Developing a population target for an overabundant ungulate for ecosystem restoration

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Summary

1. Ecosystem restoration typically focuses on re-establishing native plant communities with the hope of restoring ecological processes over the long term. In contrast, endangered species management usually focuses on short-term actions that directly affect population numbers. Here, we present an intermediate approach. We develop an ecologically based population target for the overabundant herbivore, moose *Alces alces*, with the goal of restoring a predator–prey system and thus preventing the extinction of the endangered ungulate, woodland caribou *Rangifer tarandus*.

2. Forest harvesting is a major factor contributing to increases in the number of moose, which in turn increases predator populations. Caribou populations decline as a result of increased predation representing a form of apparent competition between moose and caribou. This presents a unique conservation challenge as recovery of caribou through forest restoration would take decades, while the alternative of directly reducing predator numbers is a short-term solution. A third option is to reduce moose numbers to also maintain predators at low numbers, but the question is to what density should moose be reduced?

3. We created a statistically based target for moose abundance under conditions without forest harvesting by developing a habitat-based population model for moose under current conditions. We then calculated the habitat quality in the same area but under simulated 'pristine' conditions. We also evaluated three measures of ecological carrying capacity to determine the reliability of using current moose abundance to back-calculate numbers for the pristine landscape.

4. Our analysis suggests an 81·6% (71·0–89·9%, 95% CI) reduction in moose habitat quality under pristine conditions. All three measures indicated that moose numbers in the current landscape were near carrying capacity, suggesting that the current abundance could be used to approximate numbers for the pristine landscape and thus be used as an ecological target.

5. *Synthesis and applications.* There are few experimental tests designed to alleviate predator-mediated apparent competition by reducing overabundant prey. Our target will now be used in an adaptive management framework to evaluate the success of this recovery option for caribou, and inform whether this approach can be applied to other systems involving species endangerment from the apparent competition mechanism.

Key-words: *Alces alces*, apparent competition, bootstrapping, geographic information system, moose, predator–prey, *Rangifer tarandus caribou*, restoration, woodland caribou

Introduction

Restoring ecosystems after broad-scale alteration by humans poses a tremendous challenge to scientists and managers seeking to retain the components of community composition and structure (Dobson, Bradshaw & Baker 1997). When forested ecosystems with rare natural disturbance (e.g. rain forests) are harvested, it can take centuries for succession to achieve former levels of structure and biomass (Franklin *et al.* 2002). Yet ecosystem restoration has typically focussed on re-establishing

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vegetation with the assumption that processes at higher trophic levels will follow. This approach is critical for the long-term restoration of ecosystems but may not prevent extinctions in the short term. Interim action at higher trophic levels may be necessary to maintain key processes and species until conditions at lower trophic levels recover.

Temperate forested ecosystems with high precipitation (>100 cm/year) produce climax stands of large, old trees. These ecosystems are highly productive (Meidinger & Pojar 1991), and there is a substantial shift in structure when they are logged, as forests with closed canopies and little understorey are replaced by openings with dense shrubs. Consequently, harvested landscapes gain organisms that thrive in early seral conditions but lose those adapted to late-successional forests. One such ecosystem is the inland temperate rain forest found from Idaho, USA, to central British Columbia (BC), Canada.

The mammal of greatest conservation concern in this system is the mountain caribou *Rangifer tarandus caribou*, which is an endangered ecotype of woodland caribou. Their numbers have been declining for many decades and were recently found in 18 subpopulations; six have <20 animals and two are now extinct (Wittmer *et al.* 2005). Currently, the proximate cause of their decline appears to be apparent competition (Holt 1977) with other ungulate species (Seip 1992; Wittmer, Sinclair & McLellan 2005). When shrubs become abundant after forest harvesting, moose *Alces alces* and deer *Odocoileus* spp. increase in number (Rempel *et al.* 1997; Latham *et al.* 2011). Wolves *Canis lupus* are strongly dependent on ungulate biomass (Fuller, Mech & Cochrane 2003), so their numbers correspondingly increase. Because caribou have lower fecundity than other ungulates (Shackleton 1999), the incidental predation on caribou can cause population decline without influencing predator abundance because they depend on other prey species (Seip 1992; Wittmer, Sinclair & McLellan 2005). This apparent competition mechanism is consistent with many woodland caribou population declines across North America (Bergerud & Elliot 1986; Schaefer 2003; James *et al.* 2004; Courtois *et al.* 2007), as well as other species in other ecosystems (Norbury 2001; Courchamp, Woodroffe & Roemer 2003; DeCesare *et al.* 2010).

