Contributed Paper

The Role of Translocation in Recovery of Woodland Caribou Populations

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Abstract: *Maintenance of viable populations of many endangered species will require conservation action in perpetuity. Efforts to conserve these species are more likely to be successful if their reliance on conservation actions is assessed at the population level. Woodland caribou (*Rangifer tarandus caribou*) were extirpated recently from Banff National Park, Canada, and translocations of caribou to Banff and neighboring Jasper National Park are being considered. We used population viability analysis to assess the relative need for and benefits from translocation of individuals among caribou populations. We measured stochastic growth rates and the probability of quasi extinction of four populations of woodland caribou with and without translocation. We used two vital rates in our analysis: mean adult female survival and mean number of calves per breeding-age female as estimates of mean fecundity. We isolated process variance for each vital rate. Our results suggested the Tonquin caribou population in Jasper is likely to remain viable without translocation, but that translocation is probably insufficient to prevent eventual extirpation of the two other populations in Jasper. Simulated reintroductions of caribou into Banff resulted in a 53-98% probability of >8 females remaining after 20 years, which suggests translocation may be an effective recovery tool for some caribou populations.*

Keywords: allee effect, conservation reliant species, protected area, PVA, *Rangifer tarandus*, recovery plan, reintroduction, translocation

El Papel de la Translocación en la Recuperación de Poblaciones de Caribú del Bosque

Resumen: *El mantenimiento de poblaciones viables de muchas especies en peligro requerirá de acciones de conservación a perpetuidad. Es más probable que los esfuerzos para conservar estas especies sean exitosos si su dependencia en las acciones de conservación es evaluada a nivel poblacional. El caribú del bosque (*Rangifer tarandus caribou*) fue extirpado recientemente del Parque Nacional Banff, Canadá, y se ha estado considerando la translocación de caribús a Banff y al Parque Nacional Jasper adyacente. Utilizamos análisis de viabilidad poblacional para evaluar la necesidad y beneficios de la translocación de individuos entre poblaciones de caribú. Medimos las tasas de crecimiento estocásticas y la probabilidad de cuasi extinción de 4 poblaciones de caribús del bosque con y sin translocación. Utilizamos 2 tasas vitales en nuestros análisis: supervivencia promedio de hembras adultas y el número promedio de crías por hembra en edad reproductiva como estimaciones de la fecundidad promedio. Aislamos la varianza de cada tasa vital. Nuestros resultados sugieren que es probable que la población de caribú Tonquin en Jasper se mantenga viable sin translocación, pero que la translocación probablemente es insuficiente para prevenir la eventual extirpación de las otras 2 poblaciones en Jasper. Las reintroducciones de caribú simuladas en Banff resultaron en una probabilidad de*

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53-98% de que permanecieran >8 hembras después de 20 años, lo que sugiere que la translocación puede ser una herramienta efectiva para la recuperación de algunas poblaciones de caribú.

Palabras Clave: área protegida, AVP, efecto Allee, especies dependientes de la conservación, plan de recuperación, *Rangifer tarandus*, reintroducción, translocación

Introduction

The long-term conservation of many endangered species may require sustained conservation effort, and most likely these species will never recover to the point where they can be delisted (Doremus & Page 2001; Scott et al. 2010). Such species have been called conservation reliant (Scott et al. 2005). Scott et al. (2005) hypothesized that the level of recovery attainable for different species varies as a function of the level of effort needed to ensure the species' persistence. The extent to which populations of a given species that differ in size or level of exposure to threats are conservation reliant also may vary. Quantification of the level of conservation reliance among populations could provide information on the likely efficiency of proposed recovery actions (Bottrill et al. 2008; McDonald-Madden et al. 2008).

