Populations in variable environments: the effect of variability in a species' primary resource

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Mechanistic models for herbivore populations responding to rainfall-driven pasture are used to explore the effect of temporal variability in a primary resource on the abundance and distribution of a species. If the numerical response of the herbivore to pasture is a convex function, then gains made over time intervals with above average rainfall do not compensate for losses incurred when rainfall is below average. Populations therefore fare worse when rainfall is variable compared with when rainfall is reliable. It is demonstrated that this result is independent of the distribution of rainfall. Sensitivity of a species to variability, and hence the limit to its distribution in variable environments, is directly proportional to the difference between population growth rate under ideal conditions and the estimated rate of decline as the species' resource tends to zero. When density dependence is included in the numerical response, the average abundance of a species declines with increasing variability in its primary resource. However, a model for the dynamics of pasture and rabbits (*Oryctolagus cuniculus*) and red foxes (*Vulpes vulpes*) in southern Australia, is used to illustrate that trophic interactions can reverse the effect of variability: in the absence of foxes, the mean abundance of rabbits declines with variability as expected, but in the full model the mean abundance of rabbits increases.

Keywords: numerical response; environmental variability; trophic interactions; predator–prey

1. INTRODUCTION

The relationship between the dynamics of animal populations and the variability of their environment is a central concern of applied and theoretical ecology, if only due to the long-standing debate over the roles of density-dependent and density-independent factors in determining animal abundance (e.g. Sæther 1997). There is a gradation between predictable environments and those that are highly variable that is quite apart from the gradation between cold or wet environments and those that are hot or dry. Much of southern and central Australia is characterized by extreme climatic variability. The coefficient of variation in summer rainfall, for example, can be close to unity. In these environments, models of wildlife population dynamics have emphasized the numerical response (Solomon 1949) to variable resources, rather than density-dependent processes. This is the approach that was taken by Caughley (1987a) and subsequently used by others to analyse the population dynamics of both native and introduced herbivores in Australia (Cairns & Grigg 1993; Caley 1993; Choquenot 1998; Pech & Hood 1998; Pech *et al.* 1999; Brown & Singleton 1999; Cairns *et al.* 2000). In each case the authors proposed a numerical response of the herbivore to either rainfall or pasture biomass. Pech & Hood (1998) used a similar form of the numerical

response for the interaction of red fox populations with their prey.

The change in the numbers of a predator in response to the density of its prey was termed the 'numerical' response by Solomon (1949). The term has since been used more generally (May 1981) to describe how the rate of increase of an animal population changes in response to its food supply. The numerical response may be modelled as either an instantaneous rate or as a finite rate over a discrete time interval. Some of the different functional forms that have been used are listed by May (1981). The numerical response is commonly a component of interactive models that describe the dynamics of two or more species, but it can be used in single-species models. In addition, changes in the rate of increase can be modelled as a response to a climatic variable where this is a good predictor of food supply. For example, in at least some parts of southern Australia there is a tight relationship between lagged rainfall and pasture biomass (Robertson 1987), and Bayliss (1987) used lagged rainfall as the independent variable in an Ivlev form (Ivlev 1961) of the numerical response of populations of red kangaroos (*Macropus rufus*).

The exponential rate of increase is related to the numbers of individuals in a population by

$$r_t = \ln \left(\frac{N_{t+1}}{N_t} \right), \quad (1.1)$$

where N_t represents the abundance (or some index of abundance) at time t . The Ivlev form of the numerical response of a population is given by

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$$r_t = -a + c(1 - e^{-dV_t}), \quad (1.2)$$

where a , c and d are positive constants, and V_t represents the abundance of the population's primary resource at time t . Each of the parameters in equation (1.2) have been interpreted as representing a biological process (Bayliss 1987): a represents the maximum rate of decrease of the population when food is scarce ($V_t \rightarrow 0$), c determines the maximum rate of increase, r_m , when food is abundant ($r_m = c - a$), and d , referred to as the demographic efficiency of the population, reflects the sensitivity of the population to changes in the availability of food.

