

Predation by wolves interacts with the North Pacific Oscillation (NPO) on a western North American elk population

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Summary

1. Recent research reveals the widespread influence of the North Atlantic Oscillation (NAO), a large-scale climatic variation, on northern ungulate populations. Little is known, however, about the influence of the North Pacific Oscillation (NPO), a similar climatic index, on ungulates.

2. The influence of the NPO on elk population dynamics in Banff National Park (BNP) was examined using a 15-year time-series of three elk subpopulations exposed to different levels of predation by wolves. NPO was strongly related to local climate data including snow depth ($r = +0.61$) and winter temperatures ($r = -0.51$).

3. Higher NPO values reflected increasing winter severity, reducing elk population-growth rate irrespective of wolf-predation pressure. Elk population-growth rate, however, declined more strongly in areas with wolf predation through the interaction with winter severity, indexed by NPO. Effects of NPO were weaker in the absence of wolf predation.

4. Differences between the effects of snow and NPO were revealed that depended on wolf-predation pressure. Without wolf predation, NPO reduced elk population-growth rate, suggesting overall climate was important. With wolf predation, snow depth was more important than NPO, suggesting a mechanism of increased wolf-predation rates in deeper snow.

5. This study is the first to demonstrate the influential role of Pacific climate on western North American ungulate population dynamics and provides further evidence of the role of large-scale climatic variation in terrestrial ecosystem dynamics.

Key-words: climate, North Pacific Oscillation (NPO), population dynamics, predator–prey.

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Introduction

Winter climate influences population dynamics of ungulates through effects on locomotion (Telfer & Kelsall 1984), thermoregulation (Cook *et al.* 1998), reproduction (Portier *et al.* 1998), predator–prey processes (Post *et al.* 1999; Hebblewhite, Pletscher & Paquet 2002) and access to food resources (Turner *et al.* 1994). These effects often interact with population density in populations of northern ungulates (Portier *et al.* 1998; Milner, Elston, & Albon 1999; Coulson *et al.* 2001). Early studies used snow depth (Messier 1991), snow-

water equivalents (Turner *et al.* 1994) or local climatic indices (Picton 1984) to measure the effects of climate on population dynamics. Recent studies reveal widespread effects of large-scale climatic variations such as the North Atlantic Oscillation (NAO; Hurrell, Kushnir & Visbeck 2001; Stenseth *et al.* 2003) on ungulate population dynamics (Post & Stenseth 1999; Patterson & Power 2001).

The NAO climatic phenomenon is measured by the NAO index, a sea-surface pressure-difference index measured between the Azores and Iceland. The effects of the NAO have been demonstrated on population dynamics of soay sheep (*Ovis aries* L.) in the north sea (Coulson *et al.* 2001), red deer (*Cervus elaphus* L.) in the north sea and Norway (Post & Stenseth 1999), white-tailed deer (*Odocoileus virginianus* L.) in New Brunswick and Minnesota (Post & Stenseth 1998;

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Patterson & Power 2001) and moose (*Alces alces* L.) on Isle Royale (Post *et al.* 1999). The NAO also links predator–prey dynamics in lynx (*Lynx canadensis* L.)–snowshoe hare (*Lepus americanus* L.) cycles (Stenseth *et al.* 1999) and wolf (*Canis lupus* L.)–moose population dynamics (Post *et al.* 1999). The mechanisms linking the NAO to local climate may be spatially idiosyncratic. For example, negative NAO values were related to high snowfall in inland areas of Norway, yet warmer, moister winters in coastal areas (Mysterud *et al.* 2000). In eastern North America, positive NAO values were related to cold, snowier winters (Hurrell *et al.* 2001). The ecological effects of NAO are pervasive across terrestrial ecosystems throughout the northern hemisphere (Ottersen *et al.* 2001; Stenseth *et al.* 2002; Stenseth *et al.* 2003).

While the NAO has been related to population dynamics of mammals in western North America, relationships were not always as strong as in eastern North America (Stenseth *et al.* 1999). This difference may be because of the dominance of Pacific climate effects, such as El Niño, or the North Pacific Oscillation (Trenberth & Hurrell 1994) in western North America. South Pacific climate indices such as the El Niño Oscillation (ENSO) influenced mammalian predator–prey systems in Chile (Lima, Stenseth, & Jaksic 2002). Despite growing interest in the ecological effects of the NAO (Stenseth *et al.* 2002, 2003), few studies have investigated the effects of Pacific climate indices on population dynamics in North America (Stenseth *et al.* 2003). In North America, Pacific climate variation has been related to mountain hemlock (*Tsuga mertensiana*) growth (Peterson & Peterson 2001), phenology of flowering plants (Beaubien & Freeland 2000), seabird survival (Jones, Hunter & Robertson 2002) and reproduction (Gjerdrum *et al.* 2003) and Pacific salmon (*Onchorhynchus* spp.) populations (Beamish & Bouillon 1993; Mantua *et al.* 1997). Few, if any, studies have investigated Pacific climate indices impacts on mammalian population dynamics.

I investigated the effects of the North Pacific Oscillation (NPO hereafter) in a wolf–elk time-series from 1985 to 2000 in Banff National Park (BNP) (Hebblewhite *et al.* 2002) to test the hypothesis that elk population-growth rates (r_t) were affected by the NPO. Wolves recolonized BNP through dispersal in the mid 1980s. Similar to density–climate interactions, wolf predation interacts with climate through increased predation rates with increasing snow depths (Nelson & Mech 1986; Huggard 1993; Post *et al.* 1999). Therefore, I tested for effects of the NPO on elk in three different subpopulations that differed in the amount or timing of wolf predation in order to tease apart predation and climate impacts (Hebblewhite *et al.* 2002). I examined relationships between the NPO, NAO and local climatic indices to investigate mechanisms of any emergent relationship between wolf–elk dynamics and the NPO. Finally, I compared the strength of relationships between the NPO and local climate measures on wolf–elk dynamics.

