The anatomy of predator–prey dynamics in a changing climate

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Summary

1. Humans are increasingly influencing global climate and regional predator assemblages, yet a mechanistic understanding of how climate and predation interact to affect fluctuations in prey populations is currently lacking.

2. Here we develop a modelling framework to explore the effects of different predation strategies on the response of age-structured prey populations to a changing climate.

3. We show that predation acts in opposition to temporal correlation in climatic conditions to suppress prey population fluctuations.

4. Ambush predators such as lions are shown to be more effective at suppressing fluctuations in their prey than cursorial predators such as wolves, which chase down prey over long distances, because they are more effective predators on prime-aged adults.

5. We model climate as a Markov process and explore the consequences of future changes in climatic autocorrelation for population dynamics. We show that the presence of healthy predator populations will be particularly important in dampening prey population fluctuations if temporal correlation in climatic conditions increases in the future.

Key-words: age structure, ambush predation, autocorrelation, climate change, cursorial predation, density dependence, global change, Isle Royale, lions, population dynamics, wolves, Yellowstone.

Introduction

In 1966, David Mech published a landmark study arguing that the wolves and moose of Isle Royale had reached a state of equilibrium where fluctuations in one species would be absorbed by the other (Mech 1966). Since then, however, the wolves and moose of Isle Royale have fluctuated dramatically, leading ecologists to shift from this 'balance of nature' view of herbivore population dynamics towards a dynamical view where fluctuations are regarded as the norm. Advances in statistical analysis and increasing availability of long-term data sets of individuals and populations have allowed ecologists to make great strides in elucidating the relative influences of density-dependent and density-independent factors on population dynamics

(Royama 1992; Saether 1997; Bjornstad & Grenfell 2001; Engen *et al.* 2007). Of particular interest has been the role of climate in this relationship. Using large-scale indices of climatic variability, ecologists have made progress in understanding the role of environmental factors on population dynamics. Variation in the North Atlantic Oscillation, for instance, has been found to mediate the influence of density dependence (Forchhammer *et al.* 2002) and predators (Post *et al.* 1999; Vucetich & Peterson 2004; Wilmers *et al.* 2006b) on, and drive synchrony (Post & Forchhammer 2002, 2004, 2006) in, the population dynamics of various mammals. While the use of various statistical tools has succeeded in identifying many of the drivers of population fluctuations such as density dependence, climate and predation, mechanistic models are required to understand more fully how these factors interact to yield the dynamics observed in the natural world.

Determining what drives the magnitude and frequency of population fluctuations is crucial because,

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within a species, populations that fluctuate dramatically may be more vulnerable to extinction (Heino 1998). Fluctuating populations have lower effective population sizes, which increases their vulnerability to disease and/or deleterious recessive genes. The ecological impacts of a prey population that fluctuates widely might also be important. Many scavenger species depend on carrion for survival and reproduction (Wilmers et al. 2003a, 2003b). A prey population that fluctuates widely, going through boom and bust cycles, provides a less stable food supply to scavengers than a population that is maintained at roughly constant levels (Wilmers et al. 2003a; Wilmers & Getz 2004).

Many environmental drivers of animal population dynamics are now changing due to anthropogenic effects. From mesoscale (2–2000 km) changes in temperature and precipitation to disturbances such as hurricanes (Emanuel 2005; Katz, Brush & Parlange 2005), general circulation models (GCMs) predict both increased and decreased climatic variability in different areas over much of the earth (Easterling et al. 2000; Houghton et al. 2001). Increases in climatic variability might result in longer-lasting sequences of favourable or unfavourable conditions for individual species, as climatic conditions persist in the extremes of their distributions, rather than simple increases in maximum and/or decreases in minimum favourability (Houghton et al. 2001).

Recent theoretical attempts to understand the influence of climatic variation on population fluctuations have thus focused on the role of environmental autocorrelation. Tuljapurkar & Haridas (2006) showed that temporal autocorrelation had sizeable effects on the growth rates of structured density-independent populations, larger in many cases than the influence of interannual variability itself. The degree of compensation in density dependence has also been shown to interact importantly with autocorrelation to influence population fluctuations in non-structured models (Ripa & Heino 1999). Previously, we developed a general density-dependent, age-structured model which revealed that long sequences of favourable conditions, which are common in positively correlated environments, act as a ratchet on density dependence in successive life history traits, leading to large crashes in unfavourable years (Wilmers, Post & Hastings 2007).

