The overall annual survival for the entire population using the most parsimonious model (model 1; Table 2a) was 0.709 (95% CI = 0.644–0.766). Therefore, for further analysis we used the model with no sex or age effect as the base model.

Table 2
Analysis of the influence of (a) intrinsic (sex and age) and (b) extrinsic factors on survival (S) of the Vancouver Island marmot using radio-telemetry data (1992–2007) and known-fate models. Akaike's Information Criterion corrected for small sample size (AIC_c), differences in AIC_c values (ΔAIC_c), AIC_c weights (w_i), and the number of parameters (np) are shown for each model. The most parsimonious model in the first set of analysis testing (for intrinsic differences in survival) was used as the base model for the second set of analysis testing for effects of extrinsic factors. In both analyses, the most parsimonious models are highlighted in bold.

No.	Model	AIC_c	ΔAIC_c	w_i	np
(a)[a]					
1	**$S(\cdot)$**	**593.65**	**0.00**	**0.275**	**1**
2	S(sex)	594.21	0.56	0.208	2
3	S(2-age-class)	595.17	1.52	0.129	2
4	$S(\text{2-age-class + sex}_{\geqslant 2\text{year}})$	595.26	1.61	0.123	3
5	S(2-age-class + sex)	595.74	2.08	0.097	3
6	S(3-age-class)	597.09	3.44	0.049	3
7	S(2-age-class ∗ sex)	597.25	3.59	0.046	4
8	S(3-age-class + sex)	597.61	3.96	0.038	4
9	$S(\text{3-age-class + sex}_{2\text{year}})$	597.74	4.09	0.036	4
(b)[b]					
1	**$S(\text{4-season + site}_{A,F})$**	**552.75**	**0.00**	**0.645**	**5**
2	S(4-season + site)	555.59	2.84	0.156	5
3	$S(\text{4-season + site}_{S,A,F})$	556.69	3.94	0.090	5
4	S(4-season)	557.86	5.11	0.050	4
5	S(3-season)	558.27	5.51	0.041	3
6	S(2-season)	560.10	7.34	0.016	2
7	S(time)	567.32	14.57	0.000	13
8	S(site)	590.91	38.16	0.000	2
9	$S(\cdot)$	593.65	40.90	0.000	1
10	S(habitat)	595.22	42.47	0.000	2

[a] Age-classes are yearlings, 2-year-olds, and adults for the 3-age-class models. Age classes for 2-age-class models are yearlings and adults. Subscripts indicate age-class(es) for which the model allows the age class to affect survival (⩾2 year = 2-years of age or older; 2 year = 2-year old; ad = adults).

[b] The 4 "seasons" were spring/early summer (S, emergence-July 31), August (*A*, August 1–28), fall (*F*, August 29-immergence), and winter (*W*, hibernation); the 3-season model combined August and fall; and the 2-season model combined the entire active season. Subscripts indicate allowing survival to differ between sites only during season(s) noted. Pluses (+) indicate additive effects and asterisks (∗) indicate interactive effects. The dot (·) indicates a constant parameter value.

Using the most parsimonious model in the preceding analyses (model 1, Table 2a), as a base model we tested for the effects of seasons (models 4–6, Table 2b). Of the seasonal models, the 4-season model was the highest ranked; however, the 3-season model that combined the August and fall seasons, was equally well supported (<1 ΔAIC_c: compare model 4 with model 5 in Table 2b). Using the top ranked seasonal model (model 4, Table 2b), 2-week estimates of survival were intermediate ($S = 0.982$; 95% CI = 0.973–0.989) during summer, low during August ($S = 0.963$; 95% CI = 0.938–0.978) and fall ($S = 0.979$; 95% CI = 0.963–0.988), and high during the winter ($S = 0.996$; 95% CI = 0.992–0.998).

Table 1
Summary of records included in each analysis. For known-fate analyses, value represents number of marmot-years (one record per marmot per year); for the analysis of combined radio-telemetry and mark-resight data, values represent number of mark-recapture histories (roughly equal to number of marmots; however, one marmot can be included in the capture-mark-resight group in 1 year and the radio-telemetry group in another year depending on implantations and radio failures).