Materials and methods

STUDY AREA

Banff National Park (BNP), 6641 km² in area, is on the eastern slope of the continental divide of the Canadian Rocky Mountains (1400–3400 m, 51°15′/116°00′, Fig. 1). The climate is continental with long, cold winters and infrequent warm weather caused by Pacific-influenced Chinook winds and short, relatively dry summers. Holland & Coen (1983) describe vegetation in the study area. Elk are the most abundant ungulate of a diverse ungulate community and comprise 40–70% of the diet of wolves (Hebblewhite *et al.* 2004). Mean winter snow-pack depth in the valley-bottom was 43 cm at Banff (Hebblewhite *et al.* 2002) but increased at higher elevations. I divided the Bow Valley of BNP into three zones that followed elk subpopulation dynamics and that differed in wolf-predation pressure; the eastern zone (67 km²), the central zone (43 km²), and the western zone (181 km²) (see Hebblewhite *et al.* 2002 for more details).

CLIMATIC DATA – NORTH PACIFIC OSCILLATION (NPO)

The NPO is based on sea-surface temperature anomalies measured over the North Pacific Ocean (Trenberth & Hurrell 1994; Fig. 2). The NPO index is an area-weighted measure of mean sea-surface pressure over the North Pacific from 30° to 65°N, 160°E to 140°E (Trenberth & Hurrell 1994). Trenberth & Hurrell (1994) and others (Mantua *et al.* 1997) describe decadal length oscillations linked to the ENSO in the NPO time-series. In the Rocky Mountains, positive NPO index values are related to cooler winter temperatures, increased snowfall and increased frequency of winter storms (Trenberth & Hurrell 1994; Mantua *et al.* 1997). The Canadian Rocky Mountains show some of the strongest continental correlations ($r = -0.50$) with NPO indices of storm frequency, December–February precipitation, and November–March surface air temperatures (Trenberth & Hurrell 1994; Mantua *et al.* 1997). Standardized NPO anomaly values (which



Fig. 1. Location of Banff National Park, Alberta, Canada.

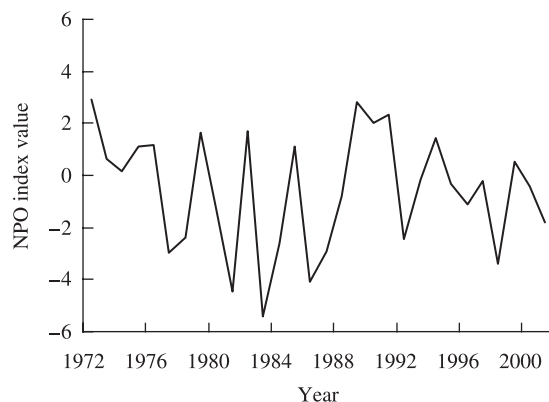


Fig. 2. The standardized North Pacific Oscillation (NPO) Anomaly Index for November to March, 1972–2003 (data from the Climate Analysis Section of the National Centre for Atmospheric Research (NCAR), USA, <http://www.cgd.ucar.edu:80/cas/climind>). Positive values relate to more severe winters in the Canadian Rocky Mountains (Trenberth & Hurrell 1994).

measure deviations) for November–March obtained from the Climate Analysis Section of the National Centre for Atmospheric Research (NCAR), USA (available from <http://www.cgd.ucar.edu:80/cas/climind>) were used for analyses. Refer to Trenberth & Hurrell (1994) for more detail on the NPO.

RELATIONSHIPS BETWEEN NPO AND LOCAL CLIMATE DATA

I tested for relationships between the NPO and local climate data between 1970 and 2001, and within the shorter 15-year time-series to confirm patterns. First, I related NPO to local snow depth, measured by Hebblewhite *et al.*'s (2002) mean snow-depth index consisting of averaged snow depths measured at 15-day intervals between 15 October and 30 April, 1972–2000, in the centre of the study area (1700 m). Next, I tested for relationships between NPO and mean monthly winter temperatures obtained from Environment Canada at the town of Banff (1545 m). Both local snow depth (Huggard 1993) and local temperatures (Env. Canada, unpublished data, Holland 1983) reflected conditions experienced throughout the Bow valley elk zones. For example, Huggard (1993) found strong covariation in snow depth between three sites in the central and western zones. I tested for relationships between local and large-scale climate indices using Pearson correlations in SYSTAT (Wilkinson 1998). While Post & Stenseth (1999) noted the importance of time-lag effects of snowfall on ungulate population growth and survival (but see Messier 1995), Hebblewhite (2000) found no support for such effects on elk in BNP. Therefore, I used only the previous winter's snow depths. Finally, I tested correlations between the NAO winter values obtained from the NCAR (available at <http://www.cgd.ucar.edu:80/cas/climind>), the NPO and local climate indices for BNP.

