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## Getting Back to Normal: Space Use and Behaviour of Reintroduced and Wild Vancouver Island Marmots

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### Abstract

I report on initial conservation efforts to reintroduce captive-reared Vancouver Island marmots (*Marmota vancouverensis*) into historical natural habitat. The home range size, movements, time allocation, and behaviour of 25 reintroduced and 30 wild free-living Vancouver Island marmots were studied over 3 active seasons (May through October 2003-2005) to assess the performance and challenges influencing survival of reintroduced animals. Activity budgets, frequency of vigilance, and ranging behaviour of wild and reintroduced marmots were generally similar. Poor survival of reintroduced marmots appears to be associated with low site fidelity. It remains unclear whether experiences during captive-rearing encourages individuals to seek out inappropriate habitats, or whether stress induced during transport and release into unfamiliar environments precipitates long distance movements.

**Key Words:** Endangered Species, Flight Distance, Immersion Distance, Marmot Behaviour, Population Recovery, Time Allocation.

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## INTRODUCTION

The use of reintroductions for recovery of endangered mammals has become common practice where risk of extinction is deemed immanent (Kleiman 1989; IUCN 1998; Grey-Ross *et al.* 2009). Patterns among successful and failed reintroductions are emerging that point to common outcomes (Seddon *et al.* 2007; Roe *et al.* 2010). For example, translocating wild-born animals is generally more successful than the use of captive-bred individuals (Ginsberg 1994; Fischer and Lindenmayer 2000; Jule *et al.* 2008). Soft releases produce better outcomes than hard releases (Bright and Morris 1994; Werner 2015), and pre-release training can increase the initial survival of naïve recruits (Biggins *et al.* 1999). Finally, releasing a minimum number of individuals (Wolf *et al.* 1996, 1998; Veltman *et al.* 1996; Green 1997) into intact historical habitat (Griffith *et al.* 1989) typically improves the survivorship and site fidelity of captive-reared animals. Notwithstanding the many advances to the praxis of mammalian reintroductions, the process of captive rearing and release remains costly, and the survival of reintroduced individuals remains low (Griffith *et al.* 1989; Fischer and Lindenmayer 2000).

The case of the endangered Vancouver Island marmot (*Marmota vancouverensis*) illustrates several of the trade-offs that recovery managers grapple with when attempting to avert population extinction. By the early 2000s the wild population had declined to less than 35 individuals (Bryant 2005); a captive-breeding program was initiated to support a future release program (Janz *et al.* 2000; VIMR Team 2008). Despite continued low post-release survivorship of reintroduced animals (Aaltonen *et al.* 2009), the reintroduction of nearly 500 individuals (2003-present) has resulted in 2 self-sustaining sub-populations each estimated to exceed 100 marmots (Pendergast and Reid 2007, 2008; Reid *et al.* 2009; Jackson and Lester 2016).

The purpose of this study was to compare the behaviour, movements, and space-use of reintroduced and wild Vancouver Island marmots. This study constitutes the only comparison of this kind and contributes to our understanding of the outcomes of these recovery efforts and to reintroduction praxis in general. Because the initial release groups were small (1-7 marmots), male-biased (approximately 2:1), and composed primarily of young unrelated animals (typically 2 years of age), I expected to observe low social cohesion among reintroduced animals and a tendency toward large exploratory movements consistent with the need to relocate to a 'suitable colony'. Some survival skills likely have a learned or socially transmitted component (Shier and Owings 2007; Reader and Biro 2010). Because captive conditions offer less

opportunity for individuals to identify natural forage and sources of risk, or to acquire skills necessary to balance wariness with food acquisition, I expected reintroduced marmots to be less vigilant and less sensitive to sources of danger. This prediction is consistent with the observation that reintroduced Vancouver Island marmots have lower survival than their wild counterparts (Werner 2005; Aaltonen *et al.* 2009). Because patterns of time allocation are a complex response to physiological needs and to environmental variation, time budgets of wild and naïve individuals were expected to differ. However, given the manifold ways in which these differences might be expressed no specific predictions were made.

## METHODS

### Study species

The Vancouver Island marmot is a large (4–6 kg), fossorial rodent endemic to Vancouver Island, British Columbia, Canada. The species was once widely distributed across the 31,000 km<sup>2</sup> island (Nagorsen *et al.* 1996), but by 2006 the wild population consisted of only 32 adult animals divided among 6 colonies (Brashares *et al.* 2010). Approximately 170 animals were held in 4 captive-breeding facilities. The marmot is presently redlisted by the IUCN as critically endangered (Nagorsen *et al.* 2013). The species is genetically different from other marmots (Kerhoulas *et al.* 2015) as well as having distinct skull morphology and pelage (Nagorsen *et al.* 1996; Cardini *et al.* 2009), behaviour (Heard 1977), and vocalizations (Blumstein 1999). The Vancouver Island marmot is a diurnal generalist herbivore (Martell and Milko 1986; Werner 2012) that uses burrow systems for shelter and escape during a 5-month active season (May–September) prior to hibernation (October–April). Breeding occurs shortly after emergence from hibernation (early May) and 1-7 pups (mean 3.4) are born after ~30 d of gestation. Young males face reproductive suppression and aggression from adult males and often disperse to new colonies when 2 or 3 years of age (Janz *et al.* 2000).