Given that most caribou populations will continue to decline or go extinct before old-growth forests are restored (Serrouya & Wittmer 2010; Wittmer, Ahrens & McLellan 2010), maintaining caribou over the short term is reliant on managing the higher trophic levels where there are two plausible recovery options (Seip 2008). The first option is to reduce predators until their primary prey (non-caribou ungulates) decline as existing early seral habitats transition to older forests that have few preferred shrub species. The second option is to reduce primary prey by sport hunting to indirectly reduce predator abundance. Although predator reductions positively affect caribou recruitment and in some cases abundance (Bergerud & Elliot 1986; Orians *et al.* 1997; Hayes *et al.* 2003), predators quickly recover once control has stopped, and predator control is much less acceptable to the public than it once was (Orians *et al.* 1997; but see Boertje, Keech & Paragi 2010). Given the social and ecological constraints, the best solution may be to reduce both predators and primary prey concurrently (Courchamp, Woodroffe & Roemer 2003). A critical management question is to what level should these populations be reduced. Eliminating predators and primary prey to allow the recovery of mountain caribou is one extreme but is not socially acceptable (Orians *et al.* 1997). An alternative target would be to reduce primary prey and predators to the number expected before alteration in the system by human activities.

Our objective was to estimate the number of moose that would have occurred in an ecosystem prior to it being heavily modified by forest harvesting. This estimate could be used to set targets for both moose and wolf abundance so a more natural predator–prey system can be re-established, helping maintain caribou populations until the vegetation recovers to a state where moose forage is less abundant. Our ultimate hypothesis was that these targets would be compatible with caribou persistence because they are more likely to represent historic conditions in this rain forest ecosystem.

Materials and methods

STUDY AREA

The study was located in BC, Canada, near the city of Revelstoke (51°32′, −118°31′). The Monashee Mountains to the west and the Selkirk Mountains to the east attain heights of ≈ 3400 m. Between these mountains at 600 m is the Revelstoke Reservoir, a portion of the Columbia River that was dammed in 1983, flooding 114 km^2 of low-elevation forest. The overall study area was 6368 km^2 and includes Revelstoke National Park (Appendix S1, Supporting Information). Average annual valley-bottom snowfall was 396 cm ($n = 100$ years, SD = 120) and 1427 cm ($n = 39$ years, SD = 263, Parks Canada files) at 1875 m (i.e. caribou late-winter habitat; Apps *et al.* 2001). Total precipitation is 200 cm/year, and plant communities were described by Apps *et al.* (2001). The winter range of moose was restricted by snowfall to 1050 km^2, but in summer moose dispersed to higher elevations, covering about three times the area (R. Serrouya, unpublished telemetry data). Mule deer *Odocoileus hemionus*, white-tailed deer *O. virginianus*, mountain goat *Oreamnos americanus* and mountain caribou are present at low densities, and carnivores include wolves, a few cougars *Puma concolor* ($n < 6$, H. van Oort, C. Bird, G. Mowat, C. Gaynor & L. De Groot, unpublished data) and bears *Ursus americanus* and *U. Arctos*, which are more common. Beginning in 2003, moose numbers were reduced using sport hunting to increase hunting opportunity and to reduce apparent competition with caribou, although no population target was developed.

Four of 16 remaining subpopulations of mountain caribou are in our study area. From 1994 to 2009, these subpopulations declined from 117 (105–130; 90% CI) to 10 (Columbia South), 232 (203–272) to 142 (142–200; Columbia North), 34 (27–47) to 12 (Frisby-Boulder) and 17 to 3 (Central Rockies) (Wittmer *et al.* 2005; McLellan, Serrouya & Furk 2008).

