

# Climatic amplification of the numerical response of a predator population to its prey

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**Abstract.** We evaluated evidence of an effect of climate on the numerical response of a coyote (*Canis latrans*) population to their keystone prey, snowshoe hares (*Lepus americanus*), in a Canadian boreal forest. Six a priori hypotheses of the coyote numerical response were developed that postulated linear, nonlinear, additive, and interactive effects of prey and climate. Model selection procedures showed the North Atlantic Oscillation (NAO) had the strongest effect on the coyote numerical response via its interaction with snowshoe hare density, while other large-scale climate indices had very weak effects. For a given snowshoe hare density, a negative value of the NAO amplified the abundance of coyote and a positive NAO decreased coyote abundance. We hypothesize that the coyote numerical response is ultimately determined by the coyote functional response influenced by winter conditions determined by the NAO.

**Key words:** Climate; coyote; North Atlantic Oscillation; numerical response; predation; snowshoe hare.

## INTRODUCTION

Predator–prey interactions can be influenced by weather conditions. For example, hunting success by wolves (*Canis lupus*) on moose (*Alces alces*) is higher in winters of deep snow (Post and Stenseth 1998, Post et al. 1999, Wilmers et al. 2006) and coyote (*Canis latrans*) predation of white-tailed deer (*Odocoileus virginianus*) is also related to snow depth (Patterson et al. 1998). In southern Africa, predation of large mammalian herbivores by lions (*Panthera leo*) is related to rainfall (Mills et al. 1995) while in the African Serengeti, the hunting success rate of lions killing and eating on wildebeest (*Connochaetes taurinus*) is related to plant abundance, rainfall, and to the El Niño Southern Oscillation (ENSO; Sinclair et al. 2013).

Coyotes (Keith et al. 1977, O'Donoghue et al. 1997) and lynx (*Lynx canadensis*; O'Donoghue et al. 1997, Hone et al. 2011) in Canada show a strong numerical response to fluctuating snowshoe hare (*Lepus americanus*) abundance, directly correlated with hare numbers the previous year. The numerical response is defined here as the relationship between predator abundance and prey abundance (Sinclair et al. 2006). Coyotes exhibit a broad diet, but can show strong preferences for particular mammalian prey. The main prey species for

Canadian (and Alaskan) coyotes in western North America are snowshoe hares (O'Donoghue et al. 1998a, b, 2001, Prugh 2005) and in eastern North America are white-tailed deer (Patterson et al. 1998, Patterson and Messier 2001).

We extend the work of O'Donoghue et al. (1997) to evaluate the hypothesis that climate as an extrinsic factor has an influence on the numerical response of coyotes in the Kluane region of the Yukon Territory, Canada. The North Atlantic Oscillation (NAO) has an interactive effect on the numerical response of lynx to hares (Hone et al. 2011) and the same may occur for coyotes and hares. We do not study the effects of climate on snowshoe hares, such as through effects on plants as hare food.

## MATERIALS AND METHODS

### Models

There is a plethora of predator–prey models (Bonsall and Hassell 2007, Arditi and Ginzburg 2012). In our study, the ecological starting point for model development was the numerical response of coyotes to the prior abundance of snowshoe hares (O'Donoghue et al. 1997; models 1 and 4 here), and the effect of climate on that relationship (models 2, 3, 5, and 6 here).

Model 1 (Fig. 1a) is a linear relationship between coyote density ( $C_t$ ) and hare density the previous winter ( $H_{t-1}$ ; O'Donoghue et al. 1997) and assumes no effect of climate

$$C_t = a + bH_{t-1}. \quad (1)$$

When the intercept,  $a$ , is zero, model 1 can be converted to a ratio-dependent model by dividing both sides of the