One common recovery tactic is the translocation of animals to either reintroduce populations or to increase the number of individuals in extant populations (Scott et al. 2005; Armstrong & Seddon 2008). Translocations of endangered species rarely are successful (Fischer & Lindenmayer 2000), although many translocations have not considered the population ecology of the species in detail (Seddon et al. 2007). Retrospective analyses have been used to assess the demographic outcomes of past translocation programs (Van Houtan et al. 2010), and population viability analyses (PVA) allow the a priori comparison of population persistence given different translocation scenarios (Morris & Doak 2002). Given that few individuals typically are translocated, demographic stochasticity and Allee effects may affect whether translocations increase the probability of species recovery (Deredec & Courchamp 2007; Van Houtan et al. 2010). Population viability analysis can be used to quantify the extent to which populations of endangered species are reliant on translocation or other conservation interventions by allowing the comparison of projected population outcomes under different scenarios.

The woodland caribou (*Rangifer tarandus caribou*) is listed as endangered in the United States and as threatened across most of its range in Canada. Evidence that populations of woodland caribou are conservation reliant is mounting along the southern edge of the species' range (Schaefer 2003), where translocation (Compton et al. 1995), habitat protection (Mosnier et al. 2003), and predator control (Gross 2008) have been used to maintain extant populations. Extirpations of populations of woodland caribou occurred recently in British Columbia

(Wittmer et al. 2010), and several other southern populations have high probabilities of extirpation in the near future (Boisjoly et al. 2010; Schneider et al. 2010; Wittmer et al. 2010). Anthropogenic land use is hypothesized to be the primary driver of the decline of woodland caribou. Human activities have caused habitat loss (Schaefer 2003) and may have indirectly caused asymmetry in wolf- (*Canis lupus*) mediated apparent competition (DeCesare et al. 2010) between caribou and primary prey species (such as moose [*Alces alces*]), which increase in abundance in areas of anthropogenic land use (Wittmer et al. 2007). In addition, at low population densities caribou may be susceptible to Allee effects (Wittmer et al. 2005; McLellan et al. 2010).

Protected areas alone may not be sufficient to conserve caribou (Brashares 2010), as evidenced in Banff and Jasper national parks. The only population in Banff was extirpated in 2009 (Hebblewhite et al. 2010), and two of four remaining populations in Jasper have declined to ≤10 individuals. Hebblewhite et al. (2010) and Serrouya and Wittmer (2010) argue that caribou conservation in Canada's national parks was ineffective because there were episodically high levels of wolf predation, delays in production and implementation of a recovery plan, a lack of political will to conserve the taxon, and disagreements about the roles of passive and active recovery strategies. Translocation may be the most aggressive approach to caribou conservation given lack of societal support for predator control (Garrott et al. 1993; Bruskotter et al. 2009), particularly within the national parks (Serrouya & Wittmer 2010). We conducted PVAs of four populations of woodland caribou in Banff and Jasper national parks to assess the efficacy of translocation-based recovery.

Methods

Study Area and Caribou Populations

Our study area included portions of the Canadian Rockies within Banff and Jasper national parks (Banff and Jasper hereafter) in Alberta, Canada (Fig. 1; 52°N, 117°W). Banff and Jasper combine with adjacent federal and provincial protected areas to form one of the largest protected landscapes (>20,000 km²) in North America. Elevations in Banff and Jasper range from 1000 to 3500 m and the mean slope is 20°. Winters are long and cold, and summers are short. Most precipitation occurs in spring.
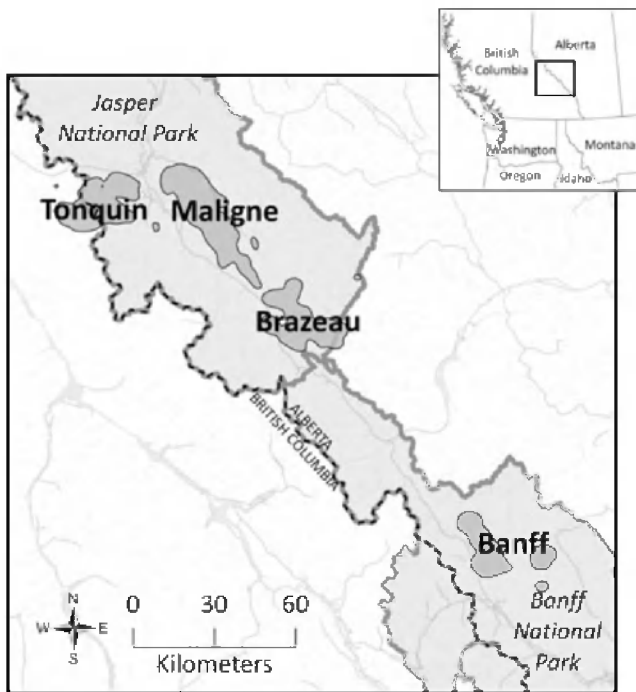
Figure 1. Home ranges (shaded polygons) of woodland caribou in three extant populations in Jasper National Park and the recently extirpated population in Banff National Park, Alberta, 2001–2009.