During our study, the vegetation within the harvestable forest (areas outside parks and economically viable to log) consisted of 46% primary (>250-year-old) forest, 33% regenerating cutblocks, 6% 'mid seral' (30- to 80-year old) and 6% was 140- to 250-year-old forest. The remaining 8% included natural openings such as avalanche paths and marshes. Additionally, forests that contain old trees but are uneconomical to harvest covered 35% of the study area. Above these forests are alpine areas, glaciers and rocky peaks that cover

27% of the study area. As a result of legally binding land-use plans, 67% of the remaining old harvestable forest is protected for mountain caribou, which corresponds to 48 000 ha in our study area (RHLPO 2005).

ANALYSIS

Our analyses were based on creating a habitat-based population estimate for moose (Boyce & McDonald 1999). We used 1994–2010 moose censuses using stratified random block (SRB) surveys and pellet transects to estimate the abundance of moose under current, human-altered landscapes (see Appendix S1, Supporting Information for the details of methods used to monitor moose abundance). We then created a resource selection function (RSF; Manly *et al.* 2002) using these censuses and ecological covariates thought to be important to moose habitat selection. Covariates were represented as spatial data bases in a geographic information system (GIS). We validated the RSF using independent data from moose fitted with radio-collars in the same area but collected from 2004 to 2010. We then simulated a landscape in the same area that excluded human-caused early seral vegetation (cutting units and hydro-electric powerlines), which we term the 'pristine' landscape. The final step was to apply the RSF to the pristine landscape to estimate the change in moose habitat quality and thus moose population size, by using the ratio of RSF values of the pristine to the current landscape (*sensu* Patthey *et al.* 2008).

MOOSE ABUNDANCE IN THE HARVESTED LANDSCAPE

To back-calculate moose numbers for the pristine landscape, we used the 2003 population estimate to represent the ecological carrying capacity under current landscape conditions. The 2003 estimate was based on a SRB aerial census, with a sightability correction factor based on a radiomarked sample of moose (Quayle, MacHutchon & Jury 2001). We defined ecological carrying capacity as an abundance that is limited by a combination of food and natural predation. We provide three indications that moose were near ecological carrying capacity in 2003. First, moose had been lightly hunted ($<4\%$, males only) for at least 12 years and were rapidly increasing prior to 2003. Secondly, we compared moose recruitment in our study area after 2000, to earlier periods and other areas because recruitment should decline near carrying capacity (Nicholson 1933). We also compared recruitment to 65 other moose surveys in BC. Thirdly, we compared moose densities in our system with those from other areas in BC.

MOOSE HABITAT MODEL

We used logistic regression to model the RSF based on habitats selected by moose in winter. The binary response was moose locations recorded during winter aerial population censuses and random locations were considered 'available' (i.e. Design I, Manly *et al.* 2002). Random locations were distributed throughout the study area (Appendix S1, Supporting Information), and we increased their number until the proportions of habitat types varied by $<1\%$ as new random locations were added. The RSF model can be summarized using the equation:

$$W(x) = e^{(\beta_1 x_1 + \beta_2 x_2 \ldots + \beta_n x_n)} \qquad \text{eqn 1}$$

where $W(x)$ is the relative probability of occurrence as a function of the covariates $x_1, x_2, \ldots x_n$, and $\beta_1 \ldots \beta_n$ are the respective parameter estimates obtained from logistic regression. There is no intercept or asymptote to this function because it is considered to

predict the relative probability of occurrence, not an absolute probability (Boyce & McDonald 1999).

We developed RSF models for the winter season. Although annual energy budgets may limit ungulate populations (Parker *et al.* 1996), winter is considered the limiting season in mountainous ecosystems because deep snow restricts their distribution and movements and forage is least available (Poole & Stuart-Smith 2006). In summer and autumn, moose can remain in valleys or spread out into the mountains where there is abundant forage.

We considered seven factors as potential predictors of moose habitat selection. Two were human-caused early seral habitats: cutting units (<30 years old) and hydro-electric powerlines, which were combined into one variable called 'human seral.' Three factors represented natural types of early seral vegetation: marshes, avalanche paths and wildfires <30 years old. We also considered age of the forest stand and closest distance to any early seral vegetation. The distance variable was included because moose often forage in early seral areas but move in and out of adjacent forest. Finally, we considered elevation because this variable influences many ecological processes in mountainous ecosystems (Apps *et al.* 2001). We developed nine *a priori* candidate models but did not include factors that were highly correlated ($r > |0{\cdot}7|$). To assess model fit, we present the area under the receiver operating curve (ROC). Although this metric can be biased because of the use-available design employed (Boyce *et al.* 2002), biases would not compromise comparisons between models. To rank the relative weight of evidence for each model, we used Akaike's Information Criteria (AIC; Burnham & Anderson 2002).