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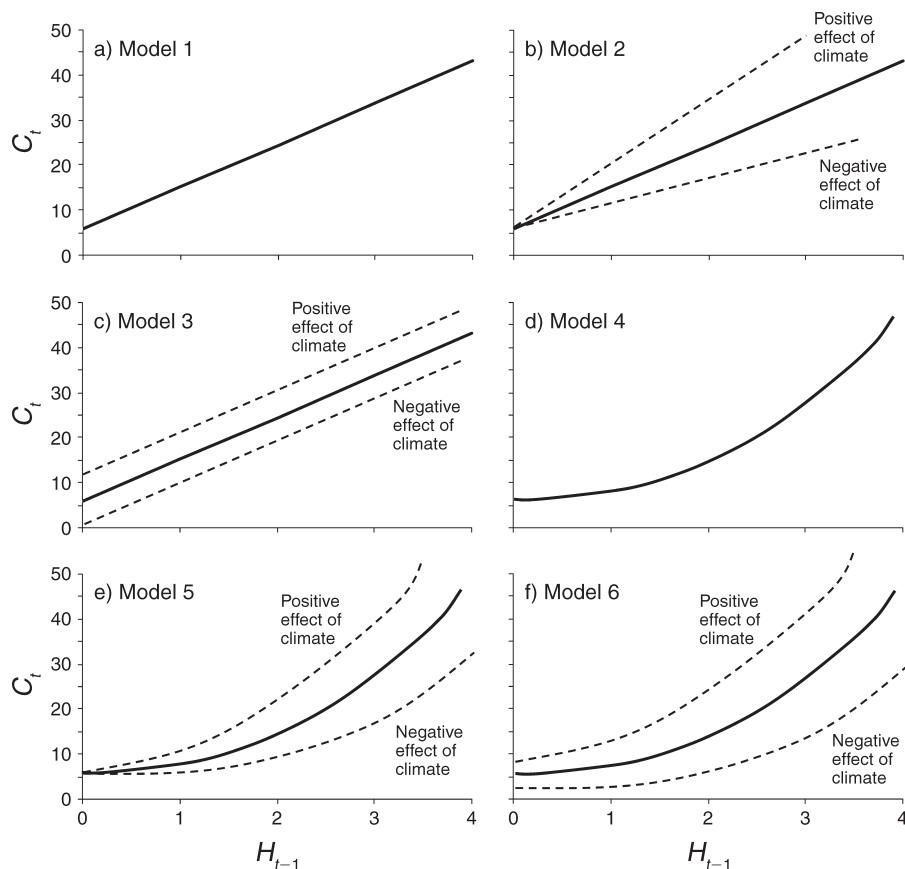


FIG. 1. Graphical hypotheses (models 1–6) of the coyote numerical response.  $C_t$  is coyote winter density at year  $t$ ;  $H_{t-1}$  is snowshoe hare autumn density at year  $t-1$ . Density values are hypothetical. Models 4, 5, and 6 show a hypothesized concave up relationship (i.e.,  $h > 1$ ). The relationship will be concave down if  $0 < h < 1$ , where  $h$  is the exponent in hypothesized nonlinear numerical responses.

equation by the coyote abundance in the previous time period ( $C_{t-1}$ ), so  $C_t/C_{t-1} = \lambda = b(H_{t-1}/C_{t-1})$ , which shows that the coyote population annual finite growth rate ( $\lambda$ ) is determined by the ratio of prey to predators ( $H_{t-1}/C_{t-1}$ ). Similarly for models 2 and 3. Several ratio-dependent models have been described for lynx and snowshoe hares (Hone et al. 2007) and wolves and moose (Arditi and Ginzburg 2012).

Particular winter conditions such as weather severity, snow depth, and snow hardness have been shown to influence coyote hunting efficiency (Todd et al. 1981, Patterson et al. 1998, Prugh 2005). Coyotes can be disadvantaged in snow because they have a high foot load (low foot-surface to body-mass ratio) and can readily sink if the snow is too deep and soft. These conditions can adversely influence coyote foraging and hunting ability and success in relation to snowshoe hares (Keith et al. 1977, Todd et al. 1981, Murray and Boutin 1991, O'Donoghue et al. 1998b). Conversely, increased snow depth can increase the coyote's predation success on white-tailed deer fawns, which become vulnerable under these conditions (Patterson et al. 1998). A negative effect of climate on coyote numerical response may occur

in winters of increased snow depth that can adversely influence coyote hunting ability. A positive effect of climate on coyote numerical response might be seen with much colder winters, which may reduce snowfall and snow depth. Such effects of climate may alter the slope or intercept of the coyote numerical response, so new models for each were derived as shown below.

Model 2 (Fig. 1b) assumes a positive linear effect of hare density on coyote density, but with prior climate ( $W_{t-1}$ ) influencing the slope ( $b = c + dW_{t-1}$ ) of the relationship (for example climate may influence hares via coyote hunting efficiency). Therefore

$$C_t = a + cH_{t-1} + dW_{t-1} \times H_{t-1}. \quad (2)$$

Where there is no effect of climate (i.e.,  $d = 0$ ) model 2 reduces to model 1.

Model 3 (Fig. 1c) is an additive model and assumes a linear effect of climate on the intercept ( $a = f + gW_{t-1}$ ) of the coyote–hare relationship. Then

$$C_t = f + bH_{t-1} + gW_{t-1}. \quad (3)$$

Models 1, 2, and 3 were the same as those in the lynx–hare study (Hone et al. 2011).