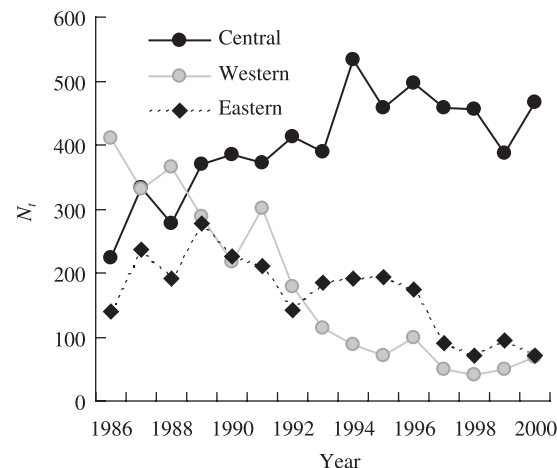


Fig. 3. Elk population time-series in Banff National Park, AB, winter 1986–2000, in the three different zones, east (wolves recolonized 1992), central (no wolves) and western (wolves recolonized 1986). Counts were converted to densities for analysis.

ELK AND WOLF POPULATION DATA

I tested for the effects of NPO on three elk subpopulations in different zones of the Bow Valley of BNP within which wolf, human and elk densities varied. Wolves recolonized the western zone first in 1986, partially recolonized the eastern zone in 1991, and failed to recolonize the central zone due to high human use (Paquet *et al.* 1996; Callaghan 2002). Elk subpopulation dynamics and movements were biologically separate between these three zones (Woods 1991). Elk populations were aerially surveyed in all three zones from 1985 to 2000 during late winter by Parks Canada (Fig. 3, see Hebblewhite *et al.* 2002). Within each zone, intrinsic elk population-growth rate (hereafter, r_t) was estimated as $r_t = \ln(N_{t+1}/N_t)$. Within each zone I used the NPO, winter elk density (N_t), counts of elk killed by humans on highways and railways, and estimates of the number of wolf-killed prey as independent variables to explain variation in r_t (variables are described in more detail in Hebblewhite *et al.* 2002). To account for highway fencing in the central zone in 1991 (Clevenger, Chruszcz, & Gunson 2001), I included a variable coding for fencing in this zone. Per-capita wolf kill-rates (elk/day/wolf) and wolf-pack sizes (number of wolves) were estimated following Hebblewhite *et al.* (2004), and their product (Messier 1994) estimates the number of elk killed per winter (181 days) in each zone. Differential recolonization provided an approximate before-after-control-impact (BACI) experimental design to evaluate the effects of wolf predation on elk (Minta, Kareiva, & Curlee 1999).

STATISTICAL ANALYSES

I tested how elk density, winter NPO index, winter wolf kill-rate, winter human-caused elk kill-rate and central zone highway fencing affected elk r_t within each of the three zones (Fig. 3) over the 15-year time-series. I also

tested for two important ecological interactions between (1) NPO and wolf kill-rate (Huggard 1993; Post *et al.* 1999) and (2) NPO and elk density (Portier *et al.* 1998). I developed a set of candidate generalized linear models (GLMs) comprising different hypotheses of factors affecting elk r_t (e.g. Burnham & Anderson 1998). GLMs were of the general form:

$$R_t = \ln \left(\frac{N_{t+1}}{N_t} \right) = b_0 + b_1 x_1(t) + b_2 x_2(t) + \dots + b_m x_m(t) + \varepsilon$$

where $t = 1-15$ years, N is population size in year t , r_t = population growth in year t , b_0 is the intercept, $b_1 \dots b_m$ are coefficients of independent variables $x_1 \dots x_m$, ε is random error where $\Sigma(\varepsilon_i) = 0$.

GLMs were estimated using maximum likelihood estimation (Type III) in SAS (PROC GENMOD in SAS 8.0, SAS Institute 1998). Models were ranked using the Akaike information criterion (AIC_c) (Burnham & Anderson 1998). Where model selection uncertainty arose, an approximate cut-off of $\Delta AIC_c = 4$ was used to estimate the top model set (Burnham & Anderson 1998). I used the sum of Akaike weights (ω_i) for each variable to rank variables by importance (Burnham & Anderson 1998: 141), following suggestions for the presentation of information-theoretic results in ecological research (Anderson *et al.* 2001). Autocorrelation is often problematic in time-series analysis (Royama 1992). Therefore, I corrected SEs in the $b_{0 \dots m}$ s following Post & Stenseth (1998) where a variance inflation adjusts the degrees of freedom for beta coefficients according to Bartlett (1946) and Priestly (1981); $N = N'[(1 - \alpha_1 \alpha_2)/(1 + \alpha_1 \alpha_2)]$, where N is the number of observations (d.f.), α_1 is the first-order autocorrelation in the dependent, and α_2 is the first-order autocorrelation in the independent variable, b_m . When one series is negatively autocorrelated, this and other approaches (i.e. Newey–West adjustment, McCullough & Nelder 1989) lead to increased degrees of freedom, hence we set $N' \leq N$ following Post & Stenseth (1998).

COMPARISON OF EFFECTS OF NPO AND SNOW DEPTH ON ELK

The relative strength of the effect of local snow depth vs. the NPO on elk r_t was evaluated by first comparing simple correlation coefficients with elk r_t across zones. Next, model fit was compared for the top model in a zone with snow and NPO effects to compare the strength of NPO vs. snow on elk population dynamics within a zone (e.g. comparing WOLF + SNOW and WOLF + NPO models). Model fit was assessed using a limited form of cross-validation (Hastie *et al.* 2001) where 1 year was randomly excluded and models were re-fitted. The top NPO or snow model in each zone was reformulated into a difference equation following Merrill & Boyce (1991) to predict N_{t+1} to compare model predictions to observed elk density. Prediction, and hence model fit, was evaluated using modified r^2 for each model (Hastie *et al.* 2002).

