IntroductIon

Captive-breeding and reintroduction programs are widely used in species recovery projects (Kleiman 1989, Seddon 1999, Seddon et al. 2007) and typically undertaken with a goal of establishing viable, wild populations (Griffith et al. 1989, IUCN 2013, Seddon et al. 2014), but relatively few programs have succeeded by that definition (Griffith et al. 1989, Beck et al. 1994a,b, Wolf et al. 1996, Fischer and Lindenmayer 2000, Armstrong and Seddon 2008). Managers reintroducing captive-bred animals necessarily make a suite of decisions related to release sites, procedures, and group composition (Kleiman 1989), often guided by expert opinion, studies of wild congeners or other release programs (Beck et al. 1994a,b). However, managers risk poor results or program failure in the absence of rigorous monitoring to identify key factors affecting success (e.g., Armstrong and Seddon 2008, Ramousse et al. 2009). In particular, because many captive-bred animals experience high mortality or other ‘release effects’ during their first year in the wild (Dama dama, Bar-David et al. 2005, Ovis canadensis, Ostermann et al. 2001, Gyps fulvus, Sarrazin et al. 1994), it is important to challenge the hypotheses underlying release decisions to
maximize subsequent survival and reproductive success (Armstrong and Seddon 2008, Runge et al. 2012).

The Vancouver Island marmot (Marmota vancouerensis, Swarth 1911), an endangered species (Munro 1978) that in 2004 numbered <35 individuals in the wild (unpublished minutes, Vancouver Island Marmot Recovery Team, November 2004), is endemic to Vancouver Island, in British Columbia, Canada (Heard 1977). Although the ultimate causes of endangerment are uncertain, recent declines were attributed to predation by cougars (Puma concolor), wolves (Canis lupus) and golden eagles (Aquila chrysaetus) (Bryant and Page 2005). A captive-breeding program was established in 1997 to support wild populations and facilitate species reintroduction (McAdie 2004).

An analysis of survival in free-living and captive-bred marmots using radiotelemetry and mark-recapture from 2003 to 2007 confirmed predation as the most frequent cause of mortality in both groups (Aaltonen et al. 2009), and also that annual survival in captive-bred marmots was 24% less (0.61, 95% CI = 0.51–0.70) than in wild-bred marmots (0.85, 95% CI = 0.76–0.92), due largely to low survival in captive-bred marmots in the active season when all marmots are most vulnerable to predation (Aaltonen et al. 2009). Prior studies of Vancouver Island marmots and their congeners suggest that sex, age (Arnold 1990a, Bryant 1996, Armitage 1999), and social cohesiveness (Downhower and Armitage 1981, Blumstein et al. 2009, Armitage et al. 2011) could affect fidelity to release site, that active season survival would be highest for site-faithful marmots (Arnold 1990b, Van Vuren and Armitage 1994), and that age (Blumstein and Arnold 1998, Bryant 1996, Lenihan and Van Vuren 1996, Appendix S1: Table S1) and hibernation behavior would predict overwinter survival (Borgo et al. 2009).

We aimed to extend the initial findings of Aaltonen et al. (2009) by asking how marmot characteristics, release practices, and site features affected three short-term measures of success for marmots in their first year in the wild: ‘site fidelity’ (fidelity to release site), ‘active season survival’ (survival to hibernation), and ‘overwinter survival’ (survival through hibernation to late spring). We defined the product of these measures expressed as probabilities as “establishment success”, or the probability that a released marmot survived to the next spring and remained within 1 km of the release site. Specifically, we estimated postrelease site fidelity and survival using a number of variables previously shown to affect fidelity or survival in marmots that were also potentially amenable to management. Our study pools captive-bred marmots released from 2003 to 2007 (Aaltonen et al. 2009) with those released from 2008 to 2010 to roughly double the number observed to estimate active season and overwinter survival (131 and 96 more marmots, respectively). This larger sample also allowed us to define three age classes (1, 2, ≥3 yr old).

