



Interacting effect of wolves and climate on recruitment in a northern mountain caribou population

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There is limited research on the influence of Pacific-based climate in large herbivore populations. Additionally, much of our understanding on the effect of large-scale climate on ungulate population dynamics has occurred on forage-limited rather than predator-limited populations. We compared the influence of the Pacific Decadal Oscillation (PDO), North Pacific Index, and local weather on recruitment in a predator-limited mountain-dwelling caribou *Rangifer tarandus caribou* population in the Yukon Territory, Canada, across a range of wolf *Canis lupus* densities. A large-scale wolf removal program allowed us to examine the role of Pacific climate and weather when wolves were reduced to ~15% of their pre-removal levels. Recruitment was best explained by the interaction of wolf density and April-PDO, with wolf density explaining the most deviance. Predicted recruitment during good springs was 0.45 (SE = 0.04) during wolf removal and 0.29 (SE = 0.03) with no wolf removal. During poor springs (low PDO, increased snow depth) predicted recruitment was 0.55 (SE = 0.10) during wolf removal and 0.12 (SE = 0.03) with no wolf removal. With non-altered wolf densities, there was a positive relationship between April-PDO and recruitment due to reduced snow depth at calving, allowing parturient females to disperse up in elevation away from predators. When wolf densities were substantially reduced there was a slight negative relationship between April-PDO and recruitment, possibly due to a more rapid vegetation green-up reducing the temporal availability of highly nutritious forage necessary for lactation and subsequent calf growth. Attempts to find general relationships between climate and ungulate population dynamics have proven difficult due to different ecological mechanisms by which climate affects individuals across populations. Temporally varying factors, such as predator density, may also play an important role in uncovering the mechanistic relationship between climate and population dynamics.

The use of large-scale indices has proven successful in enhancing our understanding of climate's influence on ecological patterns (Stenseth et al. 2003). In western Europe and eastern North America, the North Atlantic Oscillation (NAO) index sometimes better predicts ecological processes (e.g. survival) than measures of local weather, as it captures variation across multiple months (i.e. time window), spatial scales (e.g. altitude, latitude), and incorporates variation and interactions from multiple weather variables (e.g. precipitation, temperature) into one parsimonious metric (Hallett et al. 2004, Stenseth and Mysterud 2005). For mobile and/or dispersed individuals in a population, one single weather metric may not represent conditions experienced by all individuals. However, in some continental areas of Europe far from the coast, the impact of the NAO is weaker and principal component-based indices of local weather parameters were better predictors (Mysterud et al. 2007). Additionally, an integrated climate index may represent more complexity than necessary if a single local weather variable is the primary factor affecting an ecological process (e.g. population growth). For example, ungulate population dynamics

in South Africa are largely influenced by dry season rainfall limiting plant growth, rather than a large-scale climate index (Ogutu and Owen-Smith 2003).

Recently, two Pacific-based indices have been related to terrestrial vertebrate population dynamics in North America (Hebblewhite 2005, Morrison and Hik 2007, Hegel et al. 2010): the North Pacific Index (NPI) and the Pacific Decadal Oscillation (PDO). However, the identification of a 'best' Pacific-based climate index in terms of influencing terrestrial vertebrate population dynamics over a broad geographical scope, akin to that of the NAO (Stenseth et al. 2003), remains elusive and identification of such an index may enhance our understanding of ecological systems. The PDO is a measure of climatic variability in the north Pacific region characterized by shifts between warm and cool phases on an interdecadal time scale (Mantua et al. 1997, Mantua and Hare 2002). It is measured as the leading principal component of monthly sea surface temperatures (SST) in the north Pacific from 20°N poleward and 110°E–110°W. Positive (warm phase) PDO values are characterized by cool SST in the central Pacific and warm SST along coastal areas. The

PDO is related to sea level pressure (SLP) such that warm phase PDO values generally coincide with below average north Pacific SLP (Mantua et al. 1997, Stenseth et al. 2003). The NPI is an area-weighted mean SLP index summarizing the north Pacific from 30°N–65°N and 160°E–140°W (Trenberth and Hurrell 1994). Due to the negative relationship between SST and SLP in the North Pacific region, relationships between the PDO and local weather variables (e.g. snowfall) are opposite in direction to NPI – local weather relationships.

