SEX-SPECIFIC DYNAMICS OF NORTH AMERICAN ELK IN RELATION TO GLOBAL CLIMATE

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ABSTRACT: The North Atlantic Oscillation (NAO) is a continuous fluctuation in atmospheric mass balance that drives most interannual and decadal variation in winter temperatures and precipitation in the Northern Hemisphere. Effects of the NAO on the population dynamics of red deer (*Cervus elaphus*) in northern Europe and white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*) in North America are well documented. In northern Europe, analyses of sex-specific population dynamics in relation to the NAO have documented divergent responses of the sexes to winter warming, but such analyses have been lacking for North American ungulates. We investigated effects of the NAO on the sex-specific population dynamics of Roosevelt elk (*Cervus elaphus roosevelti*) on Raspberry Island, Alaska, USA. Density of females and of the total population declined after positive (cold and snowy) NAO winters. Density of males was unrelated to the NAO index. Production of young was limited by density of females and increased following positive NAO winters. Hence, in agreement with analyses of the dynamics of red deer in northern Europe, population dynamics of the herd on Raspberry Island related mainly to the influences of winter climate and density on abundance and productivity of females, rather than males.

Males and females, in sexually dimorphic mammals, exhibit such divergent strategies of growth and reproduction (Clutton-Brock et al. 1982) that the evolutionary tradeoffs between body size, survival, and reproduction apparent in their life histories leave them differentially susceptible to climatic constraints on their development (Post et al. 1999a). Predicted changes in winter climate associated with global change (Houghton et al. 1996) therefore may elicit distinct responses in population dynamics of the sexes in such species, as suggested by Kie and Bowyer (1999).

In northern Europe, sex-specific responses of red deer (*Cervus elaphus*) to large-scale variation in winter climate have been reported in several geographically distinct populations (Forchhammer et al. 1998; Post et al. 1999a, 1999b; Post and Stenseth 1999). In mainland populations in Norway, and in the island population on Rhum, Scotland, for example, increases in the total numbers of red deer following warm winters apparently related to increases in fecundity of the female segments of the populations, rather than to changes in the numbers of males (Post et al. 1999b). Such positive responses of females to increasingly warm winters likely reflect the benefits of earlier plant phenology in such years to female condition at the end of gestation and during early lactation (Bowyer 1991; Albon and Langvatn 1992; Rachlow and Bowyer 1994, 1998; Post and Stenseth 1999).

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In North America, observations of the limiting effects of large-scale variation in winter climate on population growth in large mammals have been largely confined to studies of moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*; Post and Stenseth 1998, 1999; Post et al. 1999c). The North Atlantic Oscillation (NAO) was correlated with changes in abundance of white-tailed deer and moose directly, as well as indirectly, through the influence of snow depth on hunting efficiency of wolves (*Canis lupus*; Post and Stenseth 1998, Post et al. 1999c). No study has yet examined sex-specific responses of ungulates in North America to large-scale climatic dynamics. Here, we present an analysis of the population dynamics of males and females in an introduced population of Roosevelt elk (*Cervus elaphus roosevelti*) on Raspberry Island, Alaska, USA, and discuss our results in the context of management strategies for North American ungulates in a changing climate. We tested the hypothesis that dynamics of male and female elk in this population would be constrained by density and winter climate.

Fig. 1. Location of the population of Roosevelt elk used to study climatic effects on population dynamics on Raspberry Island, Alaska, USA.

STUDY AREA

Raspberry Island lies within the Gulf of Alaska approximately 145 km below the southern tip of the Kenai Peninsula and 5 km northeast of Kodiak Island, Alaska, USA (Fig. 1); the island is 28 km wide and 11 km long. Most of Raspberry Island is undulating or mountainous, with an irregular coastline. Principal streams generally are <10 km long, flowing through narrow, well-drained valleys bordered by rolling hills.