**METHODS**

**Study species**

Vancouver Island marmots live in colonies of one or more family groups. Females can breed as yearlings (M. McAdie, personal communication) but most produce first litters at ≥3 yr of age (mean = 3.6 yr, SD = 1.2, Bryant 2005). Litters are small (mean = 3.4, SD = 1.1, n = 58) and produced annually or biennially (Bryant 2005). Vancouver Island marmots are typically active above ground April–October, but hibernate as a group for an average of 210 d yr$^{-1}$ (Bryant and McAdie 2003). Hibernation requires the accumulation of fat reserves during the active season because marmots do not store food (Ortmann and Heldmaier 2000, Legaarden et al. 2001, Armitage et al. 2003). Marmots dig burrows used as hibernacula, for sleeping and birthing, and as refugia from predators (Blumstein et al. 2001) and thermal stress (Heard 1977). Vancouver Island marmots are typically found at elevations of 1000–1400 m (Bryant and Page 2005) in steep subalpine meadows and talus slides. These habitats provide forage early in spring and are maintained by snow, which limits tree encroachment and enhances visibility (Heard 1977). Marmot habitat is patchily distributed but dispersal, most often by males at or after age 2, is common and contributes to gene flow and the viability of sub-populations (Bryant and Janz 1996, Bryant 2005).

**Captive-breeding and release program**

Between 1997 and 2004, 55 wild marmots were taken into captivity (M. McAdie, personal communication) at four Canadian breeding
facilities (Toronto and Calgary zoos, Mountain View Conservation and Breeding Centre, and Tony Barrett Mount Washington Marmot Recovery Centre, or TBMWMRC). The TBMWMRC is established close to a wild colony and operating ski resort, and release candidates not born at the TBMWMRC were brought there at least 8 months prior to release to provide an opportunity to acclimatize to native forage species and experience a winter at high elevation before release the next summer (further details in McAdie 2004 and Appendix S2). Release sites were selected from those occupied historically or identified by Vancouver Island Marmot Recovery Team managers as high-quality marmot habitat, and likely to facilitate colony distribution and dispersal. Release groups were formed to maximize the likelihood of social cohesion and eventual breeding. In total, 301 captive-bred marmots were released into the wild between 2003 and 2010 (Fig. 1). Three sample groups of 214, 199, and 144 marmots contributed to our analyses of release site fidelity, active season survival, and overwinter survival, respectively (Appendix S2: Table S1).

Definitions of site fidelity, active season and overwinter survival

We defined site fidelity as the presence of a captive-bred marmot within 1 km of its release burrow on or after October 1st of its release year. If there were multiple burrows onsite and

Fig. 1. Location of 30 release sites (2003–2010) for captive-bred Vancouver Island marmots, British Columbia, Canada.
within 50 m of one another at the time of release, we treated their midpoint as the release location. Marmots not relocated after September but detected >2 km away from a release burrow earlier in the season were recorded as not returning. In 43 cases, marmots went ‘missing’ and were not detected on- or off-site in aerial searches. We excluded those marmots from our analysis of fidelity because repeated transmitter failures made us reluctant to assume that failure to detect animals ensured site abandonment (see Armstrong et al. 2013 for an alternate approach). Five marmots that abandoned release sites in the active season were trapped and relocated to another site. Those animals were included in our analysis of site fidelity, but not active season or overwinter survival.

We defined active season survival as the survival of a marmot from release to hibernation. Because hibernation date is often hard to detect, we assumed a marmot survived to hibernation if it was alive in October and its transmitter was not found above ground the following spring, as might be expected if it were killed prior to hibernation. Overwinter survival was achieved when an animal that entered hibernation was observed to successfully emerge and survive to the end of May the following spring.

**Re-sightings and habitat characteristics**

We used ground- or air-based radiotelemetry to track marmots and confirm survival at least three times between release and hibernation, and to locate hibernacula in October and November. Although many marmots were active above ground at this time, we treated the last known location as their hibernaculum and confirmed locations the following spring. We recorded all coordinates using various global positioning system (GPS) devices to an accuracy of ±12 m and used ArcGIS 10.0 (ESRI 2010) to estimate aspect and elevation. We attempted to recover transmitters and determine cause of death in cases of mortality (Bryant and Page 2005).

