The influence of top-down, bottom-up and abiotic factors on the moose (*Alces alces*) population of Isle Royale

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Long-term, concurrent measurement of population dynamics and associated top-down and bottom-up processes are rare for unmanipulated, terrestrial systems. Here, we analyse populations of moose, their predators (wolves, *Canis lupus*), their primary winter forage (balsam fir, *Abies balsamea*) and several climatic variables that were monitored for 40 consecutive years in Isle Royale National Park (544 km²), Lake Superior, USA. We judged the relative importance of top-down, bottom-up and abiotic factors on moose population growth rate by constructing multiple linear regression models, and calculating the proportion of interannual variation in moose population growth rate explained by each factor. Our analysis indicates that more variation in population growth rate is explained by bottom-up than top-down processes, and abiotic factors explain more variation than do bottom-up processes. Surprisingly, winter precipitation did not explain any significant variation in population growth rate. Like that detected for two Norwegian ungulate populations, the relationship between population growth rate and the North Atlantic Oscillation was nonlinear. Although this analysis provides significant insight, much remains unknown: of the models examined, the most parsimonious explain little more than half the variation in moose population growth rate.

Keywords: abiotic; bottom-up; top-down; moose (*Alces alces*); North Atlantic Oscillation; wolves (*Canis lupus*)

1. INTRODUCTION

Among experiments where nutrients and zooplanktivorous fishes are added to aquatic systems, zooplankton abundance may generally be more controlled by top-down than bottom-up processes (Brett & Goldman 1997). Strong top-down effects have also been documented among terrestrial and marine systems (e.g. Estes *et al.* 1998; Schmitz *et al.* 2000; Terborgh *et al.* 2001). However, because the concurrent analysis of top-down and bottom-up processes in terrestrial systems is rare, no general characterizations exist about the relative importance of these processes for terrestrial systems. Some terrestrial studies suggest that both top-down and bottom-up influences are important (e.g. de Ruiter *et al.* 1995; Polis *et al.* 1998; Sinclair *et al.* 2000; also Dyer & Letourneau 1999). However, consistent with previous speculation (e.g. Chase 2000), patterns revealed by other studies seem complex, and suggest that the regulation in terrestrial systems cannot be simply divided into top-down and bottom-up components (Ritchie 2000; Dawes-Gromadzki 2002; Moran & Scheidler 2002). Nevertheless, discovery of generalities depends on the analysis of additional systems.

Most top-down/bottom-up studies assess how average abundance changes shortly after experimental manipulation (e.g. Brett & Goldman 1997; Schmitz *et al.* 2000). An equally important, but less studied aspect of population regulation is how interannual variation in population dynamics is affected by natural levels of interannual variation in top-down, bottom-up and abiotic processes (Polis *et al.* (1998) is an exception). To further our understanding of these relationships, we assessed how interannual variation over a 40 year period in a large, terrestrial herbivore (moose, *Alces alces*) population was affected by interannual variability in predator abundance, forage availability and several abiotic factors.

2. THE STUDY SYSTEM

The system, which has been studied continuously since 1959, comprises the wolves (*Canis lupus*), moose and balsam fir (*Abies balsamea*) in Isle Royale National Park, USA, an island (544 km²) in Lake Superior (Peterson *et al.* 1998). Wolves and moose interact essentially as an isolated single predator–single prey system. Moose comprise more than 90% of the biomass in wolf diet (Peterson & Page 1988); other moose predators are absent and hunting is prohibited on the island. Immigration and emigration are probably zero, or practically negligible.

The summer forage of moose in northeastern North America is abundant and diverse compared with winter forage (Crete & Jordan 1982). Although summer forage may be less limiting (if at all) than winter forage, an important cost of summer foraging is thermoregulation (Renecker & Hudson 1992). On Isle Royale, the most abundant and most used winter forage is balsam fir twigs (McLaren & Peterson 1995). Because deep snow limits mobility, the cost of foraging (Mech *et al.* 1987) and risk of predation (Post *et al.* 1999) are greater during winters with deeper snow cover.

The cause of death for many Isle Royale moose is

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related to nutritional restriction during spring. Thus, cool spring temperatures may increase death rates by delaying the spring growth of forage species (Stewart *et al.* 1976) and exacerbating the energetic consequences of a common ecoparasite, the winter tick (*Dermacentor albipictus*; DelGiudice *et al.* 1997).