The vegetation of Raspberry Island is similar to that on the Kenai Peninsula to the north and also contains elements from southeast Alaska. Two distinct vegetative formations occur on the island: a spruce shrubland and a grassland-forb-shrub formation. Plant nomenclature follows Hultèn (1974). The Sitka spruce (*Picea sitchensis*) climax area, which dominates the former, is interspersed with extensive shrublands of alder (*Alnus crispa*) and elderberry (*Sambucus racemosa*). Understory vegetation contains many species indigenous to southeast Alaska including devil's club (*Oplopanax horridus*), blueberry (*Vaccinium ovalifolium*), salmonberry (*Rubus spectabilis*), trailing bramble (*R. pedatus*), nagoon berry (*R. stellatus*), and highbush cranberry (*Viburnum edule*). Sitka spruce is a recent arrival to Raspberry Island but occurs throughout the island. The grassland-forb-shrub complex consists of extensive shrublands of alder, willow (*Salix* spp.) and salmonberry interspersed with a matrix of grasses and perennial forbs. Grasses and forbs include blue joint (*Calamagrostis canadensis*), hairgrass (*Deschampsia caespitosa*), fireweed (*Epilobium angustifolium*), geranium (*Geranium erianthum*), lupine (*Lupinus nootkatensis*), burnet (*Sanguisorba sitchensis*), cow parsnip (*Heracleum lanatum*), and angelica (*Angelica lucida*). Sedge meadows occupy poorly drained sites and a riparian shrubland of alder and willow
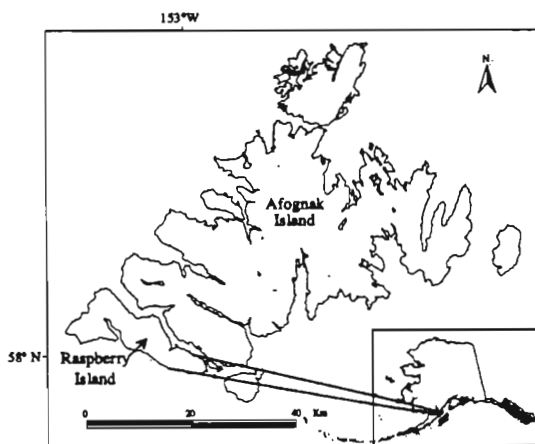
occurs along most watercourses. Above 900 m in elevation, the grassland-forb-shrub formation is replaced by an alpine vegetation dominated by extensive heath mats of crowberry (*Empetrum nigrum*), alpine azalea (*Loiseleuria procumbens*), diapensia (*Diapensia lapponica*), Kamchatka rhododendron (*Rhododendron kamtschaticum*), purple heather (*Phyllo- doce empetriformis*), Alaska heather (*Cassiope lycopodioides*), alpine bearberry (*Arctostaphylos alpina*), mountain cran- berry (*Vaccinium vitis idea*), bog blueberry (*V. uliginosum*), and dwarf willow (*Salix* sp.). In this portion of the island, spruce occurs only in isolated stands in the low- lands.

Unlike much of Alaska, Raspberry Is- land experiences a relatively mild climate throughout the year. Nearby seas tend to prevent extreme temperature variation. Temperatures range from -15° C in winter to 24° C in summer. Precipitation is abun- dant, especially in the spring and autumn, averaging about 152 cm annually. Winter precipitation consists of rain and snow. Average snow depth on Raspberry Island is unknown.

METHODS
Elk Population on Raspberry Island

Although elk likely occurred in Alaska as recently as 3,000 years ago (Guthrie 1990), Roosevelt elk are not endemic to Alaska. Roosevelt elk were successfully introduced onto Afognak Island in the Kodiak Archipelago in 1929 (Batchelor 1965). The population expanded its range and is now distributed over all of Afognak and Rasp- berry (1 km southwest of Afognak) Islands. The population ranged from 200 animals in 1948 to 1,200-1,500 elk in 1965, and is divided into 9 distinct herds, including 1 herd ranging from 115 to 175 elk on Raspberry Island. Elk are capable of swimming across the strait between Raspberry and Afognak

islands. Work conducted to determine amount of interchange among populations, however, documented a coefficient of as- sociation (Knight 1970) among elk herds of 0.51, suggesting a relatively stable elk herd in which only limited exchange of animals existed (Alexander 1973).