### Study population

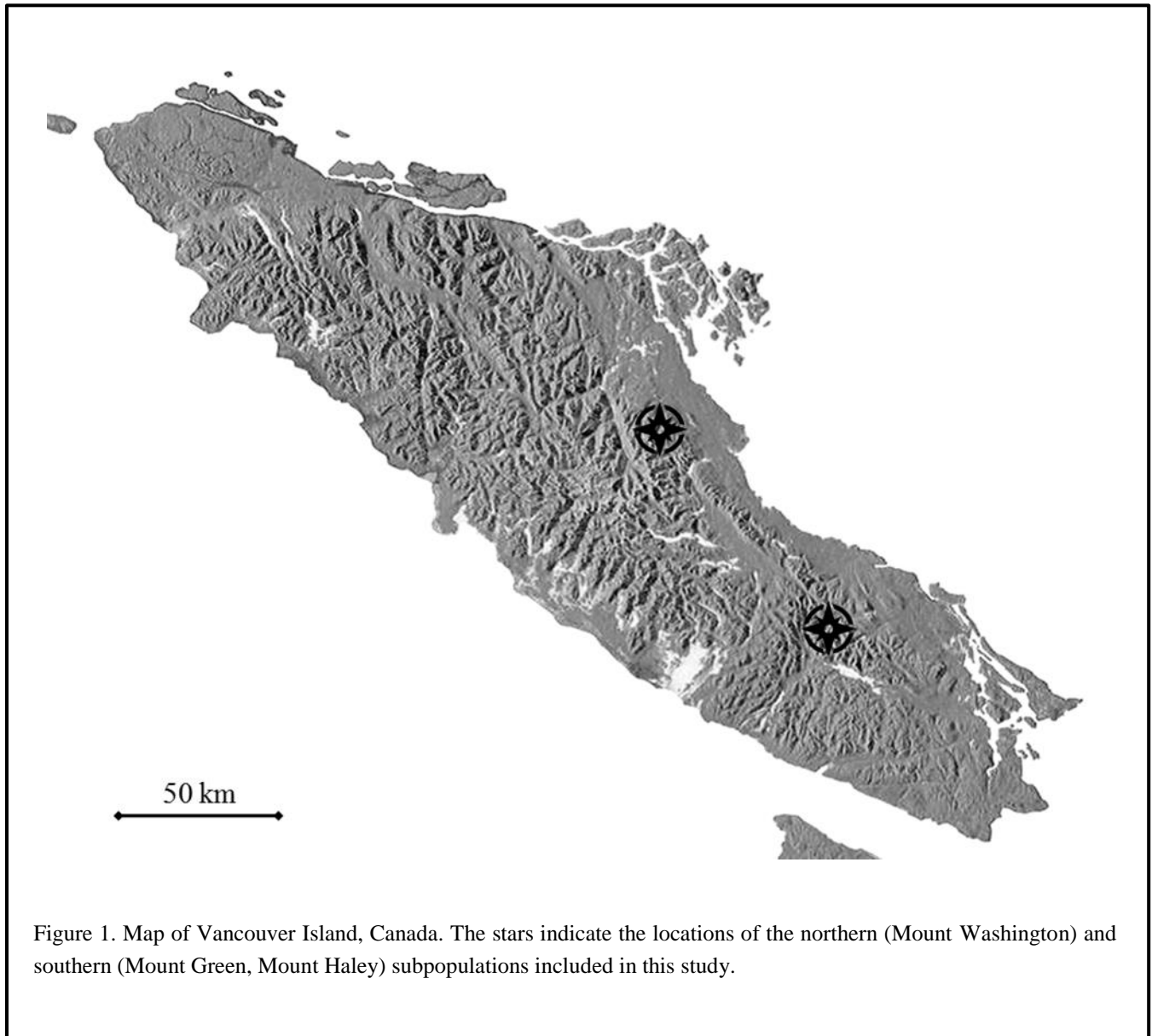
Twelve marmots raised in captivity were released and monitored during 2003-2005 at 1 active colony (Mount Washington; 4945'N 12517'E, 2004) and at 2 extinct colony sites (Mount Green, 4903'N 12420'E; Haley Bowl Ecological Reserve, 4860'N 12417'E). Four 2-year old marmots (2 ♀, 2 ♂) were released during July 2003 to Mount Green. The following year, 6 2-year marmots were released to Mount Haley (2 ♀, 4 ♂) and 2 were released to Mount Washington (2 ♀, 2 and 4 years old; Table 1). An additional 14 individuals (7 yearlings at Haley, 5 2-year-old marmots on Mount Green, and 1 4-year-old marmot on

Table 1: Minimum linear and contour (ridgeline) movement distances (km) between release site and furthest recorded location for 26 reintroduced Vancouver Island marmots during 2003-2005. Minimum distance is the straight line connecting 2 points, whereas contour movements were determined by the distance connecting 2 points by the maximum height of land (i.e., ridge connecting mountain tops).