Data set	Age class				Sex	
	Pups	Yearlings	2-Year-old	Adults	Male	Female
Radio-telemetry (1992–2007)	0	92	89	186	206	161
Radio-telemetry (2003–2007)[a]	0	66	74	115	148	107
Combined	70	98	102	316	136	137
Data set	Habitat type		Site		Origin	
	Clearcut	Natural	Nanaimo	Washington	Captive	Wild
Radio-telemetry (1992–2007)	31	336	262	105	154	213
Radio-telemetry (2003–2007)[a]	0	255	178	77	154	101
Combined	93	180	33	240	48	225

[a] Subset of radio-telemetry data were used to test for the effect of origin.

Using the most parsimonious seasonal model (model 4, Table 2b), we tested for the effects of habitat type (natural or clearcut) and site (Nanaimo or Washington) on survival (models 1–3, Table 2b). There was no evidence for the effect of habitat type on survival. The most parsimonious model (model 1 Table 2b) indicated that survival differed between sites during the latter half of the active season (Fig. 3). Estimated annual survival was higher at the Washington site ($S = 0.788$; 95% CI = 0.710–0.849) than at Nanaimo ($S = 0.678$; 95% CI = 0.606–0.742).

We used a subset of the radio-telemetry data collected during 2003–2007 to test for the effect of origin (captive-born or wild-born) on marmot survival. As in the previous analysis, first we tested for age and sex effect, and found no evidence for either (Table 3a). We used model 3 in Table 3a as a base model for further analyses because this model differed from the most parsimonious model by $\Delta \mathrm{AIC}_c < 2$, and also had fewer parameters. Next, we tested for seasonal variation in survival using the two, three, and 4-season models as described previously; all of these models were similarly supported (models 5–7, Table 3b). Because the 2-season model (model 6, Table 3b) was well supported, and also had fewer parameters, we chose this model for further analysis. Using this model, active season survival ($S = 0.770$; 95% CI = 0.701–0.827; over 24 weeks) was lower than winter survival ($S = 0.932$; 95% CI = 0.884–0.961; over 28 weeks).

The 2-season model (model 6, Table 3b) was used as a base model to test for the effect of origin (captive-born versus wild-born) and site (Washington versus Nanaimo) on survival. The most parsimonious model (model 1, Table 3b) included additive effect of season and origin, providing substantial evidence for the effect of origin on survival; overall, captive-born marmots had a much lower survival ($S = 0.605$; 95% CI = 0.507–0.696) rate than wild-born marmots ($S = 0.854$; 95% CI = 0.760–0.915). Survival of captive-born marmots was lower than that of wild-born marmots during both seasons, with a more pronounced difference during the active season (Fig. 4). There was no evidence for the cost of release (compare models 9 and 10 in Table 3b).

We also used a subset of data containing only captive-born marmots to test for the effect of age-at-release on survival. There were 46 marmots released as yearlings (74 marmot-years) and 50 marmots released as 2-year-old or older (80 marmot-years). Using a 2-season model (the same seasonal model as in previous analysis), we found that the inclusion of age-at-release improved the model ($\Delta \mathrm{AIC}_c = 1.71$). Annual survival for marmots released as yearlings was lower (0.602; 95% CI = 0.459–0.729) than for those released as 2-year-old or adults (0.774; 95% CI = 0.649–0.864).

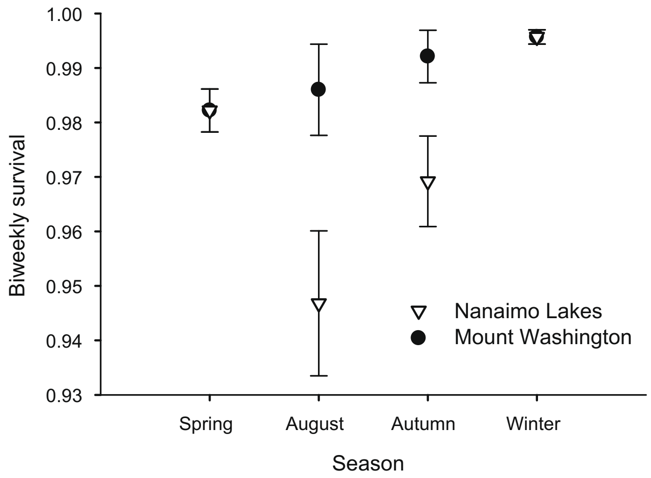

Fig. 3. Estimates of biweekly survival rates (±1SE) estimated using the most parsimonious model of the known-fate analysis (Table 2b, model no. 1). Survival differed between sites during August and fall, but not during spring/early summer or winter. For the winter interval, survival was estimated over a 2-week interval as a derived parameter; therefore, winter survival is directly comparable to biweekly survival rates during other seasons.