Results

RELATIONSHIPS BETWEEN NPO AND LOCAL CLIMATE VARIABLES

Local snow depth was strongly positively related to the NPO anomaly index between 1970 and 2001 (Fig. 4, correlation $r = +0.61$, $P = 0.0005$). During the reduced elk population time-series ($n = 15$ years), the strength of this relationship diminished, but was still positive ($r = +0.45$, $P = 0.05$). Similarly, mean monthly winter temperatures declined with increasing positive values of NPO ($r = -0.51$, $P = 0.008$) in BNP. The NAO was unrelated to NPO ($r = 0.14$, $P = 0.44$) or BNP snow depths ($r = 0.28$, $P = 0.11$).

EFFECTS OF NPO ON WOLF–ELK POPULATION DYNAMICS

Autocorrelation. Not surprisingly, original time-series were significantly autocorrelated at lag 1 for elk density (Fig. 3, eastern zone ACF $r = 0.57$, $P = 0.014$, central $r = 0.45$, $P = 0.05$, western $r = 0.68$, $P = 0.001$) and wolf predation (eastern ACF $r = 0.56$, $P = 0.016$, central $r = -0.36$, $P = 0.14$, west $r = 0.48$, $P = 0.05$) in all three zones. However, the dependent variables in all GLMs, elk population-growth rate r_t , were negatively autocorrelated (eastern ACF $r = -0.23$, $P = 0.33$, central $r = -0.57$, $P = 0.015$, west $r = -0.11$, $P = 0.64$). Therefore, using Bartlett's (1946) adjustment led to $N' > N$ for all beta coefficients, suggesting that opposite signed autocorrelations acted to counteract each other (McCullough & Nelder 1989). Hence, we set $N' = N$ for all betas and present SEs unadjusted for autocorrelation.

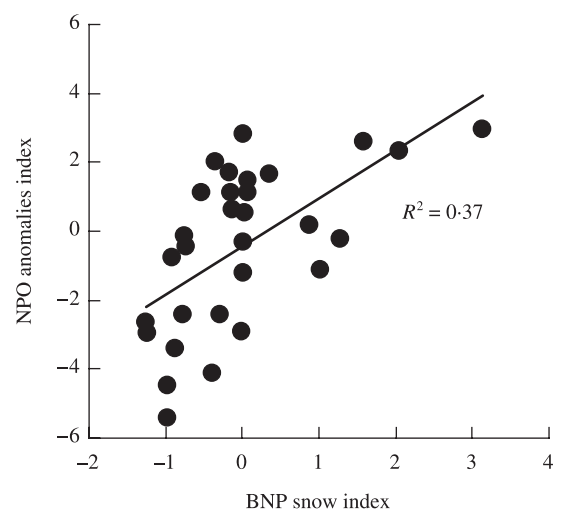


Fig. 4. Relationship between standardized North Pacific Oscillation (NPO) index and the standardized BNP snow-depth index reported in Hebblewhite *et al.* (2002) for the period from 1970 to 2001. (NPO data are from the Climate Analysis Section of the National Centre for Atmospheric Research (NCAR), USA, <http://www.cgd.ucar.edu:80/cas/climind>).

Table 1. Elk population dynamics models for the three BNP elk populations, 1986–2000, relating elk population-growth rate (r_t) to a linear function of NPO, wolf predation, human-caused elk mortality, highway fencing and elk density, with model deviance, model structure and corresponding ΔAIC_c and Akaike weight, ω_i (Burnham & Anderson 1998)

Model structure	Deviance	ΔAIC_c	ω_i	b_0	s.e.	b_1	s.e.	b_2	s.e.	b_3	s.e.
Central zone – low wolf use											
1. $b_0 + b_1(\text{ELK}) + b_2(\text{ELK} * \text{NPO}) + b_3(\text{FENCE})$	0.135	0.00	0.32	0.97	0.16	−0.12	0.08	−0.005	0.0008	0.27	0.08
2. $b_0 + b_1(\text{ELK}) + \beta_2(\text{FENCE})$	0.175	1.07	0.19	0.89	0.174	−0.11	0.023	0.23	0.09	–	–
3. $b_0 + b_1(\text{ELK}) + b_2(\text{NPO}) + b_3(\text{FENCE})$	0.145	2.06	0.11	0.997	0.17	−0.12	0.02	−0.02	0.01	0.26	0.08
4. $b_0 + b_1(\text{ELK}) + b_2(\text{FENCE}) + b_3(\text{HUMAN})$	0.157	3.28	0.06	1.03	0.19	−0.12	0.02	0.27	0.09	−0.006	0.005
5. $b_0 + b_1(\text{ELK})$	0.25	3.50	0.05	0.63	0.17	−0.12	0.02	–	–	–	–
Eastern zone models – wolf recolonization in 1991											
1. $b_0 + b_1(\text{WOLF}) + b_2(\text{NPO}) + b_3(\text{WOLF} * \text{NPO})$	0.507	0.00	0.36	0.06	0.06	−1.03*	0.57	−0.09	0.02	1.25	0.52
1. $b_0 + b_1(\text{NPO}) + b_2(\text{WOLF} * \text{NPO})$	0.619	1.20	0.20	0.06	0.05	1.63	0.54	−0.10	0.027	–	–
1. $b_0 + b_1(\text{WOLF}) + b_2(\text{ELK})$	0.808	2.00	0.13	0.42	0.19	−1.99	0.67	−0.13	0.06	–	–
1. $b_0 + b_1(\text{WOLF}) + \beta_2(\text{NPO})$	0.703	3.09	0.08	0.03	0.07	−0.071	0.028	−1.58	0.61	–	–
Western zone models – wolf recolonization in 1985											
1. $b_0 + \epsilon$	1.459	0.00	0.25	−0.120	0.081	–	–	–	–	–	–
2. $b_0 + b_1(\text{NPO})$	1.457	0.78	0.17	−0.12	0.08	−0.007	0.03	–	–	–	–
3. $b_0 + b_1(\text{ELK})$	1.364	0.99	0.15	−0.007	0.135	−0.12	0.116	–	–	–	–
5. $b_0 + b_1(\text{HUMAN})$	1.406	1.44	0.12	−0.043	0.13	−0.95	1.25	–	–	–	–
5. $b_0 + b_1(\text{WOLF})$	1.406	2.75	0.06	−0.007	0.13	−0.33	0.84	–	–	–	–