<b>Animal ID</b>	<b>Sex</b>	<b>Age (yrs)</b>	<b>Location</b>	<b>Year</b>	<b>Linear</b>	<b>Contour</b>
1	F	1	Haley	2005	11.23	16.04
2	F	1	Haley	2005	1.10	1.51
3	F	2	Green	2003	0.40	0.44
4	F	2	Green	2003	0.35	0.39
5	F	2	Green	2005	1.83	2.64
6	F	2	Green	2005	0.22	0.28
7	F	2	Wash	2004	0.94	1.45
8	F	2	Haley	2004	6.53	8.72
9	F	2	Haley	2004	0.21	0.25
10	F	4	Wash	2004	0.73	0.91
11	M	1	Haley	2005	6.75	9.96
12	M	1	Haley	2005	5.26	6.87
13	M	1	Haley	2005	1.47	2.09
14	M	1	Haley	2005	3.22	3.76
15	M	1	Haley	2005	5.24	6.93
16	M	2	Green	2003	3.39	4.12
17	M	2	Green	2005	4.04	4.53
18	M	2	Green	2005	0.25	0.36
19	M	2	Green	2005	11.08	14.11
20	M	2	Haley	2004	0.34	0.38
21	M	2	Haley	2004	5.25	6.25
22	M	2	Haley	2004	2.29	2.84
23	M	2	Haley	2004	7.20	10.87
24	M	3	Green	2003	1.33	2.07
25	M	5	Wash	2005	0.62	0.68
26	M	5	Wash	2005	1.43	1.67

Mount Washington) were released in 2005. Data from these 14 animals are limited to movement estimates from July to the onset of hibernation. Figure 1 shows the general locations of the northern and southern study populations. Excepting Mount Washington, which is an active colony ( $n \approx 10$ ), all released animals were placed in unoccupied habitats containing historical burrow systems. All sites consisted of steep forested slopes at elevations of 700-1300 m surrounding isolated patches of rock talus and sub-alpine meadow. Habitat at Mount Washington also included several ski runs.

For comparison, data from 21 wild marmots (36 animal years) were collected at 3 colonies May–October 2002-2005. Mount Washington was studied most intensively, with some data collected from Mount Green, Mount Moriarty (4900'N 12427'E) and Mount Heather (4900'N 12416'E). A detailed account of the study sites, animals, study methods and previous research is summarized by Brashares *et al.* (2010). Each wild and reintroduced individual was individually ear-tagged and implanted with a VHF radio transmitter to allow accurate tracking. Bryant (1998) described the transmitters, and capture and implant



techniques. This research was approved by The University of British Columbia Animal Care Committee in accordance with the guidelines of the Canadian Council on Animal Care (CCAC 2003).

#### Field methods

The behaviour, movement, and habitat use of reintroduced and wild marmots were recorded daily from emergence (May for wild animals) or time of release (July for released animals) to the onset of hibernation (October). A soft-release approach (Kleiman 1989) was used that included the provision of cover and food, and the use of electric fencing to exclude mammalian predators. Marmots were held for 24 h in wooden nest boxes (61 x 122 x 122 cm; packed with straw) that connected to a single natural burrow system before removing the doors (Bryant 2007). This holding

period was intended to acclimatize individuals to that burrow system. Nest boxes were left in situ for 30 d post-release to provide thermal shelter, refuge from predators, and a reference point during exploratory movements.

#### Home ranges and travel

Each day when a marmot was first located via telemetry, the observer recorded its exact location and altitude using a hand-held GPS receiver accurate to  $\pm 6$  m. Home ranges were mapped using  $>35$  locations (mean=88 for wild marmots, 61 for reintroduced marmots) collected once daily and sampled evenly across the 5 ½ -month active season (2½ months for reintroduced marmots). Specific methods used to construct individual home ranges were described by Brashares *et al.* (2010). Large dispersal-like movements ( $>2$  km) were excluded from home range analyses and evaluated separately.