We also validated the models with independent data by using locations from moose fitted with GPS and VHF collars from 2004–2010 in the study area during the late-winter season (12 January to 22 April; Apps *et al.* 2001). We accounted for biases in GPS collar fix success using D'Eon *et al.*'s (2002) equation, which was derived in the same ecosystem as ours. For each late-winter moose location, we extracted the RSF value from the census-based model, then binned the RSF scores into 10 equal categories and plotted the sum of the RSF value in each bin against the area-corrected frequency distribution of the telemetry locations. Then, we calculated the Spearman correlation between the RSF scores and the frequency distribution as the index of validation (Boyce *et al.* 2002). We also used the telemetry data to summarize the proportion of locations that were within or 200 m from human-caused early seral vegetation, as a comparison with the census-based proportions.

To create the simulated 'pristine' landscape, we converted human-caused seral habitat (cutting units and transmission lines) to mature forest by assigning the age of adjacent stand using a 'nearest neighbour' algorithm from Hawth's tools (Beyer 2004). We also calculated relevant GIS layers for the pristine landscape such as distance to seral edge, to be able to apply the RSF to the pristine landscape. The RSF value was calculated for each pixel, using the logit back transformation of the sum of the linear predictor from eqn 1. This process was carried out for both the 2003 and the pristine landscape. We then compared the sum of the RSF values for all pixels for the 2003 landscape with the pristine landscape and the corresponding pristine population estimate using

$$N_{\text{pristine}} = \left(\frac{\sum_{i=1}^{j} W(x_{\text{pristine},j})}{\sum_{i=1}^{j} W(x_{2003,j})} \right) \times N_{2003} \qquad \text{eqn 2}$$

where N is the moose population size, j is each pixel in the study area and 2003 and pristine denote the two landscapes being compared. To obtain robust confidence intervals (CIs) of the relative change between both landscapes, we bootstrapped the 2003

census data 500 times. At each iteration of the bootstrap, we obtained parameter estimates from logistic regression, calculated the RSF for both landscapes and finally calculated the ratio between the pristine and the 2003 landscape as per eqn 2. We then used the percentile method to report 95% CIs and the mean $N_{pristine}$ of the bootstrapped values. These steps were programmed in R (version 2.11.1; R Core Team 2006; see Appendix S2, Supporting Information for RSF and GIS bootstrapping code).

Results

MOOSE POPULATION TRENDS

Recent (2003–2009) aerial censuses and pellet transects indicate that moose declined from 1650 to 447 individuals (Fig. 1). Aerial censuses from the 1990s suggest lower moose numbers relative to the apparent peak in 2003. Adult male-to-female ratios in 2003 were 77:100 (66–89, 90% CI).

The calf per adult female ratio in 2003 was 22:100 (18–27), compared with 69:100 (66–72) in 1994, when the moose population was increasing rapidly (Fig. 1). The 2003 census also revealed a low calf ratio relative to 65 other surveys in BC summarized by Hatter (1999), where only four of these studies had calf ratios lower than 25:100 females. Calf per female ratios remained low in 2006 and 2007 (Fig. 1). Finally, at $1.58/km^2$, moose densities in 2003 were more than twice that of the next highest in Hatter's (1999) summary of 65 surveys (mean = $0.30/km^2$, SD = 0.22, range 0.26–0.73).

MOOSE HABITAT MODEL

During the 2003 SRB census, we observed 337 groups of moose, ranging from 1 to 10 individuals (mean = 1.9, median = 1, SD = 1.3). Once we accounted for the number of moose per group and corrected for sightability (Quayle, MacHutchon & Jury 2001), 67.0% of moose were found in cutting units despite only accounting for 20.3% of the study area. Comparing moose to random locations revealed that moose were positively associated with early seral vegetation created by humans, low elevations and marshes, but negatively associated

with avalanche chutes and increasing distance from all forms of early seral vegetation (Tables 1 and 2). Based on AIC weights, the most influential of these factors were human-created early seral vegetation, distance to early seral vegetation, elevation and avalanche chutes, whereas marsh areas were less important. Both top models had high ROC scores (0.95), indicating a reliable discrimination between used and random locations.