Caribou populations within the national parks in the Canadian Rockies are federally classified as components of caribou within the Southern Mountain National Ecological Area. There are four extant populations of caribou in Jasper: A la Pêche (northern Jasper), Brazeau, Maligne, and Tonquin. In 2009 estimated sizes of these populations were 150, 10, 4, and 74 individuals, respectively (M.B. & L.N., unpublished data). Nuclear DNA of caribou in the Canadian Rockies shows that the caribou in Banff and Jasper are distinct from neighboring populations (McDevitt et al. 2009). We did not consider the A la Pêche caribou because they generally migrate outside the national parks in winter. We focused our PVA on reintroduction of the Banff population and on translocations to restock the Brazeau, Maligne, and Tonquin populations in Jasper (Fig. 1).

PVA Scenarios

To parameterize PVA, we summarized the means and process variances of survival and fecundity of adult females of the caribou populations in Banff and Jasper from 2001 to 2009. We used these vital rates to project persistence of the populations for 20 years. We selected a projection time of 20 years because it is a feasible horizon for management and recovery planning and action in the parks. We conducted four sets of PVA. In the first set, we used the fixed-mean survival rate for each population as the stochastic survival rate. In the second set of simulations, we evaluated the effects on persistence of positive density-dependent survival (i.e., an Allee effect) (Wittmer et al. 2005; McLellan et al. 2010). We assumed the small populations in our study area remained below carrying capacity and did not model negative density dependence in vital rates. In our third and fourth sets of analyses, we considered different translocation scenarios (described below) with both fixed and density-dependent mean survival.

Estimating Vital Rates

ADULT SURVIVAL

We fitted satellite or radio collars (Lotek Engineering, Aurora, Ontario) on female caribou (≥ 1.5 years old) in the Banff ($n = 2$) (before extirpation), Brazeau ($n = 13$), Maligne ($n = 10$), and Tonquin ($n = 22$) populations from 2001 to 2009. We used helicopter net guns to capture animals (protocols approved by Parks Canada and University of Montana; Animal Use Protocol 059–09MHWB-122209).

For each of the Jasper populations, we used a staggered-entry Kaplan–Meier procedure (Pollock et al. 1989) in program Stata 10 (StataCorp 2007) to estimate population-specific mean annual survival from 1 June to 31 May (a biological year) for each year of the study. Sample size for the Banff population was insufficient to estimate a herd-specific survival rate. Thus, we considered two scenarios of mean survival in Banff: one was based on pooled data from all collared individuals and one was based on data from the Tonquin population in Jasper. Survival rates in the former scenario were lower than in the latter. We assumed survival rates of reintroduced adult female caribou in Banff would remain at or above the pooled mean over 20 years. Probability of caribou persistence in the Canadian Rockies can be theoretically estimated solely as a function of wolf density and densities of the wolves' primary prey (Hebblewhite et al. 2007). We based our assumption of female survival in Banff on the 75% decline in primary prey (elk) populations and subsequent and equivalent declines in wolf density (Hebblewhite 2006; Hebblewhite et al. 2010).

We quantified positive density dependence in survival rates by regressing annual survival rates and ln(number of females) for all biological years (sensu Wittmer et al. 2005; Supporting Information). Annual survival (S) increases linearly as ln(number of females [N_f]) increases,

$$S = 0.724 + 0.0488 * \ln(N_f). \qquad (1)$$

Although the relation was not statistically significant ($R^2 = 0.10$, $F_{1,16} = 1.85$, $p = 0.19$), it was similar to previously documented positive density dependence in

woodland caribou populations (Supporting Information; Wittmer et al. 2005; McLellan et al. 2010).