Table 3
Analysis of the influence of (a) intrinsic (sex and age) and (b) extrinsic factors on survival (S) of the Vancouver Island marmot using a subset of the radio-telemetry data (2003–2007) and known-fate models. Akaike's Information Criterion corrected for small sample size (AIC_c), differences in AIC_c values ($\Delta \mathrm{AIC}_c$), AIC_c weights (w_i), and the number of parameters (np) are shown for each model. The most parsimonious model in the first set of analysis testing (for intrinsic differences in survival) was used as the base model for the second set of analysis testing for effects of extrinsic factors. In both analyses, the selected models are highlighted in bold.

No.	Model	AIC_c	$\Delta \mathrm{AIC}_c$	w_i	np
(a)[a]					
1	S(sex)	488.66	0.00	0.322	2
2	S(2-age-class + sex)	489.79	1.13	0.183	3
3	**$S(\cdot)$**	**490.21**	**1.54**	**0.149**	**1**
4	S(2-age-class)	490.77	2.11	0.112	2
5	S(3-age-class + sex)	491.43	2.77	0.081	4
6	S(2-age-class + $\mathrm{sex}_{\geqslant 2\mathrm{year}}$)	491.44	2.77	0.080	3
7	S(3-age-class)	492.56	3.89	0.046	3
8	S(3-age-class + $\mathrm{sex}_{2\mathrm{year}}$)	493.58	4.92	0.028	4
(b)[b]					
1	**S(2-season + origin)**	**455.82**	**0.00**	**0.368**	**3**
2	S(2-season $*$ origin)	456.19	0.37	0.305	4
3	S(2-season + origin + $\mathrm{first}_{A,F}$)	457.25	1.43	0.180	4
4	S(2-season + origin + first_{W})	457.69	1.87	0.145	4
5	S(4-season)	467.92	12.10	0.001	4
6	S(2-season)	468.29	12.46	0.001	2
7	S(3-season)	470.24	14.42	0.000	3
8	S(origin)	479.60	23.78	0.000	2
9	$S(\cdot)$	490.21	34.38	0.000	1
10	S(first)	491.79	35.97	0.000	2

The "first" covariate refers to the "release cost" effect, where survival is different the first year for released marmots (or first season only as indicated by subscript) than post-first year. Pluses (+) indicate additive effects and the dot ($\cdot$) indicates a constant parameter value.

[a] Age-classes are yearlings, 2-year-olds, and adults for the 3-age-class models. Age classes for 2-age-class models are yearlings and adults. Subscripts indicate age-class(es) for which the model allows the age class to affect survival ($\geqslant$2 year = 2-years of age or older; 2 year = 2-year old; ad = adults).

[b] The 4 "seasons" were spring/early summer (S, emergence-July 31), August (A, August 1–28), fall (F, August 29-immergence), and winter (W, hibernation); the 3-season model combined August and fall; and the 2-season model combined the entire active season. Subscripts indicate allowing survival to differ between sites only during season(s) noted.

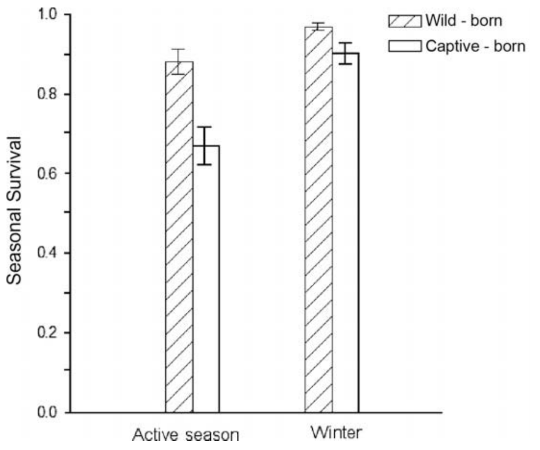

Fig. 4. Estimates of seasonal survival rates (±1SE) for captive-born and wild-born marmots estimated using the most parsimonious model from the subset analysis (Table 3b, model no. 1). Active season survival spans 24 weeks, and the winter season spans 28 weeks.