Predator–prey dynamics may be nonlinear (May 1986), so we derived such models (4, 5, and 6) by incorporating a power curve exponent ( $h$ ) into linear models 1, 2, and 3, respectively. Coyote social behavior may generate the curves. Model 4 (Fig. 1d) is a nonlinear version of model 1 being concave up if  $h > 1$ , maybe caused by accelerated surplus killing at high prey density, and concave down if  $0 < h < 1$ , the latter more likely because of territorial behavior by coyotes

$$C_t = a + bH_{t-1}^h. \quad (4)$$

Model 5 (Fig. 1e) is a modified model 2 and was

$$C_t = a + cH_{t-1}^h + dW_{t-1} \times H_{t-1}^h. \quad (5)$$

Model 6 (Fig. 1f) is a modified model 3 and was

$$C_t = f + bH_{t-1}^h + gW_{t-1}. \quad (6)$$

Model selection was undertaken using SAS version 9.0 (SAS Institute 2008), Akaike's information criterion corrected for small sample sizes (AIC<sub>c</sub>) and Akaike weights (denoted as  $\omega_i$ ) as weight of evidence (Anderson 2008).

#### *Study area and climate*

The study area of approximately 350 km<sup>2</sup> is a broad glacial valley in the boreal forest of the Kluane region, southwest Yukon Territory, Canada (60°57' N, 138°12' W; Boutin et al. 2001; Fig. 4.1). The vegetation was dominated by white spruce (*Picea glauca*) trees with scattered stands of aspen (*Populus tremuloides*), with a willow (*Salix glauca*), bog birch (*Betula glandulosa*), and soapberry (*Shepherdia canadensis*) understory (O'Donoghue et al. 1997, Krebs et al. 2001). The climate in the region is variable and cold, and precipitation is low (less than 300 mm annually). Up to 50% of the precipitation falls as snow. On average, 85 cm of snow falls over each winter with snow cover usually continuous from October to May (Krebs et al. 2001). The large-scale climate phenomena selected for analyses were the North Atlantic Oscillation (NAO), the El Niño–Southern Oscillation (ENSO), the Pacific/North American (PNA), and the North Pacific Index (NPI), based on empirical evidence of their ecological effects.

*North Atlantic Oscillation (NAO).*—The winter index is based on the difference of normalized sea level pressure between Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland since 1864. The negative NAO phase equates to colder temperatures in northwestern Canada (Stenseth et al. 1999, 2004a, b, Mysterud et al. 2003) and, at Kluane, very cold winter temperatures can act to limit snowfall (Krebs et al. 2001). NAO data were obtained from the Climate Analysis Section of the National Center for Atmospheric Research (USA) web

site.<sup>6</sup> The NAO winter (December–March) station-based index for the period 1986–1987 to 2008–2009, inclusive, was used.

*El Niño–Southern Oscillation (ENSO).*—The Southern Oscillation Index (SOI) is a monthly index calculated from the standardized anomaly of the mean sea level pressure difference between Tahiti and Darwin, Australia (Stenseth et al. 2003, Bureau of Meteorology 2010a). Western Canada experiences warmer winters with less precipitation, shallower snow depth, and less snow cover during El Niño (very negative SOI values) events, with the opposite cooler and wetter conditions seen with La Niña events (Environment Canada, available online).<sup>7</sup> Mean winter SOI values were obtained by calculating the average of the monthly SOI values for October to March (i.e., Canadian winter coyote tracking months) for the years 1986–1987 to 2008–2009 inclusive using data from the Bureau of Meteorology (2010b).

*Pacific/North American (PNA).*—The PNA is a large-scale northern hemisphere winter phenomenon that relates the atmospheric circulation pattern in the central Pacific Ocean, with centers of action over western Canada and the southeastern United States (Wallace and Gutzler 1981, NOAA 2010). The positive phase of the PNA is associated with above average temperatures over central and western Canada (NOAA 2010). Mean winter PNA values were obtained by calculating the average of the monthly PNA values for October to March (i.e., the Canadian winter coyote tracking months) for the years 1986–1987 to 2008–2009 inclusive using data from NOAA (2010).