Since Darwin (1859), and perhaps earlier, scientists have recognized the importance of climatic conditions in mediating the outcome of species interactions. The quest to predict changes in community dynamics due to anthropogenic climate change now places an added emphasis on understanding how regional changes in climate will affect these interactions. With few exceptions (e.g. Post & Forchhamer 2001) current approaches for forecasting community change due to global warming, however, ignore species interactions, treating communities as super organisms that follow climate envelopes through time and space (Schmitz et al. 2003). This approach is likely to lead to significant errors in predictions of species occurrence and abundance, as the faunal record reveals that species showed highly divergent occurrence patterns after previous large-scale changes in global climate (Graham et al. 1996).

While research has emerged simulating the effects of climate change on plant–herbivore interactions, theoretical studies examining the effects of climate change on higher-level trophic interactions have been few. Recent empirical work on grey wolf (*Canis lupus*)-mediated food chains in Isle Royale and Yellowstone National Parks indicates that predators may buffer the effects of large-scale climate phenomena on the population dynamics of their prey (Wilmers et al. 2006b) and on the community of scavengers which they subsidize with carrion (Wilmers & Getz 2005; Wilmers & Post 2006a). Our analysis of 40 years of data from a three-level food chain on Isle Royale revealed that when moose are controlled by wolf predation, climatic effects on moose population dynamics are small and the population displays a low amplitude cycle. Conversely, in the absence of regulation by wolves, climatic effects on moose population dynamics are large, and the population displays irruptive dynamics with a large increase followed by a severe crash. This work suggests that predators play an important role in mediating the response of their prey to changes in climate. Here we integrate our age-structured prey model with different types of predators in order to understand mechanistically how predation interacts with climate and prey life-history traits to influence population fluctuations.

Methods

The basic framework of the density-dependent age-structured prey model with yearly time step t is introduced in Wilmers et al. (2007) and described briefly here in Appendix S1 (see Supplementary material). The model incorporates Eberhardt's hypothesis (Eberhardt 1977), developed originally for marine mammals but tested extensively in ungulates (Gaillard, Festa-Bianchet & Yoccoz 1998), that as an age-structured population increases, the effects of density dependence should be seen first as declines in juvenile survival, followed by adult fecundity, and lastly adult survivorship. Our model also accounts for variation in environmental conditions, with density dependence felt more strongly when conditions are poor than when they are good (Boyce, Haridas & Lee 2006). Here we consider the effects of predation on this prey population.

In order to model the effects of predators on an age-structured prey population, we first distinguish between compensatory, M_c, and additive, M_a, mortality. Compensatory mortality is simply the number of prey individuals consumed that would have died in the absence of predators. Given a prey population vector x, and transition probability vector p, where the elements, x_i and p_i are, respectively, the number of prey in age class i and their corresponding probability of living to the next time step, compensatory mortality is given by:

$$M_c(t) = \sum_{i=1}^{n} x_i(t) - \sum_{i=1}^{n} p_i(t) x_i(t). \qquad \text{eqn 1}$$

Additive mortality is then the difference between total consumption and compensatory mortality:

$$M_a(t) = M(t) - M_c(t) \quad \text{for} \quad M(t) \geq M_c(t)$$
$$= 0 \qquad\qquad \text{for} \quad M(t) < M_c(t), \qquad \text{eqn 2}$$

where M is the total number of predator kills.