To characterize habitat type near each release site, we used ArcGIS to examine fused SPOT-5 (5 m resolution) and Landsat 5 (30 m resolution) panchromatic images from 2004 to 2007 (Province of British Columbia 2011). Preferred habitat for most marmot species provides ample forage and refuge opportunities and long lines of visibility (M. flaviventris, Blumstein et al. 2006, Carey 1985, M. marmota, Bibikov 1968, in Herrero et al. 1994, Ferrari et al. 2009). Therefore, we expected sites with greater amounts of ‘meadow’ and ‘talus’ habitat and lesser amounts of ‘forest’ to be positively associated to site fidelity and survival. Because philopatric marmots spend most of their time within 100–1000 m of a home burrow (Bryant and Page 2005), we digitized habitat polygons within a 1-km radius around each release burrow. Habitat types were distinguished by color and texture, and reviewed by field crew with >15 yr of experience hiking to and flying over release sites. Using 1:5000 scale images, we digitized all habitat polygons with a patch size ≥25 m² in area and comprised of ≥75% cover of a single habitat type. We then summed habitat types as the percentage of each within a 1-km radius, and standardized the percentages as z-scores to ensure parameter estimates of similar magnitude.

To evaluate the landscape-level context of habitat attributes, we used maps provided as digital shapefiles by landowners (Island Timberlands Limited Partnership 2011, Western Forest Products Incorporated 2011) to calculate the amount of recently logged habitat (forest aged 0–15 yr) within a 3-km radius of each release burrow in each year. TimberWest Forest Corporation (2011) provided these calculations in spreadsheet form. Between July and early September of 2010–2011, we also sampled fine-scale forage and visibility characteristics within 60 m of release burrows at a subset of 39 release burrows on 21 mountains.

**Data analyses**

We used an information-theoretic approach to evaluate alternative models based on Kullback–Leibler relative distance, an estimate of the information lost when using one probability distribution to approximate another (Burnham and Anderson 2002). We used the second-order form of Akaike’s information criterion (AICc, Hurvich and Tsai 1989) to estimate the K-L relative distance, and accommodate small sample sizes relative to model parameters estimated. All analyses were performed in R (R Development Core Team 2012).
We fitted generalized linear mixed-effects models to our data as response variables were binary in each case (link function = logit), and each set of models included both fixed and random effects (year, mountain, and aspect at the hibernation site, lme4 package, Bates et al. 2012). Prior analyses of captive-bred Vancouver Island marmots tested for sex, age, and release effects on active season survival (Aaltonen et al. 2009). Our analyses also included variables potentially in the control of managers that had not been previously evaluated for their influence on release success. In order to explore all relationships of interest, we used an ‘all-subsets analysis’ (Neter et al. 1996, Montgomery et al. 2012) to model every possible combination of literature- or et al. 1996, Montgomery et al. 2012) to model every possible combination of literature- or management-supported covariates, allowing us to compare a complex set of existing hypotheses that are being actively discussed by managers (Symonds and Moussalli 2011, Appendix S3). We calculated the ‘events per variable ratio’ (EPV) for each data set as the smaller of the number of outcome events per parameter estimated for fixed effects (Vittinghoff and McCulloch 2007).

We used differences in AICc (Δi) to calculate Akaike weights (wi), estimates for the likelihood of a model being ‘best’ given the other candidates. As expected, no model emerged with ‘good’ support (wi >0.9, Burnham and Anderson 2002), so we selected a subset of models with strong to moderate support (differing by the AICc ‘best’ model by <7, Burnham and Anderson 2002) for further exploration. To evaluate relative support for covariates, we summed the subset-adjusted Akaike weights for each model in which they were included. ‘Relative importance’ for predictors therefore ranged from 0 (not included in any models) to 1 (included in all models). We next applied weighted multimodel inference to estimate parameters and predict random effects, allowing us to avoid bias inherent in selecting a single model to use in predictions. Finally, we used the revised equation in Burnham and Anderson (2004) applied with the R MuMIn package (Barton 2012) to calculate the unconditional standard errors for parameter estimates and to construct 95% confidence intervals around fixed effects with greater than 0.5 relative support.