*North Pacific Index (NPI).*—The NPI is the area-weighted mean sea level pressure over the North Pacific region, with a geographic coverage extending over Alaska and western Canada (Trenberth and Hurrell 1994). Below normal (low) NPI values relate to a deeper-than-normal Aleutian low pressure system and are strongly associated with above normal surface temperatures and precipitation across northwestern Canada (Trenberth and Hurrell 1994, Hurrell 1996, Deser et al. 2004). Opposite conditions prevail for above normal (high) NPI values. The winter (November–March) index was used for years 1986–1987 to 2008–2009 inclusive using data from National Center for Atmospheric Research.<sup>8</sup>

#### *Estimation of coyote abundance*

Coyote population density was estimated during the northern winters of 1987–1988 to 2009–2010 using snow track counts in accordance with the methods outlined by O'Donoghue et al. (1997). A 25-km transect that traversed our study area east to west was run each day

<sup>7</sup> <http://www.ec.gc.ca/meteo-weather/default.asp?lang=En&n=D4AF53AA-1>

<sup>8</sup> <https://climatedataguide.ucar.edu/climate-data/north-pacific-np-index-trenberth-and-hurrell-monthly-and-winter>

<sup>6</sup> <https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based>

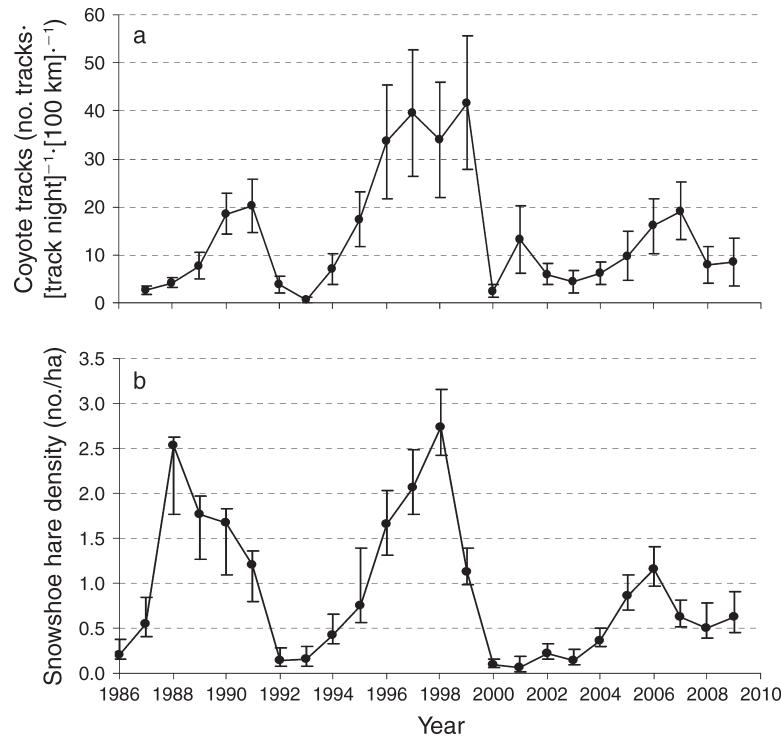


FIG. 2. (a) Number of coyote tracks in the winter (mean number of tracks per track night per 100 km) for the period 1987–1988 (shown as 1987) to 2009–2010 (shown as 2009). Vertical bars show 95% confidence intervals. (b) Autumn density of snowshoe hares for the period 1986–2009. Vertical bars show 95% confidence intervals.

by snowmobile after fresh snowfalls from October to April inclusive, continuing on subsequent days for as long as fresh coyote tracks could be distinguished. The same transect was used within and between winters and it was traversed an average of 26 times each winter. The data are expressed as the mean number of tracks per track night per 100 km. Such track counts were found by O'Donoghue et al. (1997) to be highly correlated (Spearman rank correlation coefficient = 0.88;  $P = 0.01$ ) with population estimates obtained by other means, namely telemetry and extensive snow-tracking, over the course of the first recorded population cycle (1987–1996; O'Donoghue et al. 1997). Hence, the mean number of coyote tracks is being used herein as a proxy (linear index) for coyote density.

#### Estimation of snowshoe hare density

Snowshoe hare population density was estimated during 1986 to 2009 by live-trapping using methods outlined by O'Donoghue et al. (1997) and the spatially explicit mark–recapture estimator of Efford et al. (2009). Namely, snowshoe hares were live trapped each autumn (August–September) on two 60-ha grids that were 16 km apart. Each grid contains a minimum of 86 live traps spaced 42 m apart. Hares were processed in accordance with the methods outlined in the Yukon Ecological Monitoring Protocols (Anonymous 2012) to reduce handling stress. The data are expressed as mean density

of hares per hectare. The hare grids were located within the same area as the transect used for coyote snow tracks.