Considering these aspects of moose ecology, we assessed how moose population dynamics are influenced by: (i) wolf abundance (a top-down process); (ii) indexed abundance for balsam fir forage (a bottom-up process); and (iii) moose abundance, which we assume represents intraspecific competition for forage. We also assessed the influence of several abiotic factors: (i) winter precipitation; (ii) the North Atlantic Oscillation (NAO) index, which may be associated with winter climate (see below); and (iii) average spring and summer temperature.

3. FIELD METHODS AND DATA SOURCES

Measures of abundance for wolves, moose and balsam fir forage on Isle Royale between 1959 and 1998 have been reported elsewhere (e.g. McLaren & Peterson 1994; Peterson *et al.* 1998, 2004). We briefly summarize the methods used to obtain these measures of abundance.

The entire wolf population was censused annually from a fixed-wing aircraft each January and February (Peterson *et al.* 1998). Confidence in census accuracy is provided by the frequent visibility of entire wolf packs at a single location and time, and making several complete counts during each winter survey. Moose abundance was estimated annually from 1979 to 1998 by aerial survey using fixed-wing aircraft (Peterson & Page 1993). From 1958 to 1991 moose abundance was estimated by cohort analysis. Our method of cohort analysis is similar to that described by Solberg *et al.* (1999). For complete details, see www.isleroyalewolf.org. Between 1979 and 1991 estimates of moose abundance are available for both aerial surveys and cohort analysis. The results presented below are based on cohort-analysis-derived estimates from 1959 to 1991 and aerial survey estimates from 1991 to 1998. Nevertheless, the results are qualitatively identical and quantitatively nearly identical when cohort analysis estimates are replaced with aerial survey estimates during the period of overlap.

An index of abundance for balsam fir forage was based on tree ring growth patterns from 16 trees (height 90–600 cm) sampled from areas of Isle Royale where fir is common. Because the size distribution and impact of herbivory differs dramatically on the east and west ends of Isle Royale (McLaren & Janke 1996), we sampled eight trees from each end of Isle Royale. For each tree, ring widths were measured across four radii at each of 30–40 cross-sections from throughout the length of each stem. Growth data from each tree were summarized as a time-series according to the methods described by Chouinard & Filion (2001). The time-series for trees from each end of Isle Royale were averaged to obtain two time-series (one for each end of Isle Royale) indexing the abundance of fir forage (figure 1*b*).

We obtained winter precipitation and temperature data for northeastern Minnesota from the United States National Climatic Data Center (www.wrcc.dri.edu/spi/divplot1map.html). Northeastern Minnesota is *ca.* 40 km west of Isle Royale. Winter precipitation represents the cumulative precipitation between 1 November and 31 March, summer temperature is the average temperature between 1 June and 31 August, and spring temperature is between 1 April and 30 May. We also obtained
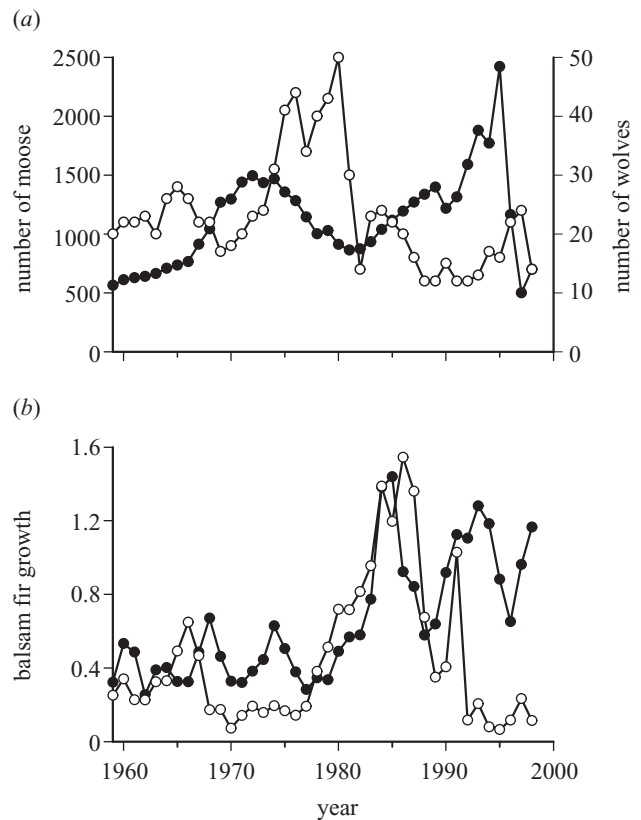
Figure 1. The abundance of wolves (open circles) and moose (filled circles) in Isle Royale National Park between 1959 and 1998 (*a*), and an index of abundance for balsam fir forage based on dendrochronological analyses of tree ring growth (*b*). Each of the two indices were based on fir trees sampled at the east (filled circles) and west (open circles) ends of Isle Royale.