3.2. Cause-specific mortality

There was a significant difference in mortality rates between captive and wild-born individuals from eagles, cougars, and over winter ($p = 0.018$, 0.039, 0.010, respectively). For each of these causes, mortality was higher for captive-born marmots than wild-born marmots (Fig. 5). Mortality due to unknown causes was higher for captive-born marmots than wild-born marmots ($p = 0.054$). Wolf predation was the only cause for which wild-born marmots had higher mortality than captive-born; however, there was not a significant difference between these rates ($p = 0.150$).

Predation by eagles was the most important known cause of death for captive-born marmots, whereas predation by wolves was the primary known cause of death of wild-born marmots (Fig. 5). As a percentage of known mortality (i.e., cause-specific mortality rate/total mortality rate), eagle predation accounted for 25% of captive-born deaths and 13% of wild-born deaths. Cougar predation and winter mortality also were relatively more important sources of mortality for captive-born marmots than wild-born marmots. In contrast, wolf predation accounted for 30% of known wild-born marmot mortality and only 6.4% of captive-born marmot mortality. Mortality due to unknown causes accounted for about a third of known deaths for marmots of both origins.

3.3. Analysis of combined (radio-telemetry and CMR) data

Using the combined dataset, we first tested for the effect of age, sex, and additive and interactive effects of the two on survival and recapture rate (Table 4a). There was evidence to support age-specificity; the most parsimonious model included 3-age-classes for survival (pups, yearling = adult, and 2-year-old) and 2-age-classes for resighting rate (yearlings = adults and 2-year-old). Estimated annual survival rate was lowest for pups ($S = 0.500$; 95% CI = 0.375–0.616), but generally high for yearlings and adults ($S = 0.656$; 95% CI = 0.604–0.705), and 2-year-old ($S = 0.649$; 95% CI = 0.527–0.754). Recapture rate was high for yearlings and adults ($\rho = 0.917$; 95% CI = 0.844–0.958) and lower for 2-year-old ($\rho = 0.677$; 95% CI = 0.464–0.836), the dispersing age class (model 1, Table 4a)

Apparent survival differed between sexes only in the 2-year-old age-class, with females surviving better than males. Survival for 2-year-old males was much lower ($S = 0.471$; 95% CI = 0.331–0.615) than survival of 2-year-old females ($S = 0.792$; 95% CI = 0.629–0.895; Fig. 6a). Therefore, we continued our analysis with the model including age-specific survival and recapture rates and sex-specific survival in the 2-year-old age-class only (model 1, Table 4a).

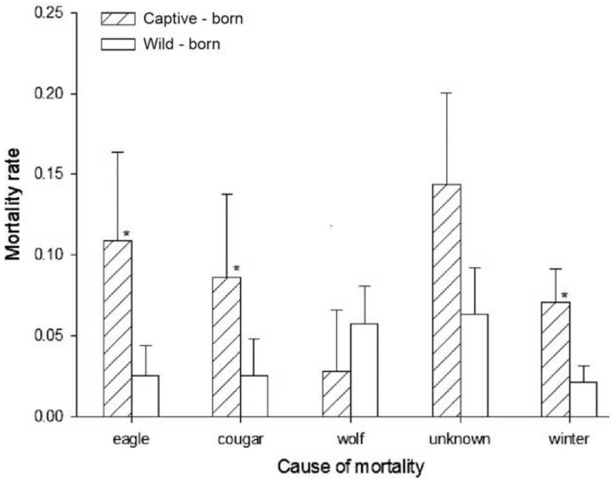

Fig. 5. Estimates of cause-specific mortality rates (mean ± 1SE) for captive-born and wild-born marmots estimated using the nonparametric cumulative incidence function estimator. Significant differences are indicated by an asterisk (∗). Most of the "unknown" cases of mortality represented cases in which predation was known to have been the cause of death, but for which forensic clues precluded identification of the predator species involved.

Next, we tested for the effects of habitat type (natural or clearcut) on survival. We found evidence for an effect of habitat type on apparent survival in the 2-year-old age-class only. The most parsimonious survival model included the additive effects of both sex and habitat type on the apparent survival of 2-year-old age-class (Table 4b, model 1). Two-year-old in clearcut habitat had lower apparent survival ($S = 0.446$; 95% CI = 0.263–0.646) than those in natural habitat ($S = 0.719$; 95% CI = 0.569–0.833). The additive effects of both sex and habitat type on the apparent survival of 2-year-old age-class are presented in Fig. 6b. There was evidence for site-specific differences in apparent survival (model 1, Table 4b), with marmots at Washington surviving better than those at Nanaimo.