#### Partial correlation analyses

To examine if coyote track counts during 1987 to 1996 were an artifact of the climate variable in question, we used partial correlation analysis in SAS version 9.0 (SAS Institute 2008). Removing the effect of coyote density would show whether track counts were correlated with weather conditions or not. The relationships between track count and each climate variable, after removing the effect of the population estimate, were nonsignificant ( $P > 0.05$ ), except for a just significant negative relationship with the North Pacific Index ( $r = -0.71$ ,  $P = 0.05$ ). The assiduous manner in which the track data are collected support the assessment of this as a spurious correlation. Snow track count surveys only occur when conditions are ideal, namely immediately following fresh snowfalls, and only while tracks remain distinguishable and uncompromised by too much coyote activity or thaw events caused by extreme maximum temperatures (O'Donoghue et al. 1998b; Liz Hofer, *personal communication*).

#### RESULTS

Over the period 1987–2010, the mean number of coyote tracks per track night per 100 km peaked three

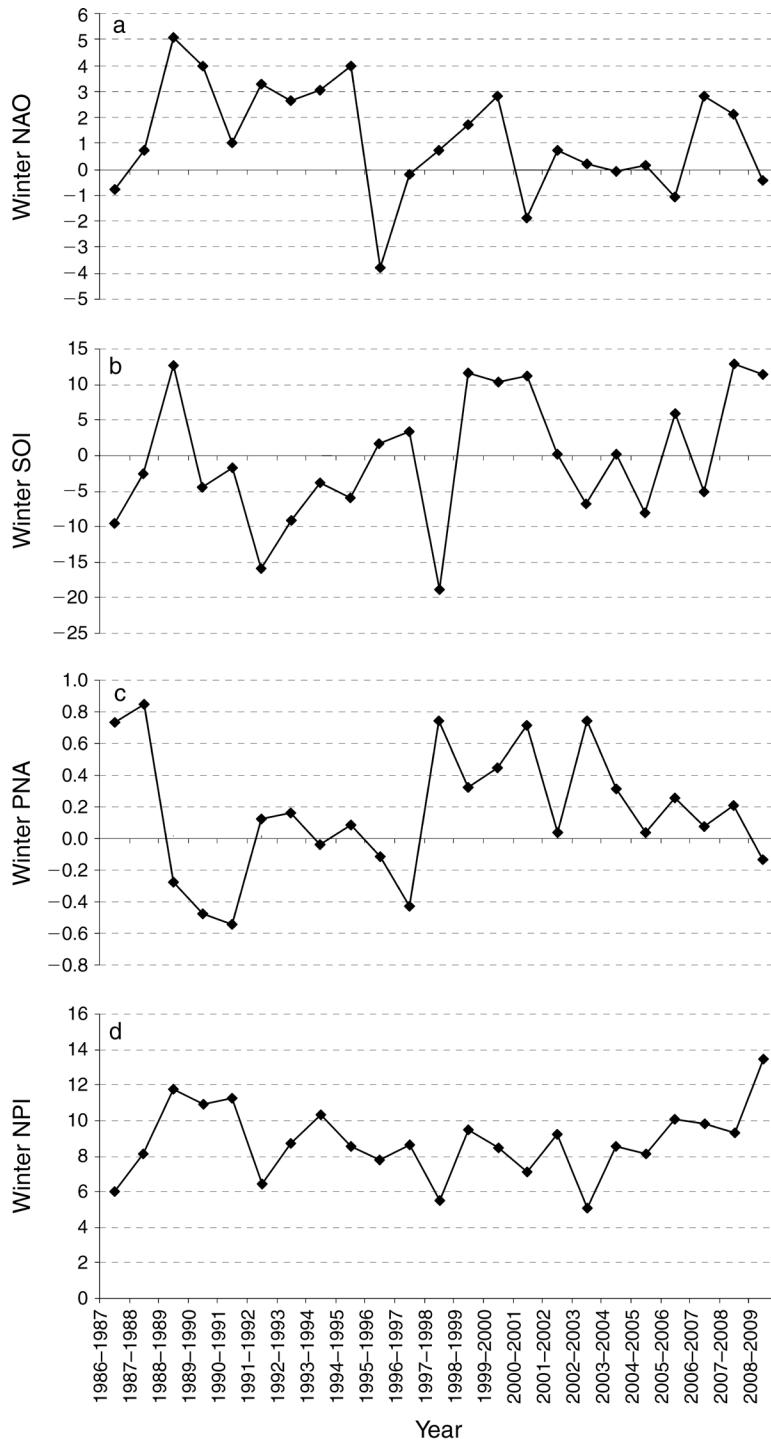


FIG. 3. Changes for the years 1986–1987 to 2008–2009 in the (a) winter North Atlantic Oscillation (NAO), (b) winter Southern Oscillation Index (SOI), (c) winter Pacific/North American Index (PNA), and (d) winter North Pacific Index (NPI).

times in the winters of 1991–1992, 1999–2000, and 2007–2008 (Fig. 2a). Snowshoe hare densities peaked three times in the autumns of 1988, 1998, and 2006 (Fig. 2b). The climate indices varied across years (Fig. 3). There

were no significant ( $P \gg 0.05$ ) relationships between coyote density ( $C_t$ ) and any of the four climate indices during the same year (highest  $R^2$  was 0.036) or the previous year (highest  $R^2$  was 0.033).