annual measures of cumulative snowfall (Nov.–Apr.) in nearby Thunder Bay, Ontario (*ca.* 25 km northwest of Isle Royale) from Environment Canada (www.ec.gc.ca).

The NAO is a large-scale fluctuation in air pressure between the subtropical and subpolar regions of the North Atlantic that affects winter climate in portions of northeastern North America (Hurrell 1995). The NAO also appears to be associated with the dynamics of several ungulate populations (Ottersen *et al.* 2001), including those on Isle Royale (Post & Stenseth 1998). We obtained values of the winter (Dec.–Mar.) NAO index (as described in Hurrell (1995)) from www.cgd.ucar.edu/~jhurrell/nao.stat.winter.html#winter.

4. STATISTICAL METHODS AND DATA PREPARATION

To assess the relative influence of top-down, bottom-up and abiotic factors on moose population growth rate, we constructed several multiple linear-regression models. For each model we assessed the contribution of each predictor variable to that model's coefficient of multiple determination. The contribution of predictor variable x (denoted R_x^2) is its standardized partial regression coefficient multiplied by the correlation coefficient between x and the response variable (Schumacker & Lomax 1996). Unless otherwise mentioned, none of the models described below suffered from high levels of multicollinearity or autocorrelated residuals, nor did inspection of residual plots reveal obvious nonlinear relationships. We also assessed model

parsimony with Akaike's Information Criterion (AIC$_c$; Burnham & Anderson 1998) and ΔAIC$_C$. ΔAIC$_C$ equals the AIC$_C$ for the model of interest minus the smallest AIC$_C$ for the set of models being considered. By definition, the best model has a ΔAIC$_C$ of zero, and models with ΔAIC$_C < 2$ are generally considered worthy of consideration.

For all models, the response variable was log-transformed growth rate of moose (r_t). That is, $r_t = m_{t+1} - m_t$, where m_t is the natural logarithm of the estimated abundance of moose in year t (figure 1a). Also, when included as a predictor variable, abundances of wolves, moose and fir were first log-transformed.

Although each of our two indices of balsam fir growth reflect the relative growth of fir at their respective ends of Isle Royale (figure 1b), the indices do not reflect differences in the absolute and relative abundance of fir at each end of the island which are dramatic (McLaren & Janke 1996). Because we have little *a priori* appreciation for the relative influence of east- and west-end fir growth on population growth rate, we considered the following statistics: the correlation between moose and fir growth, averaged across the east and west ends of the island, was 0.31. The correlation between population growth rate and west-end fir growth was -0.01, and the correlation between population growth rate and east-end fir growth was 0.39. On the basis of these correlations, we used the index of fir abundance from the east end of Isle Royale to represent fir abundance.

Two of the estimated population growth rates (i.e. $r_{1995} = -0.73$ and $r_{1996} = -0.84$) are extreme statistical outliers. Although we have no reason to think that these observations are contaminated by unusually large measurement error, these observations are less than the mean population growth rate by more than seven times the standard deviation. During these years, mortality rate and population density were exceptionally high, winter severity was greater than ever recorded in the twentieth century, and the moose population was afflicted with an unusually severe outbreak of winter tick.

Because of the unusual circumstances associated with the 1995 and 1996 observations, we constructed and compared pairs of models. The first model in a pair included parameters for each process being considered (e.g. abundance of wolves, moose, balsam fir forage). A second corresponding model included the parameters of the first model in addition to two extra parameters (one for each of the two outlying data points) to represent the hypothesis that the coincidence of the extreme environmental conditions in these years represented a unique response, with respect to the other 38 years of data. We used AIC$_C$ to assess whether the extra parameters were justified.

5. RESULTS

For each pair of models that we assessed, the model containing the two extra parameters for the extraordinary years of 1995 and 1996 outperformed the model without these two parameters (i.e. ΔAIC$_C > 50$ for the models without the extra parameters). For this reason, hereafter, we report proportions of variation explained by each explanatory variable based on the total variation calculated from the entire dataset minus the 1995 and 1996 observations.