Climate can have both direct and indirect effects operating through trophic interactions (Myserud et al. 2008). Most research on trophic interactions has focused on bottom-up effects (Post and Stenseth 1999, Myserud et al. 2001, but see Stenseth et al. 2004 for dynamics of Canada lynx *Lynx canadensis*); however, climate may also affect top-down interactions with predators (Hebblewhite 2005, Wilmsers et al. 2006). For example, Hebblewhite (2005) reported that in elk *Cervus elaphus* populations exposed to wolf *Canis lupus* predation, snow depth explained more variation in population growth rate than the NPI, whereas in populations absent of wolves the NPI was a better predictor. Winter and spring PDO is also negatively correlated with snowmelt phenology (Morrison and Hik 2007, Hegel et al. 2010) such that high values indicate an earlier first snowfree day of the year.

Northern mountain-dwelling caribou *Rangifer tarandus caribou* in the Yukon Territory, Canada (Yukon; Farnell et al. 1998) are regarded as predator-limited (Hayes et al. 2003), primarily through predation on newborn calves (Adams et al. 1995, Gustine et al. 2006) which limits recruitment. As with most ungulate populations that occur with natural predators, density dependent factors regulating population growth are weak (Crête 1999, Wang et al. 2009). Previous research indicates that recruitment dynamics in these populations are influenced by climate affecting environmental conditions at calving (Hegel et al. 2010). However, there is variability in the relationship between climate and recruitment across populations (Grøtan et al. 2009), not unlike the variable response in red deer *C. elaphus* body weight to environmental conditions across Europe (Martínez-Jauregui et al. 2009). One possible explanation for this is that the effect of climate at calving is related to variable predator densities. At calving, parturient female caribou move up in elevation to separate themselves from predators and other parturient females (Bergerud and Page 1987). In years with high snow depth during the calving season, this upward movement may be limited, resulting in higher predation rates on neonates (Bergerud and Page 1987, Adams et al. 1995). Thus, the effect of climate on recruitment may be modified by the number of predators present on the landscape.

We used long-term recruitment data from the Finlayson caribou population (herd) in the Yukon to test three hypotheses regarding the influence of large-scale climate, local weather, and predator density on recruitment dynamics. Local weather and wolf abundance data were available for the Finlayson herd allowing us to focus explicitly on the influence of a predator-climate (local weather) interaction on recruitment. First (H1: regional climate vs local weather hypothesis), we tested the prediction (H1a) that large-scale climate indices would better explain observed patterns in recruitment than local weather variables (Hallett et al. 2004) versus the prediction

that local weather was a better explanatory variable (H1b). If local weather better explained observed recruitment patterns, we predicted that this would be most evident with respect to those weather variables related to environmental conditions at calving, such as winter snowfall, given the high predation on neonates in mountain caribou populations. Second (H2: PDO vs NPI hypothesis), we tested the hypothesis that the PDO and NPI are equally supported in their ability to explain observed recruitment patterns. Due to the lack of direct comparative analyses between Pacific-based climate indices on ungulate population dynamics we had no a priori basis to assume one index would outperform the other. Finally (H3: climate-predation interaction hypothesis), we predicted that the influence of seasonal climate, or local weather, on caribou recruitment would change (Table 1) with reduced wolf densities following a large-scale predator removal program (Farnell and McDonald 1987, Hayes and Harestad 2000).

Methods

Study area and population data

The Finlayson mountain-dwelling caribou herd (~62°N, 128°W), a member of the Northern Mountain ecotype of woodland caribou, is located in the east-central Yukon (Farnell et al. 1998) and is a part of a multi-predator (e.g. wolf, grizzly bear *Ursus arctos*, black bear *U. americanus*), multi-prey system (e.g. Dall sheep *Ovis dalli*, moose *Alces alces*). Details regarding the environmental characteristics of its range are described by Farnell and McDonald (1987) and Hayes and Harestad (2000).

Aerial surveys were conducted during rutting (breeding) season (late September to mid-October) with total counts of observed calves and adult females used to estimate recruitment (calf:cow ratio; Farnell et al. 1998). The dataset used here consisted of 27 annual estimates during the period 1982–2008, and recruitment ranged from 0.09–0.62 (Fig. 1). The total number of animals classified during the surveys ranged from 393 to 2247. The recruitment estimates used here represent a combined measure of fecundity and calf survival to approximately four months of age. Age ratios such as the calf:cow ratio used here are positively correlated with population growth rates (Harris et al. 2008). During the rut, animals are aggregated above treeline in high alpine habitats reducing misclassification errors and increasing detectability of calves. A recent comparison of recruitment estimated aerially with one derived concurrently from individually captured females indicated no meaningful difference in recruitment rate (0.10 vs 0.095, Hegel unpubl.).