Variance estimation for stochastic modeling should isolate process from sampling variance (White 2000), which is possible when estimates of both within- and among-year variances are available (Morris & Doak 2002). We calculated within-year variance of annual survival estimates pooled among all populations according to Greenwood (1926) and then used White's (2000) method to isolate process variance (V_c).

FECUNDITY

Fecundity ($\hat{F}$) in female-based, prebirth pulse, matrix models is the product of multiple vital rates, including pregnancy, fetal survival, fetal sex ratio, and calf survival through the first year. Although survival of woodland caribou calves is poorly studied, recruitment is commonly monitored with spring aerial surveys that quantify the mean number of calves per breeding-age female ($\hat{R}$) (McLoughlin et al. 2003). The mean number of calves per breeding-age female can be adapted for use in prebirth matrix models by combining multiple vital rates into a single matrix element that parameterizes the contribution of 1-year-old calves at the end of each time step per adult that entered the time step. From 2004 to 2009, we conducted aerial counts of calves and females in March and used data pooled across Jasper populations to estimate the mean and process variance of fecundity. We estimated within-year mean number of calves per breeding-age female from survey counts per year (i) as

$$\hat{R}_i = \frac{\sum y_i}{\sum c_i}, \qquad (2)$$

where y_i and c_i are the numbers of calves and females ≥ 1.5 years old detected during an annual survey, respectively.

We estimated within-year variance of mean number of calves per breeding-age female with a binomial estimator (Thompson 1992):

$$\mathrm{var}\left(\hat{R}_i\right) = \left(\frac{C_i - c_i}{C_i}\right) \frac{\hat{R}_i(1 - \hat{R}_i)}{c_i - 1}, \qquad (3)$$

where C_i is the estimated number of females in the population on the basis of population-wide surveys. We used White's (2000) method to estimate process variance of $\hat{R}$ across all years of monitoring.

March mean number of calves per breeding-age female did not correspond directly to $\hat{F}$ for matrix projections, so we adjusted stochastically derived values of $\hat{R}$ in three ways. First, we divided the denominator of Eq. (2) by a concurrent stochastic value for 10-month adult survival ($S_i^{10/12}$), which converted the number of females detected each March to an estimate of number of females that entered the time step the previous June. Second, we multiplied the numerator by the same stochastic value

for adult survival adjusted to 2-month survival, which converted the number of calves detected each March to an estimate of number of calves surviving to the end of the time step the following May (assuming calf survival = adult survival in April to May). Third, we multiplied the numerator by 0.5 to account for an estimated sex ratio of 1:1. Thus, we estimated fecundity as

$$\hat{F}_i = \hat{R}_i \times \frac{\hat{S}_i^{\frac{2}{12}} \times 0.5}{1/\hat{S}_i^{\frac{10}{12}}}, \qquad (4)$$

which reduces to

$$\hat{F}_i = \hat{R}_i \times \hat{S}_i \times 0.5. \qquad (5)$$

Current Viability

We constructed a stochastic, female-based, age-structured, prebirth pulse, Leslie matrix to model caribou life history and population growth for each of our four study populations (Leslie 1945). We did not model senescence in survival or fecundity. Instead, we assumed survival and fecundity estimates were representative of the entire age distribution across all breeding age classes. We used code adapted from Morris and Doak (2002) to conduct stochastic simulations in both programs MATLAB (version R2009a, The MathWorks, Natick, Massachusetts, U.S.A.) and R (version 2.11.1, R Development Core Team 2010). We based initial simulations on fixed, population-specific, mean survival rates by drawing random values of adult survival and March mean number of calves per breeding-age female (adjusted to fecundity with Eq. 5) from beta distributions with estimated means and process variances. Simulations in which survival was density dependent were similar, except that stochastic survival rates were generated from beta distributions with a density-dependent mean survival rate derived from Eq. 1.

