NRC Research Press

ARTICLE

Managing wolves (*Canis lupus*) to recover threatened woodland caribou (*Rangifer tarandus caribou*) in Alberta

Dave Hervieux, Mark Hebblewhite, Dave Stepnisky, Michelle Bacon, and Stan Boutin

Abstract: Across Canada, woodland caribou (*Rangifer tarandus caribou* (Gmelin, 1788)) populations are declining because of human-induced changes to food webs that are resulting in apparent competition-induced increases in predator-caused caribou mortality. We tested the hypothesis that wolf (*Canis lupus* L., 1758) population reduction could reverse declines in a woodland caribou population following a BACI (before-after-control-impact) design conducted over a 12-year period in west-central Alberta, Canada. We monitored annual survival for 172 adult female caribou and calf recruitment from 2000 through 2012 and conducted a provincial government delivered wolf population reduction program annually during the winters of 2005–2006 to 2012 (inclusive) in an area centered on the Little Smoky range. Wolf removal translated to a 4.6% increase in mean population growth rate of the Little Smoky population mostly through improvements in calf recruitment. In contrast, the Red Rock Prairie Creek control population exhibited a 4.7% decline. Although the wolf population reduction program appeared to stabilize the Little Smoky population, it did not lead to population increase, however, with λ remaining approximately equal to 1. Therefore, we recommend, if required, predation management be combined with effective habitat conservation and long-term planning to effect the recovery of species, such as woodland caribou, which are declining as a result of habitat-mediated apparent competition.

Key words: woodland caribou, endangered species, recovery plan, *Species at Risk Act*, predation, *Canis lupus*, *Rangifer tarandus caribou*.

Résumé : Partout au Canada, les populations de caribous des bois (*Rangifer tarandus caribou* (Gmelin, 1788)) sont en déclin en raison de modifications des réseaux trophiques induites par les humains qui entraînent des augmentations de la mortalité des caribous par prédation découlant d'une apparente concurrence. Nous avons testé l'hypothèse voulant qu'une réduction de la population de loups (*Canis lupus* L., 1758) puisse inverser les diminutions d'une population de caribous des bois, en utilisant une expérience de type BACI (avant-après, témoin-impact) menée sur une période de 12 ans, dans le centre-ouest de l'Alberta (Canada). Nous avons surveillé la survie annuelle de 172 caribous femelles adultes et le recrutement de veaux de 2000 à 2012 et réalisé annuellement un programme du gouvernement provincial de réduction de la population de loups, de 2005–2006 à 2012 (inclusivement) dans une zone centrée sur la chaîne Little Smoky. Le retrait de loups s'est traduit par une augmentation de 4,6 % du taux de croissance moyen de la population des Little Smoky, principalement par l'amélioration du recrutement de veaux. En comparaison, la population témoin de Red Rock Prairie Creek présentait une baisse de 4,7 %. Bien que le programme de réduction de la population de loups ait semblé stabiliser la population de la chaîne Little Smoky, il n'a pas entraîné son augmentation, le λ demeurant à peu près égal à 1. Nous recommandons donc que, au besoin, la gestion de la prédation soit combinée avec des mesures efficaces de conservation de l'habitat et une planification à long terme pour permettre le rétablissement d'espèces qui, comme le caribou des bois, sont en déclin en raison d'une concurrence apparente associée à l'habitat. [Traduit par la Rédaction]

Mots-clés : caribou des bois, espèce en voie de disparition, plan de rétablissement, *Loi sur les espèces en péril*, prédation, *Canis lupus*, *Rangifer tarandus caribou*.

Introduction

With increasing human disruption of ecosystems worldwide, conservation biology often includes managing or controlling abundance of invasive or native species to conserve endangered species (Goodrich and Buskirk 1995; Lessard et al. 2005; Martin et al. 2010). Well-known examples include controlling feral pigs (*Sus scrofa* L., 1758) and native Golden Eagles (*Aquila chrysaetos* (L., 1758)) to prevent extinction of the Channel Island fox (*Urocyon littoralis* (Baird, 1858)) (Roemer et al. 2002; Courchamp et al. 2003), control of harbor seals (*Phoca vitulina* L., 1758) to enhance threatened salmon (genus *Oncorhynchus* Suckley, 1861) (Yurk and Trites 2000), reducing Common Raven (*Corvus corax* L., 1758) densities preying on endangered Mojave Desert Tortoises (*Gopherus agassizii* (Cooper, 1861)) (Kristan and Boarman 2003), and feral cat (*Felis catus* L., 1758) eradication to conserve island biodiversity (Nogales et al. 2004). In many of these examples, apparent competition-induced changes in food webs following human disruption or introduction of non-native species renders endangered species more vulnerable to predation by native predators (DeCesare et al. 2010; Wittmer et al. 2013). Indeed, recent reviews of recovery actions for reversing declines in songbirds show that predator management is often more or as effective as habitat management (Smith et al. 2010; Hartway and Mills 2012). Another endangered species that may benefit from such an approach is woodland caribou (*Rangifer tarandus caribou* (Gmelin, 1788)) (Wittmer et al. 2013).

Received 30 May 2014. Accepted 21 October 2014.

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Threatened throughout their range (Festa-Bianchet et al. 2011), woodland caribou conservation is perhaps the most widespread wildlife conservation issue currently facing Canada, with implications for >1.5 million square kilometres of boreal forest. Across provincial, territorial, and federal jurisdictions in Canada, woodland caribou are listed as threatened or endangered, and recovery plans all list reduction of mortality as a critical action to recover caribou (Alberta Woodland Caribou Recovery Team 2005; Alberta Sustainable Resource Development and Alberta Conservation Association 2010; Environment Canada 2011). A growing number of studies demonstrate declining woodland caribou populations coinciding with rapidly increasing industrial activities (i.e., oil and gas development, forestry, mining) during the past 3 decades (McLoughlin et al. 2003; Wittmer et al. 2005). Human activities can alter the spatial distribution of predation risk by creating linear features such as roads, which wolves (*Canis lupus* L., 1758) use preferentially for travel (Latham et al. 2011; Whittington et al. 2011; DeCesare 2012). In addition, human-induced increases in early seral habitats leads to an asymmetric effect on population dynamics among ungulate prey species, resulting in disproportionately high predator-caused mortality on secondary prey such as woodland caribou (Holt and Lawton 1994; DeCesare et al. 2010). Empirically, the effects of apparent competition-induced mortality have already resulted in extirpation of various local populations of woodland caribou in Canada and the US (Wittmer et al. 2005; Hebblewhite et al. 2010).

Nowhere is the question of how to recover woodland caribou in the face of industrial development more crucial than in Alberta where oil and gas and forestry developments are critically important economically (Naugle 2010), and because of the extraordinarily high net present value of oil and gas development leases in Alberta's caribou ranges (Schneider et al. 2010). In large part because of this conflict, most woodland caribou populations in Alberta are rapidly declining (Boutin et al. 2012; Hervieux et al. 2013), and across their range in Canada, Alberta boreal-ecotype woodland caribou populations face the highest extinction risk (Environment Canada 2011). A recent Federal review of boreal woodland caribou landscape condition and critical habitat under the *Species at Risk Act* (SARA) assessed the Little Smoky (LSM) population in west-central Alberta as the most at risk of immediate extirpation across the country (Environment Canada 2011).