TABLE 1. The goodness of fit of models of the numerical response of coyotes (coyote winter density at year  $t$ ;  $C_t$ ) to snowshoe hares (autumn density in year  $t - 1$ ;  $H_{t-1}$ ) with the effect of four climate indices, the North Atlantic Oscillation (NAO), Southern Oscillation Index (SOI), Pacific/North American (PNA) and North Pacific Index (NPI).

Model	Climate index	RSS	$K$	$\Delta AIC_c$	$\omega$
1	na	2057.948	3	18.919	0
<b>2</b>	<b>NAO</b>	<b>794.913</b>	<b>4</b>	<b>0</b>	<b>0.783</b>
3	NAO	1243.538	4	10.292	0.005
4	na	2053.600	4	21.830	0
5	NAO	771.300	5	2.614	0.212
6	NAO	1243.400	5	13.597	0.001
2	SOI	1997.891	4	21.197	0
3	SOI	2056.145	4	21.858	0
5	SOI	1991.700	5	24.433	0
6	SOI	2052.400	5	25.123	0
2	PNA	2020.162	4	21.452	0
3	PNA	2046.368	4	21.749	0
5	PNA	2018.400	5	24.739	0
6	PNA	2044.300	5	25.033	0
2	NPI	1783.596	4	18.588	0
3	NPI	1988.333	4	21.087	0
5	NPI	1730.900	5	21.205	0
6	NPI	1981.600	5	24.316	0

Notes: Abbreviations are na, no effect of climate in model; RSS, residual sum of squares;  $K$ , number of parameters;  $\Delta AIC_c$ , difference between Akaike information criterion corrected for small sample sizes ( $AIC_c$ ) of model  $i$  and the “best” model; and  $\omega_i$ , Akaike weight of model  $i$ . The model with the most support is shown in boldface type.

Model selection analysis showed that the model with the highest Akaike weight ( $\omega_2 = 0.783$ ) was model 2 with climate indexed as the winter NAO (Table 1). Model 2 had a highly significant and positive effect ( $\beta_1$ ) of hare

density and a highly significant negative interactive effect ( $\beta_3$ ) of NAO and hare density. The intercept ( $\beta_0$ ) was not significantly different from zero (Table 2). The overall regression was highly significant ( $F_{2,20} = 32.00$ ,  $P$

TABLE 2. Parameter estimates for models of the numerical response of coyote abundance ( $C_t$ ) to snowshoe hares ( $H_{t-1}$ ) and broad-scale climate indices (NAO, SOI, PNA, NPI).

Model	$\beta_0$	$\beta_1$	$\beta_2$	$\beta_3$	$\beta_4$
No effect of climate in model					
1	5.4723 (3.1506)	9.4389 (2.6107)	na	na	na
4	4.3193 (7.4310)	11.0879 (9.5690)	na	na	0.8521 (0.7261)
NAO					
<b>2</b>	<b>2.7249 (2.0648)</b>	<b>18.2722 (2.2847)</b>	<b>na</b>	<b>-3.2325 (0.5734)</b>	<b>na</b>
3	6.4509 (2.5241)	12.2901 (2.2237)	-3.0731 (0.8491)	na	na
5	4.3728 (2.7945)	15.4673 (4.1473)	na	-2.9135 (0.6859)	1.2156 (0.3009)
6	6.2838 (4.9509)	12.5360 (6.5845)	-3.0709 (0.8729)	na	0.9809 (0.4729)
SOI					
2	5.1190 (3.2134)	9.9141 (2.7062)	na	-0.1211 (0.1562)	na
3	5.4093 (3.2612)	9.4926 (2.7046)	-0.0314 (0.2371)	na	na
5	6.4876 (4.9875)	7.7223 (7.2004)	na	-0.1247 (0.1352)	1.2701 (0.9957)
6	4.3447 (7.5164)	11.0260 (9.7220)	-0.0261 (0.2447)	na	0.8611 (0.7499)
PNA					
2	5.3389 (3.2061)	9.4503 (2.6506)	na	2.4744 (4.0456)	na
3	6.0668 (3.6882)	9.1249 (2.8262)	-1.9089 (5.6682)	na	na
5	6.0559 (5.5815)	8.3796 (7.4015)	na	2.5921 (4.2861)	1.1109 (0.8113)
6	5.2220 (7.8221)	10.3166 (9.7316)	-1.7469 (5.9204)	na	0.8885 (0.7916)
NPI					
2	4.8492 (3.0265)	23.1131 (8.1843)	na	-1.4080 (0.8028)	na
3	12.9356 (9.4667)	9.9844 (2.7091)	-0.9034 (1.0796)	na	na
5	8.1638 (3.3032)	14.1431 (11.0310)	na	-1.0229 (0.7913)	1.8153 (0.9697)
6	11.5748 (11.7152)	12.1298 (10.1046)	-0.9210 (1.1082)	na	0.8240 (0.6833)

