FEATURE PAPER

Optimizing release strategies: a stepping-stone approach to reintroduction

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Abstract
Evaluation of alternative management strategies enables informed decisions to accelerate species recovery. For reintroductions, post-release survival to reproductive age is a key parameter influencing population growth. Here, we trial a ‘stepping-stone’ method to maximize the success of captive-bred animals when the availability of more suitable wild-born release candidates is limited. Our approach makes use of relatively safe and established wild populations to prepare captive-bred individuals for eventual translocation to a final release destination, thus building resilience through establishment of multiple populations over time. We developed a novel multiple-event model integrating encounter history and biotelemetry data to evaluate reintroduction strategies for the critically endangered Vancouver Island marmot Marmota vancouverensis. We compared post-release survival of 176 individuals (52 wild-born, 47 captive-bred marmots released directly to destinations, and 77 captive-bred marmots released with a stepping-stone approach). Survival estimates to prime breeding-age (PBA), were then used to quantify expected success of potential release strategies. Our analysis indicates that post-release survival varies by source population and release method, as well as age, season, year, and years since release. Conditional on an objective of maximizing survival to PBA, our results suggest that using wild-born marmots for translocations as often as possible, and stepping-stone captive-bred marmots prior to final release, will result in the best outcomes. There was a 0.86 probability that survival to PBA was greater for captive-bred marmots released as yearlings using a stepping-stone approach (survival to PBA mode = 0.13, 95% CRI = 0.05–0.30) than for captive-bred animals that were directly released to destination sites as one-year-olds (survival to PBA mode = 0.04, 95% CRI = 0.01–0.24). Consequently, the stepping-stone approach yields much higher population establishment or growth potential than previous release strategies that used captive-bred marmots. Optimizing the combination of release candidates, sites and timing can thereby increase the effectiveness of reintroductions.

Introduction
Reintroduction and other conservation translocations – intensive recovery actions for species conservation – are increasingly utilized worldwide (Seddon et al., 2014). Reintroduction is often used as a strategy for reducing extinction risk by increasing extent of occurrence and creating multiple independent or semi-independent populations (Rout, Hauser & Possingham, 2007). Post-release survival to reproductive age is crucial to the establishment and persistence of reintroduced populations (Armstrong & Seddon, 2008; Parlato & Armstrong, 2013). Post-release survival of individuals frequently varies among multiple release sites depending on factors such as food availability or predation pressure (Chauvenet et al., 2010). In a metapopulation context, establishment can be more difficult at some release sites than others depending on available resources and threats. Therefore, some release sites may require more time, effort and conditioning of release candidates to effectively reintroduce or reinforce populations.

Post-release effects (Armstrong & Reynolds, 2012) result in reduced survival during the acclimation phase, and can vary depending on age, sex, behavior and source population (Armstrong et al., 2017). Captive-bred animals generally fare worse than wild-born counterparts after release (Letty, Marchandeu & Aubineau, 2007; Rummel et al., 2016). Yet captive-bred animals may be an essential resource if wild-born individuals are unavailable or if the viability of remnant
populations would be unacceptably compromised by extraction of animals for translocation (Todd, Jenkins & Bearlin, 2002; Todd & Linterman, 2015). Increasing the contribution of captive-bred animals to population establishment could bring about wide-reaching benefits because conservation breeding is extensively used to support North American reintroduction efforts (Brichieri-Colombi et al., in press).

To overcome post-release challenges and aid post-release survival, various release strategies can be evaluated (Barton, Abbott & Richardson, 2015). Commonly, release strategies will include variations in source, numbers of individuals released, cohort structure, timing, techniques (hard/immediate or soft/delayed) and locations (Ewen & Armstrong, 2007; Converse, Moore & Armstrong, 2013a; Moehrenschlager & Lloyd, 2016). Evaluation of alternative reintroduction strategies over time can lead to identification of optimal methods and improve outcomes (Sarrazin & Barbault, 1996; Ewen & Armstrong, 2007; Runge, 2013; Converse & Armstrong, 2016).