There were sufficient winter telemetry data from 28 moose (20 GPS and eight VHF) for independent model validation. The census-based RSF bins and the area-adjusted frequency of telemetry locations were highly correlated (R^2 = 0.85, Spearman r = 0.93; Fig. 2). During winter, 59.8% of the telemetry locations were in 'human seral' and 18.5% were < 200 m from these young stands; thus, 78.3% of the moose locations were in 20.3% of the landbase associated with human-created early seral conditions.

When we applied the census-based model to the current landscape (Fig. 3a), the sum of the RSF values for all pixels was 13 074. The sum of all RSF values of the pristine landscape (Fig. 3b) was 2401, suggesting a decline in habitat quality of 81.6%. Bootstrapping the 2003 census data resulted in 95% confidence intervals of 71.0–89.9%. Assuming a linear relationship between RSF values and population size (eqn 2; *sensu* Boyce & McDonald 1999), and using 2003 as the approximate ecological carrying capacity under current landscape conditions, then the pristine landscape was predicted to have 303 (167–478; 95% CI) moose.

Discussion

Restoration efforts benefit from having clear goals with associated targets to help estimate achievement (Margules & Pressey 2000), yet there continues to be a debate on how to develop these targets. Some argue for landscape conditions set to a specific time period (Loh *et al.* 1998), whereas others suggest the use of protected areas as benchmarks (Arcese & Sinclair 1997). In our case, we simulated a landscape free from human-caused disturbance and applied a model derived under current conditions to estimate a target for restoration. Although this
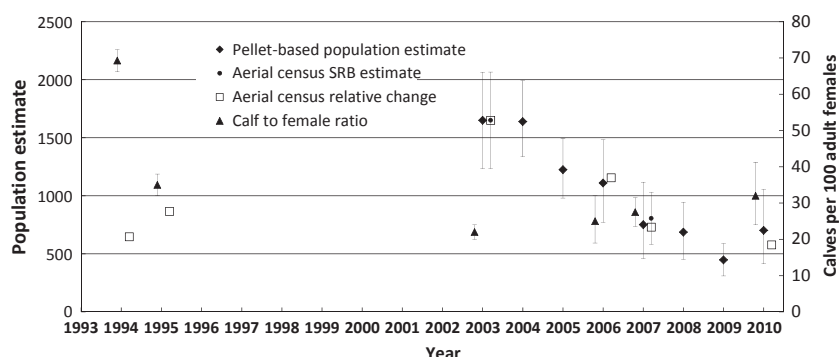

Fig. 1. Changes in moose abundance in the Lake Revelstoke Valley from 1994–2010. Three different methods are presented (see Appendix S1 Supporting Information): (i) Abundance estimates using a stratified random block design aerial census (SRB; circles); (ii) relative change based on aerial counts of moose from a sample of five survey blocks (open squares); and (iii) relative change based on 17 pellet transects (diamonds). Both relative indices were set to the 2003 SRB estimate as the initial value. Also shown are calf-to-adult female ratios (triangles; secondary *y*-axis). Error bars are 90% CIs.

Table 1. Logistic regression results for top models (0–2 AIC units) for factors predicting moose habitat selection, based on census data from the Lake Revelstoke Valley, January 2003

Model structure[a]	ROC	AIC	k	LogL	ΔAIC	AICω
Human_seral + Seral_distance + Avalanche_path + Elevation	0·95	835·86	5	−412·9	0·00	0·54
Human_seral + Seral_distance + Marsh + Avalanche_path + Elevation	0·95	837·85	6	−412·9	1·99	0·20

AIC, Akaike's Information Criteria; ROC, receiver operating curve.
[a]Human_seral is any early seral vegetation caused by humans; Seral_distance is the distance to any early seral vegetation; Marsh is open meadows or marshes; Avalanche_path is where snow avalanches occur regularly, maintaining early seral vegetation; Elevation is elevation a.s.l.