One fundamental aim of ecology is to understand what determines the abundance and distribution of species. The purpose of this paper is to explore how temporal variability in the resources required by a species affects its distribution and abundance. More specifically, what is the effect of increasingly unreliable rainfall on herbivore populations (and their predators) that respond to rainfall-driven growth and senescence of pasture? These populations are affected by environmental variability quite differently to ungulate species for which climatic variables are known to have a direct effect on vital rates (Saether 1997; Gaillard *et al.* 1998; Coulson *et al.* 2000). However, it is a form of environmental variability that is faced by a range of species that stretches from mice (*Mus domesticus*) in Australia (Pech *et al.* 1999), to coyotes (*Canis latrans*) in New Mexico (Windberg *et al.* 1997) to greater kudu (*Tragelaphus strepsiceros*) in Africa (Owen-Smith 1990).

The paper is divided into two sections that develop models for the effect of environmental variability on population dynamics. Both sections deal with herbivore populations in which the numerical response of the herbivore to rainfall, or rainfall-driven pasture, is a central component. The models are used to document the role that variability in rainfall plays in determining the abundance, dynamics and persistence of herbivore populations and, in the second section, their predators. Section 2 presents a class of single-species models for those herbivore populations that do not have a significant influence on their food supply and where lagged rainfall may be used as an index of pasture. Section 3 presents a parameterized model with three trophic levels: pasture, herbivore and predator. In this model the growth and senescence of pasture is determined by rainfall and there is a feedback mechanism such that the abundance of the herbivore affects the amount of pasture available to the herbivore population at a future time.

2. PERSISTENCE AND ABUNDANCE OF POPULATIONS IN VARIABLE ENVIRONMENTS

(a) Long-term growth rate

A numerical response to rainfall (rather than pasture) implies a grazing system that is non-interactive (Caughley & Lawton 1981), that is, the grazing of the herbivore population does not reduce the amount of food available to either themselves or later generations. If the amount of rainfall over one period is independent of the amount that fell in preceding periods, then the realized values of V_t in equation (1.2) may be represented as a set of independent samples of a random variable V . If the distribution of V is specified, then together with equation

(1.2), a stochastic process is defined for the dynamics of the population. These dynamics may be characterized by the stochastic growth rate (Tuljapurkar 1997, p. 70), representing the mean long-term growth rate of the population, and is defined as

$$\lim_{t \rightarrow \infty} \frac{1}{t} E[\ln \Lambda_t(\omega)], \quad (2.1)$$

where

$$\Lambda_t(\omega) = \frac{N_t(\omega)}{N_0}, \quad (2.2)$$

and ω denotes a particular sample path of the stochastic process. The expectation (average, E) in equation (2.1) is taken over all possible sample paths. A population will not persist if the mean long-term growth rate is negative. In the case of equation (1.2) the stochastic growth rate is just the expected value of r . This follows by rewriting $\Lambda_t(\omega)$ as

$$\Lambda_t(\omega) = \frac{N_t(\omega)}{N_{t-1}(\omega)} \frac{N_{t-1}(\omega)}{N_{t-2}(\omega)} \cdots \frac{N_1(\omega)}{N_0}, \quad (2.3)$$

and substituting this expression into equation (2.1), giving

$$\begin{aligned} \lim_{t \rightarrow \infty} \frac{1}{t} E[\ln \Lambda_t(\omega)] &= \lim_{t \rightarrow \infty} \frac{1}{t} E \left[\sum_{i=1}^t \ln \left(\frac{N_i(\omega)}{N_{i-1}(\omega)} \right) \right] \\ &= \lim_{t \rightarrow \infty} \frac{1}{t} E \left[\sum_{i=1}^t r_i(\omega) \right] = \lim_{t \rightarrow \infty} \frac{1}{t} \sum_{i=1}^t E[r_i(\omega)] \\ &= \lim_{t \rightarrow \infty} \frac{1}{t} \sum_{i=1}^t E[r] = E[r], \end{aligned} \quad (2.4)$$

because, from equation (1.2), r is independent of both time t and the path ω .