In addition to home range estimates, the minimum linear distance between successive independent (minimum 24 h apart, mean=56.4 h) locations was used to assess travel costs and to compare movement patterns between wild and reintroduced marmots. This distance was measured using the formula:

$$d = \sqrt{(x_2 - x_1)^2 + (y_2 - y_1)^2}$$

where  $d$  is the shortest distance between 2 successive locations, and  $x_1$ ,  $x_2$  and  $y_1$ ,  $y_2$  are the Northing and Easting bearings for each point in Universal Transverse Mercator. Changes in elevation during travel are not included in this calculation.

Where marmot movements from the release site were extensive, such movements were measured as the linear distance between the point of release and the furthest recorded location. Several very distant coordinates were obtained by provincial government staff via helicopter telemetric searches. Because marmots likely follow ridges when moving between mountains, more realistic distances were also estimated by measuring the most direct ridge systems connecting locations (using NTS 1:50,000 topographic maps).

#### **Sociality and time allocation**

Individual marmots were located and observed daily according to schedules constructed 14 d in advance. These schedules ensured field observers did not bias results by choosing when to initiate or terminate a focal observation. A randomized protocol was used to achieve equal coverage of animals and sample times, and to minimize observer and sampling biases related to the duration, onset, and termination times of a sampling event. Behavioural data were gathered using a focal sampling approach (Altman 1974). To obtain unbiased estimates of time allocated to below and above ground activity, behaviour sampling sessions also included the time an individual spent underground. Specifically, a single marmot's activity was scored at 1-min intervals for 60 consecutive minutes. Recorded were the animal's body position (sitting, lying, standing, moving, alert posture), head position (up or down), orientation (up, down, or across-slope), social interactions (Heard 1977), feeding, movement, and use of burrows. Every alarm call was also recorded (Barash 1989). For consistency, I used Heard's (1977) ethogram during behaviour sampling. Approximately 300 h of behavioural observations were collected for the 12 captive-bred marmots released in 2003 and 2004, and over 1,500 h were collected for 21 wild marmots (36 animal-years; see data analysis). Most focal observations were conducted between 06:00 and 20:00 when transmitters were active. The behavioural sampling methods

were described in greater detail elsewhere (Werner 2005; Brashares *et al.* 2010). Individuals were identified from their radio-telemetry frequencies and distinctive molt pattern. Behaviours were observed from 50-300 m using 10x binoculars and 60x spotting scopes.

#### **Immergence distances**

Because most predator mortalities occurred within several meters of a burrow (personal observation made during the recovery of transmitters), immergence distance was measured at the moment a solitary marmot retreated to underground safety in response to an advancing threat. Flight initiation distances were not measured. However, marmots typically initiated movement in response to sources of threat at distances greater than 40 m (Werner 2005). Individual marmots were approached from a proximity of >120 m (distance determined using a Leica DISTO E7500i range finder) within 5 min of being located. Single animals were approached steadily at a walking pace of 0.5m/sec from an across slope position until that marmot entered a burrow. When the marmot entered a burrow, the observer ceased moving and the linear distance between the observer and the animal's chosen refuge was recorded using a 60-m open reel tape measure. Flight and behavioural measurements were conducted on separate days. This was done to avoid biasing either study from induced wariness associated with the stress of being approached, or from reduced wariness resulting from habituation to an observer. An equal number of measurements was undertaken in the morning (48%) and afternoon (52%) for each individual. A maximum of 1 flight measure was obtained per marmot per week between July 15 and October 15, 2014. Total samples sizes for immergence distances were 11 wild and 9 reintroduced individuals.

#### **Data analyses**

Descriptive and non-parametric statistics were used with the program JMP version 4.0 (SAS institute Inc., Cary, North Carolina, USA). Kolmogorov-Smirnov tests were used to compare distributions, and Mann-Whitney  $U$  tests to compare medians of data that were not distributed normally. Having confirmed that variation between years was greater than that recorded between individuals, observations of individuals from different years were treated as independent (see also Barash 1989; Hoogland 1995; Blumstein and Arnold 1998). Results were considered significant when  $P < 0.05$ , and are presented as means  $\pm$  SE. Data for wild marmots were limited to the overlapping duration of the experimental releases (marmots were released in July).

Home ranges were plotted using the fixed non-parametric kernel (density probability; Worton 1987) method (grid resolution = 255). Data points were plotted using Home Range, Movement and X-tools extensions in ArcView 3.2 (ESRI 1996; Hooge 1999) and the Home Ranger program

(Hovey 1998). Kernels reflect the intensity of use, and do not assume a single center of activity or any particular shape (Worton 1995; Seaman and Powell 1996). The adaptive kernel method was not employed because it is subject to greater bias and exhibits more error in surface fit (Seaman *et al.* 1999). The  $h$  values (smoothing factor) were calculated as outlined by Worton (1989), rather than the least squares cross validation method, due to the large number of multiple observations in identical (or near identical) locations (Silverman 1986; Tufto *et al.* 1996; Seaman *et al.* 1998).