In all simulations we explicitly modeled demographic stochasticity so as to treat vital rates as probabilistic individual outcomes rather than population-level averages (Morris & Doak 2002). We projected abundances of all populations 20 years into the future and ran 10,000 simulations of each scenario. Because we only observed one movement of a radio-collared individual among populations, we treated populations as demographically isolated. We reduced extant populations to female-only vectors by distributing minimum number of adult females detected in 2009 into a stable age distribution according to the right eigenvector of the mean matrix and by assuming a 1:1 sex ratio of calves. Correlations between survival and fecundity within and among years were not statistically significant, and the parameterization of correlated vital rates in simulations had minimal effects on

results. Thus, we report simulation results assuming no within- or among-year vital-rate correlation.

Small populations may be affected by stochasticity (e.g., inbreeding depression or susceptibility to catastrophic events) that increases the probability of extirpation when abundance is below a quasi-extinction threshold (Ginzberg et al. 1982; Gilpin & Soulé 1986). We incorporated a quasi-extinction threshold in the interpretation of PVA results equal to our maximum observed group size to account for the increased probability of extirpation when all females are in a single group. During winter population surveys from 2004 to 2009, female caribou group size in Jasper ranged from 1–8 ($\bar{x} = 3.1$, $n = 81$ groups), which is similar to the size of summer groups in British Columbia ($\bar{x} = 3.8$, $n = 2099$ groups; McLellan et al. 2010). Therefore, we used a threshold of eight females as the quasi-extinction threshold, which also represents the minimum population size at which recovery efforts are feasible in other populations of woodland caribou (Compton et al. 1995; Stronen et al. 2007). We summarized the results of all simulations with the cumulative probability of quasi extinction ($n \le 8$ females at any point in time) over 20 years and the stochastic population growth rate (λ_S), estimated as a geometric mean across simulations.

Viability with Translocation

We used similar methods to simulate scenarios in which caribou were translocated into each of the four populations. Caribou translocations typically involve the introduction of 30–60 caribou over 1–3 years (e.g., Stronen et al. 2007). Thus, we simulated the translocation of 15 caribou/year over 1, 2, and 3 years, respectively, which represented the translocation of 15, 30, and 45 females, or 20, 40, or 60 total caribou, respectively, assuming the inclusion of males in translocations at a sex ratio of 3 females to 1 male. We also assumed translocated caribou fit the stable age distribution. Translocated animals can have lower probabilities of apparent survival than residents due to mortality and emigration, although survival probabilities can increase gradually to equal resi-

dent survival (Warren et al. 1996). We modeled 3 years of post-translocation survival depression, with 30%, 20%, and 10% decreases in annual adult survival probabilities for the first 3 years when projecting populations of translocated individuals, and we assessed the effect of post-translocation survival depression by simulating all scenarios with and without survival depression.

Results

Current Viability

Pooled mean annual survival of adult female woodland caribou (S) was 0.874 during the study period; raw variance (s^2) was 0.00985 and isolated process variance ($V_c[S]$) was 0.00693. Mean population-specific, annual survival differed among extant populations within Jasper (Table 1), although 95% CIs overlapped among all populations. The pooled mean number of calves per breeding-age female (R) was 0.284, raw variance was 0.01230, and process variance ($V_c[R]$) was 0.01030. Simulations of extant population sizes in which mean vital rates were either fixed or density dependent generated a high probability of quasi extinction ($\mathrm{pr}[n_f \le 8] = 1.0$) for the Brazeau and Maligne populations. The Banff population was extirpated in 2009, and the Brazeau and Maligne populations had low initial population sizes (Brazeau $n_{f,t=0} = 6$; Maligne $n_{f,t=0} = 3$) and low adult female survival (Brazeau $S = 0.806$; Maligne $S = 0.842$), which resulted in declining stochastic growth rates (Brazeau $\lambda_{S,\mathrm{FMS}} = 0.874$, $\lambda_{S,\mathrm{DDS}} = 0.851$; Maligne $\lambda_{S,\mathrm{FMS}} = 0.916$, $\lambda_{S,\mathrm{DDS}} = 0.845$). The median times to extirpation ($n_f = 0$) for both the Brazeau and Maligne populations were 16 years, assuming fixed mean survival, and were 14 and 8 years, respectively, assuming density-dependent survival.