The total number of prey killed by predators in year t is derived from the functional response $g[x(t), y(t)]$ where y is the number of predators. In discrete time formulations of Lotka–Voltera-type models, the functional response is often assumed to occur on the same time scale as the numerical response. As we are modelling systems that tend to have a pronounced birth pulse, the time step of one year is appropriate for the numerical response, but is likely to generate inaccurate results for the functional response which operates on a faster time scale. Many mammals, for instance, breed once a year (numerical response), but they are killed by predators throughout the year (functional response). Consequently, we integrate the functional response over the year in order to take into account the effect of a declining prey population on predator kill rates. While numerous forms of functional responses have been suggested for predators, we base our analyses on the type II ratio dependent formulation because this has the best empirical support for large predators such as wolves (Vucetich, Peterson & Schaefer 2002; Jost *et al.* 2005). This formulation is given by:

$$g(x(t), y(t)) = \frac{\mu N(t)}{y(t) + \mu h N(t)} \qquad \text{eqn 3}$$

where $N(t)$ and $y(t)$ are the total number of prey and predators at the beginning of year t, respectively, and μ and h are constants representing the saturation rate of the functional response and the predator handling time, respectively. After integrating the functional response over a year and taking the first order terms from a Taylor expansion, it can be shown (Hassell 1978) that the total number of predator kills during year t is given by:

$$M(t) = N(t) \left[1 - e^{-\mu \left(\frac{y(t)}{y(t) - \mu h N(t)} \right)} \right] \quad \text{for} \quad y(t) > \mu h N(t). \qquad \text{eqn 4}$$

Predator hunting strategies often influence the age classes of prey that they kill, and the relative amount of compensatory and additive mortality. Cursorial predators such as wolves (*Canis lupus*) and wild dogs (*Lycaon pictus*) chase down their prey over long distances. As such, they tend to kill weaker individuals, especially juveniles and senescent adults (Mech 1970; Kruuk 1972; Smith *et al.* 2004). Ambush predators such as mountain lions (*Puma concolor*), African lions (*Panthera leo*) and tigers (*P. tigris*) surprise their prey,

often killing them in their sleep or after a short chase (Husseman *et al.* 2003; Schaller 1972). The kill composition of ambush predators therefore tends to be correlated less with condition and age than that of cursorial predators (Husseman *et al.* 2003). In our model, we treat each predation strategy differently. Cursorial predators prey on all age classes but they prey additively only on juveniles and senescent adults. They kill each of these age classes additively in proportion to their availability. Ambush predators, conversely, kill any age class additively in proportion to their abundance in the total population.

The number of prey at time $t+1$ under cursorial predation is given by:

$$x_1(t+1) = \sum_{i=2}^{v-1} p_i(t) x_i(t) f_i(t)$$
$$+ \sum_{i=v}^{n} \left[p_i(t) x_i(t) - \frac{M_a(t) x_i(t)}{N(t)} \right] f_i(t)$$

$$x_2(t+1) = p_1(t) x_1(t) - \frac{M_a(t) x_1(t)}{N(t)}$$

$$x_i(t+1) = p_{i-1}(t) x_{i-1}(t) \qquad\qquad \text{for } i = 3, \ldots, v-1$$

$$= p_{i-1}(t) x_{i-1}(t) - \frac{M_a(t) x_{i-1}(t)}{N(t)} \quad \text{for } i = v, \ldots, n-1$$

$$x_n(t+1) = \sum_{j=n-1}^{n} p_j(t) x_j(t) - \frac{M_a x_j(t)}{N(t)}, \qquad \text{eqn 5}$$

where f is a vector giving the age-class specific fecundities, v is the age at which senescence sets in, n is the total number of age classes and:

$$N(t) = x_1(t) + \sum_{j=v}^{n} x_j(t), \qquad \text{eqn 6}$$

is the number of prey available to predators.

Under ambush predation, equation 5 becomes:

$$x_1(t+1) = \sum_{i=2}^{n} \left[p_i(t) x_i(t) - \frac{M_a(t) x_i(t)}{N(t)} \right] f_i(t)$$

$$x_i(t+1) = p_{i-1}(t) x_{i-1}(t) - \frac{M_a(t) x_{i-1}(t)}{N(t)} \quad \text{for } i = 2, \ldots, n-1$$

$$x_n(t+1) = \sum_{j=n-1}^{n} p_j(t) x_j(t) - \frac{M_a x_i(t)}{N(t)} \qquad \text{eqn 7}$$

and equation 6 for vulnerable prey becomes:

$$N(t) = \sum_{j=1}^{n} x_j(t). \qquad \text{eqn 8}$$

Ambush predators therefore can be thought of as a special case of cursorial predators and, as evidenced by substitution of equations 6 or 8 into equation 4, might kill more prey. Predator population dynamics are given by:

$$y(t+1) = eM(t) + (1-d) y(t), \qquad \text{eqn 9}$$

where *e* is the efficiency with which predators convert prey into new predators and *d* is the predator death rate.