For the Ivlev form of the numerical response, equation (1.2), the expected value of r is given by

$$E[r] = -a + c(1 - E[e^{-dV}]) = -a + c(1 - m_V(-d)), \quad (2.5)$$

where m_V is the moment generating function of V (Mendenhall *et al.* 1981). For many distributions (such as the normal and gamma distributions) the moment generating function has a closed form. In these cases the stochastic growth rate may be written as a simple function of the parameters of the Ivlev numerical response and of the mean and variance of V .

The numerical response of red kangaroos to rainfall, as an annual rate of increase, was given by Bayliss (1987) and is shown in figure 1a. If annual rainfall may be adequately represented by a gamma distribution (with mean μ and variance σ^2) then, as an example of equation (2.5), the stochastic growth rate of red kangaroos is given by

$$E[r] = -a + c \left(1 - \left(1 + \frac{d\sigma^2}{\mu} \right)^{-\mu^2/\sigma^2} \right), \quad (2.6)$$

where $a = 0.57$, $c = 1.14$ and $d = 0.004$. This expression is shown as a surface in figure 1b. It is an increasing function of the mean rainfall and a decreasing function of the variability of rainfall. At high values of the standard deviation, the stochastic growth rate is negative implying population decline and eventual extinction. This is perhaps the most interesting feature of equation (2.5) as it implies that a population may have a positive rate of increase for the

Figure 1. (a) The numerical response (curved line) of red kangaroos to lagged rainfall (Bayliss 1987) (filled circle, mean rainfall) and (b) the stochastic growth rate (contour lines) of red kangaroos as a function of the mean and standard deviation of rainfall. The distribution of rainfall is represented by a gamma distribution. At the site at which Bayliss (1987) measured the numerical response of red kangaroos, the mean annual rainfall between 1883 and 1984 was 236 mm and the standard deviation was 107 mm (shown in (b) as a filled circle) and hence the coefficient of variation was 0.45.

mean value of rainfall but have a negative stochastic growth rate. This means that in a variable environment, the value of V for which $r=0$ in equation (1.2) has less ecological meaning than the contour in figure 1b, where the mean stochastic growth rate is zero.

The conclusion that variability in V reduces the stochastic growth rate of a population does not depend on the distribution assumed for V . Intuitively, the stochastic growth rate is reduced by variability because the numerical response is convex: the benefit of a positive deviation from the mean does not compensate for losses incurred by a negative deviation from the mean. The net loss caused by such deviations increases with the magnitude of the deviations. This was illustrated by Caughley (1987b) for a symmetrical distribution for V , but it is in fact true for any distribution. This can be shown by taking the expectation of equation (1.2) and comparing the result with the same equation evaluated at $V = E[V] = \mu$. The latter gives

the growth rate of the population if there was no variability at all. Thus,

$$E[r] = -a + c(1 - E[e^{-dV}]) < -a + c(1 - e^{-d\mu}), \quad (2.7)$$

because by Jensen's inequality (e.g. Karlin & Taylor 1975, p. 249),

$$E[e^{-dV}] > e^{-d\mu}, \quad (2.8)$$

for any distribution V , provided that $c > 0$ and $d > 0$ (which ensure that the Ivlev form of the numerical response is convex).

(b) The distribution of species

A consequence of equation (2.6) is that for a fixed value of the mean of V , the sensitivity of the stochastic growth rate to changes in the variance of V is proportional to the parameter c ,

$$\frac{\partial E[r]}{\partial \sigma} \propto -c. \quad (2.9)$$

The parameter c represents the difference between the maximum rate of increase, r_m and the maximum rate of decrease, a . This means that the slope, in the direction of σ , of the surface given by equation (2.6) (and illustrated in figures 1b and 2b) can be related to the difference between the lower and upper limits of the rate of increase.