After 20 years only the Tonquin population was extant (Table 2 & Fig. 2). Projections of population size for the Tonquin population were considerably more responsive than those for other populations to whether mean survival values were fixed or positively density dependent. When mean survival was fixed, abundance

Table 1. Population-level annual survival of adult females (S), pooled March mean number of calves per breeding-age female (R), and pooled process variance (V_c) estimates for woodland caribou in Banff and Jasper national parks, Alberta, Canada, 2001–2009.*

				Adult female survival			March mean number of calves per breeding-age female	
Population	$n_{monitored}$	$n_{mortalities}$	Days	S	95% CI	$V_c(S)$	R	$V_c(R)$
Banff	2	2	1996	–	–	–	–	–
Brazeau	13	7	2425	0.806	0.670–0.916	–	–	–
Maligne	10	5	2792	0.842	0.605–0.925	–	–	–
Tonquin	22	5	2425	0.944	0.871–0.976	–	–	–
Pooled	47	19	2792	0.874	0.808–0.919	0.0069	0.284	0.0103

*Key: $n_{monitored}$, number of females monitored; $n_{mortalities}$, number of mortalities; days, length of survival-monitoring period in days.

Table 2. Probability of quasi extinction (pr[$n_f \leq 8$]), geometric mean stochastic growth rates (λ_S), and starting number of females without translocation (n_f) for the Banff, Brazeau, Maligne, and Tonquin populations of woodland caribou under different translocation scenarios.[a]

| | pr($n_f \leq 8$) | | | | | | | | | λ_S^c | | | | | | | | |
| | Brazeau ($n_f = 6$) | | Maligne ($n_f = 3$) | | Tonquin ($n_f = 33$) | | Banff ($n_f = 0$) | | | Brazeau ($n_f = 6$) | | Maligne ($n_f = 3$) | | Tonquin ($n_f = 33$) | | Banff ($n_f = 0$) | | |
Number of translocated females[b]	FMS	DDS	FMS	DDS	FMS	DDS	FMS med	FMS high	DDS	FMS	DDS	FMS	DDS	FMS	DDS	FMS med	FMS high	DDS
0	1.000	1.000	1.000	1.000	0.008	0.286				0.874	0.851	0.916	0.845	1.040	0.962			
15	0.993	0.855	0.969	0.936	0.003	0.118	0.937	0.550	0.986	0.873	0.894	0.913	0.877	1.041	0.992	0.949	1.038	0.859
30	0.965	0.528	0.830	0.670	0.002	0.052	0.606	0.073	0.796	0.873	0.935	0.916	0.917	1.042	1.012	0.956	1.042	0.898
45	0.916	0.265	0.650	0.351	0.001	0.025	0.344	0.016	0.472	0.875	0.966	0.920	0.955	1.043	1.027	0.960	1.043	0.938

[a]Scenarios included different numbers of translocated females and either fixed (FMS) or density-dependent (DDS) survival. Results were generated from population viability analyses with translocation (Banff) or restocking (Brazeau, Maligne, Tonquin) as the mode of reintroduction of caribou.
[b]Translocated animals were subject to 30%, 20%, and 10% decreases in survival probability for the first 3 years, respectively, after translocation.
[c]Years during which population sizes were affected by animals added to the population through translocation and survival depression after translocation were excluded from the estimation of stochastic growth rates (λ_S).