Table 2. AIC weights (AICω) for each variable present in the top model, weighted parameter estimates and 95% confidence intervals (CIs; based on 500 bootstrap iterations)

Variable[a]	Parameter estimate[b]	95% CIs[b]	AICω
Elevation	−0·81	−0·72 to −0·93	1·00
Seral_distance	−0·65	−0·38 to −1·19	0·98
Human_seral	40·77	116·30 to −12·05	0·88
Avalanche_path	−80·84	1·28 to −179·62	0·87
Marsh	0·53	34·71 to −30·14	0·37

[a]ROC is the area under the receiver operating curve, AIC are Akaike Information Criteria units, k is the number of parameters, LogL is the log likelihood, ΔAIC is the difference in AIC units between the top model and the *i*th model, and AICω are Akaike weights. See Table 1 for acronyms.
[b]×100.
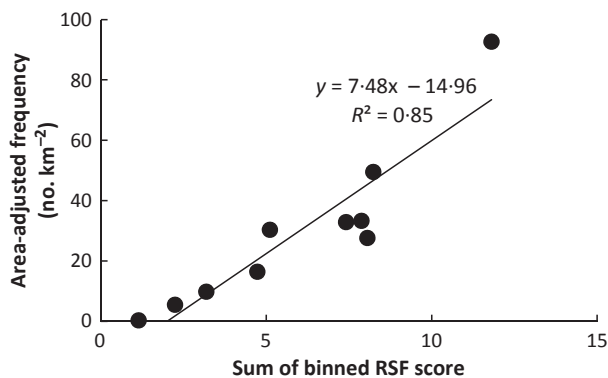
Fig. 2. Independent validation of the moose winter habitat model. The winter model was based on 2003 aerial census data (corrected for sightability), and the validation was conducted using radiotelemetry data from 2004–2010 (black dots, solid line).

model was robust to independent validation, we recognize that it is being extrapolated beyond the range of conditions from its development. A substantial change in moose foraging behaviour in a landscape dominated by old forests would change the selection coefficients we presented here and thus affect our pristine estimate. However, given the inverse relationship between mature forests and moose abundance documented elsewhere at broad scales (Schwartz & Franzmann 1991; Rempel *et al*. 1997), any change in selection would not be strong enough to change our general conclusions. Alternative approaches to deriving targets also have shortcomings. Protected areas in mountainous systems are often biased to

high-elevation, scenic sites with less productive ecosystems (Margules & Pressey 2000; Scott *et al*. 2001) compared with the low-elevation forests in our study area. Protected areas are also rarely large enough to contain large mammal predator–prey systems (Noss *et al*. 1996). Given these constraints, our approach of deriving a statistically based target moose population was likely to be the most appropriate (see Nielsen *et al*. 2007 and Patthey *et al*. 2008 for similar examples).

There is disagreement whether moose were rare or entirely absent from southern BC (Hatter 1950; Spalding 1990; Kay 1997), but it is clear that moose were far more abundant during the past decade than historically. Our prediction of 303 (167 – 478) moose in a pristine landscape is similar to 204 moose estimated in 1984 (Bradley 1986; a decade after broad-scale logging began), but re-sightability was low so the precision was poor (±159, 95% CIs). Higher recruitment in the 1990s suggests that moose were not regulated by forage at that time, but when numbers doubled by 2003, there appeared to be a density-dependent reduction in recruitment to among the lowest recorded in BC. Furthermore, the 2003 wintering density (1·58/km^2) in our system was the highest recorded in BC, > 5 times higher than the mean reported in Hatter's (1999) summary. The 2003 density estimate was also above what is considered 'high density' habitat in Alaska (1·1/km^2; Gasaway *et al*. 1992; Keech *et al*. 2000). The central portion of our study area (Goldstream Valley) had a density of 4·8/km^2 (35% of the study area estimate), higher than the 50-year peak value from the unexploited island system of Isle Royale National Park (4·5/km^2, though the mean density since 1959 in Isle Royale was less than half this value; Vucetich & Peterson 2004). These recruitment and density comparisons suggest moose were near ecological carrying capacity in 2003.