Available evidence supports apparent competition as the proximal mechanism for woodland caribou declines and that predation by wolves is the leading cause of mortality (McLoughlin et al. 2005; Wittmer et al. 2005; DeCesare et al. 2012*a*). Despite the broad consensus that predator management may be an effective way to reverse caribou declines (Wittmer et al. 2005), there have been few rigorous tests of its efficacy. Wittmer et al. (2013) recently reviewed conservation strategies in the face of apparent competition and recommended three main strategies: (1) predator reduction, (2) reduction in the density of apparently competing prey, or (3) simultaneous reduction of both. Despite the conceptual advantage of simultaneous reduction, insomuch that it might more effectively restore long-term ecosystem dynamics (e.g., Serrouya and Wittmer 2010), most often, predator removal as a strategy is highlighted. Regardless of the controversy surrounding predator reduction (Musiani and Paquet 2004), few studies have tested whether predator reductions could feasibly recover species experiencing apparent competition-induced declines. Perhaps this is because well-designed, long-term experimental studies are needed to disentangle the effects of predation from other factors (Orians et al. 1997; Hayes et al. 2003).

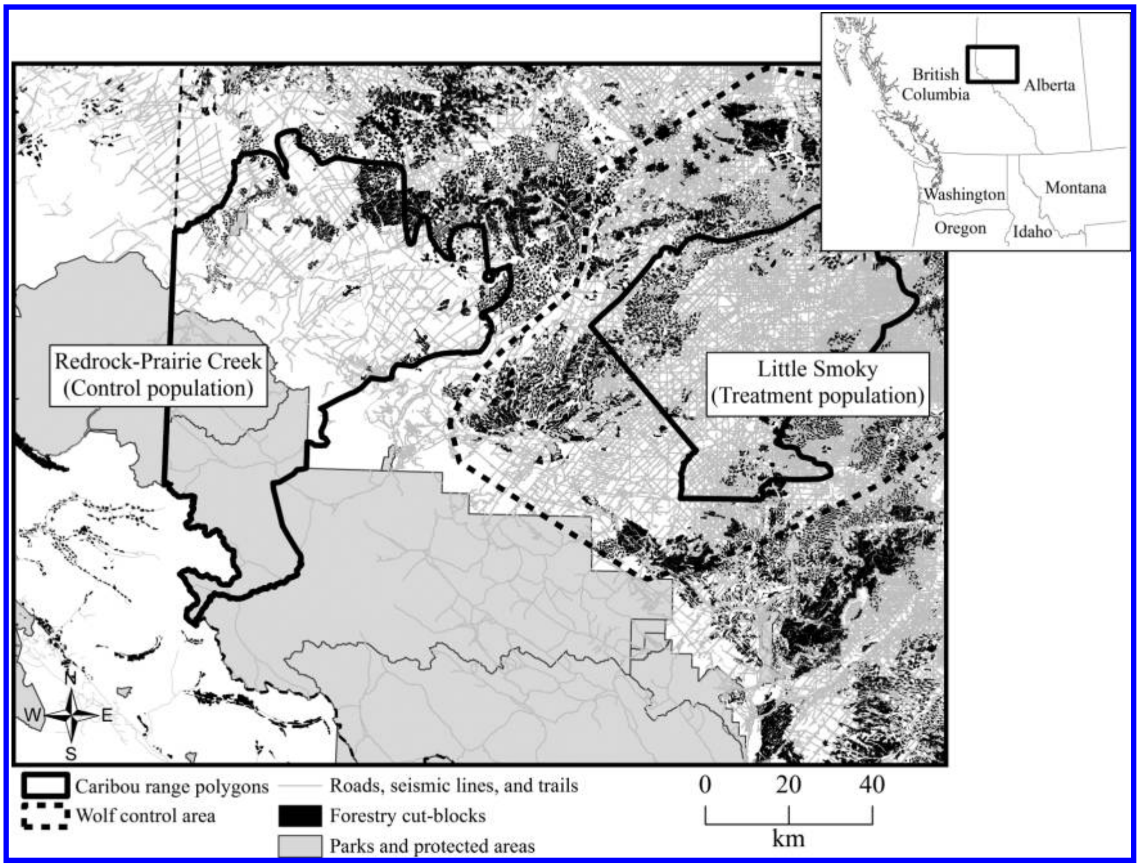
Our goal was to test whether wolf reduction could be an effective strategy for preventing further declines and avoiding extirpation of woodland caribou populations facing apparent competition-induced declines. Wolves are abundant across Canada and not listed as endangered or threatened under provincial or federal legislation, allowing management flexibility to recover woodland caribou. We tested the hypothesis that wolf reduction would increase woodland caribou population growth rate (λ) with a before-after-control-impact (BACI) design (Underwood 1997). We compared effects of wolf reduction in the Little Smoky woodland caribou population (LSM; the treatment population) to an adjacent woodland caribou population without wolf reductions, the Redrock-Prairie Creek population (RPC; the experimental control population). We monitored adult female caribou survival and calf recruitment in 2000 through 2012 for both the LSM and RPC populations, and conducted a provincial government delivered wolf population reduction program annually during the winters of 2005–2006 to 2011–2012 (inclusive) in an area centered on the LSM range. Such knowledge has widespread implications for recovery of endangered species beyond woodland caribou facing apparent competition-induced declines, including endangered Sierra Nevada Bighorn Sheep (*Ovis canadensis sierrae* Grinnell, 1912) declining from unsustainable mountain lion (*Puma concolor* (L., 1771)) predation rates (Johnson et al. 2013), roan antelope (*Hippotragus equinus* (É. Geoffroy Saint-Hilaire, 1803)) in Kruger National Park declining because of lion (*Panthera leo* (L., 1758)) predation (Harrington et al. 1999), or critically endangered South Andean huemul deer (*Hippocamelus bisulcus* (Molina, 1782)) suffering increased predation from culpeo foxes (*Lycalopex culpaeus* (Molina, 1782)) because of introduced ungulate and lagomorph prey (Wittmer et al. 2013).

Materials and methods

Study area

The study was conducted in an approximately 20 000 km² study area containing the LSM and RPC caribou populations in west-central Alberta (Fig. 1). The wolf reduction area surrounding the LSM caribou range was approximately 10 000 km² (Fig. 1). The LSM population range was 3084 km² and the RPC population range was 4281 km², both delineated from all available caribou radio-collar telemetry locations (beginning in the 1980s), caribou winter track surveys, and in some cases, assessments of land forms and habitat types. Although these populations represent different ecotypes of woodland caribou (i.e., LSM are sedentary boreal ecotype and RPC are southern mountain ecotype demonstrating annual movements between winter habitats in lower elevation forests and summer habitats in alpine areas), the geographic proximity of the ranges along with similarities in vegetation communities, large-mammal species, and patterns of anthropogenic disturbance make RPC the most appropriate experimental control for comparison with LSM. Comparatively, the LSM had higher human development impacts than the RPC, with 8.94% of the LSM covered by clearcuts compared with 1.54% in the RPC, and a mean of 3.558 km/km² of linear disturbance in the LSM compared with 0.373 km/km² in the RPC by 2012 (DeCesare et al. 2012*b*). Both forestry and oil and gas developments continued in LSM and RPC during 2000–2012 (Alberta Sustainable Resource Development and Alberta Conservation Association 2010). Both caribou population ranges support populations of other ungulates, including moose (*Alces alces* (L., 1758)), elk (*Cervus elaphus* L., 1758), white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)), and mule deer (*Odocoileus hemionus* (Rafinesque, 1817)). In addition, bighorn sheep (*Ovis canadensis* Shaw, 1804) and mountain goat (*Oreamnos americanus* (Blainville, 1816)) occur at low densities within the RPC range. On a biomass scale, moose comprise the main prey of wolves (42% of biomass in the diet), followed by deer species (27.2%), and elk (16%), with caribou comprising only 4.7% of the diet, yet wolf predation was the leading cause of caribou mortality in western Alberta (e.g., Hebblewhite et al. 2007; Whittington et al. 2011), a prediction of apparent competition (DeCesare et al. 2010). Predators in the area include wolf, grizzly bear (*Ursus arctos* L., 1758), black bear (*Ursus americanus* Pallas, 1780), cougars, lynx (*Lynx*

Fig. 1. Little Smoky and A La Peche woodland caribou (*Rangifer tarandus caribou*) ranges (solid-line outline), Little Smoky wolf (*Canis lupus*) population reduction treatment area (broken-line outline), and industrial disturbance features in west-central Alberta, Canada.



canadensis Kerr, 1792), wolverine (*Gulo gulo* (L., 1758)), and coyotes (*Canis latrans* Say, 1823).