Notes: Variables are  $\beta_0$ , intercept;  $\beta_1$ , regression coefficient for  $H_{t-1}$ ;  $\beta_2$ , regression coefficient for climate;  $\beta_3$ , regression coefficient for interaction between climate and  $H_{t-1}$ ;  $\beta_4$ , power curve exponent. Values are estimates with SE in parentheses. The abbreviation “na” stands for not applicable. The model with the most support is shown in boldface type.

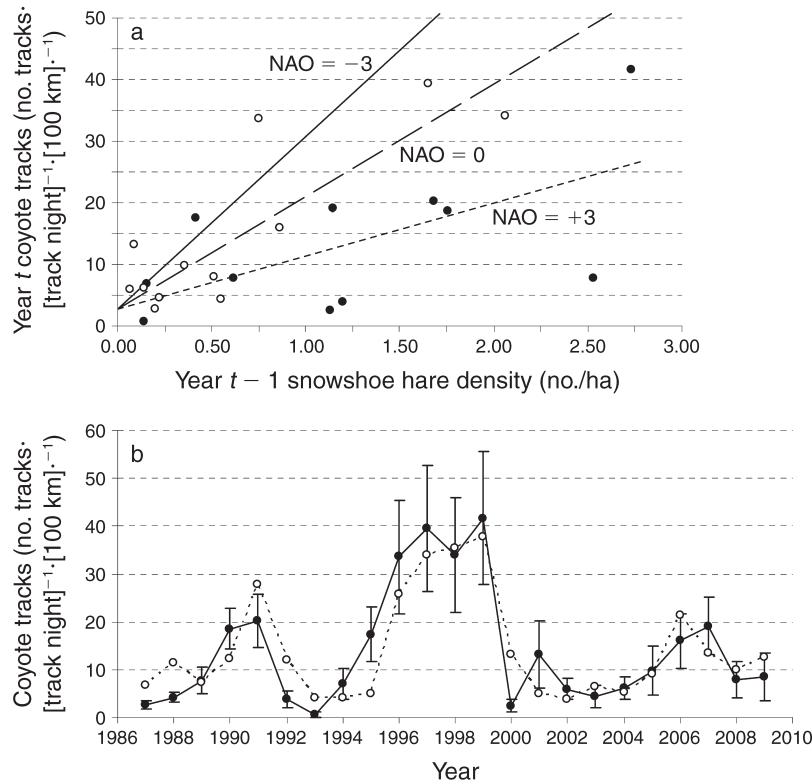


FIG. 4. (a) The coyote numerical response (mean number of coyote tracks per track night per 100 km) to snowshoe hare density for three values of the winter  $NAO_{t-1}$  using model 2 parameter estimates. The observed data are shown as solid circles ( $NAO > 1$ ) and open circles ( $NAO < 1$ ), (b) Observed data (solid line) and estimates (dotted lines and open circles) of coyote track counts reconstructed from the first ranked model (model 2) using the winter NAO as the climate index. Vertical bars show 95% confidence intervals.

$< 0.0001$ ,  $R^2 = 0.76$ ). The fitted regression of model 2 (Table 2) was

$$C_t = 2.725 + 18.272 H_{t-1} - 3.233 NAO_{t-1} \times H_{t-1}.$$

Fig. 4a shows the increase in the slope of the coyote numerical response with a negative NAO phase, and a corresponding decrease in the slope with a positive NAO phase. Model 2 was a good reconstruction of coyote abundance ( $C_t$ ), although the reconstruction demonstrated some over- and underestimation outside of the observed data 95% confidence intervals (Fig. 4b).