SIMULATIONS

Many of the dominant hemispheric atmospheric patterns such as the North Atlantic Oscillation (NAO) and the Pacific-North American and west Pacific teleconnections have been shown to behave like first-order Markov processes (Feldstein 2000). In order to explore the relationship between environmental stochasticity and predation on prey population dynamics, therefore, we simulate climate using a simple Markov chain model. We assume that each year is either good or bad for the age-structured prey population. The probability of having a good year, g, or a bad year, b, is then represented by the transition matrix:

$$P = \begin{bmatrix} P_{gg} & P_{gb} \\ P_{bg} & P_{bb} \end{bmatrix}, \qquad \text{eqn 10}$$

where P_{ij} is the probability that, if a given year is of type *j*, it will be followed by a year of type *i*. Each column of the Markov matrix sums to 1, therefore $P_{bg} = 1 - P_{gg}$ and $P_{bb} = 1 - P_{gb}$. Varying these parameters allows us to control the frequency of good years relative to bad and the autocorrelation of resources, as influenced by climate, over time.

The response variables that we consider are the co-efficient of variation (CV), and a statistic ϕ (e.g. see Wilmers *et al.* 2007) that quantifies the amount that the total prey population *N* fluctuates from year to year. The statistic ϕ is given by:

$$\phi = \frac{\dfrac{1}{(yr-1)} \sum_{t=1}^{yr-1} (N(t+1) - N(t))^2}{\dfrac{1}{yr} \sum_{t=1}^{yr} (N(t))^2}, \qquad \text{eqn 11}$$

where *year* is the total number of years in the simulation. Whereas the CV of the population time-series quantifies overall variability, the statistic ϕ is more sensitive to year-to-year fluctuations in the time series. For instance, two time-series might fluctuate between 100 and 1000 individuals, one on a yearly basis, the other on a decadal basis. Over the long term, both will have similar CVs but the former will have a much higher ϕ. Populations exhibiting large values of ϕ therefore may be more vulnerable to extinction due to stochastic events and reduced genetic diversity (from repeated bottlenecks) than comparable populations with low values of ϕ.

The stability properties of deterministic age structured prey–predator models have been well explored previously (Hastings 1982, 1983, 1984). Here we focus on the parameter ranges that yield extant populations of predators and prey as well as positive values of additive predation. First we conduct a full sensitivity analysis of the predator–prey model for both cursorial and ambush predation as described in Appendix S2 (see

Supplementary material). We then explore the influence of additive predation on prey population fluctuations in both positively and negatively autocorrelated environments. To do this, parameter values for the prey model were chosen randomly from the ranges described in Table S1 of Appendix S2. The model was then run 1000 times keeping these prey parameters fixed, and for each run drawing new predation parameters at random from the ranges described in Table S1, Appendix S2 (see Supplementary material). For each run, the level of additive predation and fluctuation statistic ϕ were recorded. After 1000 runs, a regression line was fitted to the data with ϕ as the dependent variable, and the slope and *y*-intercept recorded. This procedure was then repeated 100 times, and the mean and standard error of these regression lines were recorded and plotted. This analysis was performed for both positively ($P_{gg} = 0.8$, $P_{gb} = 0.5$, autocorrelation $\rho = 0.3$ given by the subdominant eigenvalue of the Markov matrix) and negatively ($P_{gg} = 0.2$, $P_{gb} = 0.5$, $\rho = -0.3$) autocorrelated environments. We discarded runs for which either the prey or predator goes extinct. In addition, the prey population occasionally settles at a very low unrealistic equilibrium. As such, we treat runs for which the prey population averages less than a hundred individuals as functionally extinct.