Monitoring caribou demography

We monitored annual adult female caribou survival and recruitment rates and used population modeling to estimate population growth rate, described in detail elsewhere (DeCesare et al. 2012*a*; Hervieux et al. 2013); we provide a brief review here. Between 1999 and 2012, we captured and radio-collared 92 and 80 adult female caribou in the LSM and RPC populations, respectively, using helicopter net-gunning under Alberta Wildlife Animal Care Committee class protocol No. 008. We maintained, on average, 25 radio-collared females per population-year (range 19–38). We estimated adult female caribou survival rates within biological years (1 May to 30 April) from 1999–2000 to 2011–2012, using a staggered entry Kaplan–Meier estimator (Pollock et al. 1989). We estimated the empirical mean of adult female survival within each population as the geometric mean of annual rates and bootstrapped 95% confidence intervals using the geometric means of 10 000 resampled sequences of the same set of annual rates (Morris and Doak 2002). We estimated recruitment rates and its variance using a ratio estimator of the number of calves per 100 cows (Krebs 1989; Thompson 1992). We adjusted calf:cow ratios, X, to estimate recruitment, R, according to $R = (X/2)/[1 + (X/2)]$ (DeCesare et al. 2012*a*), and then estimated geometric mean R for each period and study area with bootstrapped 95% confidence intervals using the geometric mean of 10 000 resampled sequences of annual ratios within each population.

We estimated annual population rate of increase (λ) and its variance using a stochastic version of Hatter and Bergerud's (1991) equation, $\lambda = S/(1 - R)$, where S is female adult survival and R is female recruitment rates (DeCesare et al. 2012*a*; described in Hervieux et al. 2013). We estimated the empirical mean λ per population as the geometric mean of annual estimates because population growth is a multiplicative process over time. We then estimated 95% confidence intervals for geometric mean estimates of λ by randomly drawing sets of annual λ estimates from the annual distributions (mean, SD) of survival and recruitment 10 000 times using Monte Carlo simulations using the beta distribution for binomial survival and lognormal distribution for recruitment (following Morris and Doak 2002 in Hervieux et al. 2013), and similarly followed Hervieux et al. (2013) if there were zero mortalities within a year to estimate the variance on survival rates. We report both empirical and stochastic mean λ to provide insight into the effects of demographic stochasticity on caribou (e.g., stochastic λ is expected to be less than the empirical λ; Mills 2007). Rigorous estimates of actual population size were unavailable because of extremely low sightability of woodland caribou within the two population ranges. As such, we estimated realized changes in population size relative to the initial year of monitoring as the successive product of annual λ estimates and estimated 95% confidence intervals of realized population change for each population-year using the same 10 000 sequences of simulated population vital rates and growth rates as described above.

Reducing wolf abundance

Prior to initiating the wolf reduction in winter 2005–2006, we conducted an aerial census of wolves using aerial back-tracking (Hayes and Harestad 2000). Using a fixed-wing aircraft, from 17 to 23 December 2005, a skilled observed (D. Dennison, Blackhawk Aviation) flew approximately 100 h during ideal snow conditions to locate wolf tracks in our LSM study area. We then forward-tracked wolf tracks observed from the fixed-wing until encountering all wolves in each pack and obtained a minimum estimate of

Table 1. Mean and 95% confidence intervals of woodland caribou (*Rangifer tarandus caribou*) adult female survival, calf:cow ratios, and population growth rate in the Little Smoky (LSM) wolf (*Canis lupus*) population reduction treatment and the Redrock-Prairie Creek (RPC) experimental control areas, from 2000 to 2012, before and after the wolf reduction treatment.

	LSM		RPC	
Demographic parameter	Before wolf reduction	After wolf reduction	Before wolf reduction	After wolf reduction
Adult female survival	0.894 (0.830–0.951)	0.907 (0.868–0.943)	0.830 (0.719–0.936)	0.793 (0.749–0.832)
Calf:cow ratio	0.115 (0.066–0.163)	0.186 (0.148–0.228)	0.188 (0.128–0.238)	0.171 (0.132–0.202)
Empirical population growth rate (λ)	0.945 (0.860–1.001)	0.991 (0.922–1.041)	0.908 (0.823–0.972)	0.861 (0.770–0.938)
Stochastic population growth rate (λ)	0.939 (0.860–1.002)	0.988 (0.921–1.04)	0.901 (0.821–0.969)	0.855 (0.767–0.932)

wolf abundance and thus density within the treatment area. We did not obtain a before treatment aerial density estimate in the RPC population prior to initiation of the wolf treatment in LSM.

Beginning in the winter of 2005–2006, a seasonal (mid-winter) wolf reduction program was conducted in the LSM. Wolf packs were located from a helicopter and one or more wolves per pack were captured using net-gunning techniques and fit with a VHF radio collar. Using a helicopter, we then subsequently attempted to lethally remove all remaining members of each pack through aerial-shooting throughout the winter (sensu Courchamp et al. 2003; Hayes et al. 2003), with the radio-collared wolves removed at the end of winter. Wolf captures were conducted according to Alberta Wildlife Animal Care Committee class protocol No. 009 (Alberta Sustainable Resource Development 2005). We also established toxicant bait stations, using strychnine, to augment aerial-shooting and to target wolves that could not be found or removed using aerial-shooting. Strychnine is permitted for use in Alberta for the purpose of predator control (authorized by Government of Canada Pest Management Regulatory Agency following specific provisions outlined in Alberta Fish and Wildlife Division's "Standards and Procedures Manual 1999"). Beginning in the winter of 2005–2006 and continuing to 2011–2012 (with the exception of winter 2009–2010), on average, 15–20 toxicant bait stations were active within the LSM caribou range at any given time during mid-winter to late winter only. Bait stations were set up using techniques to target wolves and avoid mortalities of nontarget species. Bait stations were checked, on average, every 8 days; at which time, any wolf carcasses were promptly removed and incinerated. All baiting stations were removed prior to the onset of spring thaw. Nongovernment-affiliated fur trappers remained active within and adjacent to both the LSM and the RPC caribou ranges during all years of the government wolf removal program in the LSM.

Testing predator reduction as a caribou recovery strategy

We predicted that (*i*) adult female survival, (*ii*) calf:cow ratio, and (*iii*) population growth rate (λ) of the LSM caribou population should significantly increase following the wolf removal treatment compared with the before wolf removal treatment. If the predicted increase in these demographic parameters for the LSM population was a direct result of our wolf reduction program, then the RPC population should show no increase in adult female survival, calf:cow ratio, or population growth rate over the same time period. To test these predictions, we used a two-factor ANOVA to determine the effect of treatment and time on adult female survival and calf:cow ratio with year as the sample unit assuming no pairing between years in treatment and control. However, to test overall differences in population growth rates between populations and treatments, because λ was itself composed of recruitment and adult survival (Morris and Doak 2002), we used Monte Carlo randomization tests based on the geometric means of both vital rates (survival and recruitment) and their empirical distributions using PopTools in Excel (Hood 2001). As there was no a priori reason to believe that wolf reductions would have a negative effect on caribou demographics (adult female survival, calf:cow ratio, and population growth rate), we calculated one-tailed *P* values and used an α value of 0.10 to minimize type II error.