In response to perceived poor recruitment and a declining population, a recovery program was initiated for the herd during 1983–1989 (Farnell et al. 1998). During late-winter, wolves were removed from the herd's range to < 20% of pre-removal levels (Farnell and McDonald 1987). Hence, the wolf population was reduced substantially during the years of active removal (Fig. 1) with numbers increasing following removal efforts to pre-removal level (Hayes and Harestad 2000). During this time wolf numbers were estimated annually (Farnell and McDonald 1987) as described in Hayes and Harestad (2000). We did not have absolute wolf density estimates for

Table 1. Predicted relationships (a) and mechanisms (b) between seasonal PDO (NPI relationship in parentheses) and local weather variables, and mountain-dwelling caribou recruitment, with unaltered and reduced (following wolf removal) wolf density in the Yukon Territory, Canada (+: positive relationship; -: negative relationship).

a) Seasonal relationships

Seasonal climate/weather variable	Predicted relationship with unaltered wolf density	Predicted change in magnitude of the relationship with reduced wolf density	Mechanism
April-PDO (NPI)	+ (-)	decrease	1
May-PDO (NPI)			
Winter-PDO (NPI) ^a	+ (-)	decrease	2
Late winter-PDO (NPI) ^b			
April-Snow ^c	-	decrease	1, 2
May-Snow	-	decrease	1

b) Mechanism

- 1 Conditions resulting in increased snow depth at calving results in greater predation on neonates and hence reduced recruitment. These conditions should become less influential as wolf densities decrease.
- 2 Increased snowfall during winter results in calves born in poorer condition with reduced survival during their first summer, and higher snow depth at calving which increases predation. With reduced wolf density, more pregnant females may enter winter in poorer condition and thus be more sensitive to winter conditions, suggesting a strengthening relationship with winter climate/weather. However, given the role of winter snowfall on predation of neonates, the effect of winter climate/weather following wolf reduction could also be expected to weaken (i.e. similar to mechanism 1). Due to the substantial influence of predation on recruitment in these populations, we ultimately expect the weakening of effect size (i.e. mechanism 1) to outweigh any strengthening of due to increased sensitivity to in utero conditions.

^awinter (November–April); ^blate winter (March–May), ^coverwinter snow accumulation measured the beginning of April.

the full range of the Finlayson caribou recruitment time-series; therefore, we generated a relative wolf density index (Wolf) ranging on the unit interval (0, 1). This index represents the proportion of the pre-removal (i.e. not reduced via management actions) wolf population in a year, calculated by:

$$W_t / 10.3 \quad (1)$$

where W_t was the wolf density estimate in year t and 10.3 was the wolf density (wolves/1000 km²) estimated prior to wolf removal activities (Environment Yukon unpubl.). Years prior to wolf removal and following the wolf population's return to pre-removal levels were valued at 1.0. The relative wolf density index ranged from 0.126–1.0 (Fig. 1).

Climate and local weather data

We used seasonal PDO values obtained from the Joint Institute for the Study of the Atmosphere and Ocean at the

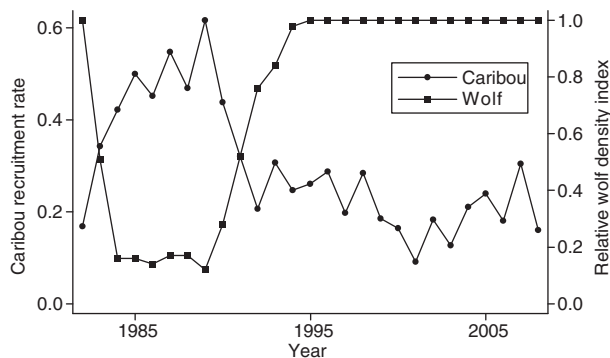


Figure 1. Annual caribou recruitment rates (calf:cow ratio) for the Finlayson caribou herd in the Yukon Territory, Canada, and relative wolf density index values in the herd's range (1982–2008).

Univ. of Washington (Mantua et al. 1997) (<<http://jisao.washington.edu/pdo>>). NPI values were obtained from the Climate Analysis Section of the National Center for Atmospheric Research (Trenberth and Hurrell 1994) (<www.cgd.ucar.edu/cas/jhurrell/npindex.html>). Seasons for which index values were obtained are described in Table 1 and were selected because they were identified as potentially influencing recruitment in northern mountain caribou in the Yukon. Seasonal PDO values were positively correlated with local weather, such as precipitation and temperature, across the Yukon (Hegel et al. 2010) and this study area (Table 2). Relationships between local weather and NPI (Table 2) were in the expected opposite direction to those between the PDO and local weather (Mantua et al. 1997, Yang et al. 2005).