We explored changes in the predicted probability of success for each response variable by varying the values of the most influential fixed effects (>0.5 relative importance) by quartiles, while maintaining covariates at their medians or modes (Peak 2007). To evaluate the predictive ability of averaged models, we dichotomized continuous success predictions at a threshold of 0.5 (<0.5 = failure, >0.5 = success) and used R package caret (Kuhn 2012) to calculate ‘sensitivity’ (the proportion of correct predictions of success, Wilson et al. 2005), ‘specificity’ (the proportion of correct predictions of failure, Wilson et al. 2005), and Cohen’s kappa coefficient (the proportion of correct predictions after accounting for chance, Cohen 1960). We also used sensitivity and specificity to calculate the ‘true skill statistic’ (TSS = sensitivity + specificity − 1, Allouche et al. 2006), a measure of accuracy independent of prevalence that evaluates the improvement of a model on the accuracy that could be expected by chance prediction alone (0 = chance, 1 = perfect accuracy, Allouche et al. 2006).

Results

Site fidelity

Of 214 marmots tracked to hibernation, 67.8% (SE = 3.2, n = 145) exhibited site fidelity by hibernating within 1 km of their release burrow (Table 1). Of 69 dispersers, 71.0% (SE = 5.5, n = 49) traveled straight-line distances of 1–5 km and 29.0% (SE = 5.5, n = 20) dispersed further. The longest straight-line distance recorded in a release year was just over 20 km, by a 2-yr-old male in 2006. Four pups were ‘missing’ at hibernation, but this was suspected to be a function of transmitter issues and not site abandonment or mortality. Of the 19 located pups, 100% exhibited site fidelity.

Our all-subsets analysis included 5121 models to predict site fidelity and resulted in 392 models with ΔAICc < 7 used in a subset to estimate model-averaged parameters. Although the best model in the subset had an Akaike weight of only 0.025, the frequency of variable selection suggested marked variation in influence overall. In particular, release date emerged as a variable with strong relative importance and model influence through its inclusion in 100% of subset models (Appendix S3: Fig. S1). Marmots released in late June were 49% less likely to remain onsite than marmots released in mid-September (Fig. 2). We also found strong support for a negative influence of a resi-
dent female on site fidelity, indicating a 29% higher likelihood of site fidelity at sites where there were no resident females. Resident male presence near release sites was less influential of fidelity, as were group composition variables of age class, sex, group size, relatedness, or release of adults with their own pups (Appendix S3: Fig. S1). Habitat variables and landscape-level disturbance metrics were also weak predictors of site fidelity, but we found no influence of site-specific forage species or visibility characteristics on site fidelity, active season survival, or overwinter survival. A sex by age interaction was not selected in any site fidelity model, but all other predictors were selected at least once. Model-averaged parameter estimates for variables with >0.5 relative importance in the 392 model ΔAICc < 7 subset are summarized in Table 1 (Appendix S3: Table S1 lists the complete set of model-averaged parameter estimates for all predictors).

### Table 1. Rates of site fidelity, active season and overwinter survival in newly released marmots. Estimated success, parameter estimates, unconditional standard errors, and 95% unconditional confidence intervals are provided for variables with >0.5 relative importance to predictive models of site fidelity, active season, and overwinter survival. Models for each success metric were constructed using ‘all-subsets analysis’, and parameter estimates were attained by averaging models with AICc Δi < 7 (see Methods).