4. Discussion

Low numbers, restricted and sparse habitat, small geographic distribution, and anthropogenic influences on marmot habitat continue to cause concern regarding the persistence of Vancouver Island marmots. Given the extremely small population size, the marmot population is at substantial risk of extinction due to demographic stochasticity alone (Caswell, 2001; Caughley and Gunn, 1996; Morris et al., 2002). This risk is exacerbated by the harsh and dynamic environment *M. vancouverensis* inhabits, and with changing ecosystem and predator-prey dynamics. Thus, it is likely that conservation measures are necessary in the foreseeable future to ensure long-term persistence of marmots. Our goal was to assist Vancouver Island marmot conservation efforts by providing rigorous estimates of survival rates, evaluating factors influencing survival of marmots, and making recommendations for the reintroduction program.

4.1. Survival rates and sex- and age-specific differences

Using radio-telemetry data (1992–2007), the overall annual survival of marmots (excluding pups) was 70.9%. There was no evidence that survival differed between sexes or among age classes. Our results regarding the effects of sex on survival of radio-tagged marmots as well as estimates of annual survival rate are similar to those reported by Bryant and Page (2005).

Analyses of combined dataset (i.e., radio-telemetry and mark-resight) revealed strong evidence for age-specific differences in survival, with annual apparent survival of pups ($S = 51.6\%$) being substantially lower than that of other age-classes ($S \geqslant 65\%$). Pups typically remained close to and hibernated at their natal burrow, and resighting rate of pups (as yearlings the next year) was generally high.

Sex effect was apparent only in apparent survival of 2-year-old marmots. Survival of 2-year-old males (47%) was much lower than survival of 2-year-old females (79%). Vancouver Island marmots typically disperse at 2 years of age, and males in most species of marmots have a greater propensity to disperse than females (Armitage, 1999; Arnold, 1990; Barash, 1989; Bryant, 1998; Van Vuren and Armitage, 1994). We believe that low apparent survival for 2-year-old males may be a consequence of male-biased dispersal. This speculation was further supported by the observation that capture probability for 2-year-old was substantially lower than that for other age-classes.

The low apparent survival rate for the dispersing age class has been observed in other species of marmots (Farand et al., 2002;

Table 4
Analysis of the influence of (a) intrinsic (sex and age) and (b) extrinsic factors on survival (S) and recapture rate (ρ) of the Vancouver Island marmot using a combination of radio-telemetry and capture–recapture data and multi-state models. Akaike's Information Criterion corrected for small sample size (AIC_c), differences in AIC_c values (ΔAIC_c), AICc weights (w_i), and the number of parameters (np) are shown for each model. The most parsimonious model in the first set of analysis (testing for intrinsic differences in survival) was used as the base model for the second set of analysis testing for effects of extrinsic factors. In both analyses, the most parsimonious models are highlighted in bold.