Wildlife managers endeavor to sustain the population at $\leq 1,000$ animals on both islands. The population level is maintained via a permit system of human hunting and the kill is monitored annually through sur- veys and herd composition counts. The open season for resident and nonresident hunters for Raspberry Island is by drawing permit only (for males and females), with an average of 60 permits issued and a total harvest of between 4 and 17 elk.

One observer in a Piper PA-18 aircraft completed aerial composition counts annu- ally in July-September (Smith 1996). Sup- plemental counts of herds > 50 animals were made from color print photographs taken during the survey. In August 1994-1996, Alaska Department of Fish and Game personnel made a composition count from the ground. Continuous data on herd composition and size are available from 1985 through 1996 for the population on Raspberry Island.

The North Atlantic Oscillation and Cli- mate in the Northern Hemisphere

The NAO is the dominant atmospheric process in the Northern Hemisphere, influ- encing interannual and decadal fluctuations in temperature and precipitation during win- ter throughout the Northern Hemisphere (Hurrell 1996, Hurrell and Van Loon 1997). This oscillation is quantified by the NAO index, calculated as an annual winter (December-March) index based on the dif- ference in normalized sea-level pressures (SLP) between Lisbon, Portugal, and Stykkisholmur, Iceland, from 1864 through 1995 (Hurrell 1995). Detailed information

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on the NAO index and its monthly, running 3-month seasonal and annual values are available at the Climate Indices website: http://www.cgd.ucar.edu:80/cas/climind. Although we lacked local data on winter temperatures and precipitation, we tested for correlations between the NAO index and temperature and precipitation for December-March, as well as yearly means for those months, with data from nearby stations at Anchorage International Airport and Juneau, Alaska, for the study period (1985-1996). Those data were obtained from the NOAA/CMDL World Climate Data Global Historical Climatology Network for Alaska (http://arcss.colorado.edu/Catalog/arcss014.html).

Incorporating the NAO into a Model of Elk Population Dynamics

Forchhammer et al. (1998) developed a model for analyzing the effect of density dependence and climatic variation on population dynamics. Specifically, the model focused on interrelations between climate, plants, and animals where climatic variation was due to the NAO. The general form of the model derived was:

$$N_t = N_{t-1} \exp(\beta_o + \sum_{n=1}^{l} \beta_n X_{t-n} + \sum_{m=0}^{k} \omega_m NAO_{t-m} + \varepsilon_t), (1)$$

where, N_t is density in year t, X_t is ln(density) in year t, NAO_t is the NAO winter index in year t, and ε_t is stochastic variation not captured by the deterministic components of the model. After logarithmic (ln) transformation of both sides of this equation, the model takes the linear-additive form:

$$X_t = \beta_0 + (1 + \beta_1) X_{t-1} + \beta_2 X_{t-2} + \sum_{n=3}^{l} \beta_n X_{t-n} + \sum_{m=0}^{k} \omega_m NAO_t + \varepsilon (2)$$

which also reduces heteroscedasticity. The subscripts l and k include time lags ≤ 3 years (Post and Stenseth 1999). In equation (2), the coefficient $(1+\beta_1)$ quantifies statistical direct density dependence, the significance of which is tested as difference from 1 due to the ln-scale transformation, whereas β_2

is the coefficient of delayed density dependence. The coefficient β_2 incorporates the influence of plant forage on herbivore dynamics (Forchhammer et al. 1998). Hence, this model investigates both the direct and delayed influences of climate on ungulate abundance, as well as the influences of direct density dependence $(1+\beta_1)$ and delayed density dependence (β_2), which operates, at least in part, through the influence of forage.

We used linear autoregression with maximum likelihood estimation (PROC AUTOREG; SAS Institute 1996) to determine the most parsimonious dimension (Royama 1992), or order of statistical density dependence (Bjørnstad et al. 1995), of the time series on total density and densities of the male and female segments of the population separately. We considered the model with the lowest Akaike Information Criterion (AIC) score to be the most parsimonious (Bjørnstad et al. 1995). After determining the dimension of each time series, we tested for significance of direct and delayed climatic effects by including the NAO index at lags of 1 and 2 years. Significance of direct density dependence (i.e., coefficient, $1 + \beta_1$, from equation [2]) was determined with the t-test of difference from 1 (Bjørnstad et al. 1995) due to the natural log-scale; significance was assessed at the 0.05 level.