While various analyses have considered the optimal allocation of animals among sites based on financial or demographic considerations (e.g. Chauvenet et al., 2010; Collazo et al., 2013; Helmstedt & Possingham, 2016; Converse et al., 2018), few have evaluated how variation in release site characteristics can be exploited to reduce post-release effects and increase establishment success in metapopulation restoration efforts. A ‘two-stage translocation’ between subpopulations of wild-born Hawaiian monk seals Monachus schauinslandi was suggested to help overcome food short-ages for certain age classes in a metapopulation (Baker, Harting & Littman, 2013). For many bird translocations, techniques of temporarily or permanently ‘marooning’ populations on predator-free islands, generally outside the indigenous range of the species, have been used in a metapopulation context for recovery (Robertson et al., 2011; Jones & Merton, 2012; Parker, 2013). Within many plant translocations involving propagated individuals, ‘hardening’ has been used to transition plants to acclimatize to wild conditions prior to release (Parthibhana, Kummar & Raoa, 2015). However, to the best of our knowledge, the use of established conservation translocation sites within the species’ indigenous range to prepare captive-bred individuals for eventual release at other sites has not been tested. We term this relatively novel release strategy a ‘stepping-stone’ approach.

The stepping-stone approach makes use of an established and relatively safe wild population to help captive-bred individuals gain wild experience (e.g. foraging, predator avoidance, conspecific interactions) prior to translocation to a final release destination. The approach differs from soft-release techniques involving pre-release enclosures (e.g. Mitchell et al., 2011), supplementary feeding (e.g. Chauvenet et al., 2012), or predator control (e.g. Armstrong et al., 2006) to facilitate population establishment. Instead of expensive and logistically difficult soft-releases at various sites, an established site known to have high survival despite the potential presence of predators can be used as a stepping-stone to potentially reduce release effects and thereby increase survival at a final release location. Our goal was to evaluate this approach for the Canadian-endemic Vancouver Island marmot Marmota vancouverensis, which is critically endangered (IUCN Red List, 2017).

In 2003, fewer than 30 Vancouver Island marmots remained in the wild (Jackson et al., 2015) at four locations (i.e. colonies; Vancouver Island Marmot Recovery Team, 2017). In 1997, conservation breeding for release was initiated. From 2003 to 2016, >490 captive-bred Vancouver Island marmots (hereafter marmots) were released into the wild, primarily into two metapopulations: the southern Nanaimo Lakes metapopulation (14 mountain colonies) and the northern Strathcona metapopulation (nine mountain colonies) on Vancouver Island (Vancouver Island Marmot Recovery Team, 2017). Released captive-bred marmots had greater mortality during their first wild hibernation which contributed to lower annual survival compared to resident wild-born marmots (Aaltonen et al., 2009; Jackson, Schuster & Arcese, 2016a). However, captive-bred marmots surviving their first hibernation had similar survival to wild-born individuals for subsequent over-winter periods (Jackson et al., 2016a) suggesting an acclimation period of 1 year.

Given low survival in the first post-release year for captive-bred marmots, a decision was made to evaluate three release methods varying by level of wild experience: (1) captive-bred direct release to the wild (i.e. no wild experience; hereafter ‘captive-wild’); (2) wild-born marmots translocated from a wild source population (i.e. full wild experience; hereafter ‘wild-wild’); and (3) a novel stepping-stone method for captive-bred marmots (i.e. limited wild experience; hereafter ‘stepping-stone’). The stepping-stone method exposed captive-bred marmots to wild conditions for 1 year at a site known to have high survival (Mt Washington) before translocation to a more challenging colony in Strathcona Provincial Park. To evaluate alternative approaches for reintroduction of Vancouver Island Marmots, we aimed to, (1) develop a survival estimation model to account for the challenges of monitoring marmots; (2) estimate survival as a function of release method, including the novel stepping-stone approach; and 3) identify the optimal combination of release method and age for captive-bred release candidates to maximize survival to prime breeding-age.

Materials and methods

Study species

The Vancouver Island marmot is a large, herbivorous and semi-fossorial rodent within the Sciuridae family. The species is an island endemic found only in the interior mountains of Vancouver Island, British Columbia, Canada (Nagorsen, 1987). Marmots inhabit steep subalpine meadows and talus habitats on mountain slopes at elevations between 1000 and 1400 m (Bryant & Page, 2005). Similar to congeners, marmots are a social species living in small colonies made up of one family group. Marmots typically hibernate for >200 days each year (Bryant & McAdie, 2003), from October to April or May. Reproduction occurs in early

October to April or May. Reproduction occurs in early
spring with pups emerging from their natal burrows in July. Female marmots give birth to their first litter at 3.6 years average age (Bryant, 2005). Male sex-biased dispersal is suggested for marmots (Aaltonen et al., 2009). However, both sexes have been known to disperse up to 30 km in a year (COSEWIC, 2008).