Maximum likelihood estimates (MLE, type III) for coefficients in the models are presented with standard errors, coefficients with likelihood ratio χ^2 probabilities < 0.05 are highlighted in black, and < 0.10 marked by *. Coefficients are reported in the order in the model, i.e. for $\beta_{s,i} = 1$ if the model has only one parameter.

to be conservative. Confirmatory analyses using the Newey–West estimator yielded identical results (unpublished data).

CENTRAL ZONE

The central zone elk population was regulated by elk density, experienced higher population-growth rate after fencing and had reduced population-growth rates during positive (more severe) NPO winters (Table 1). Models of r_t fitted the data well in the central zone (Table 1), and all top models explained a high proportion of the deviance (Table 1). Across all models, individual variables were ranked in order of importance as elk density ($\omega_{\text{elk density}} = 0.95$), fencing ($\omega_{\text{fencing}} = 0.69$), the interaction between elk density and NPO ($\omega_{\text{elk} * \text{NPO}} = 0.28$), NPO itself ($\omega_{\text{NPO}} = 0.26$), wolf predation ($\omega_{\text{wolf}} = 0.162$) and human-caused mortality ($\omega_{\text{human}} = 0.13$).

EASTERN ZONE

Eastern zone elk population-growth rate declined with increased wolf predation, positive NPO values and through the interaction of NPO and wolf predation (Table 1). The model fit in the top set was adequate (Table 1, all deviances < 1). Elk r_t was related to variables in the following order of importance; wolf predation ($\omega_{\text{wolf}} = 0.90$), NPO ($\omega_{\text{NPO}} = 0.85$), the interaction between wolf predation and NPO ($\omega_{\text{elk} * \text{NPO}} = 0.68$), elk density ($\omega_{\text{elk density}} = 0.25$) and human-caused mortality ($\omega_{\text{human}} = 0.11$).

WESTERN ZONE

Model fit was poor across all top models (Table 1, all deviances > 1), and the best model was a constant rate of decline of $r_t = -0.12$ in the western zone. Models in the top model set were restricted to simple one-parameter models, suggesting that model fit was too poor to accommodate additional parameters.

COMPARISON OF EFFECTS OF NPO AND SNOW DEPTH ON ELK POPULATIONS

Snow depth was more strongly correlated with elk population-growth rate in zones with wolf predation (Table 2), whereas NPO was more important in zones without wolf predation (Table 2). Similarly, cross-validation revealed snow-depth models generally were better predictors of elk population-growth rates in zones with wolf predation (Table 3), and NPO was a better predictor in the zone without wolf predation (Table 3).

Table 2. Correlation coefficients between elk population-growth rate, with NPO and BNP snow-depth indices from Hebblewhite *et al.* (2002)

Zone	Snow models		NPO models	
	r	P -value	r	P -value
East	−0.396	0.04	−0.09	0.11
Central	−0.156	0.24	−0.30	0.04
Western	−0.75	0.10	−0.37	0.22

Table 3. Cross-validation of top NPO models from this study and snow-depth models from Hebblewhite *et al.* (2002) for each zone showing correlations between predicted and observed population-growth rate for elk in BNP

	Cross-validation r^2
Central zone	
Elk + snow + fence	0.61
Elk + NPO + fence	0.69
Eastern zone	
Wolf + NPO + (WOLF * NPO)	0.63
Wolf + snow + (WOLF * SNOW)	0.58
Western zone	
NPO	0.03
SNOW	0.16

Discussion

This study demonstrates the effects of large-scale Pacific climate variation on a western North American ungulate population, confirming similar responses found in ungulate populations to the NAO in eastern North America and Europe (Post & Stenseth 1998; Post *et al.* 1999; Patterson & Power 2001). This research is the first to confirm similar effects on North American ungulates, revealing the influence of Pacific climate on terrestrial dynamics as far inland as the Canadian Rockies. Both local climatic comparisons to the NPO (Fig. 4), and more extensive meteorological comparisons (Trenberth & Hurrell 1994; Mantua *et al.* 1997) support the important role of Pacific climatic variation affecting local climate. Through these large-scale climatic effects, elk population-growth rate was affected by the NPO through interaction with predation by wolves and, to a lesser degree, interaction with elk density in the absence of wolves (Table 1).