An assumption of our temporal habitat comparisons is that resources selected by organisms reflect a positive fitness choice. Van Horne (1983) cautioned that this tenet was incorrect, but since then many studies have shown that resources selected by a range of vertebrates based on indices of animal density can have links to abundance (Wheatley, Larsen & Boutin 2002; Bock & Jones 2004). Van Horne's (1983) concerns dealt with areas modified by humans that can create ecological traps because animals had not adapted to these novel habitats. Considering that moose evolved with early seral vegetation and associated predators, it appears this vegetation is not novel habitat for these ungulates. Therefore, the RSF we created probably reflects resource choice that relates to the fitness of the
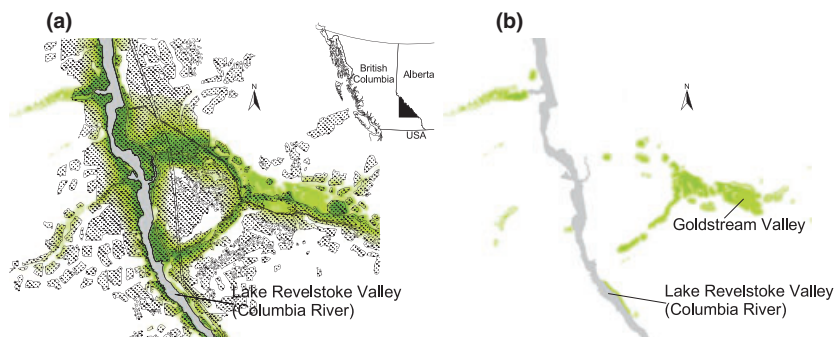
Fig. 3. Resource selection function (Tables 1 and 2) for moose in a small portion of the study area (the Goldstream Valley is a tributary of Lake Revelstoke) for (a) current (2003) logged landscape and (b) a simulated pristine landscape. Darker green indicates higher habitat quality, and speckled polygons are human-caused early seral vegetation (clearcuts and hydro-electric powerlines). The effects of removing this vegetation can be seen by comparing the two maps. The moose habitat that remains in the pristine landscape is from natural openings such as marshes and wetlands. Note how habitat quality decreases with increasing distance from early seral vegetation and increasing distance from valley bottoms (i.e. elevation; Tables 1 and 2).

animals (Boyce & McDonald 1999; McLoughlin *et al.* 2006, 2007). It is likely that the selection patterns are robust to a range of ecological conditions including density and resource availability because our estimates of selection were consistent using a variety of techniques. These included a broad representation of moose using aerial census data, fewer moose but across time (and thus density) using radiocollar data, and match the outcome of a third study based on systematic snow track transects (R. Serrouya & R. G. D'Eon, 2003).

Several factors may cause an underestimate of historical moose numbers including the habitat loss from flooding the Columbia River at Revelstoke in 1983. However, considering the current abundance of clearcuts and existing natural openings, habitat loss from flooding in 1983 amounts to only 1–2% of the current habitat area (Utzig & Holt 2008; R. Serrouya unpublished data). Dynamic factors associated with expanding moose populations could also affect our historic target. When organisms occupy a new region, they sometimes exceed carrying capacity (Simard *et al.* 2008) and then drop below this level leading to dampening oscillations towards an equilibrium (Caughley 1970). Although we provide evidence that moose were approaching carrying capacity, if our 2003 benchmark was below or above this level, our pristine estimate would be affected correspondingly.

Processes associated with small populations were not considered in our estimate of historic moose carrying capacity because we assumed a direct relationship between habitat change and population change. For example, as some ungulate species decline, so do their average group size, making them more vulnerable to predation and contributing to a dispensatory predation rate (McLellan *et al.* 2010). Moose group sizes have shown declining patterns in our study area (McLellan *et al.* 2010). In addition, given that moose habitat in the pristine landscape is more fragmented compared with the current landscape (Appendix S3, Supporting Information), other demographic factors associated with isolated and small subpopulations (Soulé 1986) could make moose viability more difficult under pristine conditions.