| Success metric         | Estimated success | Top variables | Parameter estimate | SE       | Lower 95% CI   | Upper 95% CI   |
|------------------------|-------------------|---------------|--------------------|----------|----------------|----------------|
| Site fidelity           | 68%               | Release date  | 0.039              | 0.011    | 0.017          | 0.061          |
|                        |                   | Female presence | −1.214            | 0.9022   | −2.983         | 0.554          |
| Active season survival  | 84%               | Release date  | 0.047              | 0.016    | 0.015          | 0.079          |
|                        |                   | Age (2 yr old) | 1.043              | 0.726    | −0.380         | 2.465          |
|                        |                   | Age (≥3 yr old) | −1.334            | 0.738    | −2.780         | 0.111          |
|                        |                   | Sex (female)  | 0.928              | 0.604    | −0.256         | 2.112          |
|                        |                   | Talus          | 0.893              | 0.743    | −0.563         | 2.349          |
| Overwinter survival     | 58%               | Release date  | −0.041             | 0.021    | −0.082         | −0.001         |

**Active season survival**

Marmots experienced high active season survival overall (84.4%, SE = 2.6, n = 199, Table 1). Predation was the implied cause of mortality in 61% of 31 deaths recorded, including seven by eagles, five by cougars, one each by a wolf and black bear, and five attributed to predation but not to species. One marmot died by falling and one via suspected bacterial infection (M. McAdie, personal communication). We did not recover 10 marmots confirmed dead by telemetry. Ninety-five percent of pups (SE = 5.3, 18 of 19) survived the active season; the deceased pup was not recovered.

Of 1025 models predicting active season survival, 106 had ΔAICc < 7, with the best model having a weight of 0.077. Four variables had
greater than 0.5 relative importance and all were selected at least once (Appendix S3: Fig. S2). The averaged model was most sensitive to age class and release date (Table 1). Two-year-olds were predicted to survive 5% better than yearlings and 21% better than adults (Fig. 3a). Marmots released at the end of June were 31% less likely to survive to hibernation than those released in mid-September. In addition, females were predicted to be 9% more likely to survive than males (Fig. 3b), and marmots released to sites with the maximum local representation of talus habitat were 9% more likely to survive the active season than those released at sites with the least talus (Fig. 3c).

Fig. 3. Predicted probabilities of active season survival in newly released captive-bred marmots. The plotted lines represent estimates of the probability that an animal released on that date would survive to hibernation, and were calculated using model-averaged parameter estimates and varying (a) age class, (b) sex, and (c) talus cover, while maintaining covariates at their medians or modes. Active season survival is predicted to increase with release date and was higher for females, 2-yr-olds and marmots released to sites with talus cover within 1 km of the release burrow.
Birth facility, release group size, and the amount of disturbance around release burrows had little or no influence on active season survival.

**Overwinter survival**

Fifty-eight percent of 144 captive-bred marmots used in our primary analyses survived overwinter (SE = 4.1, \( n = 84 \), Table 1). Between 2006 and 2010, survival of new releases ranged from 29 to 92%, but was <40% in 2009 (14 of 41) and 2010 (6 of 21). In contrast, survival of wild-born and established marmots averaged 99% of 122 and 98% of 118 marmots, respectively (Fig. 4). Fifty percent of 16 captive-bred pups survived overwinter (SE = 12.9).

We used 129 models to predict overwinter survival and included 51 in the \( \Delta \text{AICc} < 7 \) subset, with the best model weighted at 0.133. Release date was the only variable with greater than 0.5 relative support (Appendix S3: Fig. S3) and was negatively related to overwinter survival (Fig. 5a, averaged parameter estimates in Table 1 and Appendix S3: Table S1). The model subset included the null model, which differed from the best model by 3.6 AICc. Distance class traveled, prerelease hibernation at Mt. Washington, age class, sex, elevation at hibernation and birth facility all received less support as factors potentially affecting overwinter survival. Weighted average survival of marmots from release through the active season and overwinter periods was predicted to be highest for marmots released in late June to early July (Fig. 5b).

**Model assessment**

We aimed for a global EPV of at least five (Vittinghoff and McCulloch 2007), and achieved it for site fidelity (EPV = 5.4), and overwinter survival (EPV = 8.6), but not for active season survival (EPV = 2.9). The averaged models for release site fidelity and active season survival showed high degrees of sensitivity, but poor specificity (Table 2). Our overwinter survival model had high values of sensitivity (0.90), specificity (0.85), and kappa and TSS (0.75), indicating substantially higher discrimination.
and sensitivity than observed for our site fidelity or active season survival models (Table 2).