Finally, we explored the dynamics of the model for a particular parameter set, which we felt was representative of the model output as a whole, to changes in climate over time. Specifically, we simulated 200 years of environmental data and increased the frequency of good years every 50 years. We began with $P_{gg} = P_{gb} = 0.2$ and incremented these by 0.2 every 50 years. All simulations were conducted in Matlab 7.

Results

Sensitivity analysis of the predator–prey model reveals that the more additive predation there is, the less the prey population fluctuates [Fig. 1; see Appendix S2 (see Supplementary material) for precise sensitivities of each parameter in the model]. Increasing the autocorrelation in environmental conditions magnifies prey population fluctuations, and decreases the ability of predators to control these fluctuations. While increasing the amount of additive predation still decreases prey fluctuations, the effect is not as strong as when environmental conditions are correlated negatively, as seen by the increase in slope between additive predation and fluctuations. A comparison of the cursorial (Fig. 1a) and ambush (Fig. 1b) predator–prey models reveals that ambush predators are slightly more effective at suppressing the fluctuations of their prey, for a given amount of additive predation, than cursorial predators.

As the frequency of good years relative to bad years increases, the prey population in the absence of predation experiences larger and larger amplitude fluctuations (Fig. 2). As we describe in Wilmers *et al.* (2007), this is
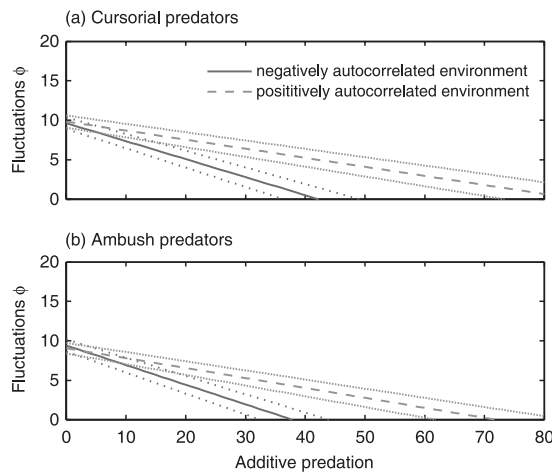
Fig. 1. Mean influence of (a) cursorial and (b) ambush predators on the population fluctuations of an age-structured prey in positively (dashed line, $\rho = 0\cdot3$) and negatively (solid line, $\rho = -0\cdot3$) autocorrelated environments. Dotted lines represent standard errors of simulation runs (see Methods for details).

due to the fact that as good years become increasingly common, the population is able to build to the point that when there is a bad year, the population experiences strong density dependence not only in juvenile survival but also in adult fecundity and survival, thus
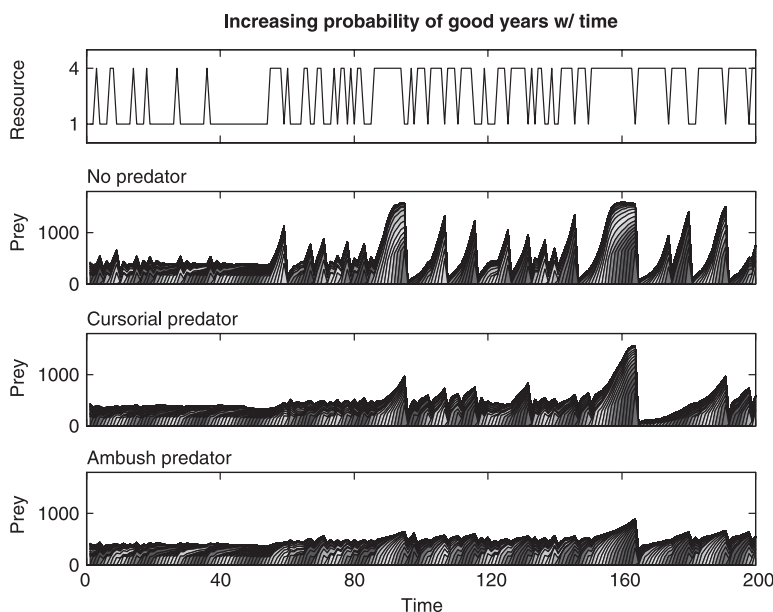