**Study site**

Our study area was in central Vancouver Island, British Columbia, Canada. It included Mt Washington and 12 release sites within Strathcona Provincial Park (hereafter ‘Strathcona’) in the northern Strathcona metapopulation (Fig. 1). The landscape was rugged and dominated by open heath, meadows, and talus slides interspersed with copses of stunted mountain hemlock, subalpine fir, and yellow cedar (Jackson et al., 2016b). The elevation of sites ranged from 1000 to 1700 m. Most of these sites had minimal human disturbance; however, Mt Washington features an active ski resort. Associated human activities on Mt Washington may deter predators, accounting for higher survival. Thus, Mt Washington was a relatively safe place for marmots to be exposed to wild conditions.

**Field methods**

**Pre-release**

Four facilities – Calgary Zoo, Toronto Zoo, Mountain View Conservation and Breeding Centre, and the Tony Barrett Mt Washington Marmot Recovery Centre (hereafter ‘Recovery Centre’) – bred marmots for reintroduction during this study. Marmots from other facilities were transferred to the Recovery Centre in preparation for release. Subsequently, all marmots underwent a quarantine period of ≥30 days. Marmots released in 2013-2016 hibernated at their respective facilities and were moved to the Recovery Centre in the spring before their release (usually late April/early May). Marmots released in 2011 and 2012 were transferred to the Recovery Centre in the previous fall and hibernated there. Each captive release candidate had a transmitter surgically implanted into the intraperitoneal cavity two to six weeks prior to initial release.

![Figure 1](map.jpg)  
**Figure 1** Map of Vancouver Island with Vancouver Island marmot reintroduction locations indicated. Release sites for this study were located within the black square.
Most marmots received a Holohil radio transmitter (model A1-2TH, Holohil Systems Ltd, Carp, ON) with a battery life of ~60 months. A few marmots received an ATS transmitter (model 1240T, Advanced Telemetry Systems Inc., Isanti, MN) with a life expectancy of 50 months. Wild-born marmots were re-released to the wild immediately after transmitter implantation. Capture of marmots in the wild was conducted using baited one-door Havahart\textsuperscript{®} traps. Field methodology was approved by Wildlife Act permit VI11-70146.

Releases into Strathcona
In most years, releases into Strathcona took place in July (2013–2016), after the breeding season, with plenty of time for marmots to become established prior to hibernation. In earlier years, marmots were released in either July or September (2011–2012; see Jackson et al., 2016a). Marmots were released in groups (2–22, median = 4) selected to promote social cohesion and future breeding opportunities. Whenever possible, release groups included marmots with all three levels of experience (wild-wild, stepping-stone, captive-wild; see Fig. 2). Sex and age-class ratios were balanced to the extent possible between the three experience levels tested (See Table S2, in Appendix S1). Releases were either reinforcements of existing colonies or reintroductions to areas that previously supported colonies. All release sites were within two km of successful hibernacula. All release sites were within two km of successful hibernacula.

Data collection and processing
Radio-tracking of marmots started in September 2011 and ended in October 2016. Helicopter surveys to detect signals occurred May – October each year (and November 2011 and 2012). Transmitter signals were detected using a Lotek STR_1000 receiver (Lotek Wireless Inc., Aurora, ON) and two, three-element Yagi antennas attached to helicopter skids (Wildlife Materials International, Murphysboro, IL). Ground-based surveys were used to detect transmitters and recover dead individuals at Mt Washington. During each survey, field staff members searched for a subset of transmitters based on previous location and status.

Radio-transmitters were temperature-responsive, with a pulse rate of ~35 bpm at euthermic body temperatures of 38°C and a progressively diminishing pulse rate at lower temperatures. Fast signals (≥30 bpm) represented active individuals. A slow signal during the marmot active season (summer) implied a dead individual. A slow signal during the fall or spring periods indicated that the individual was present, and either alive and hibernating or dead.

Encounter data were grouped by month. When an individual was detected multiple times in the same month, the last observation was used. All marmots were censored 48 months after release to separate non-detections from transmitter failure (minimum transmitter life expectancy = 50 months). Marmots released at Mt Washington that could not subsequently be captured for translocation to Strathcona were censored at the end of their first wild year.