The first regression model that we analysed included only wolf, moose and fir abundance (figure 1) and explained 32% of the variation in moose population growth rate (figures 2a and 3). For this model, wolf and

fir abundance explained similar amounts of variation in population growth rate ($R_w^2 = 0.11$, $R_f^2 = 0.08$). If moose density is considered a bottom-up process, then bottom-up influences explain twice the variation in population growth rate that top-down influences explain (i.e. ($R_f^2 + R_m^2$)/$R_w^2 = 2.0$). Importantly, for this model, unidentified variables account for most of the variation in population growth rate (i.e. $1 - R^2 = 0.68$).

Because some theories of population biology are based on the *per capita* (rather than absolute) abundance of a resource (e.g. Berryman *et al.* 1995), we also considered the ratios of moose to wolf abundance, and fir to moose abundance as predictor variables. (Statistically, these variables may be interpreted as interaction terms.) For this model (figures 2b and 3), the *per capita* abundance of fir explains substantially more variation in population growth rate ($R_{f:m}^2 = 0.26$) than does the number of moose per wolf ($R_{m:w}^2 = 0.01$). The interpretation of this model may be more reliable because the moose to wolf ratio and fir to moose ratio are uncorrelated ($r = -0.02$, $p = 0.90$), but wolf and fir abundance (variables in figure 2a model) are significantly correlated ($r = -0.49$, $p < 0.01$; see Hamilton 1987). Again, unidentified variables account for most of the variation in moose population growth rate ($1 - R^2 = 0.73$).

Of the models that we constructed which included abiotic variables, the most parsimonious included the influence of wolves, moose, fir, spring temperature and NAO (ΔAIC$_c = 0$). This model explains 58% of the variation in population growth rate (figures 2c and 3). Of the variation explained, bottom-up processes account for about three times more than do top-down processes (i.e. ($R_f^2 + R_m^2$)/$R_w^2 = 3.2$), and abiotic processes explain *ca.* 80% more than bottom-up processes (i.e. ($R_{NAO}^2 + R_{temp}^2$)/($R_f^2 + R_m^2$) = 1.8).

The second-best-performing model (ΔAIC$_c = 1.1$), explains 57% of the variation in population growth rate, and included the influence of the ratio of moose to wolves, the ratio of fir to moose, spring temperature and NAO (figures 2d and 3). Of the variation explained by this model, abiotic factors account for approximately two-thirds, bottom-up processes account for approximately one-third and top-down processes account for virtually none of the variation in population growth rate.

For both of these models (i.e. figure 2c,d) warmer springs were associated with depressed growth rates ($p = 0.06$ and 0.05). The relationship between NAO and population growth rate was complex. First, population growth rate was influenced by NAO of the current year and of the two preceding years. The population growth rate of year t was most influenced by NAO of year $t - 2$. Moreover, the terms describing NAO's influence in each year are second-order terms (i.e. NAO^2). Models including only second-order terms outperformed models including linear terms (NAO) and third-order terms (NAO^3), either alone or in combination with other-order terms. The simple bivariate relationship between NAO$_{t-2}$ and population growth rate in year t illustrates the nature of this nonlinear relationship (figure 4a).