Fig. 2. Climate change scenario depicting the influence of predation and an increasing frequency of favourable environmental conditions on the population fluctuations of an age-structured prey. As the frequency of favourable years increases, population fluctuations increase in magnitude because favourable conditions allow the population to grow to large densities which, when a poor year occurs, leads to density dependence in multiple vital rates and a crash. Predators dampen the magnitude of these crashes because they retard the growth of the population during good years. A climate change scenario depicting a decreasing frequency of favourable conditions through time can be visualized by reading the figure right to left. Parameter values were as follows: prey model $\alpha = 0\cdot1, \delta_{JS} = 5, \delta_F = 5, \delta_{AS} = 5, \gamma_{JS} = 300, \beta_1 = 200, \beta_2 = 200, v = 11, n = 16, b_1 = 0\cdot75, b_{2,\ldots,v-1} = 0\cdot95, b_{v,\ldots,n} = 0\cdot5, c_1 = 0, c_{2,\ldots,v-1} = 1\cdot3, c_{v,\ldots,n} = 0\cdot8$, cursorial model $\mu = 0\cdot80, h = 0\cdot01, e = 0\cdot2, d = 0\cdot95$, ambush model $\mu = 0\cdot45, h = 0\cdot12, e = 0\cdot50, d = 0\cdot95$.

precipitating a crash in the population. When cursorial predators and ambush predators are added to the model, the fluctuations are almost fully attenuated when good years are rare (Fig. 2, early years), and attenuated partially when good years are common (Fig. 2, later years). When good years are common, predators are less effective at keeping the prey population from increasing to the point where they experience density dependence in adult fecundity and survival. This then leads to the fluctuations observed in the later years. The fluctuations are less frequent and less pronounced under ambush predation than cursorial predation, however, because the prey population builds more slowly under ambush predation. By killing all age classes of the prey population, ambush predators suppress the growth rate of the prey population when years are good. This reduces the frequency of years when density is high enough to lead to density dependence in adult survival and thus high mortality. While the difference in influence of ambush predators vs. cursorial predators on the fluctuations of their prey over the length of the time-series is small in general (as shown in Fig. 1 as well), it can be quite important in certain years. For instance, in year 164 (Fig. 2) the prey population experienced a large crash in the cursorial predator scenario after many consecutive good years had allowed the population to grow to such a high level that when a poor year arrived, strong density dependence in all three vital rates precipitated a large die-off in the population. Under the ambush predator scenario the population also grew during the good years, but much more slowly, such that when a poor year arrived, density dependence in adult vital rates was weaker, leading to only a small crash in the population.

Discussion

When additive predation is strong, we have shown that predators can have a strong effect on the response of age-structured prey populations to changes in climate. In particular, additive predation serves to decrease the amplitude and frequency of prey population fluctuations. These results shed new light on Mech's (1966) 'balance of nature' hypothesis regarding predators and prey. Variation in climate, in particular when this variation is correlated positively through time, leads to strong fluctuations in age-structured prey populations. Predators suppress these fluctuations by retarding the growth of the prey populations during good years, such that when a bad year arrives the prey population is not yet at a size where density dependence is strong. In Wilmers *et al*. (2007), we describe how a correlated climate acts as a ratchet, exposing successive life history traits (juvenile survival, adult fecundity, adult survival) to density dependence. The greater the number of successive years of favourable conditions, the greater the number of life history traits exposed to density dependence and the larger the subsequent crash in the population. Predators act in opposition to this ratchet

by retarding the rate of population growth in good years, thus preventing later life history traits from experiencing density dependence. When there are very many good years in a row, however, the prey population may escape this predator pit and reach high densities anyway, whereupon it crashes when a bad year arrives. The stronger this climate ratchet becomes, as indicated by an increase in autocorrelation, the smaller the counteracting force of predation becomes (see Figs 1 and 2).

