

# Ecosystem consequences of wolf behavioural response to climate

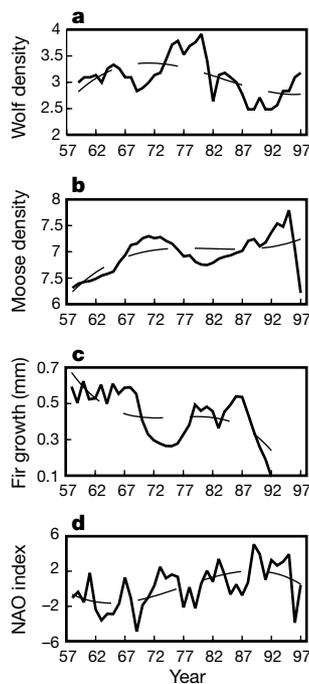
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Because apex predators exert considerable influence on the structure and function of top-down ecosystems<sup>1–3</sup>, their responses to climate may shape responses at lower trophic levels<sup>4</sup>. Previous reports of trophic cascades and ecosystem dynamics induced by predators have focused on changes in their abundance<sup>5–8</sup>, whereas we investigated whether changes in predator behaviour could precipitate cascades of similar ecological scale. Here we report the ecological consequences of predator behavioural response to global climatic variation using 40 years of data on wolf predation from Isle Royale, USA, where wolves limit abundance of moose<sup>9</sup>, which limit productivity of fir trees<sup>10</sup>. In response to increases in winter snow related to the North Atlantic Oscillation, wolves hunted in larger packs and, consequently, tripled the number of moose killed per day compared with less snowy years when they hunted in smaller packs. Following increased predation rates, moose abundance declined, and, following release from heavy browsing, growth of understory fir increased. Hence, cascading



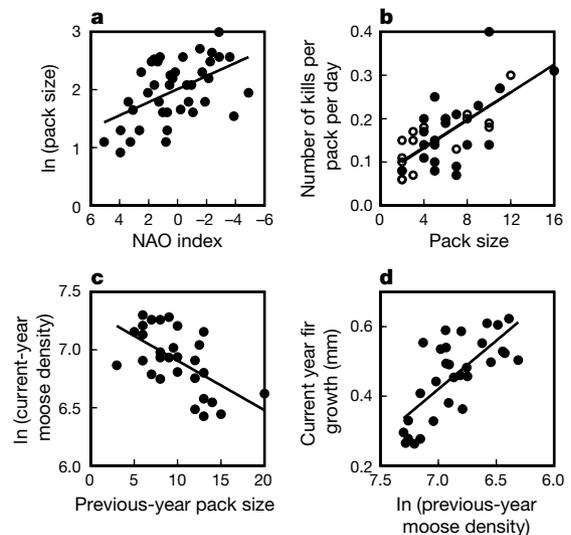
**Figure 1** Dynamics of the three-trophic-level system on Isle Royale, USA, and the North Atlantic Oscillation index, 1958–97. **a**, Interannual variation in wolf abundance (ln-transformed). **b**, Interannual variation in moose abundance (ln-transformed). **c**, Interannual variation in the mean annual growth increment (in millimetres) of balsam fir trees. **d**, The winter (December–March) North Atlantic Oscillation (NAO) index. The NAO index<sup>17</sup> correlates negatively with snow accumulation on Isle Royale during the current winter and up to six previous winters<sup>9</sup>. Dashed lines are multi-annual trends estimated with third-order polynomial regression. Density is measured in number of animals over the area studied.

behavioural responses of apex predators may be a substantial link in the pathway from climatic change to ecosystem function.