No.	Model	AIC_c	$\Delta\ \text{AIC}_c$	w_i	np
(a)[a]					
1	**$S(\text{3-age-class} + \text{sex}_{\text{2year}})\rho(\text{2-age})$**	**765.81**	**0.00**	**0.644**	**6**
2	$S(\text{3-age-class} + \text{sex}_{\text{2year}})\rho(\text{2-age} + \text{sex}_{\text{2year}})$	767.59	1.77	0.265	7
3	$S(\text{2-age})\rho(\text{2-age})$	771.44	5.62	0.039	4
4	$S(\text{4-age} + \text{sex}_{\geqslant\text{2year}})\rho(\text{2-age})$	773.02	7.21	0.018	7
5	$S(\text{3-age})\rho(\text{2-age})$	773.15	7.33	0.016	5
6	$S(\cdot)\rho(\text{2-age})$	774.73	8.92	0.007	3
7	$S(\text{4-age})\rho(\text{2-age})$	775.18	9.37	0.006	6
8	$S(\cdot)\rho(\text{3-age})$	776.95	11.14	0.002	4
9	$S(\text{sex})\rho(\cdot)$	778.97	13.16	0.001	3
10	$S(\cdot)\rho(\cdot)$	779.54	13.73	0.001	2
11	$S(\text{sex})\rho(\text{sex})$	780.56	14.75	0.000	4
12	$S(\cdot)\rho(\text{sex})$	780.81	15.00	0.000	3
(b)					
1	**$S(\text{3-age} + \text{sex}_{\text{2year}} + \text{site} + \text{habitat}_{\text{2year}})\rho(\text{2-age})$**	**755.28**	**0.00**	**0.753**	**8**
2	$S(\text{3-age} + \text{sex}_{\text{2year}} + \text{site})\rho(\text{2-age})$	758.04	2.76	0.189	7
3	$S(\text{3-age} + \text{sex}_{\text{2year}} + \text{habitat}_{\text{2year}})\rho(\text{2-age})$	761.49	6.21	0.034	7
4	$S(\text{3-age} + \text{sex}_{\text{2year}} + \text{site}_{\geqslant\text{2year}})\rho(\text{2-age})$	763.72	8.45	0.011	7
5	$S(\text{3-age} + \text{sex}_{\text{2year}} + \text{habitat}_{\geqslant\text{2year}})\rho(\text{2-age})$	765.12	9.85	0.005	7
6	$S(\text{3-age} + \text{sex}_{\text{2year}})\rho(\text{2-age})$	765.81	10.54	0.004	6
7	$S(\text{3-age} + \text{sex}_{\text{2year}} + \text{habitat})\rho(\text{2-age})$	766.02	10.75	0.003	7

[a] Age-classes are pups, yearlings, 2-year-olds, and adults. For recapture rate, 3 age-class models consider yearling, 2-year-old, and adult differently; and, 2 age-class models consider yearling and adult recapture rate to be equal but different from 2-year-old recapture rate. For apparent survival, 2 age-class models are pups and older marmots (>1 year); 3 age-class models are where pup and 2-year-old apparent survival differ, and yearling and adult survival are set equal. All subscripts refer to the age-class(es) for which the individual covariate was considered ($\geqslant$2 year = 2-years of age or older; 2 year = 2-year old; ad = adults). Pluses (+) indicate additive effects and the dot ($\cdot$) indicates a constant parameter value.

Ozgul et al., 2006). While it is often thought that dispersing marmots face a greater risk of mortality and therefore have lower survival (Ozgul et al., 2006; Van Vuren and Armitage, 1994; Van Vuren, 2001), this trend was not apparent in the known-fate analysis of radio-telemetry data. The lower apparent survival of 2-year-old males obtained from CMR analysis than survival estimated from radio-telemetry data most likely was due to the fact that CMR-based methods cannot distinguish between death and permanent emigration (Williams et al., 2002).

Our findings (based on the analysis of combined data) that survival of pups was lower than that of other age-classes, and that apparent survival of dispersing age class was lower than that of yearling and adult marmots, are similar to those reported for other species of ground-dwelling sciurids (Armitage, 2003; Bronson, 1979; Bryant, 1998; Farand et al., 2002; Griffin et al., 2008; Ozgul et al., 2006; Sherman and Runge, 2002). However, annual apparent survival for pups (50%) was lower than those reported for Alpine marmot pups (62%, Farand et al., 2002), yellow-bellied marmot pups (Ozgul et al., 2006), and most relevantly, Olympic marmot pups (60% from tagging, Griffin et al., 2008). Our estimates of age-specific apparent survival for older age-classes of *M. vancouverensis* were generally lower than those reported for other species of marmots (Farand et al., 2002; Ozgul et al., 2006).

4.2. Seasonal and site-specific variation

Analysis of radio-telemetry data revealed substantial seasonal variation in survival (Table 2b, Fig. 3), with higher survival during hibernation than during late summer/fall (also see Bryant and Page, 2005). However, support for 2-, 3-, and 4-season models was similar, suggesting that the primary cause of seasonal variation was the substantially higher survival during hibernation than during the active season. Marmots are not exposed to predators and other mortality factors linked with activity above ground during hibernation, and are thought to be efficient hibernators (Bryant and McAdie, 2003); consequently, survival rates are higher during winter than during the active season. Comparison of our results with those of Bryant and Page (2005) suggests that seasonal variation in survival, throughout the year and particularly during active season, may have become less pronounced in recent years (i.e., mortality is more evenly spread throughout the active season, instead of higher mortality during August and fall relative to spring and early summer).