was stable to increasing over 20 years ($\lambda_{S,FMS}$ = 1.040; pr[$n_f \leq 8$] = 0.008). Because the estimated population size for 2009 was low relative to recent years ($n_{f,t=0}$ = 33), density-dependent survival led to a decrease in population size and possible quasi extinction in 20 years ($\lambda_{S,DDS}$ = 0.962; pr[$n_f \leq 8$] = 0.286).
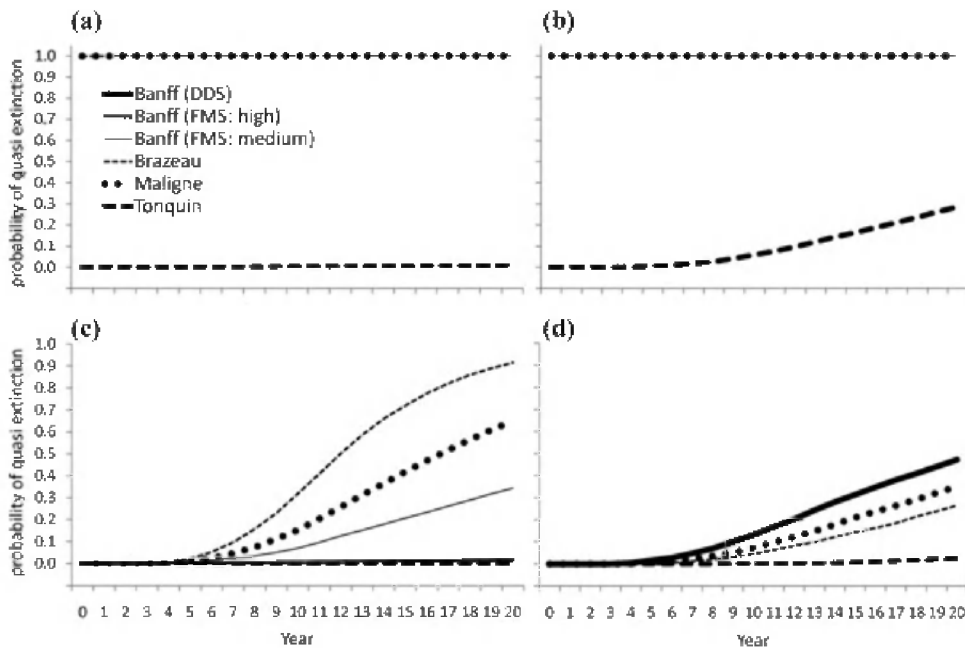
Viability with Translocation

The effect of translocation on population viability depended on whether survival was fixed or density dependent. When mean survival was fixed, translocations increased population sizes and minimally increased stochastic growth rates (Table 2). When survival was positively density dependent, translocations increased both initial population sizes and stochastic growth rates (Table 2 & Fig. 2). Although positive density dependence accelerated population declines of the Brazeau and Maligne populations when no individuals were translocated, it led to increased survival when individuals were translocated. Stochastic growth rates of 0.966 and 0.955 in the Brazeau and Maligne populations, respectively, resulted from translocation alone (Table 2).

Stable to positive growth rates were generated by translocation in the Tonquin population under all scenarios (λ_S = 0.992–1.043), whereas in Banff stable to positive growth rates were achieved only when survival rates were fixed and high (λ_S = 1.038–1.042). Simulations in which 45 females (60 total) were translocated to Banff resulted in a 53–98% probability of the population containing >8 females in 20 years, and the stochastic population growth rates were 0.938–1.043. We assumed 3 years of post-translocation survival depression in all simulations, which resulted in an average 40% decrease in the median number of females after 20 years.

Discussion

Our results suggest there is variation in the extent to which persistence of different woodland caribou populations in Banff and Jasper rely on translocation. The Brazeau and Maligne populations are likely to be extirpated in <20 years without translocation. Although translocation efforts may reduce the short-term probability of extirpation of these populations, translocation does not appear sufficient to reverse declines in abundance. The Tonquin population appears viable without translocation. If caribou are reintroduced into Banff, the population may be viable without further translocation if high survival probabilities are realized. Thus, managers of conservation-reliant populations may wish to consider differentially prioritizing recovery actions, such as translocation, among populations of endangered species.