Isle Royale, USA, is a protected national park and the focus of the longest continuous study of an undisturbed, three-trophic-level system involving grey wolves (*Canis lupus*), moose (*Alces alces*) and their primary winter forage, balsam fir (*Abies balsamea*) (Fig. 1). Moose play a pivotal role in ecosystem function on Isle Royale because they are the primary prey of wolves<sup>11,12</sup>, and because their heavy browsing on balsam fir and other woody species determines fir seedling establishment<sup>13</sup>, sapling recruitment<sup>14</sup> and growth rates<sup>10</sup>, forest litter production<sup>15</sup> and edaphic nutrient dynamics<sup>16</sup>. Recently, we reported that large-scale climatic variability influences wolf–moose dynamics in this system<sup>9</sup> through interannual and decadal fluctuations in snow depth related to the North Atlantic Oscillation (NAO)<sup>17</sup> (Fig. 1). Here we present the hypothesis that wolf predatory behaviour links climate and ecosystem dynamics on Isle Royale through wolf–moose and moose–fir dynamics.

Wolf-pack dynamics and hunting behaviour on Isle Royale are recorded systematically during winter aerial surveys initiated in 1959, shortly after wolves colonized the island. Variation in the annual mean size of packs between 1959 and 1998 showed a close correlation with the state of the NAO (Fig. 2a), which correlated negatively with winter snow depth<sup>9</sup> on Isle Royale. In turn, as pack size increased in response to winter snow depth, the number of moose killed per pack per day rose during the same period (Fig. 2b). Hence, moose winter mortality was strongly dependent on wolf-pack size, which related directly to large-scale variation in winter climate.

Examination of carcasses of moose killed by wolves during winter revealed that as pack size increased, wolves also killed more calves (correlation coefficient  $r = 0.52$ , significance level  $P = 0.01$ ) and old moose ( $r = 0.55$ ,  $P = 0.05$ ). For old moose, this reflected both an increase in pack size with snow depth and a direct influence of climate on the susceptibility of old moose to predation, as the partial correlation between old moose killed and the NAO index ( $r = -0.52$ ,  $P < 0.05$ ) was independent of pack size. Additionally,



**Figure 2** Progression of climatic influence on ecosystem function from wolf behaviour to growth of fir trees. **a**, Increase in the mean size of wolf packs during snowy (negative NAO) winters, 1959–98 ( $r = -0.51$ ,  $P < 0.02$ ). **b**, Increase in the winter kill rate of wolf packs with pack size, 1972–98, for the East Pack (solid circles,  $R^2 = 0.37$ ,  $P < 0.01$ ) and West Pack (open circles,  $R^2 = 0.69$ ,  $P < 0.001$ ). Trend lines for each pack overlap completely. Common regression:  $R^2 = 0.49$ ,  $P < 0.001$ . **c**, Decline in moose density one year after increase in size of winter wolf packs, 1959–88 ( $r = -0.58$ ,  $P < 0.05$ ). **d**, Increased growth of fir trees one year after decline in moose density, 1958–88 ( $R^2 = 0.52$ ,  $P < 0.001$ ). Density is measured in number of animals over the area studied; pack size is measured in number of wolves per pack.

in support of earlier observations<sup>9,18,19</sup>, the condition and survival of adult moose declined after snowy winters. Examination of summer wolf faeces revealed increases in both the per cent occurrence ( $r = 0.79$ ,  $P = 0.02$ ) and biomass ( $r = -0.83$ ,  $P = 0.01$ ) of adult moose following negative (snowy) NAO winters.

Direct observations of numbers of wolf pups, together with estimates of the percentage of calves and numbers of old moose in the population, indicated that wolf productivity was positively related to both moose production and the availability of calves and old moose (Table 1) (total multiple regression coefficient  $R^2 = 0.34$ ,  $P = 0.037$ ). Also, annual mortality of wolves, which was density-dependent, declined following winters in which wolves hunted in large packs (Table 1) (total  $R^2 = 0.55$ ,  $P = 0.001$ ). Hence, availability of calves and old moose determined productivity of wolves<sup>20</sup>, and winter wolf-pack size influenced survival of wolves.

Because the amount of food acquired per individual wolf declines with increasing pack size<sup>21,22</sup>, it is not obvious that wolves hunting in larger packs should enjoy both greater productivity and survival. However, analysis of estimates of hunting success per individual wolf<sup>23</sup> revealed that, in addition to the increased kill rate per pack during snowy winters (Fig. 2b), the kill rate per individual wolf also increased during snowy winters (Table 1), indicating that moose were easier to kill during the snowiest winters. Thus, the parallel increase in hunting efficiency with winter snow translated into greater food acquisition by mating pairs and their offspring. The tendency of both moose and wolves to travel along the shorelines of Lake Superior and inland lakes during snowy winters increases the frequency of encounters between the two species<sup>24</sup>, and, together with greater pack sizes, probably also contributed to the higher kill rates observed during snowy winters.