Local weather was represented by snow depth data collected at the Hoole River snowcourse station (61°32'N, 131°36'W) located within the Finlayson herd's range (data provided by Water Resources Branch, Environment Yukon). Two snow measurements (cm), collected at the beginning of the month, were used: May-snow represented snow levels immediately prior to calving (May-Snow), and April-snow represented the overwinter (in utero) accumulation of snow. Separate April and May snow depth measurements were used because spring snowmelt often begins in April. Thus, May snow depth is related to both April climatic conditions and overwinter snowfall. Data from multiple seasons were used to allow for a direct comparison of seasons with differing mechanistic effects on recruitment (Table 1).

Statistical analysis

We modeled caribou recruitment by fitting a suite of candidate generalized additive models (GAM; Wood 2006) which allowed us to account for possible non-linearity (Myerud et al. 2001). If non-linear relationships were not supported,

Table 2. Correlation between seasonal values of the PDO and NPI and local weather variables in the Finlayson caribou herd range in east-central Yukon Territory, Canada (1982–2008). ($p > 0.05$ for all correlations).

Weather variable	Winter ^b		April		Late winter ^b	
	PDO	NPI	PDO	NPI	PDO	NPI
Winter snowfall ^a	-0.30	0.22			-0.18	-0.07
May snow depth ^a	-0.08	0.10	-0.17	0.26	-0.19	0.24

^adata from the Hoole River snowcourse station (61°32'N, 131°36'W);
^bwinter: November–April; late winter: March–May.

generalized linear models (GLM) were fitted instead. All models were fitted using the binomial family and a logit link function. All models were fitted using the 'mgcv' package (Wood 2006) for the statistical software R 2.9.2 (R Development Core Team 2009). We fitted a suite of candidate models using Wolf and the seasonal NPI, PDO, and local weather variables (Table 1), specified as interactions. For GAMs, a tensor-product smooth term represented the interaction. Candidate models were also fitted in which Wolf and the climate/weather variables were specified with separate terms (i.e. no variable interaction). A null model (i.e. no predictors) was also fitted for comparison. We did not include more than one seasonal variable in a model as we regarded this time-series too short to estimate more complex models. All GAM smooth terms were penalized thin-plate regression splines with the degree of smoothing, limited to a maximum of four degrees of freedom ($DF = 4$), selected using generalized cross-validation (Wood 2006).

Candidate models were ranked using the Akaike information criterion adjusted for small sample size (AIC_c ; Burnham and Anderson 2002). For each model (i) we calculated ΔAIC_c , which is AIC_c minus the minimum AIC_c from all models in the candidate set. Models with $\Delta AIC_c < 2$ and large Akaike weights, indicating the probability that model i is the top model among the candidate set, were interpreted as having the strongest support (Burnham and Anderson 2002).

Results

The best model of recruitment was represented by the interaction of relative wolf density (Wolf) and April-PDO (Table 3, Fig. 2). It explained 80.5% of the deviance relative to the null model and had an Akaike weight of 0.99. Wolf

Table 3. Parameter estimates of the top generalized linear model of recruitment rate for the Finlayson caribou herd in the Yukon Territory, Canada (1982–2008). The model explained 80.5% of the deviance relative to the null model.

Parameter	Coefficient	SE ^a
Intercept	0.312	0.227
Relative wolf density index	-1.823	0.272
April-PDO	-0.191	0.176
April-PDO × Relative wolf density index	0.509	0.229

^aBootstrapped standard errors estimated from 1000 simulations.

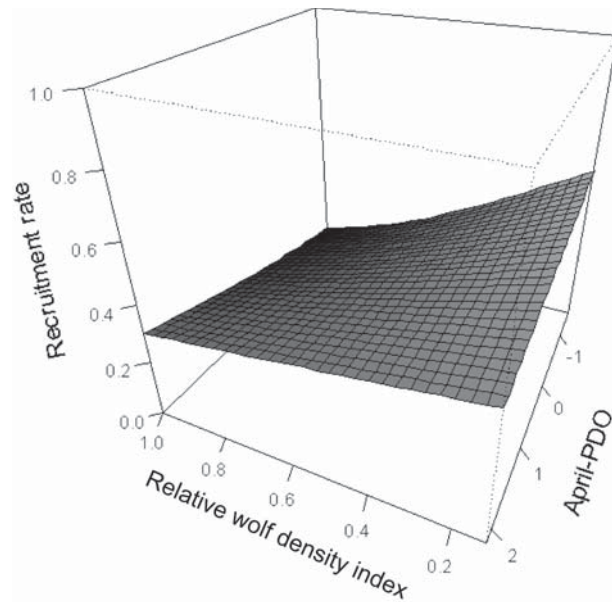


Figure 2. Relationship between recruitment (calf:cow ratio) and the Relative wolf density index × April-PDO interaction, estimated from a generalized linear model, for the Finlayson caribou herd in the Yukon Territory, Canada.