**DISCUSSION**

We found that poor overwinter survival was the limiting factor in first-year reintroduction success for captive-bred Vancouver Island marmots. Release date was the variable most predictive of success, but was positively associated to site fidelity and active season survival and negatively associated with overwinter survival. We now develop these results in the context of literature on congeners, hibernators and other reintroduced or translocated species, to make recommendations for future release candidates, site characteristics, and procedures.

**Site fidelity**

Captive-bred animals are often released with the goal of establishing a local population, but many animals move unpredictably before becoming established (e.g., *Mandrillus sphinx*, Peignot et al. 2008, *Vulpes vulpes*, Robertson and Harris 1995, *Mystax palmeri*, Tweed et al. 2003, *Marmota marmota*, Borgo et al. 2009). Site fidelity of captive-bred Vancouver Island marmots was most influenced by release date, and marmots released later in the active season were more likely to hibernate within 1 km of the release site. Given the advantages of finding a mate and hibernaculum prior to fall (Arnold 1990a), and the circannual activity patterns of wild *Marmota* in late summer and fall (Heard 1977, Taulman 1990, Perrin et al. 1993, Armitage et al. 1996), high site fidelity in marmots released later in the active season is probably related to several factors.

We estimated a 29% decline in site fidelity for captive-bred marmots released as groups within 500 m of an established captive-bred or wild resident female (Fig. 2, Table 1) but found little support for an effect of release group structure (Appendix S3). This suggests that interactions...
with individuals outside release groups were more influential of site fidelity than those within release groups, supporting similar reports for *Lutra lutra* (Sjöåsen 1996), *Martes americana* (Davis 1983), and *Marmota marmota* (Ramousse and Le Berre 1993).

Habitat safety is also thought to affect survival in *M. flaviventris* (Carey 1985, Carey and Moore 1986, Blumstein et al. 2006), and *M. vancouverensis* (Milko 1984). Surprisingly, we found little effect of landscape-level habitat descriptors on site fidelity, perhaps due to the narrow range of qualities exhibited at release sites, or because site fidelity was not strongly affected by proximity to talus, meadow or old or harvested forest patches within 1 km of release burrows.

**Active season survival**

Predation was the main cause of active season mortality in recently released, captive-bred marmots and release date was a strong positive predictor of active season survival (Fig. 3, Table 1), probably because marmots released later in the active season were less available to predators. Our results support the suggestion by Aaltonen et al. (2009) that eagles and cougars are predators of captive-bred marmots, but provide some contrary estimates of postrelease survival rate. Aaltonen et al. (2009) estimated that captive-bred marmots released at ≥2 years of age achieved an annual survival rate higher than that experienced by yearlings (0.77, 95% CI = 0.65–0.86 vs. 0.60, 95% CI = 0.46–0.73, respectively). In contrast, we estimated that 2-yr old and yearling marmots both survived the postrelease active season at high rates (86%, CI = 76–92 and 91%, CI = 71–97, respectively), but that adults ≥3 years old survived much less well (75%, CI = 48–91). Our results also suggest females survived ~9% better than males on average. Thus, although Aaltonen et al. (2009) estimated annual survival, we estimated active season survival (2–4 months) and overwinter survival (7 months) separately. Including an additional age class also allowed us to show that 2-yr-old marmots survived better than yearlings but that older marmots, which have spent longer in captivity, survived the worst. Because Vancouver Island marmots sometimes breed as polygamous groups (Bryant 1996; D. Doyle, personal communication), modest sex-ratio skews in surviving adults may have limited consequences for population growth unless cumulative sex-biased survival amplifies those observed in captive-bred, released marmots.