RESULTS

The NAO index correlated negatively with mean winter temperature, averaged for December-March, at the Anchorage weather station ($r = -0.87$, $P = 0.024$), and with January mean temperature at the Juneau station ($r = -0.79$, $P = 0.06$). The NAO index correlated positively with January precipitation at Juneau ($r = 0.89$, $P = 0.04$). Those results indicate, though not overwhelmingly, that positive NAO winters were colder and snowier than usual at our

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study site.

Although the total population, and the male and female segments of the population separately, were best described by a first-order autoregressive process, direct density dependence was significant only in the male and female segments of the population when analyzed separately (Table 1). Plots of the autoregressive coefficients quantifying direct and delayed density dependence for the total population, and for males and females separately, indicated that all 3 segments of the population displayed damped oscillations (Fig. 2).

Inclusion of the NAO as a covariate improved the fit of the model for the total population and for the female segment of the population, but not for males (Table 1). Density of females, but not males, declined after positive NAO winters ($R^2 = 0.53$, $P < 0.01$; Fig. 3a). Density of males was unrelated to the NAO index ($R^2 = 0.12$, $P = 0.28$; Fig. 3b). As with females, density of the total population decreased following positive NAO winters ($R^2 = 0.43$, $P < 0.02$; Fig.

3c). Production of young (i.e., percentage of young) was limited by density of females ($R^2 = 0.46$, $P = 0.02$; Fig. 4a) but not males. Accordingly, the multiple regression model revealed that, following positive NAO winters when density declined, production of young increased ($R^2 = 0.37$, $P = 0.04$; Fig. 4b).

DISCUSSION

As with populations of red deer in northern Europe (Post et al. 1999b), dynamics of elk on Raspberry Island, Alaska, USA, were driven by changes in the numbers of females, but not males. Moreover, dynamics of females in this population related mainly to large-scale variation in winter climate, with only slight but significant influences of direct density dependence. In contrast to red deer in Norway and on the Isle of Rhum, Scotland, however, elk on Raspberry Island declined after positive NAO winters. We suggest that this outcome reflects the opposing influences of the NAO on local winter climate in the 2 regions. Positive NAO

Table 1. Analysis of the dynamics of elk on Raspberry Island, Alaska, USA, 1985-1996. Shown are parameter estimates describing direct and delayed density dependence, and coefficients of covariates quantifying climatic limitation of population growth, from the statistical population model in equation (2). AIC refers to the Akaike Information Criterion, the minimum values of which identify the most parsimonious model for each population; d refers to the dimension of the model, where "1" indicates the first-order model and "2" indicates the second-order model; $(1 + \beta_1)$ is the coefficient of direct density dependence; β_2 is the coefficient of delayed density dependence due to trophic interactions; and NAO refers to the coefficient of the North Atlantic Oscillation index. An asterisk (*) indicates significance at $P < 0.05$.

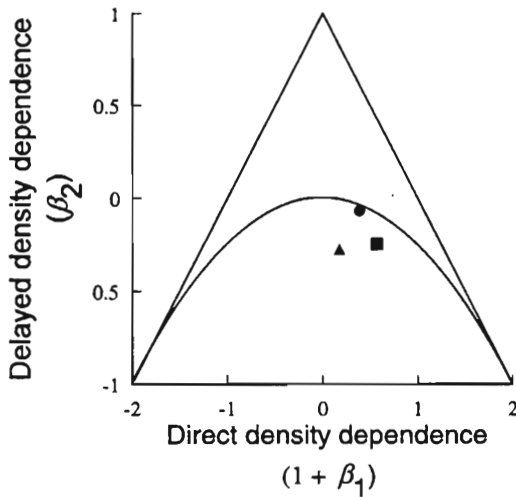| Population	AIC	d	$(1 + \beta_1) \pm SE$	$\beta_2 \pm SE$	NAO $\pm$ SE	R^2
Total	1.77	1	0.48±0.29	—	—	0.23
	3.11	2	0.58±0.33	-0.25±0.34	—	0.28
	-0.53	1	0.25±0.41	—	-0.05±0.02*	0.46
Males	40.04	1	0.14±0.35*	—	—	0.02
	41.4	2	0.18±0.37*	-0.28±0.38	—	0.08
	40.74	1	-0.03±0.36*	—	-0.16±0.15	0.12
Females	3.22	1	0.37±0.30*	—	—	0.15
	5.16	2	0.40±0.34	-0.07±0.35	—	0.15
	-1.99	1	0.04±0.41*	—	-0.07±0.02*	0.53