Methods for quantifying activity budgets for feeding, resting (lying or sitting) and in-burrow follow those of Martin and Bateson (1993). Infrequent behaviours, such as social interactions, were expressed as occurrences per animal per hour of observation. Data for activity budgets and rates of behaviour for wild marmots during 2002, 2003 and 2004 were pooled after finding no significant inter-annual differences (Brashares *et al.* 2010).

## RESULTS

### General observations

Upon release, most animals used the temporary nest boxes and fed on supplemental food pellets and water for several days, before adapting to local forage. Individuals appeared to select forbs over grasses, and flower heads over leaves/stems. Some individuals dispersed long distances during the first several weeks of release. Within 2 weeks non-dispersing marmots located to nearby burrow complexes containing talus and large boulders.

Twenty-one (81%) of the 26 captive-bred animals released in 2003-2005 dispersed or made exploratory movements (400 m to ~12 km) from their release burrow (Table 1). Seven (33%) of these dispersers selected appropriate habitat on open south-facing meadows or boulder slopes. One 2-year-old male settled in a clearcut and was subsequently translocated to Mount Green. Another 2-year-old male spent most of the active season in steep, heavily forested habitat which held few natural burrows and little forage.

### Home ranges and movements

The average home range size of reintroduced females (33.2 ha) was roughly half that of wild females (65.5 ha) ( $U=57$ ,  $n_1=7$ ,  $n_2=10$ ,  $P=0.03$ ). The average home range size of reintroduced males (123.9 ha; range=33-250 ha), was not significantly different from that of wild males (97.6 ha; range=27-201ha) ( $U=51.5$ ,  $n_1=19$ ,  $n_2=6$ ,  $P=0.71$ ). Several of the reintroduced marmots that did not disperse or undertake large movements (>300 m) had small home ranges (~30 ha). The mean maximum linear movement that reintroduced marmots made from their point of release was  $3.14 \text{ km} \pm 0.57$  ( $n=26$ , range=0.3-10.8 km). Assuming these animals

travelled along ridges connecting mountain tops, the mean maximum movement increased to  $4.25 \text{ km} \pm 0.81$  (range=0.39-16.0 km; Table 1). Comparable data are not available for long-distance movements of wild marmots because no such events were observed. Although both reintroduced and wild marmots exhibited large home ranges (Table 2), the distances between successive locations for reintroduced individuals were about half the movements of wild ones ( $129.9 \pm 28.9 \text{ m}$  vs.  $226.3 \pm 22.4 \text{ m}$ ;  $U=53$ ,  $n_1=20$ ,  $n_2=12$ ,  $P<0.01$ ).

### Sociality

Reintroduced marmots were generally more social than wild ones. Mean frequency of social interactions (per animal per hour; all individuals combined) was significantly greater in reintroduced ( $0.23 \pm 0.04$  interactions; 2003-2004) than in wild groups ( $0.18 \pm 0.04$  interactions; 2002-2004;  $U=246$ ,  $n_1=28$ ,  $n_2=12$ ,  $P<0.05$ ). Sample sizes of reintroduced animals were too small to distinguish patterns between sex or age. Both wild and reintroduced marmots exhibited a bimodal pattern of social activity. Peak social activity occurred during the months of emergence (May;  $0.33 \pm 0.05$  social interactions/h) and immergence (September/October;  $0.38 \pm 0.07$  interactions/h) for wild marmots, and the months of release (July;  $0.244 \pm 0.05$  interactions/h) and immergence (September/October;  $0.233 \pm 0.04$  interactions/h) for reintroduced marmots. The number of alarm calls recorded for reintroduced individuals during the first 10 days post-release (65;  $\approx 0.54$ /animal/day) exceeded the number recorded for wild marmots during any single year of study (highest yearly count was 31;  $\approx 0.03$ /animal/day).

### Time allocation

Reintroduced marmots allocated  $67.7 \pm 3.5\%$  of their daylight h to underground activity (in burrow), as compared to  $60.0 \pm 2.5\%$  for wild marmots. Percentage of time spent vigilant (head-up) during bouts of foraging did not differ between reintroduced ( $55.0 \pm 2.3\%$ ) and wild marmots ( $60.1 \pm 2.1\%$ ); but reintroduced animals devoted more time to bipedal alert posture ( $6.5 \pm 1.08\%$ ) than wild ones ( $1.2 \pm 0.31\%$ ) ( $U=314.5$ ;  $n_1=30$ ,  $n_2=12$ ;  $P<0.001$ ) during periods of feeding. Overall, the fraction of above ground time invested in vigilant (head up – hu) vs. non-vigilant (head down – hd) postures was nearly identical for wild (hu=66  $\pm$  2.2%, hd=34  $\pm$  1.8%) and reintroduced (hu=67  $\pm$  3.2%, hd=33  $\pm$  2.8%) individuals. Time spent feeding as a fraction of all activity was  $4.0\% \pm 0.8$  for reintroduced and  $3.5\% \pm 0.4$  for wild marmots. In short, these 2 groups allocated time similarly to above vs. below ground, in scanning vs. feeding, and in the proportion of time spent being wary vs. other activity. The only distinction was that reintroduced individuals conducted more of their scanning in an alert posture.