Greater talus cover at release sites has been suggested as improving active season survival in marmots because boulder piles facilitate predator detection and act as refugia (e.g., *M. caligata*, Barash 1973, Holmes 1984, *M. broweri*, Bee and Hall 1956, as cited in Gunderson et al. 2009, *M. flaviventris*, Svendsen 1974). Talus cover ranged from 0 to 11% in 1 km buffers around release burrows and, as expected, our results suggested that survival increased over this range (0.77, CI = 0.65–0.86; and 1, CI = 0.61–1, respectively, Table 1), but with very wide confidence intervals and weak model support.

**Overwinter survival**

Low overwinter survival was a key factor limiting first-year release success in captive-bred Vancouver Island marmots (Table 1), an interesting finding given that Vancouver Island marmots are reported to be efficient hibernators, with low rates of mass loss in captivity (Bryant

| Success metric               | EPV † | Prevalence | Sensitivity | Specificity | Kappa | TSS ‡ |
|-----------------------------|-------|------------|-------------|-------------|-------|-------|
| Site fidelity                | 5.4   | 0.673      | 0.917       | 0.486       | 0.44  | 0.40  |
| Active season survival       | 2.9   | 0.844      | 0.994       | 0.290       | 0.39  | 0.28  |
| Overwinter survival          | 8.6   | 0.383      | 0.905       | 0.850       | 0.75  | 0.75  |

† EPV = Events per variable ratio for global model.
‡ TSS = True skill statistic, a measure of a model’s improvement on chance prediction.
and McAdie 2003) and high overwinter survival in wild individuals (Bryant and Page 2005). Although explanations for why marmots cycle through torpor, arousal, and euthermia remain unclear, multiple species do so at substantial energetic cost, losing 32% of fall body mass in hibernation on average (range 12–52%, Armitage 2014, Arnold 1990b, 1993, Blumstein and Arnold 1998). We found that overwinter survival in newly released captive-bred marmots was consistently lower than for captive-bred marmots in their second and subsequent wild hibernations and for wild marmots (Fig. 4), but we detected no marked difference in overwinter survival between wild and captive-bred marmots after their first wild hibernation. This suggests that management to increase overwinter survival in newly released marmots may improve reintroduction success.

In particular, release date strongly influenced overwinter survival because marmots released earlier in the season survived better to the following year, in contrast to our results for active season survival. To date, managers have assumed that in captivity low energy expenditure and access to supplemental food might allow marmots to accumulate reserves more effectively than wild or early released animals, and therefore that those released later might therefore weigh more at immersgence than marmots released earlier. However, anecdotal evidence suggests that survival differences between newly released and established marmots may also arise via the timing of immersgence. Most wild-born and established marmots were known to be in torpor or plugged hibernacula by the end of October annually, whereas signs of marmot activity above ground at new release sites were often observed in November (D. Doyle, personal communication). Some newly released marmots may therefore delay immersgence, rely on senesced plants as food, more often experience inclement weather, and potentially deplete body condition prior to hibernation. However, we also note that captive-bred marmots experienced much lower overwinter survival after releases in 2009 and 2010 than 2006–2008 (Fig. 4), suggesting that variation in climate, snowpack, or other factors also affect overwinter survival (see also Armitage 2014:333). Because climate varies as a consequence of deterministic and stochastic factors, monitoring timeframes of one to several decades may be required to detect these effects on population vital rates (e.g., Wilson and Arcese 2003, Ozgul et al. 2010).

It is also possible that abnormal hibernation behavior in newly released marmots develops as an artifact of captivity. In arctic ground squirrels (Urocitellus parryii), thermoregulatory behavior differed in free-living squirrels and those in captivity, with about 60% of captive but only 26% of free-living squirrels experiencing prehibernation bouts of torpor and arousal (Sheriff et al. 2012). Bryant and McAdie (2003) studied Vancouver Island marmots in the wild and at breeding facilities to find that, on average, captive marmots entered hibernation 6 weeks later and emerged 5 weeks earlier than wild marmots. However, because immersgence and emergence dates were determined differently for wild and captive marmots and we were unable to observe all wild animals regularly, we were unable to estimate differences in hibernation timing here.