Ambush predators are more effective than cursorial predators at prolonging the predator pit and hence suppressing prey population fluctuations. While this effect is small overall, it can be very important in certain years (e.g. year 164 in Fig. 2). By preying on the prime-aged adult part of the population, ambush predators suppress the reproductive capacity of the prey population, hence delaying population growth. It is important to note that while we limit cursorial predators to kill only the young and senescent age classes, and allow ambush predators to kill all age classes, this might not always be the case in nature. The vulnerability of adult prey to different styles of predation is likely to depend on many attributes of both the prey and the predator. When hunting large prey such as elk, moose or bison, for instance, wolves are likely to kill primarily the old and the young (Smith *et al.* 2004). When hunting smaller prey such as mule deer, wolves might kill prime-aged adults additively as well. Similarly, African lions may kill all age classes of wildebeest but when hunting elephants are limited to killing primarily calves (Schaller 1972). The important metric to measure when trying to understand the impact of predation on prey is how much additive predation there is on each age category, particularly on prime-aged adults.

A recent analysis of elk population fluctuations in Yellowstone National Park since wolf reintroduction in 1995 reveals that wolf predation on elk has been primarily compensatory to date (Vucetich, Smith & Stahler 2005). Although the elk population has declined since wolf reintroduction, year-to-year variability in elk population growth rate is primarily a factor of human hunting and multiple years of below-average precipitation. While the analysis of Vucetich *et al.* (2005) does not consider the effects of age structure (so that it is not possible to tell whether predation is compensatory on all age classes or just prime-aged adults for instance), its findings are generally consistent with our model. Wolf predation on elk in Yellowstone is highly skewed towards young and old age classes (Wright 2003). During years of below-average precipitation and/or severe winters, therefore, wolf predation on these age classes is likely to be compensatory as these individuals would have probably died anyway. When conditions improve in Yellowstone, our model predicts wolf predation on these age classes to be additive. Excluding other mortality factors (and in Yellowstone, where there are mountain lions, grizzly bears and human hunters, these are not trivial), the rate of elk population increase will depend primarily on if and how much additive predation there is on each age category, particularly prime-aged elk.

By using a simple Markov climate model, we were able to explore the mechanisms by which changes in climate and predation interact to affect prey population fluctuations. By either increasing or decreasing the frequency of good years, we were able to explore how prey population dynamics respond to a changing climate with different kinds of predators (Fig. 2). If the frequency of good years increases in the future, then the presence of predators in the ecosystem becomes increasingly important in order to dampen the increasing fluctuations in population size. Conversely, if good years decrease in the future, predators may be more important in dampening fluctuations now than later.

These results are in accordance with a recent analysis of wolf–moose interactions on Isle Royale (Wilmers *et al.* 2006b). This study revealed that when wolves had a top-down impact on moose population growth, the moose population experienced a low amplitude cycle. Conversely, when the top-down effect of wolves on moose population dynamics was removed effectively by a disease outbreak in the wolf population, the moose population displayed irruptive dynamics whereby it increased rapidly in response to favourable climatic conditions, then crashed precipitously, losing almost four-fifths of the population during a severe winter.

We have shown how autocorrelation in environmental conditions interacts with predation to influence prey population fluctuations. Our model reveals that predators may have a strong effect on prey population fluctuations. Models with multiple prey and/or multiple predators are likely to yield different results. Models with multiple prey, for instance, are likely to permit substantial reductions in at least one prey species through apparent competition when predator numbers are maintained by an alternate prey (Wittmer *et al.* 2007). We predict that the main result of this paper, namely that predators provide a countervailing force to climate in suppressing prey population fluctuations, will be robust to inclusion of multiple species because the same mechanism will apply to all such models: by preying on herbivores, predators suppress population growth rate, thereby reducing the effect of density dependence on later life history traits. Our study also reveals that a crucial detail in linking the effects of climate change to the outcome of species interactions is knowledge about how global warming is likely to effect year-to-year correlation in climatic conditions.

Acknowledgements

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Supplementary material

The following supplementary material is available for this article.

Appendix S1. The prey model.

Appendix S2. Sensitivity analysis.

Table S1. Results of sensitivity analysis.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2656.2007.01289.x
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