Table 2. Home range sizes (mean  $\pm$  SE) for reintroduced and wild Vancouver Island marmots at the 90% kernel density.

Group	90% kernal home range (ha)	<i>n</i>
<b>Reintroduced</b>		
♀*	33.2 $\pm$ 10.0	7
♂	123.9 $\pm$ 31.8	6
<b>Wild</b>		
♀	65.5 $\pm$ 11.1	11
♂	97.6 $\pm$ 11.7	19

\*Includes 1 additional home range estimate from a female that dispersed to a new mountain.

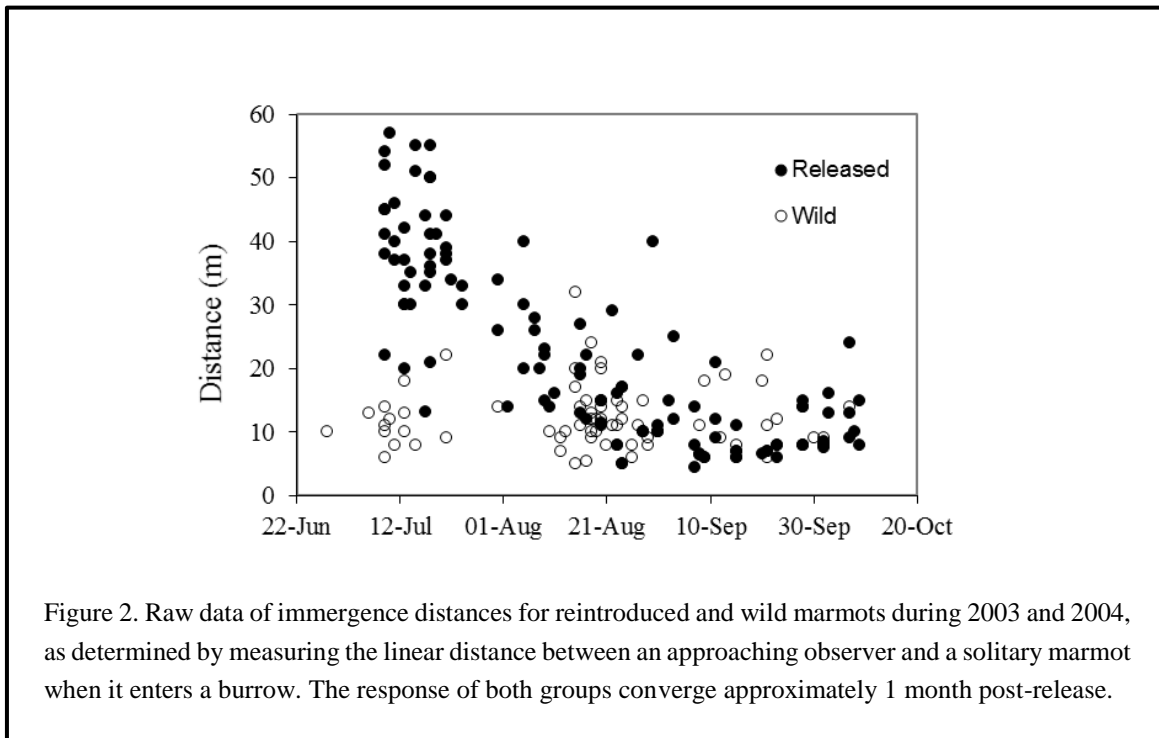


Figure 2. Raw data of immersion distances for reintroduced and wild marmots during 2003 and 2004, as determined by measuring the linear distance between an approaching observer and a solitary marmot when it enters a burrow. The response of both groups converge approximately 1 month post-release.

**Immersion distances**

A total of 122 flight responses from 9 reintroduced (5 females, 4 males) and 67 observations from 11 wild marmots (6 males, 5 females) were used to assess wariness. Immersion distances were twice as large for reintroduced (25.3  $\pm$  2.8 m) compared to wild (13.0  $\pm$  2.0 m) marmots for all months combined ( $U=89.0$ ,  $n_1=9$ ,  $n_2=11$ ,  $P<0.01$ ). Reintroduced marmots exhibited a pattern of increased

wariness during the first few weeks in their new environment, but their immersion distances decreased steadily over time (Figure 2). To ascertain whether differences between wild and reintroduced marmots were an artefact of the elevated wariness of reintroduced animals immediately after the reintroduction, these data were further partitioned into July 12–August 15 and August 15–immersion (mid-October). Early season discrepancies between wild and captive-raised

animals were highly significant ( $U=93.5$ ,  $n_1=9$ ,  $n_2=11$ ,  $P<0.01$ ), but became indistinguishable as the season progressed ( $U=34$ ,  $n_1=9$ ,  $n_2=11$ ,  $P>0.1$ ).