Data analysis
Post-release survival
We developed a multievent (Pradel, 2005) mark-recapture-recovery model to estimate marmot apparent survival (hereafter ‘survival’), detection and recovery probabilities. Our modeling approach extends the multistate mark-recapture-recovery model of Lebreton, Almeras & Pradel (1999) to incorporate auxiliary information on transmitter temperature data (via signal speed), uncertainty in the state of detected individuals, physical recovery of transmitters, and the possibility of detecting radio-transmitter signals multiple months after death.

Marmot survival (\(\phi_t\)) was modeled as a function of release type, location and year since release, with additive effects for sex, age-class, year and season. Telemetry observation events included probabilities for detecting an individual in state ‘Alive’ with a fast signal (\(p_{\text{alive}}F_t\)) or a slow signal (\(p_{\text{alive}}(1-F_t)\)). We used a multievent modeling framework (Pradel, 2005) to incorporate state uncertainty in spring and fall telemetry observation events where detections of slow signals could arise from individuals in state ‘Alive’ with probability \(p_{\text{alive}}(1-F_t)\) (i.e. alive and hibernating) or state ‘Dead (not recovered)’ with probability \(\lambda_i, r\). Newly dead individuals could also be recovered on Mt Washington with probability \(r_{ir}\), however, dead recoveries were not available from Strathcona. Encounter probabilities for states ‘Alive’, ‘Dead (not recovered)’, and ‘Dead (recovered)’ (\(p, \lambda, \text{and } r\), respectively)

Figure 2 Diagram illustrating translocation process for three release methods, varying by wild experience level, for Vancouver Island marmots (captive-wild, stepping-stone, wild-wild).
were modeled as functions of search effort, location, and logit-scale random monthly effects at Strathcona (see Appendix S1 for complete details).

Captive survival

We used a known-fate model to estimate captive marmot annual survival during 2011 - 2017. We assumed the annual number of survivors in captivity for breeding programs in each age-class, $n_{age, yr}$, is a binomial random variable, $n_{age, yr} \sim \text{Binomial}(N_{age, yr}, S_{age})$, where $N_{age, yr}$ is the number of captive marmots in each age-class and year, and $S_{age}$ is the annual age-class specific captive survival probability.

Release strategy comparison

We were interested in evaluating the probability of survival to breeding age for each captive-bred release strategy. We define an animal that has survived to breeding age as an individual ≥4 years old that had survived at the final release location (in Strathcona) until at least the second spring after release. According to Bryant (2005) 4 years old is the age at which marmots females are most likely to first wean pups. Within that study, 16% of known-age females first weaned pups at 2 years old, compared to 20% at 3 years old and 40% at 4 years old. Because marmots were released after the breeding season (July), we assumed the majority of first breeding in the wild likely occurred 2 years after release. For instance, only 11.1% of female marmots 3 years or older bred in the first spring post-release (Jackson, 2018). Hereafter, we refer to any marmot who meets our definition as a prime breeding-age (PBA) marmot.

We constructed an event tree to trace the routes a captive-bred marmot could take to becoming a PBA adult, by deriving the appropriate cumulative probabilities. The probability of a stepping-stone marmot being available for translocation from Mt Washington to Strathcona was included in this derivation. This translocation probability ($\psi$) was calculated by dividing the number of known translocated individuals by the estimated number of individuals alive at the end of their first (acclimation) year at Mt Washington. For example, a marmot that entered a stepping-stone cohort as a one-year-old would have to survive 1 year as a yearling stepping-stone individual at Mt Washington, then be successfully recaptured and translocated to Strathcona as a two-year-old, and then survive for 2 years in Strathcona to become a PBA marmot. We also calculated the probability that a given release strategy resulted in higher values of survival to PBA by monitoring the proportion of Markov chain Monte Carlo iterations where survival to PBA for a given release strategy was greater than a comparative strategy.

Analysis implementation

We analyzed the multievent and captive survival models in a Bayesian framework using JAGS (Plummer, 2003) and the jagsUI package (Kellner, 2015) accessed through R version 3.3.1 (R Core Team, 2016; see Appendix S1 for details). Due to skewed posterior distributions for some parameters results are presented as posterior modes and 95% credible intervals (95% CRI; Schaub et al., 2012).