Although sensitivity to variability is not wholly determined by c , equation (2.9) indicates that populations most sensitive to changes in the variance of V will have extreme values of both r_m and a , or at least large values for a . The distribution of these species is more likely to be influenced by variability in resources. Red kangaroos on the one hand, have evolved mechanisms, such as a reproductive response to rainfall (Lee & Cockburn 1985), which enable them to persist during periods of low rainfall, and so have a relatively small value of a . Feral pigs (*Sus scrofa*) on the other hand, which in Australia are an introduced herbivore, tend to decline rapidly during dry periods (Choquenot 1998). Published estimates of the maximum rate of decrease for red kangaroos (Bayliss 1987; Caughley 1987b; Cairns & Grigg 1993) are smaller than those for feral pigs (Caley 1993; Choquenot 1998) regardless of whether estimates are based on a fitted numerical response or simply the maximum rate of decrease observed. The numerical response for feral pigs and the stochastic growth rate predicted by equation (2.6) are shown in figure 2. Note that the response surface for feral pigs in figure 2b shows greater sensitivity to both the mean μ and the standard deviation σ of the rainfall than is the case for the red kangaroos in figure 1b.

(c) Density dependence

A key assumption for the single-species models presented so far is that population growth rate does not depend on density. This assumption is clearly not valid when a herbivore has a substantial impact on future levels of its food supply. Caughley & Krebs (1983) proposed that Ivlev's form for the numerical response could be modified by adding a linear term in density so as to introduce density dependence. Equation (1.2) becomes

$$r_t = -a + c(1 - e^{-dV_t}) - bN_t, \quad (2.10)$$

Figure 2. (a) The numerical response (curved line) of feral pigs to lagged rainfall. Values for r_m and a are those given by Choquenot (1998). In the absence of a published estimate, d was chosen such that $E[r] = 0$. This means that in the long term, the population is expected to persist but not increase. (Filled circle, mean rainfall.) (b) The stochastic growth rate (contour lines) of pigs as a function of the mean and standard deviation of rainfall. The distribution of rainfall is represented by a gamma distribution. Choquenot (1998) gives the mean annual rainfall as 193 mm and the standard deviation as 94 mm (shown in (b) as a filled circle) and hence the coefficient of variation was 0.49.

where b is a positive constant. Graphically, the final term in equation (2.10) represents a downward vertical shift of the numerical response on the axes shown in figures 1a and 2a. As abundance increases, the amount of the primary resource required to maintain positive rates of increase becomes higher such that the population cannot continually increase. This means that either the abundance of the population will tend to zero (this is the case if the stochastic growth rate calculated from equation (2.10) with $N_t = 0$ is negative), or abundance will vary about some long-term average. In the latter case, the long-term average can be found by taking the expected value of equation (2.10),

$$E[r_t] = -a + c(1 - m_V(-d)) - bE[N_t]. \quad (2.11)$$

Setting $E[r_t] = 0$ (which must be the case if abundance varies about a positive long-term average) defines

$$E[N_t] = \frac{1}{b}(-a + c(1 - m_V(-d))). \quad (2.12)$$

The similarity between equation (2.5) and equation (2.12) implies that, like the stochastic growth rate, average abundance is a decreasing function of the variance of V .

3. TROPHIC INTERACTIONS AND VARIABLE ENVIRONMENTS

(a) *Three trophic levels: foxes, rabbits and pasture*

Pech & Hood (1998) developed an interactive model for pasture, rabbits and foxes in semi-arid southern Australia. The model consists of a functional and numerical response for the predator and prey species, and a pasture growth model. The latter is largely determined by rainfall but includes a density-dependent term that prevents the amount of pasture from increasing without limit in the absence of herbivory. The model is discrete and runs on a quarterly basis. The full model given by Pech & Hood (1998) includes the presence of disease and an alternative prey species, and incorporates additional stochasticity in the growth of pasture (apart from that due to variability in rainfall). We reduce the model to the following simple interactions between rainfall and the three trophic levels:

$$\Delta V = -55.12 - 0.0153V_t - 0.00056V_t^2 + 2.5R, \quad (3.1)$$

where ΔV is the growth of pasture in the absence of herbivores, V_t is the pasture biomass at time t and R is the quarterly rainfall over the interval $(t, t + 1)$. In the presence of rabbits,