Results

Wolf reductions

We estimated a minimum density of 25 wolves/1000 km² in the LSM treatment area in December 2005, among the higher reported wolf density estimates in North America (Fuller et al. 2003). In the 5 years prior to initiation of wolf reduction in 2005–2006, fur trappers reported (Government of Alberta Registered Fur Harvest Reports) a total of 49 wolves killed in the LSM treatment area (range 3–19 wolves, mean 9.8 wolves/year), and 22 wolves in the RPC experimental control area (range 0–10 wolves, mean 4.4 wolves/year). During the wolf reduction period (2005–2006 to 2011–2012), fur trappers reported a total of 108 wolves (range 8–35 wolves, mean 15.4 wolves/year) taken in the treatment area, and 59 wolves in the control area (range 2–19 wolves, mean 8.4 wolves/year). During the LSM wolf management program, a total of 579 wolves were removed (range 54–144 wolves, mean 82.7 wolves/year) using aerial methods and a total of 154 wolves (range 0–34 wolves, mean 22 wolves/year) were removed using toxicant methods (for a tabular summary of wolf removal and nontarget species mortality see Supplementary Tables S2[1] and S3[1]). In total, 49 wolves were removed before treatment and 841 wolves were removed during treatment (Fig. 4). Translated to densities within our LSM wolf treatment area of 10 380 km², our aerial and toxicant programs annually removed a mean of 11.6 wolves/1000 km² (range 8.8–16.7 wolves/1000 km²) while trappers removed far fewer wolves (Supplementary Table S2).[1] In terms of the proportion of the wolf population removed, assuming the before treatment wolf density as a minimum estimate, we removed approximately 45% of the mid-winter wolf population each year of our treatment.

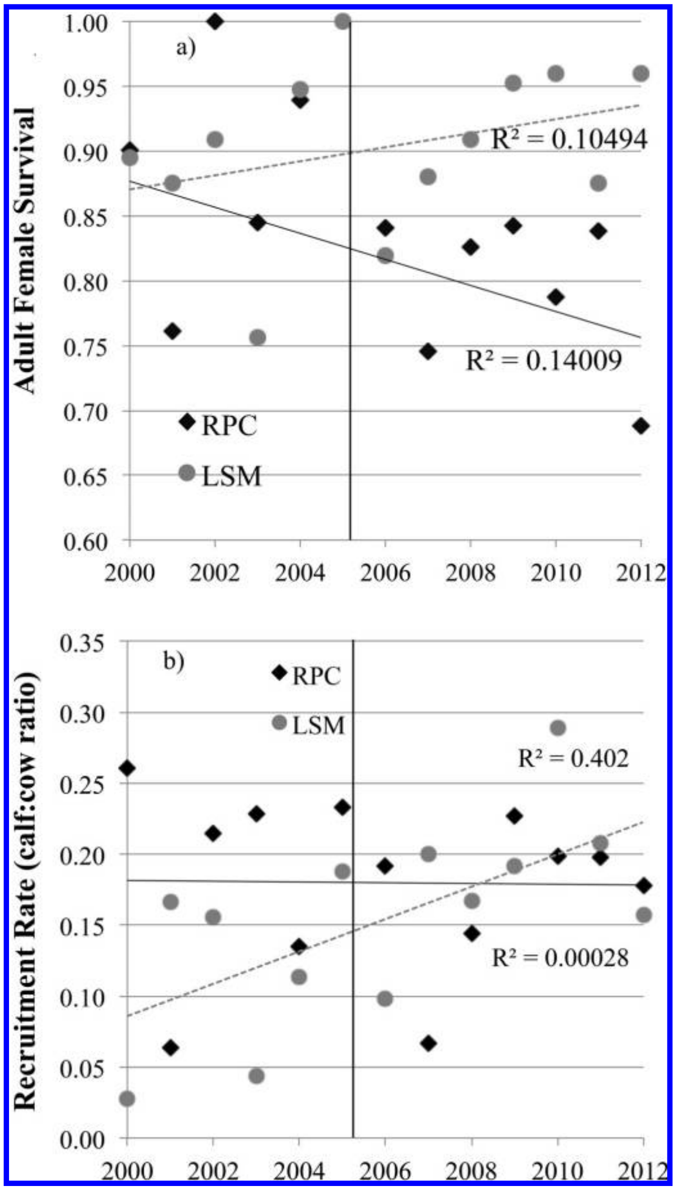
Caribou demographic response to wolf removal

Prior to initiation of the wolf reduction in the LSM, mean adult female caribou survival was 0.89, mean calf recruitment was 0.12 (as measured by calf:cow ratios), the mean empirical population growth rate was 0.95, and the stochastic population growth rate was 0.94 (Table 1; annual estimates of all parameters are given in Supplementary Table S1[1]). Following the initiation of wolf reduction, mean adult female survival was 0.91. Mean recruitment increased to 0.19 and empirical and stochastic population growth rates were $\lambda = 0.99$ and $\lambda = 0.99$, respectively (Table 1). Throughout the entire study, adult female survival did not significantly increase ($F_{[1,11]} = 1.21$, $P = 0.281$; Fig. 2*a*), but recruitment did significantly increase over time ($\beta = 1.1$ calves: 100 cows per year, $F_{[1,11]} = 7.41$, $P = 0.02$, $R^2 = 0.401$; Fig. 2*b*).

In comparison with the LSM, caribou vital rates and demography remained poor in the RPC population throughout the study period. Mean adult female survival was 0.83 from 2000 to 2005 and was 0.79 after 2005 (Table 1). Recruitment was essentially

[1]Supplementary Tables S1, S2, and S3 are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2014-0142.

Fig. 2. Changes in vital-rate components of population growth rate for both the Little Smoky (LSM) (treatment) and the Redrock-Prairie Creek (RPC) (control) woodland caribou (*Rangifer tarandus caribou*) populations, from 2000 to 2012, showing trends over the entire time period in (*a*) adult female survival and (*b*) recruitment rate (calf:cow ratio) in late winter. Our before-after-control-impact (BACI) design compared vital rates before and after initiation (denoted by the solid vertical line) of wolf reduction.



unchanged between periods, from 0.19 before wolf reduction treatment and 0.17 after wolf reduction treatment (Table 1). Resultant population growth rates were 0.91 empirical or 0.90 stochastic before treatment, and declined to 0.86 and 0.86 after treatment. Over the entire study, neither adult female survival ($F_{[1,11]} = 1.78$, $P = 0.201$; Fig. 2*a*) nor recruitment ($F_{[1,11]} = 0.1$, $P = 0.951$; Fig. 2*b*) showed any temporal trend.

Experimentally, we determined that adult female survival differed between the two populations ($F_{[1,22]} = 5.78$, $P = 0.025$), but did not differ between before and after treatment time periods ($F_{[1,22]} = 2.24$, $P = 0.6285$) nor did adult female survival vary with the interaction between treatment and population ($F_{[1,22]} = 0.64$, $P = 0.433$). However, post hoc tests revealed the LSM had adult female survival rates higher than RPC in 1 of 6 years prior to wolf removal and 6 of 7 years during removal. There was no difference in calf recruitment between before and after treatment time periods ($F_{[1,22]} = 1.19$, $P = 0.2879$) nor did calf recruitment rates differ between populations ($F_{[1,22]} = 1.37$, $P = 0.2537$). A statistically significant (at a one-tailed P value of 0.10; see Discussion) effect of the treatment on calf recruitment for just the LSM population (interaction term of the mean treatment difference was $\beta = 8.9$ calves: 100 cows, $F_{[1,22]} = 3.23$, $P = 0.0861$). Calf recruitment was higher in LSM relative to RPC in 1 of 6 years prior to wolf removal and 4 of 6 years during removal.