There is uncertainty when estimating the number of moose expected in a pristine environment, and consequently, there will be further uncertainty when estimating the number of predators. Using Fuller, Mech & Cochrane (2003) equation to predict wolf numbers from ungulate biomass, 303 (167–478) moose yields nine wolves (6·5–12·1), or a density of 8·1/1000 km^2 (5·9–11·0/1000 km^2). This wolf density is lower than recent estimates of wolves in the study area (16·4–30·9/1000 km^2 from 2007–2010). Although wolf numbers have declined in response to the moose reduction treatment (H. van Oort, C. Bird, G. Mowat, C. Gaynor & L. De Groot, unpublished data), the wolf decline is lagging behind the moose decline, as has been observed in other areas (Gasaway *et al.* 1992). This lag may increase predation on caribou because wolves must increase searching time for the less-abundant primary prey (moose), and may encounter more caribou. Elsewhere, primary prey has been reduced too quickly and predators killed more rare prey (Norbury 2001). We recommend that any further moose reduction is accompanied by concurrent wolf reduction. We predict that because there are far fewer moose on the landscape, immigration of wolves, which often follows wolf reduction (Hayes *et al.* 2003), should be reduced, thereby lessening the need for continuous wolf control. Reducing moose may also help to reduce the abundance of other predators in the system including cougars and bears, which have also been common predators of caribou at various time periods (Wittmer *et al.* 2005; Stotyn 2008).

Now that a target population has been developed for the dominant ungulate, the next step is to test the outcome of reducing the number of these animals to determine whether caribou survival and recruitment increases. This active adaptive management experiment (Walters & Holling 1990; Chee & Wintle 2010) is underway with an adjacent control where moose numbers are not being reduced. However, because some mountain caribou populations are in imminent danger of extinction (Serrouya & Wittmer 2010), moose and predator targets may need to be lower to further reduce extinction risk. If the smaller mountain caribou populations recover, then our approach and target will be useful for decision-making and adaptive evaluation until the early seral habitat recovers. Furthermore, we suggest that the approach developed here can be applied across ecosystems including the boreal forest where woodland caribou are also declining (Festa-Bianchet *et al.* in press), and to cari-

bou-deer-cougar systems that are more prevalent in southern Canada and north-western USA (Kinley & Apps 2001).

The effort required to recover mountain caribou in British Columbia highlights the importance of social values in making management decisions regarding predators and valued game species. In Alaska, elected officials have decided to use ongoing predator control to reduce wolf, grizzly and black bear populations, so moose numbers will increase allowing hunters to kill more moose (Boertje, Keech & Paragi 2010). Whereas in British Columbia (adjacent to Alaska), moose populations are being greatly reduced, so wolf control will only be needed for a short time period to allow the recovery of an endangered ungulate. To allow the recovery of caribou, a truly 'ecosystem management' (Grumbine 1994) approach would be to manage moose and predators at historic levels until the habitat recovers completely. Complete habitat recovery may be unrealistic given the economic pressure to harvest forests, but recent recovery plans have set aside substantial old-growth reserves to prevent additional forage for moose and deer, and plans include a strategy to recruit early seral stands to old forests (RHLPO 2005). Despite these protection measures, it is unlikely that a truly ecosystem-based recovery approach will be feasible and continued management of moose to historic levels will be needed in perpetuity. However, the intensity of this management should be reduced with newly enacted protection of old forests. Furthermore, we suggest that liberalized sport hunting can be used to reduce moose populations (R. Serrouya, unpublished data), despite abundant moose forage (and see Rempel *et al.* 1997). This approach appears more socially acceptable than predator control, at least in British Columbia (C. Ritchie, BC Ministry of Environment, Pers. Comm.).

The multitrophic approach to caribou recovery in British Columbia is being recognized by independent researchers to be among the most comprehensive in North America (Hebblewhite, White & Musiani 2010; Festa-Bianchet *et al.* in press). However, habitat protection, without management of the predator–prey system, will be insufficient and will result in the extinction of caribou subpopulations (Wittmer, Ahrens & McLellan 2010). These extinctions may lead to returning large areas of old-growth forest to short-term rotation forestry (Serrouya & Wittmer 2010). It is hoped that this multitrophic level approach to conservation will be evaluated and adapted as the dynamics of the large mammals respond to the treatments described here.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Methods used to estimate moose abundance from 1994 to 2010.

Appendix S2. R code for RSF and GIS bootstrapping approach to estimate precision for the moose target in the 'pristine' landscape.

Appendix S3. RSF map for the entire study area for two time periods, the 2003 and pristine landscapes.

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