$$V_{t+1} = V_t + \Delta V - C_{t+1}, \quad (3.2)$$

where C_{t+1} represents the pasture removed by rabbits over the interval $(t, t + 1)$, determined by the number of rabbits and their functional response to pasture. The number of rabbits, denoted by N_t , is determined by their numerical response to pasture, r_N , and the total predation rate by foxes per rabbit per quarter, G_P ,

$$N_{t+1} = N_t \exp(r_N - G_P). \quad (3.3)$$

The predation rate G_P is related to the functional response of foxes, denoted g_P , by

$$G_P = (365/4)(g_P P_t)/N_t. \quad (3.4)$$

Finally, the density of foxes, P_t , is determined by their numerical response to rabbits, r_P ,

$$P_{t+1} = P_t \exp(r_P). \quad (3.5)$$

The estimated numerical and functional responses of rabbits and foxes, as provided by Pech & Hood (1998), are shown in figure 3.

The only source of environmental variability in the reduced model is variability in rainfall. Pech & Hood (1998) found that when a cube-root transformation was applied to historical records of summer, autumn, winter and spring rainfall these distributions did not differ significantly from normal. Therefore to consider the effect of environmental variability in quarterly rainfall on the dynamics of pasture, rabbits and foxes, quarterly rainfall was simulated by generating values of R^3 where R was taken from a normal distribution with mean μ_R and stan-

Figure 3. The four relationships that govern the interactions between pasture and rabbits and between rabbits and foxes (from Pech & Hood (1998)). (a) The quarterly consumption of pasture per rabbit (functional response), (b) the quarterly numerical response of rabbits to pasture, (c) the functional response of foxes to the density of rabbits, and (d) the quarterly numerical response of foxes to rabbits. The pasture removed per rabbit is $C_t/N_t = v(365/4)(w^{0.75})(1 - \exp(-(V_{t-1} + \Delta V)/f))$ where $w = 0.782$ kg, $f = 138$ kg ha⁻¹ and $v = 0.068$ kg kg^{-0.75} day⁻¹ (Short 1985). The quarterly numerical response of rabbits to pasture is $r_N = -4.6 + 5.5(1 - e^{-0.0045V_{t-1}})$. The functional response of foxes, given by Pech *et al.* (1992) as a predation rate per fox per day is $g_P = (1096/782)N_{t-1}^2/(N_{t-1}^2 + 1.32^2)$ and the quarterly numerical response of foxes to the density of rabbits is $r_P = -0.56 + 0.77(1 - e^{-3.2N_{t-1}})$.

dard deviation σ_R . The average value of R^3 is related to the mean and standard deviation of R by

$$E[R^3] = \mu_R^3 + 3\mu_R\sigma_R^2. \quad (3.6)$$

In order to change the variability in quarterly rainfall while keeping the average value of R^3 constant, σ_R was varied and μ_R was determined by equation (3.6). In some parts of southern Australia rainfall is seasonal, either falling predominantly in winter or predominantly in summer. Only a single distribution for R was used so that this type of seasonal structure was not included.

The mechanistic model for foxes, rabbits and pasture was used to generate trajectories from which long-term mean values of abundance at the three trophic levels could be calculated. In order to avoid extremely low densities of foxes or rabbits (the model does not include demographic stochasticity, so it is not appropriate when population sizes are very small) the same minimum constraints as Pech & Hood (1998) were placed on N_t and P_t . In the case of the prey species this minimum density was 0.017 ha⁻¹, and for the predator 0.001 ha⁻¹. Pasture biomass was restricted to non-negative values. This means that the long-term

mean values calculated from these trajectories are incorrect for the model given by equations (3.1)–(3.5), but correct for an amended model where $N_{t+1} = \max\{N_t \exp(r_N - G_P), 0.0017\}$, with similar changes for P_{t+1} and V_{t+1} .