## DISCUSSION

Captive conditions may alter how infants develop into adults in a variety of ways. For example, captive animals are typically insulated from some of the environmental stimuli normally experienced in wild conditions. Upon release, they must quickly learn to recognize sources of risk, compulsory habitat, and suitable forage (Reading *et al.* 2013). Most captive marmots were raised in small cages that do not provide the opportunity to dig, forage, or move moderate distances. In addition, rearing facilities do not allow animals to associate freely, which may hamper development of social skills. Although captive Vancouver Island marmots were typically housed in high-density environments, individuals have little control over who they have contact with. For mammals learning how to recognize and avoid predators is often socially transmitted (Curio 1993; Zohar and Terkel 1995). Captive rearing may also encourage novel behaviours (Mason *et al.* 2006) that, although conducive to captive life, are either non-functional or maladaptive in natural settings (Reading *et al.* 2013). Marmots that are bold, for example, may suffer less stress and reproduce more successfully in captivity than those who are fearful of their handlers (McDougall *et al.* 2006). However, traits such as boldness may confer disadvantages such as increased susceptibility to predation (Bremner-Harrison *et al.* 2004; McPhee 2004) or tendency to disperse (Sih *et al.* 2012) in the wild.

The purpose of this project was to compare the behaviour, space use, wariness and time allocation of reintroduced and wild marmots. This comprises the first comparison of this kind among Vancouver Island marmots, and represents an important baseline for future investigations. I now consider how the differences reported here may bear upon the persistence of newly founded colonies.

Activity budgets and social activity remained similar between reintroduced and wild Vancouver Island marmots. When reintroduced marmots remained at the location of their release, subsequent home range sizes and daily movements were comparable to those of wild marmot males; they were, however, smaller for reintroduced females. Unfortunately, most reintroduced animals either dispersed or exhibited large exploratory travels that exceeded those of their wild counterparts in both frequency and extent. However, and contrary to expectation, reintroduced marmots were highly vigilant and wary to sources of potential danger. They also had larger initial flight distances, spent more time in alert

postures, and employed alarm calls more often than wild animals.

### Home ranges and movements

That reintroduced marmots made shorter daily movements than wild-born marmots may have been due to measurement bias; individuals which traveled to remote mountains during this study were located less often than those remaining near their location of release. Large dispersal-like movements (3–4 km) from the release sites were generally common (range 0.3–16 km) and represented a major challenge for monitoring the fates of those individuals. The movements reported here underestimate true travel distances because marmots rarely move in straight lines between locations; rather, they follow ridgelines and topographic high points. For example, in 2004, a 2-year old male released at Mount Haley was observed via routine telemetry to have moved an accumulated distance greater than 30 km while visiting several mountain systems before being predated. But for purposes of analysis, a single minimum straight-line distance connecting the point of release to the furthest recorded location was computed to be ~4 km (13% of the realised distance).

All marmot species tend to associate with permanent burrow systems at a colony site, and do not typically travel great distances except to disperse (Armitage 2014). For example, the largest recorded movement recorded for the golden marmot (*Marmota caudata* area) over a 6-year period was 950 m (Blumstein and Arnold 1998). In a telemetry study of Arctic ground squirrels, individuals with higher rates of movement (Byrom 2003) and larger dispersal distances (Byrom and Krebs 1999) were more likely to die from predation than squirrels with lower rates of movement or who did not disperse as far. Translocation experiments have also revealed a negative correlation between the propensity for a ground squirrel to travel and its probability of surviving the summer (Werner *et al.* 2015). In another example, Bremner-Harrison *et al.* (2004) correlated large movements with low survival for reintroduced swift foxes (*Vulpes velox*).

During the first 2 reintroduction attempts those that survived their first year had either remained or returned to the release site. Although philopatry is traditionally associated with habitat quality (Haughland and Larson 2004; but see Davis and Stamps 2004), in the case of the Vancouver Island marmot, release sites were carefully chosen based upon previous use, considerations of historical population dynamics at those sites, and estimates of food availability. It is therefore unlikely that reintroduced marmots left these vicinities because the habitat was of objectively poor quality. Reintroduced marmots chose a variety of habitats during their first 3 months in the wild. Some of these areas had been historically occupied, and were consistent with popular



conceptions of what constitutes suitable habitat. In other cases, clearcuts or mature forest were used. Variable habitat selection is surprising given that old colony sites were available and given the theoretical expectation that, at low population density, the narrowest range of optimal habitats should be selected for (Fretwell and Lucas 1970). Indeed, other marmot species exhibit narrow habitat choice at lower density (Borgo 2009). However, sub-optimal habitat selection has been documented in other reintroduction scenarios (Roe *et al.* 2010) and modelling exercises (Mihoub *et al.* 2009). A possible explanation is that, where conspecific cues are used in settlement decisions (Kiestler 1979), the identification of optimal habitat becomes unreliable at low population density (Stamps and Swaisgood 2007). A strong reliance on the use of conspecific cues for targeting high-quality habitat will impede population expansion via the recolonization of extinct colony sites (Smith and Peacock 1990; Werner 2015).