These trends are illustrated in the Monte Carlo randomization test of the treatment effects on the LSM and RPC population growth rates in Fig. 3. Randomization tests revealed that the difference between before and after wolf treatment λ values were not statistically significant for either the LSM population (randomization $P = 0.51$) or the RPC population (randomization $P = 0.37$). However, our BACI design revealed that while the LSM and RPC λ distributions were not different before treatment, they were significantly different during the 2005–2006 to 2011–2012 period (randomization $P = 0.039$; Fig. 3). This supports a real difference in the trajectories of the two caribou populations following the wolf reduction. These trajectories are illustrated in Fig. 4 that shows percent realized population change from 2000 to 2012 for both the RPC and the LSM populations, and for the LSM population projected without any effect of the treatment using a before treatment geometric mean empirical λ of 0.945. Thus, without the wolf treatment, the LSM population could have declined to an estimated 52% of its starting value instead of apparently stabilizing at 32%, a 20% realized difference in population size.

Discussion

Predator reduction by itself may be an effective short-term strategy to reduce the risk of population extirpation of an endangered species facing declines due to apparent competition. In our test of this recovery strategy, woodland caribou population growth rate increased to approximately stable levels during 6 years of reductions of their main predators (wolves). The strongest evidence that our treatment had its hypothesized biological effect was born through comparison of the realized trajectories of the adjacent RPC and LSM populations following the initiation of wolf reduction. Statistically similar during the before wolf reduction period, the population trajectories of LSM and RPC rapidly diverged by as much as a 14% difference in population growth rate that can be best explained by the wolf reduction. Conservatively, we annually removed 40%–50% of the initial wolf population from the caribou treatment area, and the positive response of recruitment supports the role of wolves as the proximate cause of woodland caribou declines. Given that both caribou population ranges experienced similar land-use trends, climatic conditions, and increased hunting of alternate prey (Alberta Fish and Wildlife, unpublished data), we conclude the main effect was related to the wolf reduction. However, the increased recruitment rates were not as strong as those observed during wolf removal in the Yukon (0.15 calves:cows ratio before wolf control and 0.42 calves:cows ratio during wolf control) (Hayes et al. 2005). One possible reason for the reduced response is the fact that the LSM population is small, probably with less than 50 females present. This small size increase the chances of demographic stochasticity (Mills 2007) manifested through mortality events greatly reducing the potential population benefits of wolf removal. In addition, we note that the annual reduction of wolves at the end of each winter was estimated to be approximately 45% in relation to the before treatment wolf density; this level of wolf reduction may have been inadequate to produce a more robust caribou population response compared with the 70% removal reported by Hayes et al. (2005). The relatively restricted current distribution of the LSM population and close proximity to areas of early seral forest may have also limited the benefits of wolf

Fig. 3. Distribution of annual population growth rate (λ) from 10 000 Monte Carlo simulations based on the empirical adult female survival rates and calf:cow ratios for the Little Smoky (LSM) and Redrock-Prairie Creek (RPC) woodland caribou (*Rangifer tarandus caribou*) populations before and after the wolf (*Canis lupus*) removal treatment was initiated in 2005. Lambda values of 1.0 indicate population stability.

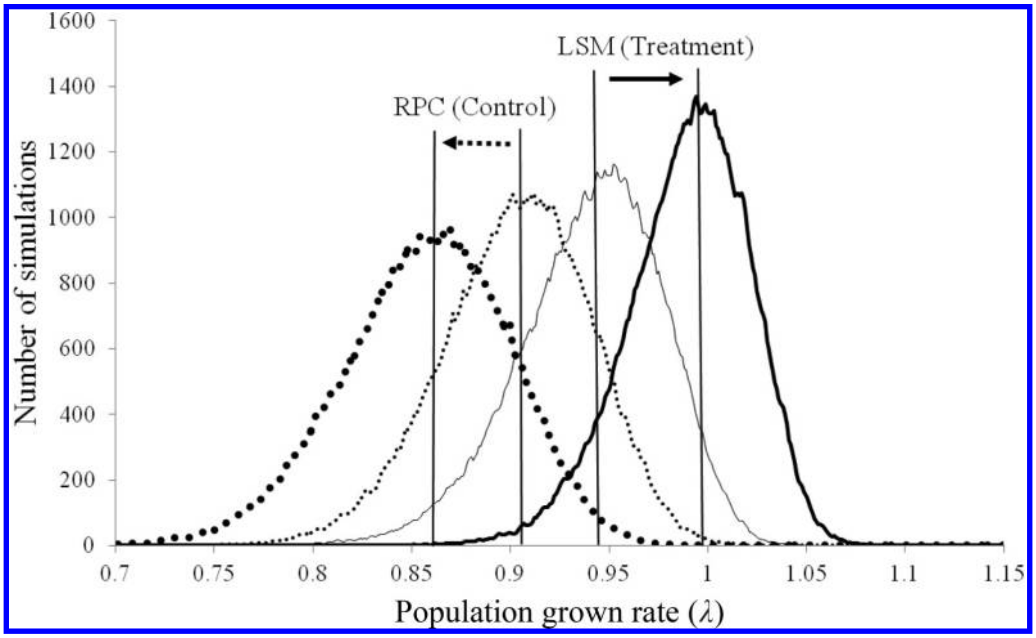
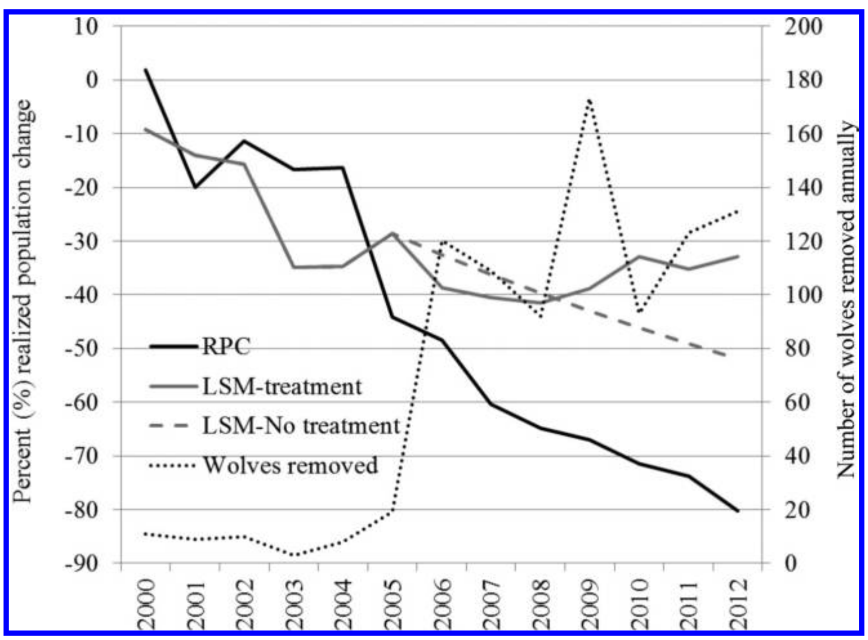


Fig. 4. Estimated percent change in population size for the Little Smoky (LSM) and Redrock-Prairie Creek (RPC) woodland caribou (*Rangifer tarandus caribou*) populations before and after initiation of wolf (*Canis lupus*) reduction showing realized LSM and RPC values and projected LSM growth rates given the before wolf removal population growth rate illustrated by the broken line showing the possible LSM population change effect without the wolf population reduction treatment.



removal. This emphasizes that waiting until threatened populations are small and subject to the negative effects of demographic stochasticity will make any recovery efforts, including wolf removal or habitat recovery, more difficult.