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Fig. 2. The parameter plane for the linear second-order density-dependent process describing the dynamics of the total population (■), and the male (▲) and female segments (●) of the population, of elk on Raspberry Island, Alaska, USA, 1985-1996. The coefficients of direct and delayed density dependence were estimated with equation (2). Outside the triangle, population dynamics are characterized by chaos leading to extinction; inside the triangle, but above the curve, dynamics are characterized by point stability; inside the triangle, but below the parabola, dynamics are characterized by damped oscillations. Dynamics inside the triangle will be characterized by persistent fluctuations if any level of stochasticity, such as that from climatic variation, is present. Royama (1992) provides a full description of the model and parameters.

winters are unusually warm in northern Europe (Hurrell 1995), but are typically cold, and perhaps snowy, in the Gulf of Alaska. Thus, on Raspberry Island, the elk population was limited by concerted influences of direct density dependence and winter climate.

Two results from this study indicate that management aimed at predicting effects of rising density and changes in climate on the future of elk on Raspberry Island should be directed toward the female segment of the population. First, large-

scale variation in winter climate influenced the dynamics of this population by limiting numbers of females (Fig. 3a). Second, production of young in this population was limited by density of females, but not males (Fig. 4a; sensu McCullough 1979), perhaps because, in female philopatric species that segregate sexually for at least part of the
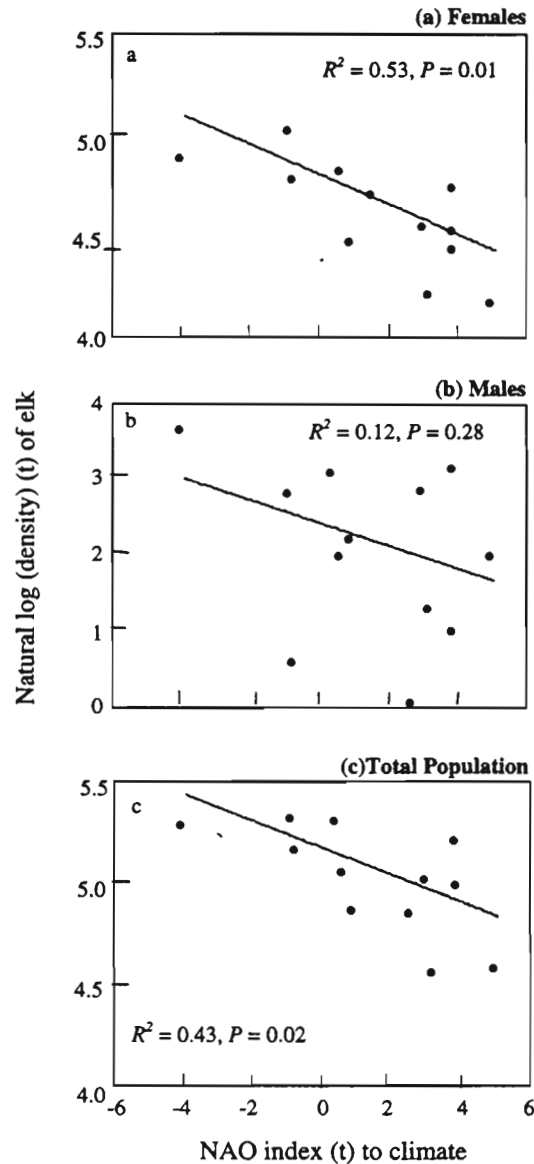