The use of large home ranges and extensive exploratory movements increases the time a marmot spends being solitary and away from refuge (Brashares *et al.* 2010). For a social species living at low densities, the release of larger group sizes or the addition of animals to pre-existing colonies could mitigate extravagant ranging. Limited experience with supplementing the Mount Washington population in 2004–2005 suggests that when naïve captive-bred marmots join their wild counterparts, their daily movements and home ranges are smaller than when released into vacant habitat (Werner, unpublished data).

#### **Behaviour and time allocation**

Reintroduced marmots partition time to specific behaviours in similar fashion to wild marmots; this suggests the manner in which competing costs are balanced amongst foraging, resting and apprehension may be more innate than learned. A greater proportion of time was allocated to vigilance (head up  $\approx 60\%$ ) for both wild and captive-reared individuals, compared to historic Vancouver Island marmot populations (Heard 1977; Brashares *et al.* 2010) and to other marmot species (e.g., Barash 1989; Carey and Moore 1986; Blumstein *et al.* 2001). This may reflect the high costs of solitary life that most wild individuals now lead (Brashares *et al.* 2010). As reintroduction methods designed to keep individuals near the release site become more refined (Aaltonen *et al.* 2009), observations from a range of release group sizes will enable managers to identify the minimum number of conspecifics necessary to obtain higher foraging efficiency.

#### **Immergence distances**

Measuring the flight response to sources of danger may help predict individual behaviour and ultimately reintroduction success (Zidon *et al.* 2009). For example,

boldness (low fear) often predicted poor survival among release candidates of swift foxes (e.g., Bremner-Harrison *et al.* 2004). That reintroduced marmots were generally more apprehensive than wild born individuals is cause for hope. However, high rates of predation remain concentrated in late summer (Bryant and Page 2005), a time when marmots are metabolically less active and less wary (Barash 1989). These results demonstrate how flight measurements of wild and reintroduced Vancouver Island marmots may help gauge the degree to which captive rearing influences sensitivity to sources of danger.

Overtaking low initial survival of captive-reared animals is a chronic challenge with reintroduction efforts (e.g., Scheeper and Venzke 1995; Black *et al.* 1997; Bryant *et al.* 2002; Green *et al.* 2005; Soorae 2011). A lack of prior experience with recognising predators, selecting native forage, or navigating spatially complex habitat typically contributes to higher initial mortality (e.g., Priddel and Wheeler 1994; Stoinski *et al.* 2003; Mathews *et al.* 2005). In addition to naiveté, abnormal manners developed in captivity or absent social behaviours derived from limited experience, will influence reintroduction success (Price 1989; Snyder *et al.* 1996).

Reintroduced marmots face the additional challenge of having to prepare for hibernation and choose an appropriate hibernaculum during the first 3 months after release. Werner (2005) found low body mass for several reintroduced individuals that died overwinter, and suggested that those individuals either did not accumulate sufficient fat reserves, chose inappropriate hibernacula, or failed to capitalise the benefits of social thermoregulation (Arnold *et al.* 1991). The survival of ex-captives over the study period is reported to have been poor, and mortality sources were predation and unsuccessful hibernation. Annual survival from time of release (July) through to July of the following year was 25% for reintroduced animals (Werner 2005). Annual survival of reintroduced marmots has since been increased to 60% through various management interventions including food addition and predator management (Aaltonen *et al.* 2009). Over the study period, survival of wild marmots was 84% (27/32; Brashares *et al.* 2010), which is higher than the long-term average ( $74 \pm 4\%$ ) reported by Bryant and Page (2005), but similar to an updated estimate ( $85 \pm 5\%$ ) reported by Aaltonen *et al.* (2009). Winter mortality is also a relatively more important source of mortality for captive-born than wild-born marmots (Aaltonen *et al.* 2009).

In summary, the activity budgets, vigilance, and ranging behaviour of wild and reintroduced Vancouver Island marmots were generally similar. Poor survival of captive-bred marmots released into the wild appears to be associated with low release-site fidelity. An individual's prior

experience may be an important factor determining its survival during the early phase of establishment to unfamiliar surroundings (Stamps and Swaisgood 2007). Whether captive-rearing encourages reintroduced individuals to seek out inappropriate habitats, or whether stress induced during transport and release into an alien environment precipitates long distance movement remains unclear.

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