Both the radio-telemetry data and combined telemetry and CMR data suggest that survival at the Mt. Washington site was higher than in the Nanaimo Lakes region. The two areas are quite different; Mt. Washington is a ski hill, where most marmots live on ski slopes. These ski slopes are technically clearcuts; however, they more closely resemble natural meadows due to stumps being removed and maintenance to prevent regeneration. Apparently, the ski slopes are suitable habitat, although differences in vegetative composition and how this affects fitness and survival of marmots have not been formally tested.

The other major difference is the amount of human activity at each site. Whereas much of the land inhabited by marmots in the Nanaimo Lakes region is private land inaccessible to the public, Washington is a popular ski slope with lots of human traffic. Griffin et al. (2007) found that high levels of tourist traffic did not negatively affect demographic rates of Olympic marmots in Olympic National Park. Although the majority of human activities at Mt. Washington occur during winter months while marmots are hibernating, summer activities have become increasingly popular in recent years. While human presence may not have a direct effect on demographic rates of marmots, there could be indirect effects (e.g., modification of behaviors; Griffin et al., 2007).

4.3. Habitat changes and Vancouver Island marmots

The landscape of Vancouver Island has undergone substantial change, especially since logging intensity increased in the

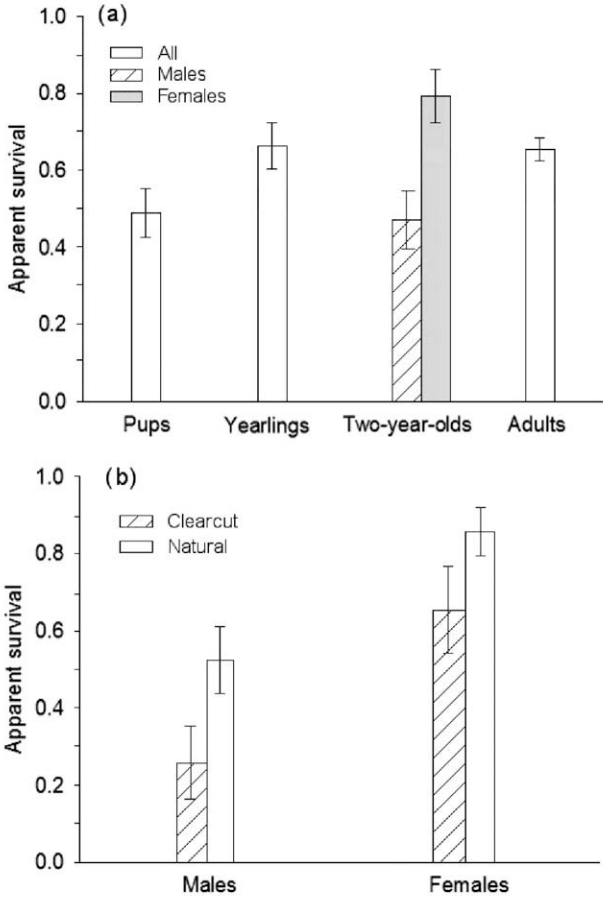

Fig. 6. (a) Age-specific annual apparent survival rates (means ± 1SE)) estimated using model no. 1, Table 4a. Apparent survival rates differed between males and feamales only for 2-year-old. (b) Sex-specific annual apparent survival rates for 2-year-old marmots by habitat type at Nanaimo Lakes based on model no. 1 in Table 4b.

1950s. High elevation clearcut logging created patches of open meadows that resembled natural marmot habitat. These newly created habitats were colonized by marmots, and by the 1990s, nearly half of the known marmot population inhabited clearcuts (Bryant, 1996; Bryant and Janz, 1996). However, most marmot colonies in clearcut habitats have disappeared and very few marmots have been observed in clearcuts in recent years. Why did marmots disappear from the clearcut habitats where they thrived during the 1980s?

One explanation is that clearcut habitat served as an ecological or evolutionary trap (Robertson and Hutto, 2006; Sherman and Runge, 2002). While marmots may have persisted in clearcuts that initially resembled natural meadows, subsequent forest regeneration rendered clearcut habitat unsuitable for marmots over a few years or decades. In addition, clearcut logging substantially changed the landscape structure and local marmot population density. These changes could have caused an increase in mortality of marmots due to predation through several mechanisms: (a) an increased proportion of open habitat in the landscape, making the area more attractive to avian predators; (b) an increase in secondary growth and edge habitat, where predation by wolves and cougars would be higher; (c) logging roads could have acted as conduits for the movement of both predators and marmots, possibly increasing the probability of encounters; and/or (d) an increase in secondary growth altering the abundance of other prey species, and consequently the abundance of predators. We note that these mechanisms are not mutually exclusive.