The power curve exponent parameter ( $h$ ) was not significantly different from 1.0 for any model, supporting linear rather than nonlinear models. Models 1, 3, 4, and 6 and non-NAO climate indices had very low support (Table 1) with the sum of Akaike weights  $\omega_i$  for those models of  $\sum \omega_i = 0.005$ . Parameter estimates and associated standard errors for all models and climate indices are shown in Table 2.

The estimated intercept ( $\beta_0$ ) of the model 2 numerical response was 2.73 (Table 2), which was not significantly different from zero. The linear relationship (model 1) between coyote density ( $C_t$ ) and snowshoe hare density the previous year ( $H_{t-1}$ ) accounted for only 38% of variation in coyote density. Hence inclusion of the

interactive effect of hare density and climate (NAO) as in model 2 increased the  $R^2$  from 38% to 76%.

#### DISCUSSION

Predator–prey dynamics are influenced by climate conditions, as shown for wolves and moose (Post et al. 1999, Wilmers et al. 2006), lynx and snowshoe hares (Hone et al. 2011), and lions and wildebeest (Sinclair et al. 2013). The results of this study show clear evidence of a numerical response relationship between coyote density and snowshoe hare density that is influenced by climate, measured as the winter NAO (Table 1). For a given hare density, a negative NAO value amplified coyote abundance and a positive NAO value decreased coyote abundance.

The results firstly extend the positive relationship between coyote and snowshoe hare densities previously reported for Canadian boreal forest coyote populations (Keith et al. 1977, Todd et al. 1981, O’Donoghue et al. 1997, Patterson and Messier 2001). Second, the results provide a level of support for the hypothesis that coyote density is related to both snowshoe hare density and the winter NAO the previous year, similar to the results reported for lynx–hares–NAO (Hone et al. 2011). The coyote climate-modified numerical response has a lower estimated slope ( $18.27 \pm 2.29$  [mean  $\pm$  SE]) than that

( $30.51 \pm 4.08$ ) reported for lynx (Hone et al. 2011). Such a difference can be predicted if coyotes are more of a diet generalist than the lynx, however, at Kluane, both predators eat mostly snowshoe hares (O'Donoghue et al. 2001) so an alternative ecological mechanism may be generating the different slope. The model with most support (model 2), with an intercept not different from zero, is a form of ratio-dependent model. Ratio-dependent models have been reported for several predator-prey systems, such as lynx and snowshoe hares (Hone et al. 2007) and wolves and moose (Arditi and Ginzburg 2012).

The following hypothesis is proposed to explain how the NAO may be affecting the coyote numerical response, that is, influencing the slope of the relationship in model 2. The negative NAO phase equates to colder temperatures in north-western Canada (Stenseth et al. 1999, 2004a, b, Mysterud et al. 2003) and at Kluane very cold winter temperatures can act to limit snowfall (Krebs et al. 2001). By contrast, warmer (milder) winters in high-latitude regions may increase the level of snowfall (Beniston et al. 2003, Räisänen 2008). If snow conditions at year  $t - 1$  were not conducive to efficient and effective hunting (i.e., increased snow depth in milder winters due to a positive NAO phase), coyote density could be influenced in two ways. First, coyotes may move to more suitable habitats that have less ground snow cover, as reported for example by O'Donoghue et al. (1998a) and Thibault and Ouellet (2005). Secondly, the added energetic costs of hunting, and reduced hunting ability and success could result in lowered body condition and demographic rates as reported for example by Todd et al. (1981), Todd and Keith (1983), and Thibault and Ouellet (2005). In both instances, coyote density (number of tracks detected) could be reduced at year  $t$ .

The results can be compared to other predator-prey systems. For Canada lynx, it was proposed that the NAO affected hunting behavior and success through its influence on temperature and snow properties, and this in turn influenced lynx population dynamics (Stenseth et al. 2004a, b). In contrast, Hone et al. (2011) considered the mechanism for the effect of the NAO on the lynx numerical response was not known clearly but may be via demographic rates. For grey wolves living on Isle Royale, Michigan USA, hunting success was significantly increased during winters of deep snow as a result of the increased vulnerability of their prey species (moose; Post and Stenseth 1998, Post et al. 1999). Coyote predation on white-tailed deer was found to increase sharply, and continue to increase disproportionately relative to the availability of snowshoe hares, as deer became increasingly vulnerable with increased snow depth (Patterson et al. 1998).

These studies on coyotes, lynx, and wolves highlight the effects of the NAO on predator numerical and functional responses. Avenues for future research would be to evaluate the influence of climate on the coyote's

functional response, and the effects of climate change on the numerical response.

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