Climatic influences on the hunting behaviour of wolves apparently cascaded down onto secondary and primary producers in this system. One year after snowy winters, increases in wolf-pack size and killing rates led directly to a decline in moose abundance (Fig. 2c), independently of density-dependent limitation of moose (total  $R^2 = 0.92$ ,  $P < 0.001$ ). Analysis of tree rings from the west end of Isle Royale, where fir are heavily and repeatedly browsed by moose<sup>10</sup>, revealed that growth of understory balsam fir saplings increased after snowy winters: the annual growth increment of fir correlated negatively with the NAO index of the current year ( $r = -0.59$ ,  $P < 0.005$ ) and previous year ( $r = -0.42$ ,  $P < 0.05$ ).

However, multiple regression revealed that the one-year-delayed effect of winter climate on growth of fir related directly to release from browsing after declines in moose abundance (Fig. 2d), whereas the current-year effect was related to the NAO (partial  $r = -0.48$ ,  $P < 0.05$ ). This suggests, in contrast to an earlier analysis<sup>10</sup>, that climate may directly influence fir growth on the west end of the island by offering protection from browsing under deep snow. In support of this suggestion, analysis of data from the east end of Isle Royale, where fir have escaped heavy browsing by moose<sup>10</sup>, revealed that fir growth there did not correlate with the NAO index or moose density (see Methods). Because deep snow hampers both moose foraging and locomotion<sup>24,25</sup>, the pathway of climatic influences on trophic dynamics in this system may begin with vulnerability of moose, but cascade down from wolves once they begin killing more frequently.

This study indicates that trophic cascades may occur in a three-level system as a result of behavioural responses of an apex predator to large-scale climatic variability. Such behaviourally induced cascades may ultimately influence ecosystem function, as primary production and edaphic nutrient dynamics are strongly influenced by herbivores such as moose<sup>13–16,26</sup>. Moreover, although pack size in wolves is believed to be limited by the minimum number of individuals needed to find and kill prey and by social competition<sup>27</sup>, the influence of climate on sociality in wolves illustrates that environment can influence behaviour in species displaying complex social organization, with ecosystem consequences. Similarly, the social behaviour of fish-eating predators links nutrient dynamics

**Table 1 Dynamics of wolf production, mortality and hunting success on Isle Royale, USA**

Variable (year)	Standardized coefficient	Partial <i>r</i>	<i>F</i>
Per cent pups ( <i>t</i> )			
Per cent moose calves ( <i>t</i> )	0.61*	0.42*	7.69*
Density of old moose ( <i>t</i> )	0.81*	0.40*	7.29*
Total moose density ( <i>t</i> - 1)	–	0.45	3.72
Wolf density ( <i>t</i> - 1)	–	-0.21	0.67
NAO ( <i>t</i> - 1)	–	0.02	0.01
Annual wolf mortality ( <i>t</i> )			
Wolf density ( <i>t</i> - 1)	0.97*	0.51*	18.34*
Pack size ( <i>t</i> )	-0.61*	-0.62*	10.22*
Number of packs ( <i>t</i> )	-0.81*	-0.41*	17.86*
NAO ( <i>t</i> - 1)	–	-0.15	0.33
Individual kill rate ( <i>t</i> )			
NAO ( <i>t</i> )	-0.44*	-0.53*	5.66*
Wolf density ( <i>t</i> )	-0.38*	-0.66*	4.57*
Pack size ( <i>t</i> )	–	0.42	2.95
Moose density ( <i>t</i> )	–	-0.36	2.15

Standardized coefficients, partial correlation coefficients and *F*-tests are shown from stepwise multiple linear regression of interannual variation in annual per cent pups (1970–91), annual mortality (1970–91), and number of moose killed per wolf per 100 days during winter (1967–85). Current-year effects are denoted with *t*.