The biological mechanism of the woodland caribou population response was consistent with recent syntheses of ungulate demography. While we observed some signs of improvements in adult female survival, none were statistically significant, and the increased population performance of the LSM was explained by an increase in caribou recruitment (although as we note above, weaker than improvements in caribou recruitment following wolf reductions in the Yukon; Hayes et al. 2005). Across ungulate populations, adult female survival drives population growth rate, but variation in juvenile recruitment explains the annual variation (Gaillard et al. 1998). Adult female survival may have high theoretical sensitivity, but because of evolutionary canalization, low practical ability for managers to affect change in this key vital rate (Wisdom et al. 2000). This is especially true for populations of declining ungulates where the relative importance of adult female versus juvenile survival may differ from reviews of "healthy" populations. For example, Johnson et al. (2010) and Hebblewhite et al. (2007) showed that in small populations of Sierra bighorn sheep and woodland caribou, juvenile survival became the most important parameter driving changes in population growth rate. Indeed, Hebblewhite et al. (2007) showed that for the now extirpated Banff woodland caribou population (Hebblewhite et al. 2010), wolf density and juvenile survival were the most important parameters driving woodland caribou population growth. Our results are also corroborated by Gustine et al. (2006), who showed wolves were the leading cause of woodland caribou calf summer mortality, followed by wolverines, in nearby British Columbia. While it is a weakness of our study that we do not know cause-specific mortality, and that black bears especially can be important causes of mortality for neonatal (<30 days old) calves (Griffin et al. 2011), given the previous literature documenting the importance of wolves as the primary source of mortality in many caribou populations in western Canada (Wittmer et al. 2005; Gustine et al. 2006; DeCesare et al. 2011) and the response of caribou recruitment and λ, we interpret our treatment effects as largely attributable to wolf reductions.

Despite a long practice of using lethal methods to reduce predation by native and non-native predators in conservation biology (Goodrich and Buskirk 1995; Martin et al. 2010), we expect that wolf reductions to recover caribou will continue to be controversial. Much of this controversy will be generated because the predator in this case is wolves, not feral cats, pigs, ravens, or other "invasive" species. Indeed, recent authors have argued that the more important question is whether we should manage wolf populations or not, rather than how to recover federally and provincially threatened woodland caribou (Wasser et al. 2012). Given the debate about such tactics in conservation, it is important to consider the policy framework for recovering endangered species. In this case, woodland caribou are protected under federal and provincial legislation, while wolf populations are healthy and abundant throughout Canada and managed by provincial or territorial management plans. Previous studies demonstrate that wolf populations can absorb mortality of 50% or greater and quickly rebound when population reduction programs end (Fuller et al. 2003; Murray et al. 2010; Webb et al. 2011). Indeed, our own removal rates showed no trend during the study, suggesting a continually replenishing local wolf population, maintained through the documented high dispersal (Fuller et al. 2003) and reproductive rates (Webb et al. 2011). Population genetics studies of wolves in the Canadian Rockies suggest wolf populations operate at an approximately 20 000 km^2 scale (Thiessen 2007), also reducing potential concerns over impacts to the wolf population itself. Nonetheless, important ethical questions regarding the practice of wolf reduction methods remain, as experienced by all conservation practitioners engaged in predator reductions (e.g., Roemer and Wayne 2003). We hope the results of our study that demonstrate some potential short-term benefit of wolf removal on threatened caribou population demography can contribute to informed debates about the role of wolf management in caribou conservation.

Like many previous predator reduction studies, our results indicate that achieving desired demographic results for caribou populations is dependent upon continued wolf population management. While our results demonstrate a significant increase in woodland caribou population growth rate between treatment and experimental control populations and achievement of approximate stability in the treatment population, our wolf reduction treatment itself did not achieve an overall mean of positive population growth rate during the period of wolf removal. Nonetheless, during a period when 10 of the 13 studied woodland caribou populations in Alberta were declining, the LSM population was 1 of only 3 populations demonstrating population stability (Hervieux et al. 2013). In the absence of annual wolf population reductions, the LSM would have likely continued to decline, with potential realized population declines of at least an additional 20% during the 7 years of wolf removals (Fig. 4, Supplementary Table S1[1]). There may have also been unmeasured lag effects in the population response of caribou in the LSM, as reflected by the suggestion of higher demographic performance in latter years of the wolf removal treatment becuase the lagged demographic effects of improved recruitment would have begun to manifest with young prime-aged females entering reproductive ages. Regardless of the uncertainty in our results, they all suggest demographic recovery of a long-lived threatened species like woodland caribou will take long-term commitment to all recovery efforts.

The application of predator reduction as a means of "buying time" in the avoidance of woodland caribou population extirpation has been associated with a call for development and implementation of long-term strategies for habitat conservation, restoration, and management (Environment Canada 2011, 2012, 2014) to achieve a lasting solution to habitat-mediated apparent competition. These habitat management actions will be needed to restore predator–prey communities to their long-term range of variation within which caribou might be able to persist. Practically, however, even were all industrial development on woodland caribou ranges to cease, it would take over 30 years (Schneider et al. 2010) or likely much longer for habitat conditions to favour caribou over moose and wolves. Thus, given extended time periods required to recover caribou habitats and the rapid declines of many woodland caribou populations in Alberta (Hervieux et al. 2013), one of the most pressing challenges will be how to employ predator reductions in combination with ongoing and enhanced habitat conservation and management to achieve the best conservation success. Provincial and territorial governments are committed under the federal SARA legislation to maintain and recover all declining boreal woodland caribou populations (Environment Canada 2012) and a similar requirement for southern mountain woodland caribou populations are anticipated (Environment Canada 2014). Therefore, despite ethical debates over reducing wolf and possibly other predator densities, delays in taking predator reduction actions to reduce woodland caribou mortality rates will dramatically increase the risk of caribou population extirpations. Decisions not to conduct predator reductions are a defacto adoption of extirpation as a management outcome for some populations (Serrouya and Wittmer 2010; Theberge and Walker 2011). While other management actions like caribou translocations can buy time, the ultimate success of caribou translocations will hinge on concurrent predator reduction as well (Compton et al. 1995; DeCesare et al. 2011). Moreover, given widespread and dramatic woodland population declines, conservation managers face increasing difficulty in finding viable source populations for reintroductions. Clearly, the coming decade will be a critical time for conservation of woodland caribou and the 1.5 million square kilometres of boreal forest habitats they and other at risk species depend on. The short-term efficacy of predator reduction, when combined with long-term habitat conservation, restoration, and management, may be the only path forward for recovering many woodland caribou populations.

Acknowledgements

We thank numerous Alberta Fish and Wildlife Division personnel and other cooperating agency personnel involved in caribou population monitoring and analyses, including, but not limited to, N.J. DeCesare, C. Stambaugh, D. Hobson, M. Russell, K.G. Smith, S. Robertson, T. Sorenson, J. Fitch, J. Kneteman, A. James, T. Skorupa, M. Bradley, and L. Neufeld. We thank Bighorn Helicopters, Pacific Western Helicopters, and Highland Helicopters for aircraft support, as well as Blackhawk aviation for assistance conducting wolf surveys. The Government of Alberta provided funding.

References

Alberta Sustainable Resource Development. 2005. Alberta Wildlife Animal Care Committee class protocol No. 009. Alberta Sustainable Resource Development, Edmonton.

Alberta Sustainable Resource Development and Alberta Conservation Association. 2010. Status of the woodland caribou (*Rangifer tarandus caribou*) in Alberta: update 2010. Alberta Sustainable Resource Development and Alberta Conservation Association, Edmonton.