Trajectories were produced for both the full model and the case without foxes. The latter case corresponds to the trophic interaction model proposed by Caughley (1987b) for red kangaroos and pasture. Figure 4 illustrates that in the absence of predation the average abundance of rabbits steadily decreases with variability in rainfall while average pasture biomass increases. Variability in the abundance of rabbits initially increases rapidly with increasing variability in rainfall but then declines for larger values of the coefficient of variation. These trends are reversed when foxes are present. Figure 5 shows that the average abundance of rabbits increases in an exponential fashion with increasing variability in rainfall. Average pasture biomass slowly declines, and the variability in rabbit abundance increases in much the same way as average abundance. The abundance of foxes declines in response to variability in rainfall. The variability in the abundance of foxes is similar to the

Figure 4. Long-term mean values of pasture biomass and the abundance of rabbits (ha^{-1}), in the absence of foxes, for increasing values of the coefficient of variation of quarterly rainfall. Means were estimated from model trajectories, each 10 000 years in length. Mean quarterly rainfall was always 95 mm. The upper and lower error bars represent the 90th and 10th percentiles. The horizontal dotted lines represent pasture biomass and abundance of rabbits when there is no variability.

variability in abundance of rabbits when foxes are absent (compare figure 5 with figure 4); at first it increases with increasing variability and then declines for higher values of the coefficient of variation.

When quarterly rainfall is as unreliable as it is for much of southern Australia, the coefficient of variation for quarterly rainfall is typically greater than 0.5. For this amount of variability the model predicts population dynamics of rabbits that are characterized by occasional eruptions (figure 6). For most of the time foxes regulate rabbits, that is, in the presence of foxes the rabbit population rarely reaches densities in excess of 2 individuals ha^{-1} . Pech *et al.* (1992) estimated 2.5 ha^{-1} as the upper limit of the densities at which foxes can regulate rabbits. At this density both the numerical and functional responses of foxes are close to their maximum values (figure 3). However, during periods of high rainfall, rabbits can increase at a rate greater than the total predation rate of foxes such that an eruption occurs. In the model, foxes respond to high densities of rabbits by increasing in number but they do so at their relatively slow maximum rate of increase, $r_m = 0.21$. This is too slow a response to prevent the rabbits from increasing at a rate close to their maximum, which they will do while pasture is plentiful. Once rabbit densities realize values exceeding 2.5 individuals ha^{-1} they tend to continue to increase. Beyond this density the rabbits are no longer regulated by predation, but by their highly variable food supply. Thus, when the period of high rainfall ends the rabbit population goes into a sharp decline that is due to insufficient pasture but is exacer-

Figure 5. Long-term mean values of pasture biomass, abundance of rabbits (ha^{-1}), and abundance of foxes (ha^{-1}) for increasing values of the coefficient of variation of quarterly rainfall. Means were estimated from model trajectories, each 10 000 years in length. Mean quarterly rainfall was always 95 mm. The upper and lower error bars represent the 90th and 10th percentiles. The horizontal dotted lines represent pasture biomass and the abundance of rabbits and foxes when there is no variability.

bated by predation from an increasing number of foxes. On these occasions rabbits are capable of reducing pasture biomass to zero (see figure 6) and often crash to the minimum density of 0.17 ha^{-1} .

The eruptive dynamics of rabbits produced by the model are in broad agreement with the dynamics of rabbits that are observed in the field (Williams *et al.* 1995; Newsome *et al.* 1997; B. D. Cooke, unpublished data). In the model, variability in rainfall is directly responsible for eruptions and the inevitable collapse to extremely low numbers. If there is no variability in rainfall then eruptions do not occur and pasture, rabbits and foxes settle on a constant value. As variability increases, the frequency of quarters in which rabbit densities are greater than 2.5 ha^{-1} (the approximate threshold for predator-regulation) increases monotonically (figure 5).