\* Significant,  $P < 0.05$ .

between maritime and terrestrial ecosystems<sup>28</sup>. Just as the importance of herbivore behavioural (rather than numerical) responses to predators in trophic cascades has gained increasing attention<sup>29,30</sup>, this study indicates a need for additional focus on links between climate and animal behaviour in ecosystem processes. □

## Methods

### Wolf dynamics and winter kill data

Abundance of wolves was estimated during aerial surveys between late January and early March, 1959–98, when sizes, numbers and locations of packs were recorded. We used natural-logarithm-transformed estimates of mean annual pack size to remedy heteroscedasticity. Raw data yielded a similar correlation coefficient ( $r = -0.47$ ,  $P < 0.01$ ). The full regression model of wolf pack size ( $R^2 = 0.73$ ,  $P < 0.001$ ) included wolf density (partial  $r = 0.66$ ,  $P < 0.02$ ), number of wolf packs (partial  $r = -0.59$ ,  $P < 0.005$ ) and the NAO index (partial  $r = -0.45$ ,  $P < 0.05$ ). Annual mortality was estimated from absolute changes in wolf abundance together with pup numbers between successive winters<sup>20</sup>. In analysing pack kill rate versus pack size, we used data from the two most enduring wolf packs, the East Pack and West Pack<sup>20</sup>. Pack kill rate was not related to moose density or wolf density for either pack.

During winter, wolf travel routes were located from the air and either followed or back-tracked to locate moose kills. Nearly all moose carcasses were examined from the ground to establish age and sex of the kill<sup>11</sup>. The proportions of calf and old (aged 10–14 years) moose in the annual winter kill were arcsine-transformed before analysis. The annual kill interval during winter for wolf packs (days per kill) was calculated from observations made while back-tracking wolves between kills for 40–60 days each winter.

Per cent occurrence and biomass of adult moose in wolf faeces during summer were estimated from macrohistological analysis of fresh faeces<sup>21</sup>. When regressing per cent occurrence and biomass of adult moose in wolf faeces versus the NAO index, we also accounted for moose density during the previous winter. Partial correlations with moose density were, for per cent occurrence,  $r = 0.82$  ( $P = 0.01$ ), and, for per cent biomass,  $r = 0.84$  ( $P = 0.01$ ).

### Moose dynamics

Annual estimates of abundance of moose and the age structure of the population during 1958–88 were based on cohort reconstruction<sup>11</sup> from remains of moose collected from 1958–97. Estimates based on aerial surveys during winter (late January–early March) extend through 1997. Annual per cent calves in the population were estimated from aerial surveys during winter. To analyse the simultaneous influences of wolf-pack size and moose density on variation in moose density (ln-transformed), we used stepwise multiple regression including 'year' to de-trend the data. The first-order autoregressive term quantifying moose density was estimated ( $\pm 1$  s.e.) as  $0.85 \pm 0.06$ ,  $P < 0.05$  (a two-tailed *t*-test was used to test for difference from one<sup>19</sup>). We analysed effects of wolf-pack size on moose density only for 1959–88 because annual aerial estimates of moose abundance beyond 1988 have not been corrected by cohort reconstruction.

### Balsam fir dynamics

We used data on growth of balsam fir saplings from the west end of Isle Royale, where trophic interactions between moose and fir are tightly coupled<sup>10</sup>. Fir trees were sampled in 1992, when 8 individuals (aged 48–60 years) were cut for examination of ring-width chronologies<sup>10</sup>. The mean annual ring-width index (in millimetres) is based on an average of 4 measurements taken on each tree at 5–10-cm intervals along their stems. In the analysis of the influence of moose density on fir growth, we used data only for the period

1958–88 (see above). Matching data from 8 trees sampled on the east end of Isle Royale, where balsam fir are not heavily or repeatedly browsed by moose<sup>10</sup>, provided a natural control for the test of our hypothesis relating climate and wolf behaviour to the dynamics of moose and fir growth. On the east end, fir growth did not correlate with the NAO index at lags of 0 ( $r = 0.074$ ,  $P = 0.69$ ) or 1 year ( $r = 0.069$ ,  $P = 0.71$ ) or with moose density at a lag of 1 year ( $r = 0.054$ ,  $P = 0.78$ ).