We found no statistical justification to include the other abiotic factors that we considered (i.e. summer temperature, cumulative winter precipitation and snowfall).
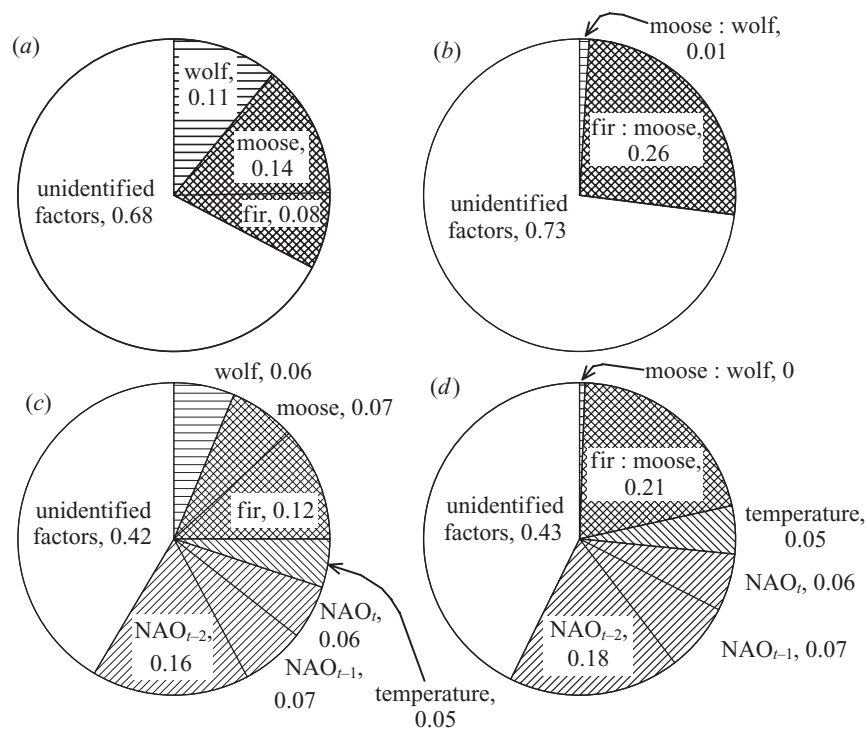
Figure 2. Proportion of interannual variation in moose population growth rate attributable to interannual variation in different biotic and abiotic factors. Each panel represents a different multiple linear-regression model, including only the factors indicated on each panel. Top-down and bottom-up processes are represented as abundances in panels (*a*) and (*c*) and as ratios in panel (*b*) and (*d*). Panels (*c*) and (*d*) are the first and second most parsimonious of all the models that we fit (see § 5).
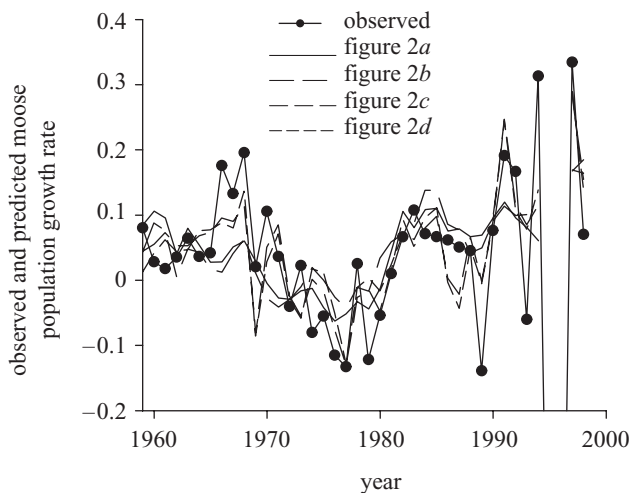

Figure 3. Observed and predicted population growth rates for Isle Royale moose, 1959–1998. Each set of predictions corresponds to one of the models depicted in figure 2. Figure 2 indicates the independent variables of each model and the proportion of variation explained by each model. For more effective visual presentation, two extreme outlying values are not shown. The observed and predicted growth rates of 1995 and 1996 were −0.73 and −0.84. Extra parameters were required to fit these observations (see § 4).

Models that included these variables, in addition to the biotic factors (i.e. figure 2*a*,*b*), had large ΔAIC_c values (i.e. greater than 4.0). Also, the significance of these variables was low when included (individually, in pairs, or all together) in models with biotic variables (i.e. $p > 0.50$).

Although growth rate was nonlinearly related to NAO, no nonlinear relationship with any of the biological terms was obvious from inspection of residuals or bivariate plots. However, because nonlinearity is considered an important aspect of many real and theorized population processes, we constructed and assessed a nonlinear model that included wolf, moose and fir abundance. Specifically, we assessed a self-excitatory threshold autoregressive (SETAR) model, which consisted of two optimal piece-wise linear models (e.g. Stenseth *et al.* 1998). Each piece is defined by the best-fitting threshold abundance of moose. Such a model roughly approximates an important nonlinear model derived from ecological principles (Stenseth & Chan 1998). On the basis of AICc, this nonlinear model did not outperform any of the linear models in figure 2. If this system exhibits nonlinearities, beyond that detected for NAO, they are either too weak to be detected with the available data, or (and) the system spends too little time in the region where nonlinearities would be more pronounced.

Finally, neither the inclusion of interaction terms between biotic and abiotic factors nor lagged terms (aside from those associated with NAO) resulted in a more parsimonious model.