explained 69.3% of the deviance, while April-PDO and the interaction of Wolf and April-PDO explained 11.9% and 5.7% respectively. No other models had $\Delta AIC_c < 10$. The constant-only (null) model ($\Delta AIC_c = 101.5$), models with either Wolf ($\Delta AIC_c = 572.74$) and April-PDO ($\Delta AIC_c = 807.66$) as single predictors, and the model with Wolf and April-PDO as separate smooth terms ($\Delta AIC_c = 67.93$) received less support. NPI and local weather were not represented in the top-ranked models, and the ΔAIC_c values of the best models including these variables were 24.56 and 46.21 respectively (Appendix 1).

The significant interaction between Wolf and April-PDO (Table 3) highlighted the important non-additive relationship between these two variables and recruitment. There was a negative effect of increasing wolf density on recruitment across the range of April-PDO values (Fig. 2), although this relationship lessened as April-PDO increased suggesting that in 'good' springs, climate partly buffered the effect of wolves. The relationship between April-PDO and recruitment was positive at high wolf densities; however with reduced wolf numbers the direction of this relationship changed to one that was slightly negative (Fig. 2, 3). For example, predicted recruitment with April-PDO at 2.0 and -1.5 was 0.29 ($SE = 0.03$) and 0.12 ($SE = 0.03$), respectively, at high wolf density (Wolf = 1.0). At low wolf density (e.g. Wolf = 0.15) there was a slight negative effect of increasing April-PDO on recruitment (Fig. 3). For example, predicted recruitment at April-PDO of 2.0 and -1.5 was 0.45 ($SE = 0.04$) and 0.55 ($SE = 0.10$) respectively. The difference in predicted recruitment between these two climatic extremes was not significant given the high amount of overlap of 95% confidence intervals of the predictions. Residuals from the top model were normally distributed (Shapiro–Wilk test: $W = 0.97$, $p = 0.59$) and an autocorrelation plot indicated no significant serial autocorrelation.

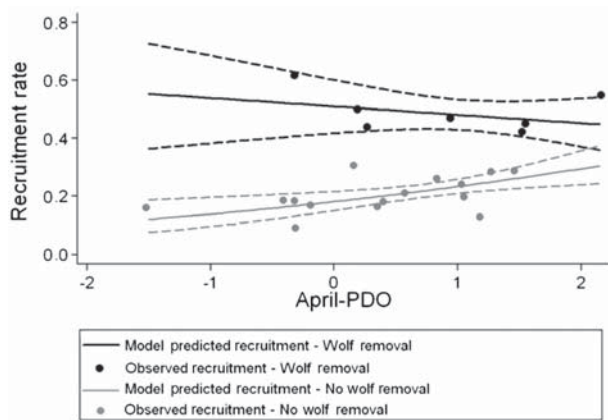


Figure 3. Predicted recruitment rates (calf:cow ratio) for the Finlayson caribou herd in the Yukon Territory, Canada, based on a generalized linear model of recruitment including April-PDO and Relative wolf density index (Wolf) as covariates (Table 3). Solid lines represent predicted recruitment rates during two extremes of no wolf removal (Wolf = 1.0, gray lines) and active wolf removal (Wolf = 0.15, black lines). Dashed lines indicate 95% CI of the predictions. Observed recruitment rates during active wolf removal (Wolf \leq 0.3, black) and no wolf removal (Wolf = 1.0, gray) are indicated by solid circles. Values of April-PDO (-1.5–2.15) used for model predictions were restricted to the range of values present in the model training dataset.

Discussion

The presence of only large-scale climate indices in the top ranked models provided support for H1a, that large-scale climate would better explain recruitment patterns than local weather metrics. The lack of the NPI in any of the top ranked models also led us to reject H2, that the NPI would be an equally good predictor of recruitment as the PDO. Finally, our results provide support for H3, that a reduction in predator density would affect the relationship between climate and recruitment.

Regional climate versus local weather

Our findings, indicating large-scale climate's greater explanatory performance than local conditions, represented by snow depth, are consistent with those previously reported for a variety of ecological systems (Attrill and Power 2002, Hallett et al. 2004). Given the strong mechanistic link between snow conditions at calving and predation on neonates in northern mountain-dwelling caribou (Bergerud and Page 1987), and the increased effect of local weather on elk population growth following wolf recolonization in the Canadian Rocky Mountains (Hebblewhite 2005), we expected snow conditions to be important for recruitment in the Finlayson caribou herd. Our snow depth measurements were obtained from within the range of the herd. However, this site may not have captured all the spatial variation in snow depth across the herd's range, both in area and elevation, making the PDO a better proxy than snow depth from a single station.