Results

Encounter probabilities

Analyses included 176 radio-tagged marmots released during 2011–2016 (77 stepping-stone, 47 captive-wild, 52 wild-wild). Mode estimates for encounter probabilities ($p$, $\lambda$, and $\tau$) at Mt Washington were all >0.85 (Table S1, Appendix S1). Strathcona encounter probabilities were lower, with mode values of 0.71 for $p$ and 0.30 for $\lambda$ (see Appendix S1). Individuals in state ‘Alive’ were primarily detected as fast signals in spring ($F_{spring} = 0.91; 95\%$ CRI 0.82–0.96) and fall ($F_{fall} = 0.84; 95\%$ CRI 0.79–0.88). Assignment parameters ($F_{spring}$ and $F_{fall}$) <1.0, however, support the hypothesis that slow signals in the spring and fall included both live (hibernating) and dead individuals.

Annual survival

Estimates for average annual survival varied between 0.27 (95% CRI 0.06–0.65) and 0.73 (95% CRI 0.38–0.89), depending on experience level, release site and years since release (Fig. 3). Stepping-stone marmots had high survival during their year on Mt Washington (0.69, 95% CRI 0.53–0.82). Annual survival dropped during the year stepping-stone marmots were translocated to Strathcona (0.34, 95% CRI 0.13–0.62) and then rebounded in the third year after release (i.e. second year in Strathcona; 0.73, 95% CRI 0.38–0.89; Fig. 3). Captive-wild marmots had the lowest survival compared to the other experience types in the first two years following release but survived at rates similar to wild-wild and stepping-stone marmots in the third year following release, suggesting a two-year time-lag for captive-wild individuals to overcome release effects (Fig. 3). In the third year since release, marmot annual survival was similar for all experience levels (Fig. 3).

Annual survival for yearlings, two-year-olds, and adult marmots while in captivity for conservation breeding was 0.99 (95% CRI 0.96–1.00; 168 survivors out of 170 total trials), 1.00 (95% CRI 0.94–1.00; 56 survivors out of 56 total trials) and 0.85 (95% CRI 0.81–0.89; 271 survivors out of 318 total trials), respectively.

Intrinsic and extrinsic factors affecting post-release survival

Survival was highest for two-year-old marmots, followed by yearlings, and lowest for adults, but was similar across sexes (Fig. 4). Seasonal survival was higher in the fall and winter compared to spring and summer (Fig. 4). Survival also varied by year, with the highest survival in 2013 and lowest in 2016 (Fig. 4).
**Release strategy comparison**

Releasing yearling captive-bred individuals under a stepping-stone release strategy resulted in the highest probability a captive-bred marmot survived to become a PBA adult in Strathcona (mode = 0.13, 95% CRI = 0.05–0.30, Fig. 5). The second-best strategy was release of yearling individuals under a captive-wild release strategy (mode = 0.04, 95% CRI = 0.01–0.24). Strategies for release of two-year-old marmots performed equally well for stepping-stone and captive-wild release types, but both resulted in lower mode estimates relative to strategies for release of yearling individuals (Fig. 5). Strategies involving release of marmots as adults were the poorest-performing strategies regardless of experience level; however, credible intervals for all scenarios overlapped (Fig. 5).

**Discussion**

Release strategies play a critical role in the outcomes of conservation translocation programs. Techniques that increase post-release survival for captive-bred individuals could have a large impact on this increasingly used global conservation action for species recovery. Consistent with release strategy studies comparing captive-bred with wild-born individuals (Letty et al., 2007), translocations of wild-born marmots from Mt Washington yielded the highest post-release survival rates. However, their limited availability necessitates a productive contribution from captive-bred animals to allow for population establishment at Strathcona, which is a relatively challenging release area. Our analysis suggests that captive-bred marmots take 2 years to overcome release effects in Strathcona and reach annual survival probabilities
comparable to those of wild-wild individuals. Before our study, a comparison of release effects between captive-bred and wild-born resident marmots was only available for one year post-release (Aaltonen et al., 2009; Jackson et al., 2016a). In the third year post-release, annual survival for all three experience levels was similar to wild-born resident marmots consistent with Jackson et al. (2016a), with greater survival for two-year-old marmots compared to other age classes, and females compared to males. Differences in survival among years are also consistent with other studies (Farand, Allaine & Coulon, 2002) and likely due to variation in seasonal weather (Armitage, 2013).