Hibernation in newly released Vancouver Island marmots might also be influenced by social or environmental stressors, or ‘release stress’ linked to their transportation or introduction to natural habitat. Stress can influence health, cognition, and behavior in released animals (Teixeira et al. 2007). However, if these effects abate with time, high overwinter survival by animals released early in the active season may reflect recovery from stress and acclimatization to social, physical, or environmental cues. For example, free-living arctic ground squirrels prepare for hibernation weeks before initiating torpor (Sheriff et al. 2012) as do yellow-bellied marmots (Armitage 2014). Few data exist for Vancouver Island marmots, but evidence suggests that captive animals may display lower body temperatures by the first week of September (M. McAdie, personal communication); thus, marmots released in August may have begun adjusting body temperature in preparation for hibernation in captivity.

**Model building and evaluation**

We included variables under management control and previously identified as potentially affecting site fidelity and active season and
overwinter survival, and then averaged parameter estimates across a subset of models to evaluate effect sizes and minimize model selection uncertainty (‘zero method’, Burnham and Anderson 2002, Nakagawa and Freckleton 2011). Less model-intensive approaches are often preferred (Burnham and Anderson 2002, 2004), but our approach allowed us to compare a complex set of existing hypotheses that are being actively discussed by managers in the hope of improving predictions and designing management experiments (Burnham and Anderson 2002, Symonds and Moussalli 2011). Therefore, our results offer timely input to managers and point to experiments able to hone success in future.

For example, our averaged model was 76% better than expected by chance at predicting overwinter survival (TSS, Table 2), and successes and failures (prevalence) were nearly balanced, leading to good model sensitivity and specificity (Table 2). Kappa and TSS values both suggested ‘substantial agreement’ of predicted and observed outcomes (e.g., 0.76 and 0.75, respectively, Landis and Koch 1977). In contrast, site fidelity and active season survival had higher prevalence of success than failure (68% and 84%, respectively), limiting the interpretation of sensitivity, specificity, or kappa (McPherson et al. 2004, Allouche et al. 2006). TSS, which is similar to kappa and independent of prevalence (Allouche et al. 2006), suggested only ‘fair’ support for these models (Table 2). In future, model performance should be evaluated with independent data (Fielding and Bell 1997), ideally gathered in ways that help managers optimize release tactics based on location, calendar date, and environmental conditions within seasons and across years.

**Conclusions**

Our results suggest that release date was highly influential of overwinter survival and somewhat influential of site fidelity and active season survival in captive-bred Vancouver Island marmots released to natural habitats. In particular, later release dates appeared to increase site fidelity and active season survival, but to reduce overwinter survival. Active season and overwinter survival are evaluated over consecutive time intervals using the same units and are therefore multiplicative, implying an optimal range of dates likely to maximize annual survival. In contrast, site fidelity may be of less interest to managers given that marmots that disperse from release sites have the potential to establish new colonies and enhance recovery success. In practice, however, release date is typically limited to a narrow window in the active season because in most winters, potential release sites remain under snow with little food or shelter until late June; and by late September, forage quality wanes and weather limits access. Weighted model estimates of active season and overwinter survival suggest releases from late June to early July resulted in the highest overall establishment success. However, emphasizing the release of 2-yr-old and yearling marmots over older animals and selecting sites with talus to increase active season survival, managers may be able to ameliorate the predicted negative effects of early release on active season survival.

Because reintroduction programs may require years to re-establish viable populations of some endangered species (Griffith et al. 1989, Kleiman 1989, Fischer and Lindenmayer 2000), it is critical to evaluate program performance early and frequently (Beck et al. 1994a,b, Seddon 1999). Our results identify release date as a variable with a large influence on first-year establishment success in newly released, captive-bred Vancouver Island marmots. However, because release date had opposite effects to those underpinning some current management practices, and influenced three indicators of establishment success (site fidelity, active season survival, overwinter survival), our results support Armstrong and Seddon’s (2008) admonition that monitoring effort must be sufficient to resolve key a priori questions potentially affecting success.

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