When one localized metric is used to represent weather conditions for a mobile species, it may not represent the full range of conditions experienced by individuals. This is particularly relevant for snow depth which may be more spatially variable than either precipitation or temperature. For species such as northern mountain caribou which disperse

away from conspecifics during calving, finding one localized weather measurement to represent the environmental conditions experienced by the population may be difficult. Indeed, northern mountain caribou are most widely dispersed during the calving season.

While snow depth is an important factor influencing predation rates (Huggard 1993), snowmelt patterns may also influence predation rates by creating a more heterogeneous landscape, which may reduce predator searching efficiency and enhance neonate survival (Bergerud and Page 1987, Eastland et al. 1989). If a heterogeneous snowmelt pattern is important for influencing neonate survival, and hence recruitment, an integrated index representing temperature and precipitation prior to calving would thus provide more explanatory power. The complexity of snowmelt patterns may be further enhanced in mountainous and topographically variable terrain. April-PDO may therefore represent the combination of temperature and precipitation during April, immediately prior to calving, which subsequently better describes snow depth and snowmelt heterogeneity, within a broader "spatial window" (Stenseth and Mysterud 2005), than a single local weather metric. The spatio-temporal complexity of how local weather translates to actual environmental conditions may explain why, in some systems, local weather variables that should in theory be strongly related to animal population dynamics, do not necessarily provide the predictive ability expected (Jonzén et al. 2005). The use of multiple local weather measurements in the Finlayson herd's range could provide a more spatially complete description of snow depth and a principal components approach to providing a single snow metric (Mysterud et al. 2007) may prove to be a better explanatory variable than a large-scale index. However, there were not sufficient numbers of weather stations available in the herd's range to allow for this. This is a typical situation in remote areas where only one station may be available (Adams 2005).

The Pacific Decadal Oscillation versus North Pacific Index

There were relatively similar relationships between the NPI and PDO and local weather, however the signal by which the PDO manifested itself into complex local weather patterns was stronger than the NPI for recruitment in the Finlayson caribou herd. In addition to caribou recruitment patterns (Hegel et al. 2010) and collared pika *Ochotona collaris* survival (Morrison and Hik 2007) in the Yukon, the PDO is correlated with a variety of broad-scale terrestrial environmental phenomena in North America including forest fires (Skinner et al. 2006) and summer drought (Shabbar and Skinner 2004). The NPI is also related to weather patterns across North America (Trenberth and Hurrell 1994, Yang et al. 2005), and showed comparable, and sometimes stronger, relationships to local weather in this study area to the PDO.

Indeed, the NPI is strongly related to snow conditions in the Canadian Rocky Mountains (Hebblewhite 2005) and may perform better than the PDO in that system. Understanding why this may occur is complicated by the uncertainty of the physical mechanisms driving Pacific decadal variability in North Pacific climate (Miller and Schneider 2000, Mantua and Hare 2002), and the additional complex relationships

between the NPI and PDO and other global indices such as the El Niño Southern Oscillation (Tianjun et al. 2002). There remains a need for more investigation, over a broad geographic region, into the performance of different Pacific-based indices in explaining ecological patterns.

Interaction of wolves and climate on recruitment

Our results demonstrate that the effect of April-PDO on recruitment in the Finlayson caribou herd may change direction with substantially reduced wolf numbers. With higher wolf numbers, recruitment increased in years with 'better' springs (i.e. higher PDO, less snow on the ground). Predation on neonatal caribou in the Finlayson herd is apparently moderated by spring climate conditions. In good springs, recruitment rates in the absence of active wolf removal approached those when the wolf population was reduced by ~85%. This "environmentally modulated predation" (sensu Newsome et al. 1989) can result from reduced predator efficiency due to an increased ability for prey to disperse in years with lower snow depths at calving thus reducing prey densities and increasing search times (Bergerud and Page 1987), increased vulnerability of prey due to environmental conditions as seen by increased wolf predation success on elk in Yellowstone National Park during severe winters (Mech et al. 2001), and the effect of snow characteristics (e.g. hard vs soft) on predation success as seen for Canada lynx (Stenseth et al. 2004). Our results are consistent with Melis et al. (2009) who found a significant interaction between winter severity and the presence of large predators affecting the densities of roe deer *Capreolus capreolus* across Europe. They found that winter severity was only a factor shaping population densities when large predators were present. Modulation of predation rates is also observed in aquatic systems where changes in environmental features such as water temperature impose physiological constraints on predator efficiency (Kashi et al. 2005). Climate can also modulate the influence of predators by directly affecting predator abundance and hence subsequent predation impacts on prey (Preisser and Strong 2004).