Fig. 3. Relationship between the density of (a) female segment, (b) male segment, and (c) total population of elk in relation to the North Atlantic Oscillation (NAO), Raspberry Island, Alaska, USA, 1985-1996.
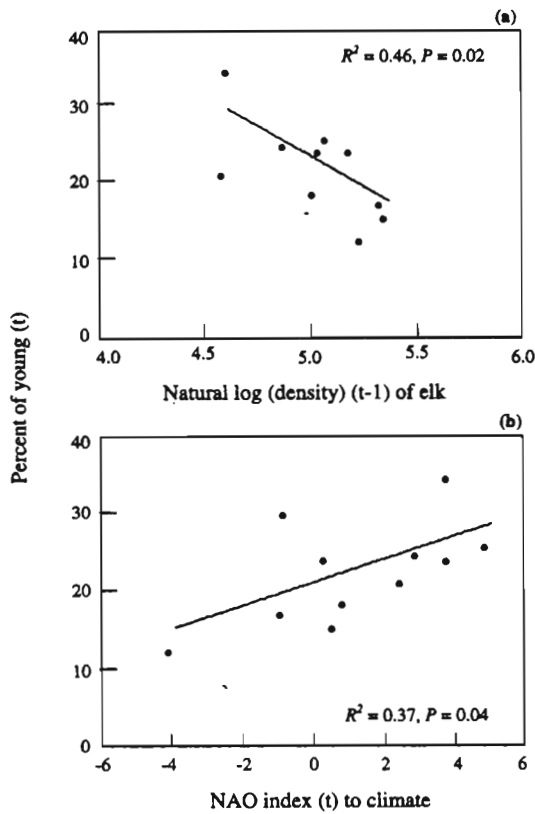
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Fig. 4. Relationship between (a) percent of young (i.e., production of young) and density of female elk and (b) percent of young and the NAO, Raspberry Island, Alaska, USA, 1985-1996.

year, intrasexual competition for forage is more intense than intersexual competition (Conradt et al. 1999).

Winter warming, such as that predicted from global circulation models of climate change (Houghton et al. 1996), may influence the fecundity of female ungulates through effects of winter climate on body size (Post et al. 1997, Milner et al. 1999), physical condition (Keech et al. 2000), and plant phenology (Langvatn et al. 1996, Post and Stenseth 1999). Moreover, climatic variation is likely the main determinant of timing and synchrony of parturition in large herbivores inhabiting strongly seasonal environments (Rachlow and Bowyer 1991,

Bowyer et al. 1998, Post and Klein 1999, Keech et al. 2000). Hence, we suggest that future monitoring of this population, and others in the far north, should involve collection of data on both the timing of parturition and total production of young. Additionally, we recommend the collection of data on local weather variables including temperature, wind speed, snow depth, and hardness to allow for a greater understanding of the complex relations among local weather, the NAO index, and survival and reproduction of elk in Alaska.

Given the negative correlation between the NAO index and local winter temperature in the Gulf of Alaska, and between the NAO index and population density of elk on Raspberry Island, we predict that increasing winter temperatures associated with global warming will elicit an increase in the numbers of elk in this population. This effect likely will be because of decreased snow depth rather than to warm temperatures, as deep snow is known to result in decreased body mass (Skogland 1986, Parker et al. 1996) and survival in large herbivores (Skogland 1985, Mech et al. 1987). Snow depth also limits habitat available for use in winter by large ungulates (Telfer and Kelsall 1984) including elk (Sweeney and Sweeney 1984). Considering, however, that production of young in this population is density dependent, and, moreover, that this population displays damped oscillations rather than chaotic dynamics (Fig. 2), the predicted increase in density following winter warming may lead to suppressed production of young and population regulation (sensu Messier 1991). Hence, once the constraint of cold and snowy winters is alleviated, this population may move from being limited by extrinsic abiotic conditions to being regulated by intrinsic biotic processes.

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