Alberta Woodland Caribou Recovery Team. 2005. Alberta woodland caribou recovery plan 2004/05-2013/14. Alberta Species at Risk Recover Plan No. 4. Alberta Sustainable Resource Development, Fish and Wildlife Division, Edmonton.

Boutin, S., Boyce, M.S., Hebblewhite, M., Hervieux, D., Knopff, K.H., Latham, M.C., Latham, A.D.M., Nagy, J., Seip, D., and Serrouya, R. 2012. Why are caribou declining in the oil sands? Front. Ecol. Environ. **10**(2): 65–67. doi:10.1890/12.WB.005.

Compton, B.B., Zager, P., and Servheen, G. 1995. Survival and mortality of translocated woodland caribou. Wildl. Soc. Bull. **23**(3): 490–496.

Courchamp, F., Woodroffe, R., and Roemer, G. 2003. Removing protected populations to save endangered species. Science, **302**(5650): 1532. doi:10.1126/science.1089492. PMID:14645839.

DeCesare, N.J. 2012. Separating spatial search and efficiency rates as components of predation risk. Proc. R. Soc. Lond. B Biol. Sci. **279**: 4626–4633. doi:10.1098/rspb.2012.1698.

DeCesare, N., Hebblewhite, M., Robinson, H., and Musiani, M. 2010. Endangered, apparently: the role of apparent competition in endangered species conservation. Anim. Conserv. **13**: 353–362. doi:10.1111/j.1469-1795.2009.00328.x.

DeCesare, N.J., Whittington, J., Robinson, H., Hebblewhite, M., Bradley, M., Neufeld, L., and Musiani, M. 2011. The role of translocation in recovery of woodland caribou populations. Conserv. Biol. **25**: 365–373. PMID:21091770.

DeCesare, N.J., Hebblewhite, M., Bradley, M., Smith, K., Hervieux, D., and Neufeld, L. 2012*a*. Estimating ungulate recruitment and growth rates using age ratios. J. Wildl. Manage. **76**(1): 144–153. doi:10.1002/jwmg.244.

DeCesare, N.J., Hebblewhite, M., Schmiegelow, F., Hervieux, D., McDermid, G., Neufeld, L., Bradley, M., Whittington, J., Smith, K.G., Morgantini, L., Wheatley, M., and Musiani, M. 2012*b*. Transcending scale dependence in identifying habitat with resource selection functions. Ecol. Appl. **22**(4): 1068–1083. doi:10.1890/11-1610.1. PMID:22827119.

Environment Canada. 2011. Scientific assessment to inform the identification of critical habitat for woodland caribou (*Rangifer tarandus caribou*), boreal population, in Canada: 2011 Update. Environment Canada, Gatineau, Que.

Environment Canada. 2012. Recovery strategy for the woodland caribou (*Rangifer tarandus caribou*), Boreal population, in Canada. Species at Risk Act Recovery Strategy Series. Environment Canada, Gatineau, Que.

Environment Canada. 2014. Recovery strategy for the woodland caribou, southern mountain population (*Rangier tarandus caribou*) in Canada. Environment Canada, Gatineau, Que.

Festa-Bianchet, M., Ray, J.C., Boutin, S., Côté, S.D., and Gunn, A. 2011. Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. Can. J. Zool. **89**(5): 419–434. doi:10.1139/z11-025.

Fuller, T.K., Mech, L.D., and Cochrane, J.F. 2003. Wolf population dynamics. *In* Wolves: behavior, ecology and conservation. *Edited by* L.D. Mech and L. Boitani. University of Chicago Press, Chicago, Ill. pp. 161–190.

Gaillard, J.-M., Festa-Bianchet, M., and Yoccoz, N.G. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends Ecol. Evol. **13**(2): 58–63. doi:10.1016/S0169-5347(97)01237-8. PMID:21238201.

Goodrich, J.M., and Buskirk, S.W. 1995. Control of abundant native vertebrates for conservation of endangered species. Conserv. Biol. **9**(6): 1357–1364. doi:10.1046/j.1523-1739.1995.09061357.x.

Griffin, K.A, Hebblewhite, M., Zager, P., Robinson, H.S., Barber-Meyer, S.M., Christenson, D., Creel, S., Harris, N.C., Hurley, M.A., Jackson, D.H., Johnson, B.K., Myers, W.L., Raithel, J.D., Schlegel, M., Smith, B.L., White, C., and White, P.J. 2011. Neonatal mortality of elk driven by climate, predator phenology and predator community composition. J. Anim. Ecol. **80**: 1246–1257. doi:10.1111/j.1365-2656.2011.01856.x. PMID:21615401.

Gustine, D.D., Parker, K.L., Lay, R.J., Gillingham, M.P., and Heard, D.C. 2006. Calf survival of woodland caribou in a multi-predator ecosystem. Wildl. Monogr. **165**: 1–32. doi:10.2193/0084-0173(2006)165[1:CSOWCI]2.0.CO;2.

Harrington, R., Owen-Smith, N., Viljoen, P.C., Biggs, H.C., Mason, D.R., and Funston, P. 1999. Establishing the causes of the roan antelope decline in the Kruger National Park, South Africa. Biol. Conserv. **90**(1): 69–78. doi:10.1016/S0006-3207(98)00120-7.

Hartway, C., and Mills, L.S. 2012. A meta-analysis of the effects of common management actions on the nest success of North American birds. Conserv. Biol. **26**(4): 657–666. doi:10.1111/j.1523-1739.2012.01883.x. PMID:22741927.

Hatter, I.W., and Bergerud, W.A. 1991. Moose recruitment, adult mortality and rate of change. Alces, **27**: 65–73.

Hayes, R.D., and Harestad, A.S. 2000. Demography of a recovering wolf population in the Yukon. Can. J. Zool. **78**(1): 36–48. doi:10.1139/z99-186.

Hayes, R.D., Farnell, R., Ward, R.M.P., Carey, J., Dehn, M., Kuzyk, G.W., Baer, A.M., Gardner, C.L., and O'Donoghue, M. 2003. Experimental reduction of wolves in the Yukon: ungulate responses and management implications. Wildl. Monogr. **152**: 1–35.

Hebblewhite, M., Whittington, J., Bradley, M., Skinner, G., Dibb, A., and White, C.A. 2007. Conditions for caribou persistence in the wolf–elk–caribou systems of the Canadian Rockies. Rangifer, **17**: 79–91. doi:10.7557/2.27.4.322.

Hebblewhite, M., White, C.A., and Musiani, M. 2010. Revisiting extinction in National Parks: Mountain caribou in Banff. Conserv. Biol. **24**(1): 341–344. doi:10.1111/j.1523-1739.2009.01343.x. PMID:19843126.

Hervieux, D., Hebblewhite, M., DeCesare, N.J., Russell, M., Smith, K., Robertson, S., and Boutin, S. 2013. Widespread declines in woodland caribou (*Rangifer tarandus caribou*) continue in Alberta. Can. J. Zool. **91**(12): 872–882. doi:10.1139/cjz-2013-0123.

Holt, R.D., and Lawton, J.H. 1994. The ecological consequences of shared natural enemies. Annu. Rev. Ecol. Syst. **25**: 495–520. doi:10.1146/annurev.es.25.110194.002431.

Hood, G. 2001. PopTools EXCEL Add-in. CSIRO, Canberra, Australia.

Johnson, H.E., Mills, L.S., Stephenson, T.R., and Wehausen, J.D. 2010. Population-specific vital rate contributions influence management of an endangered ungulate. Ecol. Appl. **20**(6): 1753–1765. doi:10.1890/09-1107.1. PMID:20945773.