The reduced and reversed effect of climate on recruitment in the Finlayson herd following wolf reduction differs from similar situations observed elsewhere. Following massive disease-related wolf losses on Isle Royale, the effect of winter NAO on moose population growth increased substantially as bottom-up factors became more influential (Wilmers et al. 2006). Our results indicate that rather than exerting a buffering capacity against climate by keeping population densities sufficiently low enough to limit density dependent effects, the presence of wolves enhanced the effect of spring climate on caribou recruitment dynamics. These contrasting results may be due to differing degrees of bottom-up limitation occurring in each population prior to the reduction of wolves (Vucetich and Peterson 2004) and that the Finlayson caribou herd would not have been as spatially limited as the island moose population of Isle Royale following population increases.

The slightly negative relationship between April-PDO and recruitment following the substantial reduction in wolf numbers suggests an alternative mechanism operating once a substantial portion of predation is removed from the system. April-PDO is positively correlated to earlier snowmelt

and temperature (Hegel et al. 2010). In springs with higher PDO, forage green-up may occur earlier and more rapidly. Rapid changes in plant productivity, following high April-PDO, may have a negative effect on calf growth (Pettoirelli et al. 2007) and subsequent survival. In mountainous environments, a very warm spring may reduce the heterogeneity of snowmelt, thus reducing the temporal availability of highly nutritious green forage available to lactating females and growing calves. Warmer temperatures may also result in reduced forage quality such as nitrogen content (Lenart et al. 2002), further affecting calf growth. That this relationship was only detected in the absence of a large portion of the primary predation source indicates the dominant effect of predation on recruitment in this population. Population density does not provide an adequate explanation for this observed pattern, as all but one of the observed recruitment rates during years with no wolf removal in Fig. 3 (i.e. the gray circles) were obtained after wolf control was implemented and thus densities were higher during these years.

Conclusion

This study indicates the potential importance of considering climate during management activities such as predator control (Reynolds and Tapper 1996) or reducing the impacts of introduced species (Harding et al. 2001), which could provide insight into their level of success (Keedwell 2002). Our results suggest that wolf removal would be most effective, in terms of increasing calf recruitment, during poor springs. In years with high April-PDO, the effect of wolf removal on recruitment may be reduced. Given the social controversy surrounding predator control (Martínez-Espíñeira 2006), its financial costs (Engeman et al. 2002), and the possible ecosystem effects of top predator reduction (Duffy 2003), understanding how climate may influence a program's success may prove useful for decision making (Knowlton et al. 1999). This could include consideration of upcoming seasonal weather forecasts. For example, the decision to undertake a predator reduction program that must occur in the winter due to logistical and other environmental constraints may use a forecast of upcoming springtime weather as one factor in deciding whether to proceed with the activities. The usefulness of such an approach would largely depend on how well future weather can be forecasted in a particular location and the ability of a management agency to adapt quickly to changing conditions. While spring climate was the most influential season in our study, the effect of seasonal climate on predation should be assessed at a local level and in other systems variables such as winter snowfall may be more influential (Hebblewhite 2005).

Our results may prove useful for understanding the factors affecting the broad-scale decline of woodland (boreal forest and mountain-dwelling) caribou across North America (McLoughlin et al. 2003, Wittmer et al. 2010). Numerous proximate and ultimate factors influence these declines, including human disturbance (Environment Canada 2008), habitat loss (Wittmer et al. 2010), and predation (Wittmer et al. 2005). Incorporating climate variables as non-additive interactions with other influential variables (e.g. % forest cover) could strengthen the predictive power of demographic and population models. Recent work suggests Allee effects

may be present in low density mountain caribou populations in British Columbia driven largely by predation and apparent competition with alternate prey (Wittmer et al. 2005). Our results suggest that in poor years (e.g. high snow depth at calving) these Allee effects could be more pronounced. Further, climatic conditions that are generally favorable to alternate prey may indirectly affect caribou through apparent competition. Ultimately, what our research and others' indicates is that the role of predation on the population dynamics of mountain dwelling caribou is complex and its effect may be best understood when considering other ecological factors.