6. DISCUSSION

Our analysis suggests that top-down processes are neither the primary nor a dominant influencer of interannual variation in moose population growth rate. Wolf density, a surrogate for top-down processes, explains only about half the variation in moose population growth rate
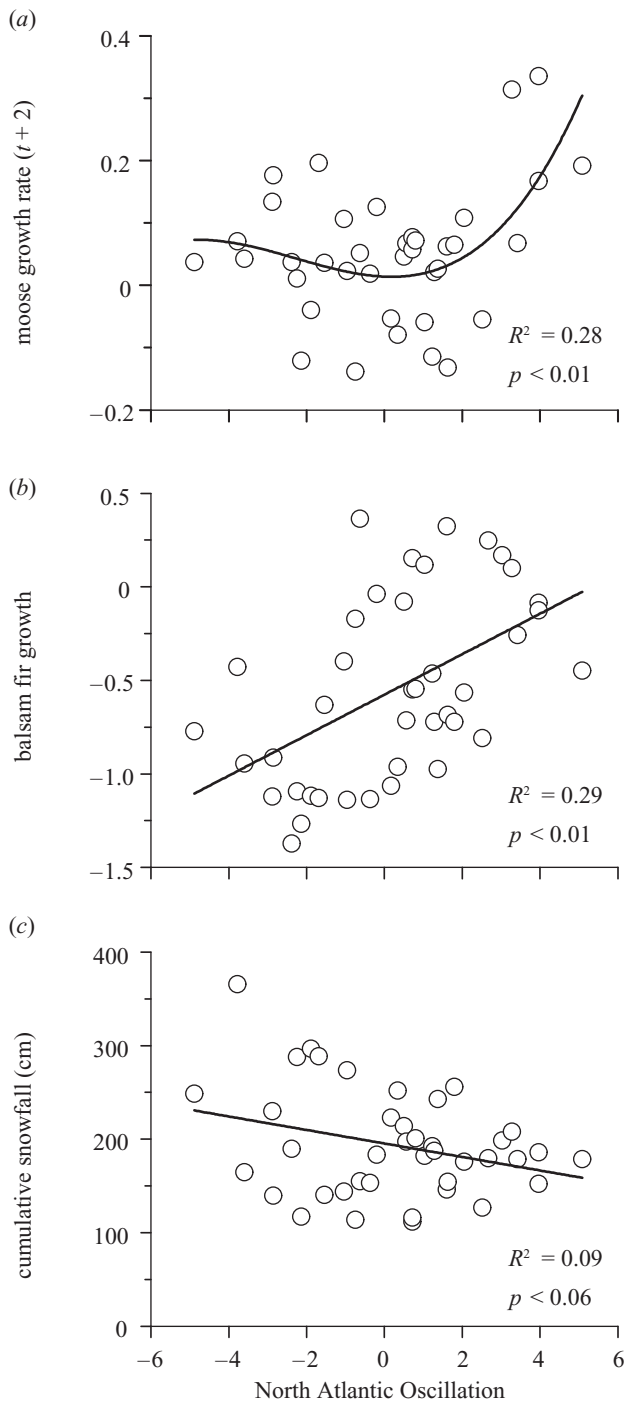
Figure 4. The relationship between the winter NAO index in year t and moose population growth rate in year $t + 2$ (*a*), growth of balsam fir in the summer of year t (*b*), and snowfall in year t (*c*). For each relationship we fit and compare models with all combinations of first-, second- and third-order polynomials. The best-performing models (according to AICc) are depicted by the lines in each panel. The line in (*a*) includes second- and third-order terms and the lines in (*b*) and (*c*) include only first-order terms.

that is explained by moose and fir density, which are surrogates for bottom-up processes (figure 2*a,c*). Also, the moose to wolf ratio, another surrogate for top-down processes, accounts for virtually none of the variation in moose population growth rate (figure 2*b,d*).