The link between local climate and the NPO was as strong, or stronger, than connections between the NAO and local climate reported elsewhere. For example, Post & Stenseth (1999) report correlation coefficients of $r = -0.33$ and -0.30 between the NAO and snow in Minnesota while this study reports $r = +0.60$ between snow depth and NPO, and -0.50 between winter temperatures and the NPO. Trenberth & Hurrell (1994) discuss the relatively stronger Pacific influence and dominant westerly flows as a continental mechanism for these strong connections to local climate. Hence, future research in western North America, especially in the Rocky Mountains and coastal areas (Trenberth & Hurrell 1994) might usefully investigate effects of the NPO on animal population dynamics.

Differences between similar analyses of local effects of snow depth on elk population dynamics (Hebblewhite *et al.* 2002) and NPO suggest different climatic mechanisms operating on elk populations. Effects of snow depth were stronger in zones with wolves, suggesting the mechanism of wolves increasing kill-rates with increasing snow depths was responsible (Nelson &

Mech 1986; Huggard 1993; Post *et al.* 1999). Without wolf predation, Hebblewhite *et al.* (2002) found no negative effect of snow depth on central zone elk r_i . However, NPO did reduce r_i in the central zone (Table 1), revealing important differences between local measures and large-scale climatic indices. Perhaps overall climate, but not snow, would still impact elk negatively due to temperature, winds and precipitation (Cook *et al.* 1998), particularly at the high elk densities in this zone (Portier *et al.* 1998). In a review of effects of NAO on ungulate populations, Post & Stenseth (1999) found NAO better-explained population dynamics in 10 of 19 ungulate time-series. This suggests, as did this study, that the influence of large-scale climate on population dynamics is varied, and may be mediated through small-scale local processes. Future analyses of ungulate population dynamics will probably benefit from the simultaneous consideration of both local and large-scale effects (e.g. Wang *et al.* 2002a).

Comparison to the snow models of Hebblewhite *et al.* (2002) showed that r_i was related more strongly to snow depth with wolf predation, and to NPO without wolf predation (Table 2). Stronger partial correlation coefficients (Table 2) and higher cross-validation r^2 -values in wolf-zones provides further evidence for the mechanism of increasing snow depth increasing predation rates by wolves (Nelson & Mech 1986; Huggard 1993; Post *et al.* 1999). Stronger local climatic effects on elk population-growth rate in the presence of wolves may help to explain why local climate effects were stronger than NAO in some populations in Post & Stenseth's (1999) review. If populations were subject to predation, the local interaction between snow depth and predation may be more important than large-scale indices, potentially contributing to differences across populations.

The interaction between wolf predation and NPO was stronger (by the ratio of Akaike weights) than the interaction between elk density and NPO (Table 1). Similarly, Hebblewhite *et al.* (2002) found no snow-density interaction without wolves, yet a stronger snow-predation interaction with wolf predation. Therefore, density-climate interactions were weak without wolf predation. Many studies documenting strong climate-density interactions are from populations without significant predators (i.e. Portier *et al.* 1998). Thus, predation may reduce densities below climate-density interaction thresholds, only to be replaced by climate-predation interactions. Further, predation may reduce densities such that the effects of environmental stochasticity are reduced (Eberhardt 2002).

The cross-zone comparison suggests wolf predation can reduce elk density below the range at which density-dependent effects play an important role (for more details see Hebblewhite *et al.* 2002), consistent with wolf limitation and regulation of ungulates reported elsewhere (Gasaway *et al.* 1992; Dale, Adams & Bowyer 1994; Messier 1994; Jedrzejewski *et al.* 2002). Before wolf recolonization elk density regulated growth

rate in the eastern zone, and after wolf predation and snow/NPO limited growth rate. Without wolves, elk density, human-caused mortality, and the NPO limited elk r_t in the central zone. The western zone highlights problems with correlative approaches to the study of population dynamics because of the near constant rate of decline (Boyce & Anderson 1999). However, elk densities were similar in all three zones prior to wolf recolonization in 1986 (Fig. 3, Hebblewhite *et al.* 2002). Elk decline in the western zone with wolf predation, when compared to eastern and central zones, suggests that wolf predation limited elk populations in concert with the NPO.

In conclusion, this is the first report of a large-scale Pacific climate variation, the NPO, influencing ungulate population dynamics in combination with wolf predation. Future research is anticipated to reveal further the important role of the NPO on mammalian population dynamics in western North America. Anticipating the impacts of future global climate change on ecological systems is an important area of applied research (Scott, Malcolm & Lemieux 2002; Stenseth *et al.* 2002; Walther *et al.* 2002). Indices such as the NPO may be used to help forecast future impacts of climate change on ungulate population dynamics (Wang *et al.* 2002b). However, I agree with Lima *et al.* (2002) that to realize the full utility of such approaches, improved knowledge of the interactions of predation and climate must be developed.