Johnson, H.E., Hebblewhite, M., Stephenson, T.R., German, D.W., and Pierce, B.M. 2013. Apparent competition limits the recovery of an endangered ungulate: quantifying the direct and indirect effects of predation. Oecologia, **171**: 295–307. doi:10.1007/s00442-012-2397-6. PMID:22791131.

Krebs, C.J. (*Editor*). 1989. Ecological methodology. HarperCollins Publishers, New York.

Kristan, W.B., III, and Boarman, W.I. 2003. Spatial pattern of risk of common raven predation on desert tortoises. Ecology, **84**(9): 2432–2443. doi:10.1890/02-0448.

Latham, A.D.M., Latham, M.C., Boyce, M.S., and Boutin, S. 2011. Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern Alberta. Ecol. Appl. **21**(8): 2854–2865. doi:10.1890/11-0666.1.

Lessard, R.B., Martell, S.J.D., Walters, C.J., Essington, T.E., and Kitchell, J.F. 2005. Should ecosystem management involve active control of species abundances? Ecol. Soc. **10**(2): 1–21.

Martin, J., O'Connell, A.F., Jr., Kendall, W.L., Runge, M.C., Simons, T.R., Waldstein, A.H., Schulte, S.A., Converse, S.J., Smith, G.W., Pinion, T., Rikard, M., and Zipkin, E.F. 2010. Optimal control of native predators. Biol. Conserv. **143**(7): 1751–1758. doi:10.1016/j.biocon.2010.04.023.

McLoughlin, P.D., Dzus, E., Wynes, B., and Boutin, S. 2003. Declines in populations of woodland caribou. J. Wildl. Manage. **67**(4): 755–761. doi:10.2307/3802682.

McLoughlin, P.D., Dunford, J.S., and Boutin, S. 2005. Relating predation mortality to broad-scale habitat selection. J. Anim. Ecol. **74**(4): 701–707. doi:10.1111/j.1365-2656.2005.00967.x.

Mills, L.S. 2007. Conservation of wildlife populations: demography, genetics, and management. Blackwell Publishing, Malden, Mass.

Morris, W.F., and Doak, D.F. (*Editors*). 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Inc., Sunderland, Mass.

Murray, D.L., Smith, D.W., Bangs, E.E., Mack, C., Oakleaf, J.K., Fontaine, J., Boyd, D., Jiminez, M., Niemeyer, C., Meier, T.J., Stahler, D., Holyan, J., and Asher, V.J. 2010. Death from anthropogenic causes is partially compensatory in recovering wolf populations. Biol. Conserv. **143**(11): 2514–2524. doi:10.1016/j.biocon.2010.06.018.

Musiani, M., and Paquet, P.C. 2004. The practices of wolf persecution, protection, and restoration in Canada and the United States. BioScience, **54**(1): 50–60. doi:10.1641/0006-3568(2004)054[0050:TPOWPP]2.0.CO;2.

Naugle, D. 2010. Energy development and wildlife conservation in western North America. Island Press, Washington, D.C.

Nogales, M., Martin, A., Tershy, B.R., Donlan, C.J., Witch, D., Puerta, N., Wood, B., and Alonso, J. 2004. A review of feral cat eradication on islands. Conserv. Biol. **18**(2): 310–319. doi:10.1111/j.1523-1739.2004.00442.x.

Orians G., Cochran, P.A., Duffield, J.W., Fuller, T.K., Gutierrez, R.J., Henemann, W.M., James, F.C., Kereiva, P., Kellert, S.R., Klein, D., McLellan, B.N., Olson, P.D., and Yaska, G. (*Editors*). 1997. Wolves, bears, and their prey in Alaska. National Academy Press, Washington, D.C.

Pollock, K.H., Winterstein, S.R., Bunck, C.M., and Curtis, P.D. 1989. Survival analysis in telemetry studies: the staggered entry design. J. Wildl. Manage. **53**: 7–15. doi:10.2307/3801296.

Roemer, G.W., and Wayne, R.K. 2003. Conservation in conflict: the tale of two endangered species. Conserv. Biol. **17**(5): 1251–1260. doi:10.1046/j.1523-1739.2003.02202.x.

Roemer, G.W., Donlan, C.J., and Courchamp, F. 2002. Golden eagles, feral pigs, and insular carnivores: how exotic species turn native predators into prey. Proc. Natl. Acad. Sci. U.S.A. **99**(2): 791–796. doi:10.1073/pnas.012422499. PMID:11752396.

Schneider, R.R., Hauer, G., Adamowicz, W.L., and Boutin, S. 2010. Triage for conserving populations of threatened species: the case of woodland caribou in Alberta. Biol. Conserv. **143**(7): 1603–1611. doi:10.1016/j.biocon.2010.04.002.

Serrouya, R., and Wittmer, H.U. 2010. Imminent extinctions of woodland caribou from National Parks. Conserv. Biol. **24**(2): 363–364. doi:10.1111/j.1523-1739.2010.01454.x. PMID:20491847.

Smith, R.K., Pullin, A.S., Stewart, G.B., and Sutherland, W.J. 2010. Effectiveness of predator removal for enhancing bird populations. Conserv. Biol. **24**(3): 820–829. doi:10.1111/j.1523-1739.2009.01421.x. PMID:20067492.

Theberge, J., and Walker, G. 2011. Managing for caribou and ecological integrity: reply to Serrouya and Wittmer 2010. Conserv. Biol. **25**(5): 858–859. doi:10.1111/j.1523-1739.2011.01721.x. PMID:21902717.

Thiessen, C.D. 2007. Population structure and dispersal of wolves (*Canis lupus*) in the Canadian Rocky Mountains. M.Sc. thesis, Department of Biological Sciences, University of Alberta, Edmonton.

Thompson, S.K. (*Editor*). 1992. Sampling. John Wiley and Sons, New York.

Underwood, A.J. (*Editor*). 1997. Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge, UK.

Wasser, S.K., Keim, J.L., Taper, M.L., and Lele, S.R. 2012. To kill or not to kill—that is the question. Front. Ecol. Environ. **10**(2): 67–68. doi:10.1890/12.WB.006.

Webb, N.F., Allen, J.R., and Merrill, E.H. 2011. Demography of a harvested population of wolves (*Canis lupus*) in west-central Alberta, Canada. Can. J. Zool. **89**(8): 744–752. doi:10.1139/z11-043.

Whittington, J., Hebblewhite, M., DeCesare, N.J., Neufeld, L., Bradley, M., Wilmshurst, J.W., and Musiani, M. 2011. Caribou encounters with wolves increase near roads and trails: a time-to-event approach. J. Appl. Ecol. **48**: 1535–1542. doi:10.1111/j.1365-2664.2011.02043.x.

Wisdom, M.J., Mills, L.S., and Doak, D.F. 2000. Life stage simulation analysis: estimating vital-rate effects on population growth for conservation. Ecology, **81**(3): 628–641. doi:10.1890/0012-9658(2000)081[0628:LSSAEV]2.0.CO;2.

Wittmer, H.U., Sinclair, A.R.E., and Mclellan, B.N. 2005. The role of predation in the decline and extirpation of woodland caribou. Oecologia, **144**(2): 257–267. doi:10.1007/s00442-005-0055-y. PMID:15891849.

Wittmer, H.U., Serrouya, R., Elbroch, L.M., and Marshall, A.J. 2013. Conservation strategies for species affected by apparent competition. Conserv. Biol. **27**: 254–260. doi:10.1111/cobi.12005. PMID:23282104.

Yurk, H., and Trites, A.W. 2000. Experimental attempts to reduce predation by harbor seals on out-migrating juvenile salmonids. Trans Am. Fish. Soc. **129**: 1360–1366. doi:10.1577/1548-8659(2000)129<1360:EATRPB>2.0.CO;2.