For both the ratio- and density-dependent models, abiotic factors (NAO and spring temperature) explain more

of the variation in population growth rate than do bottom-up processes (figure 2*c,d*). Because we expected a positive relationship between population growth rate and spring temperature (see § 2), the observed negative relationship is difficult to explain. The relationship with NAO was complex and reminiscent of previously described relationships between NAO and ungulate populations (i.e. Forchhammer *et al.* 2001; Mysterud *et al.* 2001). More specifically, the influence of NAO on moose population growth rate is at least partly attributable to the influence of NAO in year t on winter severity in year t (figure 4*b*) and balsam fir growth during the summer of year t (figure 4*c*). Similar influences of winter NAO on summer forage have been described elsewhere (i.e. Mysterud *et al.* 2001). The influence of NAO on population growth rate 2 years later may arise from an *in utero* effect, which has also been previously discussed (see Mech *et al.* 1987; Forchhammer *et al.* 2001). More specifically, moose born after a severe winter, in contrast to moose born during more benign conditions, may exhibit delayed first reproduction, and thereby moose population growth rate in year t could be affected by NAO in year $t - 2$. Confirmation of such a mechanism awaits further scrutiny.

For the two most parsimonious models that we assessed (figure 2*c,d*), a little less than half of the variation in population growth rate was not attributable to any particular variable. Some portion of the unexplained variation is probably attributable to measurement error associated with estimates of moose and fir abundance. Coefficients of variation for estimates of moose abundance average 13.0%, and the correlation between the abundance of fir forage and our measure of fir abundance (tree-ring growth) is unknown. By contrast, measurement error associated with wolf abundance is negligible, because abundance is based on a complete census rather than a partial survey.

Unexplained variation in moose population growth rate may be attributable to factors that we recognize as important, but are difficult to measure, such as snow condition, parasites, abundance of alternative forage and forage quality. It is unknown whether most of the unexplained variation is attributable to a few unidentified variables with large effects or numerous variables each with small effects. If the latter scenario is true, factors with a small, but biologically significant influence on population growth rate are likely to elude statistical detection. Finally, temporal variation in age structure of the moose population could account for substantial portions of the variation in population growth (Coulson *et al.* 2001). Because wolves exhibit strong age-selective predation, the influence of age structure could be considered an indirect top-down influence.

Although NAO and snowfall are correlated (figure 4*c*), snowfall was not a significant predictor of population growth rate. More specifically, our analysis suggests that population growth rate is either unaffected or slightly positively affected by increased winter precipitation ($R = 0.25$, $p = 0.13$) and snowfall ($R = -0.03$, $p = 0.85$). By contrast, previous analyses of Isle Royale moose have concluded that increased snowfall is importantly associated with decreased population growth (Mech *et al.* 1987) and increased kill rates (Post *et al.* 1999). The conclusion by Mech *et al.* (1987) was based on a correlation between

moose population growth and snowfall for a 13 year period. The conclusion by Post *et al.* (1999) was based on a correlation between NAO and average pack size and a second correlation between average pack size and kill rate. Our results suggest that NAO is correlated to aspects of winter climate that are important to wolf–prey dynamics, but are not easily monitored, such as snow depth (i.e. ground cover, not snowfall), snow density, snow crust and intraseasonal timing (e.g. late snows versus early snows) and duration of various snow conditions.

Previous investigations involving the analysis of the Isle Royale system have either emphasized the influence of top-down processes (McLaren & Peterson 1994; Messier 1994; Eberhardt & Peterson 1999; Peterson 1999), or argued that both top-down and bottom-up processes are important (Vucetich *et al.* 2002). These investigations may not contradict this analysis. This analysis considers how interannual variation (presumably around some equilibrium) in population growth rate is affected by naturally occurring, short-term fluctuations in wolf abundance. By contrast, these previous analyses focus more on how *average* moose abundance is affected by various *mean* levels of wolf abundance. Thus, wolf predation, the dominant cause of death for Isle Royale moose (Peterson 1977), appears to be a dominant predictor of the moose equilibrium, but has much less influence on variation around that equilibrium.

To conclude, our analysis provides a strong indication that top-down processes are not the primary influencer of interannual variation in moose dynamics. Interestingly, an analysis of the Isle Royale wolf population indicates that kill rate (i.e. bottom-up process) explains only a minor portion of the observed variation in wolf population growth rate (Vucetich & Peterson 2004). Our analysis does not contradict strong evidence that predator populations are important determinants of average abundance for ungulate populations (see figure 1 in Peterson *et al.* 2004). Our results do contrast with comparable studies of aquatic systems, where top-down processes appear dominant; and may contrast with some studies of terrestrial systems, where top-down and bottom-up forces may be similarly important (see § 1). Finally, our analysis further supports the claim that, relative to biotic processes, abiotic factors are an important and complex influencer of the dynamics of terrestrial populations (see § 1).

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