The greater support of the PDO over the NPI in predicting recruitment patterns in the Finlayson caribou herd, and the strong effect of the NPI on ungulate population dynamics elsewhere in western North America (Hebblewhite 2005), coupled with the relatively sparse literature on Pacific-based climatic impacts on terrestrial vertebrate population dynamics, highlights our lack of knowledge on its broad-scale effects, certainly in comparison to the NAO (Stenseth et al. 2003). Assuming one exists; identifying a Pacific-based index that is consistently strong in explaining ecological patterns across western North America would provide researchers a common metric for analysis, which would allow for more direct comparison across study areas and taxa. The stronger support of the PDO over snow depth suggests that while specific processes, such as predation, are assumed to have very strong mechanistic linkages to a single weather variable, these linkages may be more complex than a single metric. The complex spatio-temporal nature of snowmelt (Mysterud et al. 2000), particularly in a dynamic season such as spring, highlights the utility of using large-scale indices to explain ecological patterns, when their relationships to local weather patterns are known (Stenseth et al. 2003), as they inherently capture this variability over space and time (Stenseth and Mysterud 2005).

Finally, the non-additive effect of climate and wolf density found in this study highlights the importance of understanding the mechanistic relationship between climate and the ecological parameter of interest. Interacting ecological variables were important factors shaping roe deer densities across Europe (Melis et al. 2009). The role of large predators on population density was largely context-specific and differed depending on winter severity as well as habitat productivity. The influence of climate on recruitment in the Finlayson caribou herd was most pronounced when wolf density was also accounted for. This indicates the importance of ecological factors extrinsic to the population (e.g. predators) in determining the strength of the climatic effect, similar to the influence of intrinsic factors, such as population density (Mysterud et al. 2001), in affecting the role of climate in influencing population dynamics. Hebblewhite (2005) noted that density-climate interactions for elk in western Canada were weak without the presence of wolves. Indeed, how climate influences populations may be governed by both extrinsic and intrinsic factors, as suggested by the different response to large-scale climate following wolf reduction in the Finlayson caribou herd and the Isle Royale moose population (Wilmers et al. 2006). Generalizing the effect of climate across spatially discrete populations has proven difficult (Martínez-Jauregui et al. 2009). Our research also demonstrates that the effect of climate on a population's

dynamics may also vary temporally within that population, further complicating the attempt to find broad-scale climatic influences on ungulate population dynamics.

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Appendix 1.

Models of annual recruitment for the Finlayson northern mountain caribou herd in the Yukon Territory, Canada. The 'f' prior to a model term indicates a smoothing function estimated from the data as represented by a generalized additive model. Lack of an 'f' prior to model terms indicates a generalized linear model. Seasons are defined in Table 1.

Model	K ^a	log-likelihood	AICc	ΔAICc
Wolf × April-PDO	4	-213.60	437.01	0
Wolf × Late winter-PDO	4	-224.39	458.60	20.55
f(Wolf) + April-NPI	3.27	-227.42	462.61	24.56
Wolf × April-NPI	4	-228.64	467.10	29.05
f(Wolf × Late winter-NPI)	4.49	-230.55	472.37	34.32
Wolf × May-PDO	4	-236.95	483.71	45.66
f(Wolf × April-Snow)	4.54	-236.42	484.25	46.21
f(Wolf) + April-Snow	3.59	-238.29	485.22	47.17
Wolf + May-PDO	3	-246.73	500.49	62.45
Wolf + April-PDO	3	-249.47	505.97	67.93
Wolf + Late winter-PDO	3	-254.67	516.38	78.34
Wolf × Winter-PDO	4	-254.87	519.55	81.50
Wolf + Late winter-NPI	3	-260.02	527.08	89.04
Wolf × Winter-NPI	4	-267.35	544.52	106.47
Wolf + Winter-PDO	3	-272.07	551.18	113.14
f(Wolf) + May-Snow	3.15	-273.20	553.83	115.79
Wolf × May-NPI	4	-273.13	556.07	118.02
Wolf × May-Snow	4	-275.07	559.96	121.91
Wolf + May-NPI	3	-282.56	572.16	134.12
Wolf	2	-284.12	572.74	134.69
Wolf + Winter-NPI	3	-283.00	573.04	135.00
f(Winter-NPI)	3.44	-578.47	1165.16	727.12
f(Late winter-PDO)	3.86	-608.45	1226.30	788.26
f(April-PDO)	3.51	-618.64	1245.71	807.66
f(Winter-PDO)	3.52	-634.62	1277.70	839.65
f(May-PDO)	3.44	-639.56	1287.34	849.30
April-Snow	2	-657.61	1319.72	881.67
Late winter-NPI	2	-708.22	1420.93	982.88
f(May-Snow)	2.16	-714.02	1432.92	994.88
April-NPI	2	-720.30	1445.09	1007.04
Null	1	-723.71	1449.58	1011.53
May-NPI	2	-722.55	1449.59	1011.54

^aeffective number of model parameters.