Survival to PBA in the wild was almost three times higher for captive-bred marmots released as yearlings using a stepping-stone approach than for captive-bred animals that were directly released to Strathcona. This suggests that living a year at Mt Washington better prepared captive-bred marmots for subsequent release. Delaying release from captivity regardless of technique yielded survival rates to PBA that were so low that such individuals were highly unlikely to contribute to the population. There may be several benefits gained using Mt Washington as a stepping-stone prior to a marmot’s final release in Strathcona. Predation is a major cause of mortality for most reintroduced species (Moseby et al., 2011; Brichieri-Colombi & Moehrenschlager, 2016) and is a leading cause of mortality for marmots (Bryant & Page, 2005). Released individuals are particularly susceptible to predators after release at a new site (Letty et al., 2007). The Mt Washington colony does have a predator presence but it is likely lower than at other sites given the human presence there. Therefore, this location may allow naïve marmots to learn predator-evasion in an area with relatively low predation risk. Detecting and evading predators on Mt Washington is likely facilitated by a larger colony size and resulting benefit of social behaviors such as alarm (Blumstein & Armitage, 1997). The stepping-stone approach thereby balances keeping marmots safe until they can contribute to population growth with attempting to allow captive-bred individuals to overcome their naiveté in life in the wild.

Wild marmots have been present on Mt Washington since at least the 1940s, and the mountain has an abundance of burrows and hibernacula. Captive-bred marmots are raised using plywood nest boxes as burrows, and prior to their release, have never been underground. The abundance of burrows/hibernacula on Mt Washington gives stepping-stone marmots the chance to use burrow infrastructure and possibly learn to excavate their own burrows, which is likely a critical skill for marmots at Strathcona. Finally, hibernation in captivity does not perfectly mimic wild conditions (Bryant & McAdie, 2003; Bryant, 2005). Therefore, the stepping-stone year allows captive-bred marmots to experience wild hibernation. Marmots hibernate socially (Armitage, 1999), and observations on Mt Washington indicate that stepping-stone marmots sometimes hibernate with groups of resident marmots. Stepping-stone yearlings released to Mt Washington may be adopted into a wild marmot hibernaculum and learn key winter survival skills.

For managers aiming to rebuild a population, it is tempting to release individuals only as they approach reproductive age. This can be particularly true for species that are slow to

| Age 0 | Age 1 | Age 2 | Age 3 | Age 4 | Age 5 | Age 6 | Age 7 | P_{PBA} |
|-------|-------|-------|-------|-------|-------|-------|-------|--------|
| SS (MW) | SS (ST) | SS (ST) | PBA | 0.13 (0.05–0.30) | |
| Captive | CW (ST) | CW (ST) | SS (ST) | PBA | 0.04 (0.01–0.24) | |
| CW (ST) | CW (ST) | SS (MW) | SS (ST) | PBA | 0.02 (0.01–0.18) | |
| Captive | CW (ST) | SS (MW) | SS (ST) | PBA | 0.02 (0.00–0.25) | |
| CW (ST) | SS (ST) | SS (ST) | PBA | 0.01 (0.00–0.14) | |
| Captive | CW (ST) | SS (ST) | SS (ST) | PBA | 0.00 (0.00–0.12) | |
| CW (ST) | SS (ST) | SS (ST) | PBA | 0.00 (0.00–0.12) | |

**Figure 5** Event tree diagram describing the probability a captive marmot pup (Age 0) alive at the end of its first year survived to become a prime breeding-age adult (PBA) at Strathcona ($P_{PBA}$; mode and 95% credible interval). Event paths are unique to release strategies (stepping-stone [SS] or captive-wild [CW]) and age at release. Locations include Mt Washington (MW), Strathcona (ST), and captivity (CA). Annual survival ($\psi$) and translocation probabilities ($\phi$; probability an SS individual alive after their first year at MW is captured and translocated to ST) are derived from field estimates and are specific to release-type, age-class, location, and years since release.
reach reproductive maturity and breed infrequently. However, individuals that are released at older ages can be disadvantaged if they are less adaptable and consequently have high pre-breeding mortality (Mathews, Coates & Delehanty, 2016), or experience release effects that delay breeding (Saltz & Rubenstein, 1995). For Vancouver Island marmots, releasing captive-bred adults directly into Strathcona appears to be ineffective regardless of release method, and may be considered unethical by some (Harrington et al., 2013). In principle, a marmot maintained in captivity until reaching reproductive maturity could breed during its first spring in the wild, necessitating just ~12 months of post-release survival; however, this rarely occurs in practice with most marmots delaying reproduction post-release. Assuming delayed breeding, our results indicated a 0.85 probability that survival to PBA was greater for stepping-stone individuals released into Strathcona as two-year-olds (survival to PBA mode = 0.13, 95% CRI = 0.05–0.30) than captive-wild individuals released into Strathcona as two-year-olds (survival to PBA mode = 0.02, 95% CRI = 0.00–0.25). Ultimately, it would be most informative to evaluate release methods based on an objective of maximizing lifetime reproductive contribution (sensu Canessa et al., 2016). However, this would require much finer-scale data on age-specific breeding output as a function of release age and method. Instead, our approach was to choose a standard definition and evaluate methods against that standard. The standard we chose to define PBA adult should result, based on available information, in marmots that are more likely to become breeders compared to any other definition we could have chosen, based on both age and years since release.