### The North Atlantic Oscillation

The NAO is a meridional alternation in atmospheric mass balance between pressure centres over the Azores and Iceland. The winter NAO index is calculated on the basis of the normalized sea-level pressure difference between these two centres from December to March<sup>17</sup>. A negative difference indicates weak westerly winds across the Atlantic Ocean and unusually warm winters over north eastern North America; opposing conditions prevail during positive years<sup>17</sup>. We used data from the Climate Indices website of the National Center for Atmospheric Research, Boulder, USA (<http://www.cgd.ucar.edu/cas/climind/>). Although annual snow depth measures during the study period are not available for Isle Royale, the NAO index correlates negatively with snow depth in nearby Superior National Forest, USA<sup>9</sup>. In all regressions, degrees of freedom for tests of significance of independent variables were adjusted for autocorrelation<sup>9</sup>.

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## Allometric scaling of production and life-history variation in vascular plants

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A prominent feature of comparative life histories is the well documented negative correlation between growth rate and life span<sup>1,2</sup>. Patterns of resource allocation during growth and reproduction reflect life-history differences between species<sup>1,2</sup>. This is particularly striking in tropical forests, where tree species can differ greatly in their rates of growth and ages of maturity but still attain similar canopy sizes<sup>3,4</sup>. Here we provide a theoretical framework for relating life-history variables to rates of production,  $dM/dt$ , where  $M$  is above-ground mass and  $t$  is time. As metabolic rate limits production as an individual grows,  $dM/dt \propto M^{3/4}$ . Incorporating interspecific variation in resource allocation to wood density, we derive a universal growth law that quantitatively fits data for a large sample of tropical tree species with diverse life histories. Combined with evolutionary life-history theory<sup>1</sup>, the growth law also predicts several qualitative features of tree demography and reproduction. This framework also provides a general quantitative answer to why relative growth rate  $(1/M)(dM/dt)$  decreases with increasing plant size ( $\propto M^{-1/4}$ ) and how it varies with differing allocation strategies<sup>5–8</sup>.

Coexistence in diverse ecological communities has been thought to be due, in part, to life-history trade-offs involving allocation of resources<sup>6,9–13</sup>. There is, however, no generally accepted mechanistic framework for understanding how patterns of allocation influence variation in life histories. Here we show that a general allometric growth model for trees can provide an explanation for much life-history variation. Metabolism produces the energy and materials that are used for all biological processes. A central issue of life history is how over ontogeny the products of metabolism are allocated among maintenance, growth and reproduction. Previous work has shown how the 3/4-power scaling of metabolic rate with body mass in both animals and plants results from physical and biological constraints on the distribution of resources through fractal-like vascular networks<sup>14–16</sup>.

In Box 1, we derive a production/growth law in terms of above-ground plant mass,  $M$ , or basal stem diameter,  $D$ . Our data set (Table 1, Fig. 1) consists of a 20-year change in  $D$  ( $D(20)$ ) compared with  $D(0)$  for 45 species of trees in a tropical dry forest. In total, there were 2,283 individuals, all of reproductive age. Equation (6) predicts that  $D^{2/3}(20) = A_i + D^{2/3}(0)$ , so that a plot of  $D^{2/3}(20)$  versus  $D^{2/3}(0)$  for each species should yield a straight line with a universal slope of unity and an intercept,  $A_i$ , inversely proportional to wood density,  $\rho$ , so that  $A_i$  is proportional to  $\rho^{-1}$ . We tested this prediction by analysing the data for 45 species (Fig. 2a, Table 1). The average slope of all species, 1.04, is essentially not different from the predicted value of 1.0 (95% confidence intervals (CI): 1.01 to 1.08). Forty of the forty-five species had slopes statistically indistinguishable from the predicted value of 1 (Table 1). There was no systematic trend to deviate above or below 1; furthermore, we expect 5% ( $\approx 2.5$  species) to differ by chance alone at the 0.05 level.