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References

- Anderson, D.R., Link, W.A., Johnson, D.H. & Burnham, K.P. (2001) Suggestions for presenting the results of data analyses. *Journal of Wildlife Management*, **65**, 373–378.
- Bartlett, M.S. (1946) On the theoretical specification of sampling properties of autocorrelated time series. *Journal of the Royal Statistical Society Supplement*, **8**, 27–411.
- Beamish, R.J. & Bouillon, D.R. (1993) Pacific salmon production trends in relation to climate. *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 1002–1016.
- Beaubien, E.G. & Freeland, H.J. (2000) Spring phenology trends in Alberta, Canada: links to ocean temperature. *International Journal of Biometeorology*, **44**, 53–59.
- Boyce, M.S. & Anderson, E.M. (1999) Evaluating the role of carnivores in the Greater Yellowstone ecosystem. *Carnivores in Ecosystems: the Yellowstone Experience* (eds T.K. Clark, A.P. Curlee, S.C. Minta & P.M. Kareiva), pp. 265–284. Yale University press, New Haven and London.
- Burnham, K.P. & Anderson, D.R. (1998) *Model Selection and Inference: a Practical Information-Theoretic Approach*. Springer-Verlag, New York.
- Callaghan, C. (2002) *The Ecology of Gray Wolf (Canis Lupus) Habitat Use, Survival, and Persistence in the Central Rocky Mountains, Canada*. Department of Zoology, University of Guelph.
- Clevenger, A.P., Chruszcz, B. & Gunson, K. (2001) Highway mitigation fencing reduces wildlife-vehicle collisions. *Wildlife Society Bulletin*, **29**, 646–653.
- Cook, J.G., Irwin, L.L., Bryant, L.D., Riggs, R.A. & Thomas, J.W. (1998) Relations of forest cover and condition of elk: a test of the thermal cover hypothesis in summer and winter. *Wildlife Monograph*, **141**, 5–61.
- Coulson, T., Catchpole, E.A., Albon, S.D., Morgan, B.J.T., Pemberton, J.M., Clutton-Brock, T.H., Crawley, M.J. & Grenfell, B.T. (2001) Age, sex, density, winter weather, and population crashes in soay sheep. *Science*, **292**, 1528–1531.
- Dale, B.W., Adams, L.G. & Bowyer, R.T. (1994) Functional response of wolves preying on barren-ground caribou in a multiple-prey ecosystem. *Journal of Animal Ecology*, **63**, 644–652.
- Eberhardt, L.L. (2002) A paradigm for population analysis of long-lived vertebrates. *Ecology*, **83**, 2841–2854.
- Gasaway, W.C., Boertje, R.D., Grangaard, D.V., Kellyhouse, D.G., Stephenson, R.O. & Larsen, D.G. (1992) The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. *Wildlife Monograph*, **120**, 1–59.
- Gjerdrum, C., Vallee, A.M.J., St. Clair, C.C., Bertram, D.F., Ryder, J.L. & Blackburn, G.S. (2003) Tufted puffin reproduction reveals ocean climate variability. *Proceedings of the National Academy of Science*, **100**, 9377–9382.
- Hastie, T., Tibshirani, T. & Friedman, J. (2001) *The Elements of Statistical Learning: Data Mining, Inference, and Prediction*. Springer, New York.
- Hebblewhite, M. (2000) *Wolf and Elk Predator-Prey Dynamics in Banff National Park*. Wildlife Biology Program, School of Forestry, University of Montana, Montana.
- Hebblewhite, M., Paquet, P.C., Pletscher, D.H., Lessard, R.B. & Callaghan, C.J. (2004) Development and application of a ratio-estimator to estimate wolf killing rates and variance in a multiple prey system. *Wildlife Society Bulletin*, **31**, 933–946.
- Hebblewhite, M., Pletscher, D.H. & Paquet, P.C. (2002) Elk population dynamics in areas with and without predation by recolonizing wolves in Banff National Park, Alberta. *Canadian Journal of Zoology*, **80**, 789–799.
- Holland, W.D. & Coen, G.M. (1983) Ecological (biophysical) land classification of Banff and Jasper National Parks, 1. Summary. Alberta Institute of Pedology, Edmonton, AB.
- Huggard, D.J. (1993) Effect of snow depth on predation and scavenging by gray wolves. *Journal of Wildlife Management*, **57**, 382–388.
- Hurrell, J.W., Kushnir, Y. & Visbeck, M. (2001) The North Atlantic Oscillation. *Science*, **291**, 603–605.
- Jedrzejewski, W., Schmidt, K., Theuerkauf, J., Jedrzejewska, B., Selva, N., Zub, K. & Szymura, L. (2002) Kill rates and predation by wolves on ungulate populations in Białowieża primeval forest (Poland). *Ecology*, **83**, 1341–1356.
- Jones, I.L., Hunter, F.M. & Robertson, G.J. (2002) Annual adult survival of least auklets (Aves, Alcidae) varies with large-scale climatic conditions of the North Pacific Ocean. *Oecologia*, **133**, 38–44.
- Lima, M., Stenseth, N.C. & Jaksic, F.M. (2002) Population dynamics of a South American rodent: seasonal structure