Marmots are social, colonial animals and intrinsic effects such as age or sex may influence their behavior in important ways. In their first two years of life, marmots are not reproductively active and are generally well-tolerated by older marmots (Wey & Blumstein, 2010). Heard (1977) observed a dominance hierarchy in marmots, with adults at the top and yearlings at the bottom. For marmot translocations, this means that releasing subordinate yearlings is more likely to support social cohesion than releasing adult marmots. Our observations supported this; stepping-stone yearlings sometimes hibernated with colony residents in well-established hibernacula at Mt Washington, and this integration was not observed for older marmots.

Dispersal is acknowledged as a major source of loss of translocated individuals (Mehrensclager & Macdonald, 2003; Le Gouar, Mihoub & Sarrazin, 2012; Richardson et al., 2015). For captive-wild marmots released at any age, Jackson et al. (2016a) found 67% of newly released marmots hibernated within one km of their release site. Marmots released in July, like most marmots in this study, were less likely to be site-faithful than marmots released later in the summer, but earlier release dates were preferred because of improved overwinter survival (Jackson et al., 2016a). While we could not differentiate between mortality and permanent emigration from the study area, it is likely that most dispersing individuals do not locate a colony and are effectively lost to the population. Certainly, a more comprehensive understanding of the social and dispersal dynamics in relation to extrinsic factors will help inform evaluation of release strategies, including the stepping-stone approach.

The use of certain wild sites as stepping-stones for reintroductions should be employed with caution. It is possible that certain risks, such as increased stress due to multiple translocations, may hamper stepping-stone approaches. During translocation, individuals are exposed to various stressors (Dickers, Delehanty & Romero, 2010; Parker et al., 2015). Stress associated with capture, transport, and release should be minimized to the extent possible (Letty et al., 2007; Harrington et al., 2013). It may be helpful to provide a relatively long acclimation period at the stepping-stone site to overcome stress associated with the initial translocation.

Unfortunately, the carrying capacity on Mt Washington likely will not support a stepping-stone approach for all captive-bred marmots, most likely due to social constraints and competition for quality hibernacula. However, the Mt Washington colony is both a release site for stepping-stone marmots and a source site for wild-wild marmots, so managers must carefully consider optimal co-management of these differing release strategies. Further research on how conserving breeding facilities can best prepare captive-bred marmots for release would be valuable. Post-release dispersal is often higher in release environments that differ substantially from source environments (Roe et al., 2010; Biggins et al., 2011). Final release sites with ecological characteristics similar to stepping-stone sites could help reduce stress, decrease post-release dispersal, and increase overall success (Letty et al., 2007; Stamps & Swaisgood, 2007).

Continued monitoring and assessment will allow for increased understanding of the stepping-stone approach and inform decisions for marmots and other species. The stepping-stone approach could be applied for any species and taxon involved in conservation translocation with multiple release sites and variation in release candidates, but as with every conservation action, the associated risks need to be considered and reduced to the extent possible. This approach may be particularly useful for social species given the added benefit of learning from interactions with conspecifics. Our analytic approach will be beneficial for modeling any species with a similar observation process. In addition, this framework allows full propagation of uncertainty in release strategy survival estimates, which can be used to directly compare release strategies and better inform decision-making processes.

A truly optimal release strategy can only be identified through consideration of all relevant management objectives (Converse et al., 2013b). Therefore, we suggest that the stepping-stone approach, like any reintroduction method, should be evaluated against alternatives with full consideration of monetary costs and other relevant objectives.

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**Supporting information**

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Appendix S1.** Modeling Framework.

**Appendix S2.** AGS code for analysis of captive survival, multi-event mark-recapture-recovery model, and derived probabilities for survival until breeding age.