In a recent review of reintroduction biology, Armstrong and Seddon (2008) identify an information gap

Figure 2. Probability of quasi extinction ($n_f \leq 8$) over time in 10,000 population-projection simulations of four scenarios for the Banff, Brazeau, Maligne, and Tonquin populations of woodland caribou. Data used in simulations were collected during 2001–2009 in Banff and Jasper national parks, Alberta. The four scenarios are (a) 2009 female population size and population-specific, fixed-mean, survival rates (FMS), (b) 2009 female population size and density-dependent survival rates (DDS), (c) translocation of 15 females/year for 3 years to each population and fixed-mean survival rates, and (d) translocation of 15 females/year for 3 years to each population and density-dependent survival rates.

relative to the relation between population establishment and the number of individuals that are translocated. We believe populations respond to number of translocated individuals in three ways. First, translocations increase population size regardless of trends in abundance, which decreases the short-term probability of extirpation. Second, translocations can decrease the negative effects of demographic stochasticity by leading to small increases in stochastic population growth rates ($\lambda_{S,FMS}$ in Table 2) (Morris & Doak 2002). Third, in populations with positive density dependence, translocations may reduce the intensity of Allee effects by increasing population sizes and subsequent population growth rates ($\lambda_{S,DDS}$ in Table 2). Translocations have been correlated with increased means and reduced variances in population growth rates for ungulates (Komers & Curman 2000; Van Houtan et al. 2010). Nevertheless, the effects of translocations observed in the past may not have been independent of concurrent recovery actions (Van Houtan et al. 2010). In our work, when survival was density dependent, a threshold between positive and negative stochastic population growth occurred when the number of female caribou was approximately 50 (Table 2), although this number may be higher for populations outside protected areas (Supporting Information; Wittmer et al. 2010).

The International Union for Conservation of Nature (IUCN) recommends that individuals only should be translocated when threats have been removed and sufficient habitat is available (IUCN 1987). Our results suggest translocation alone will not lead to recovery of the Brazeau and Maligne populations unless underlying vital rates are improved naturally or through additional conservation actions. Current probabilities of persistence may be driven by wolf-mediated apparent competition among caribou and abundant primary prey species such as moose (Seip 1992), elk (*Cervus elaphus*) (Hebblewhite et al. 2007), and deer (*Odocoileus* spp.) (Latham 2009). Thus, translocation of caribou may increase probabilities of persistence of the Brazeau or Maligne populations if primary prey and wolf densities were to decline substantially. Direct manipulation of predators or primary prey species may be effective short-term recovery actions for endangered secondary prey species (Courchamp et al. 2003; Lessard et al. 2005), particularly if these actions are combined with translocations (Van Houtan et al. 2010). Although directives for managing hyperabundant species are in place within Parks Canada (Prior 2010), achieving consensus on these forms of active management for endangered species recovery is challenging for Parks Canada and other organizations (Hebblewhite et al. 2010; Serrouya & Wittmer 2010). Additionally,

conservation tactics such as predator control are often short term and proximate solutions to conservation problems (Musiani et al. 2005; DeCesare et al. 2010) that may have high social (Garrott et al. 1993; Bruskotter et al. 2009) and ecological (Wallach et al. 2010) costs.

It is difficult to measure the success of translocation projects because such projects often lack explicit goals and completion times (Fischer & Lindenmayer 2000). Many translocation programs do not distinguish between phases of initial population establishment and long-term persistence (Armstrong & Seddon 2008). To account for increased mortality and emigration during population establishment, our analysis assumed survival rates for 3 years following translocation would be reduced (Warren et al. 1996). We assumed that environmental conditions during the next 20 years will be similar to those of the past 8 years. Twenty years is a relatively short time frame for population projections, but the potential for changing climate (Post et al. 2009), anthropogenic land use (Wittmer et al. 2010), and predator–prey community (Hebblewhite et al. 2007) conditions makes longer term projections challenging. Woodland caribou and other species that have locally adapted behaviors are difficult to translocate successfully.

Most endangered species exist within multiple populations (Wilcove et al. 1993), and these populations vary in the extent to which they depend on conservation actions. We used PVA to quantify the probability of extinction and to predict the probability of recovery of populations of woodland caribou with and without translocation. Recovery efforts may be aimed at preventing the loss of a single population (Chauvenet et al. 2010) or at prioritizing populations for conservation (Bottrill et al. 2008, McDonald-Madden et al. 2008). In either case, explicit recovery priorities are needed to set quantitative recovery criteria, determine probability of extinction, and identify efficient conservation strategies.

Acknowledgments

Supporting Information

Information on the modeling of density dependence in survival rates (Appendix S1) is available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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