4.4. Captive-breeding, cause-specific mortality, age-at-release and conservation of *M. vancouverensis*

Our results clearly show that captive-born marmots suffer a higher mortality than wild-born marmots, and these results are consistent with findings of Jule et al. (2008). In addition, causes of mortality also differed between the two groups; captive-born marmots were much more vulnerable to avian predators than their wild-born counterparts. These results suggest that, whereas captive-born marmots exhibit anti-predatory responses to mammalian predators (Blumstein et al., 2001, 2006), their ability to detect and/or avoid avian predators may be compromised. Pre-release anti-predator training improves survival in the wild for some species (Shier and Owings, 2006; van Heezik et al., 1999). Exposing captive-born marmots to predators (particularly, golden eagles) before they are released may enhance their survival in natural habitats and contribute to the success of the release program; this however, is unproven and would be financially and logistically challenging to implement.

In some species, reintroduced individuals suffer a higher mortality during the first year after release; however, the survival may be similar to those of wild-born individuals thereafter (Bar-David et al., 2005; Le Gouar et al., 2008; Sarrazin et al., 1994). We tested for this effect, and found no evidence that survival of captive-born marmots improved after their first active season, winter, or full year in the wild.

Age at which captive-bred individuals are released can also influence demography of reintroduced populations (Green et al., 2005; Sarrazin et al., 1994; Sarrazin and Legendre, 2000). Marmots released as 2-year-old had an approximately 17% higher probability of survival than marmots released as yearlings (survival of marmots released as 2-year-old: 0.602 ± 0.070; survival of marmots released at an older age: 0.774 ± 0.055). Thus, marmots released at >2 year of age are more likely to survive to reproductive age and contribute to the population growth via reproduction. The initial increase in costs associated with rearing marmots for an extra year may be well worth it if, as our results suggest, it can increase the probability of success of the release program.

Acknowledgements

Project funding was provided in various years by the BC Habitat Conservation Trust Fund, BC Ministry of Environment, World Wildlife Fund (Canada), Forest Alliance of BC, Forest Renewal BC, Cowichan Valley Field Naturalists Society, Nanaimo Field Naturalists, BC Wildlife Federation, BC Hydro Bridge Coastal Fish and Wildlife Restoration Program, TimberWest Forests, MacMillan Bloedel Limited, Environment Canada (administered through the University of British Columbia), and the Marmot Recovery Foundation. One of us (AAB) was partially supported in some years by a Province of Alberta Graduate Scholarship, University of Calgary Thesis Research Grant, a Canadian Wildlife Service Research Grant, a King-Platt Memorial Award, Franc Joubin Graduate Bursary in Environmental Science, and University of Victoria (Biology) graduate award.

Other essential support was by provided by the University of Florida, Toronto Zoo, Calgary Zoo, Mountain View Breeding and Conservation Center, West Coast Helicopters, Mt. Washington Alpine Resort, BC Conservation Foundation, BC Conservation Corps, and the Nature Trust of BC. MacMillan Bloedel Limited, Weyerhaeuser, Island Timberlands, TimberWest Forests and Mt. Washington Alpine Resort allowed unrestricted field access to private forest lands.

K. Langelier DVM pioneered radio-implant techniques for Vancouver Island marmots in 1992. M. McAdie DVM subsequently performed the majority of radio implant surgeries. H. Schwantje DVM,

S. Saksida DVM and M. Smith DVM also performed implantation surgeries.

This work would not have been possible without the dedicated work of many individuals who collected and supplied field data: these include: A. Bryant, M. DeLaronde, D. Doyle, C. Jackson, D. Janz, L. Dyck, J. Lewis, K. McDonald, J. MacDermott, D. Milne, M. McAdie, D. Norton, A. Pendergast, S. Pendergast, C. Reid, W. Swain, J. Voller, L. Wilson, and A. Zeeman. Many others too numerous to list here helped with trapping, resighting and telemetry work. We thank them all. K. Armitage, V. Goswami, J. McRae, and E. Kneip provided helpful comments on the manuscript, for which we are grateful.

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