- interacting with climate, density dependence and predator effects. *Proceedings of the Royal Society of London B*, **269**, 2579–2586.
- Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M. & Francis, R.C. (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society*, **78**, 1069–1079.
- McCullough, P. & Nelder, J.A. (1989) *Generalized Linear Models*, 2nd edn. Chapman & Hall, London, UK.
- Merrill, E.H. & Boyce, M.S. (1991) Summer range and elk population dynamics in Yellowstone National Park. *The Greater Yellowstone Ecosystem: Redefining America's Wilderness Heritage* (eds R.B. Keiter & M.S. Boyce), pp. 263–273. Yale University Press: New Haven.
- Messier, F. (1991) The significance of limiting and regulating factors on the demography of moose and white-tailed deer. *Journal of Animal Ecology*, **60**, 377–393.
- Messier, F. (1994) Ungulate population models with predation: a case study with the North American Moose. *Ecology*, **75**, 478–488.
- Messier, F. (1995) Is there evidence for a cumulative effect of snow depth on moose and deer populations? *Journal of Animal Ecology*, **64**, 136–140.
- Milner, J.M., Elston, D.A. & Albon, S.D. (1999) Estimating the contributions of population density and climatic fluctuations to interannual variation in survival of Soay sheep. *Journal of Animal Ecology*, **68**, 1235–1247.
- Minta, S.C., Kareiva, P.M. & Curlee, A.P. (1999) Carnivore research and conservation: learning from history and theory. *Carnivores in Ecosystems: the Yellowstone Experience* (eds T.K. Clark, A.P. Curlee, S.C. Minta & P.M. Kareiva), pp. 323–404. Yale University Press, New Haven and London.
- Mysterud, A., Yoccoz, N.G., Stenseth, N.C. & Langvatn, R. (2000) Relationships between sex ratio, climate and density in red deer: the importance of spatial scale. *Journal of Animal Ecology*, **69**, 959–974.
- Nelson, M.E. & Mech, L.D. (1986) Relationship between snow depth and gray wolf predation on white-tailed deer. *Journal of Wildlife Management*, **50**, 471–474.
- Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P.C. & Stenseth, N.C. (2001) Ecological effects of the North Atlantic Oscillation. *Oecologia*, **128**, 1–14.
- Paquet, P.C., Wierzbowski, J. & Callaghan, C. (1996) Summary report on the effects of human activity on gray wolves in the Bow River Valley, Banff National Park. *Ecological Outlooks Project. A Cumulative Effects Assessment and Futures Outlook of the Banff Bow Valley* (eds J.C. Green, C. Pacas, L. Conrwell & S. Bayley), pp. 74 + appendices. Prepared for the Banff Bow Valley Study. Department of Canadian Heritage, Ottawa, ON.
- Patterson, B.R. & Power, V.A. (2001) Contributions of forage competition, harvest, and climate fluctuation to changes in population growth of northern white-tailed deer. *Oecologia*, **128**, 244–255.
- Peterson, D.W. & Peterson, D.L. (2001) Mountain hemlock growth responds to climatic variability at annual and decadal time scales. *Ecology*, **82**, 3330–3345.
- Picton, H.D. (1984) Climate and the prediction of reproduction of three ungulate species. *Journal of Applied Ecology*, **21**, 869–879.
- Portier, C., Festa-Bianchet, M., Gaillard, J.-M., Jorgenson, J.T. & Yoccoz, N.G. (1998) Effects of density and weather on survival of bighorn sheep lambs (*Ovis canadensis*). *Journal of Zoology*, **245**, 271–278.
- Post, E., Peterson, R.O., Stenseth, N.C. & McLaren, B.E. (1999) Ecosystem consequences of wolf behavioral response to climate. *Nature*, **401**, 905–907.
- Post, E. & Stenseth, N.C. (1998) Large scale climatic fluctuations and population dynamics of moose and white-tailed deer. *Journal of Animal Ecology*, **67**, 537–543.
- Post, E. & Stenseth, N.C. (1999) Climatic variability, plant phenology, and northern ungulates. *Ecology*, **80**, 1322–1339.
- Priestly, M.B. (1981) *Spectral Analysis and Time Series*. Academic Press, Toronto.
- Royama, T. (1992) *Analytical Population Dynamics*. Chapman & Hall, New York.
- SAS Institute Inc. (1998) *SAS User's Guide*. edn 8. SAS Institute Inc., Cary, NC, USA.
- Scott, D., Malcolm, J.R. & Lemieux, C. (2002) Climate change and modelled biome representation in Canada's National Park System: implications for system planning and park mandates. *Global Ecology and Biogeography*, **11**, 475–484.
- Stenseth, N.C., Chan, K.-S., Tong, H., Boonstra, R., Boutin, S., Krebs, C.J., Post, E., O'Donoghue, M., Yoccoz, N.G., Forchhammer, M.C. & Hurrell, J.W. (1999) Common dynamic structure of Canada lynx populations within three climatic regions. *Science*, **285**, 1071–1073.
- Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.A., Chan, K.-S. & Lima, M. (2002) Ecological effects of climate fluctuations. *Science*, **297**, 1292.
- Stenseth, N.C., Ottersen, G., Hurrell, J.W., Mysterud, A., Lima, M., Chan, K., Yoccoz, N.G. & Adlandsvik, B. (2003) Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond [Review article]. *Proceedings: Biological Sciences*, **270**, 2087–2096.
- Telfer, E.S. & Kelsall, J.P. (1984) Adaptation of some large North American Mammals for survival in snow. *Ecology*, **65**, 1828–1834.
- Trenberth, K.E. & Hurrell, J.W. (1994) Decadal atmosphere–ocean variations in the Pacific. *Climate Dynamics*, **9**, 303–319.
- Turner, M.G., Wu, Y., Wallace, L.L., Romme, W.H. & Brenkert, A. (1994) Simulating winter interactions among ungulates, vegetation, and fire in northern Yellowstone Park. *Ecological Applications*, **4**, 472–496.
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.
- Wang, G.M., Hobbs, N.T., Giesen, K.M., Galbraith, H., Ojima, D.S. & Braun, C.E. (2002a) Relationships between climate and population dynamics of white-tailed ptarmigan *Lagopus leucurus* in Rocky Mountain National Park, Colorado, USA. *Climate Research*, **23**, 81–87.
- Wang, G.M., Hobbs, N.T., Singer, F.J., Ojima, D.S. & Lubow, B.C. (2002b) Impacts of climate changes on elk population dynamics in Rocky Mountain National Park, Colorado, USA. *Climatic Change*, **54**, 205–223.
- Wilkinson, L. (1998) *SYSTAT 8-0*. Chicago, IL, USA.
- Woods, J.G. (1991) *Ecology of a Partially Migratory Elk Population*. University of British Columbia, Canada.

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