The model most clearly indicates that increasing variability in rainfall results in increasing variability at all trophic levels (figures 4 and 5). At high values of the coefficient of variation, pasture becomes increasingly unre-

Figure 6. Typical trajectories of pasture biomass, the abundance of rabbits (ha^{-1}) and the abundance of foxes (ha^{-1}) over a 100 year time interval. The coefficient of variation of quarterly rainfall was 0.8 representing a highly variable environment.

liable, rabbits tend to display eruptive dynamics and fox populations, though buffered to some extent by being the highest trophic level, fluctuate over two orders of magnitude (figure 6). Rabbit densities appear to fluctuate the most dramatically, perhaps explaining why fox densities fluctuate as much as they do. In the absence of variability, rabbit densities settle at $0.4 \text{ individuals ha}^{-1}$ but when the coefficient of variation for quarterly rainfall is 0.8, rabbit densities can exceed 55 ha^{-1} at the height of an eruption.

4. DISCUSSION

In the absence of interspecific interactions, the effect of temporal variation in rainfall on a herbivore population having a density-independent convex numerical response to rainfall-driven pasture is to reduce the stochastic growth rate of the population. A negative stochastic growth rate implies that the population must decline in the long term. Thus environmental variability, in the form of unreliable rainfall, can determine whether or not populations persist. The inclusion of either density dependence in the numerical response, or a model for pasture that accounts for the plant material consumed by the herbivore, does not

change the conclusion that in these single-species models populations do less well in variable environments than in predictable ones.

An immediate implication of the effect of environmental variability is that it may play a role in determining the range of a species if there is a geographical gradient from reliable to highly unreliable environments. For example, high variability in rainfall, combined with sensitivity to variability, is an obvious explanation for why local extinction (and recolonization) might be a feature of some herbivore species at the edge of their geographical range (e.g. Choquenot 1998; Cairns *et al.* 2000). A coarse test of the proposed effect of variability on the stochastic growth rate of populations is to compare the distribution maps for red kangaroos and feral pigs with each other, and with geographical patterns in the mean and variance of rainfall. Future work will include comparing the geographical distribution of kangaroos and pigs predicted from equation (2.6) with the actual distributions.

The questions of how variability in a species' primary resource affects its distribution and abundance may be applied to any species. Here, we have focused on a herbivore population responding to rainfall, but the theory applies to any animal population that has a convex numerical response to its primary resource, and where this resource is variable. For example, the response of foxes to increased variability in rainfall is very similar to the response of rabbits with predators removed. Just as variability in pasture decreases the average abundance of rabbits in the model for two trophic levels, the convex numerical response of the fox population means that variability in rabbit numbers decreases the average abundance of foxes in the model involving all three trophic levels. Perhaps more surprisingly this occurs even though the average abundance of rabbits increases in response to variability.

Variability in a species' primary resource may distort short- to medium-term population time-series data. During a time interval in which the resource is relatively constant a population would be expected to fare better than in time intervals in which the resource is highly variable. Differences in variability may therefore explain population trends within time-series data. Data on coyotes (*C. latrans*) in New Mexico (Windberg *et al.* 1997) may provide an interesting example of this. The authors relate the abundance of prey available to the coyotes to rainfall and suggest that a numerical response to abundance of prey is largely responsible for the population dynamics of the species. The authors draw attention to differences in variability in rainfall within the time-series data but do not propose this factor as an explanation for trends in coyote abundance.

Lewontin & Cohen (1969) demonstrated that for population growth in a random environment

$$E[r] = E[\ln \lambda] \cong \ln \bar{\lambda} - \frac{\sigma_{\lambda}^2}{2\bar{\lambda}^2}, \quad (4.1)$$

where λ is the finite rate of increase (population growth rate), $\bar{\lambda}$ is the mean of λ and σ_{λ}^2 is the variance of λ due to changing environmental conditions. The authors do not specify any interactions between the population and the environment, or between the population and other species, but suppose that λ is a random variable with no serial

autocorrelation. Their approximation to the long-term growth rate is obtained by expanding $\ln \lambda$ around $\bar{\lambda}$, taking the expectation of the resulting expansion and dropping higher-order terms. The equation reflects the difference between the average value of $\ln \lambda$ and the logarithm of the average value of λ . It states that the greater the variability in λ the lower the long-term growth rate. Other authors have since proposed similar approximations for the effects of variability in λ on the long-term growth rate, but for more complex population models (Tuljapourkar 1997; Lande 1998).

At first appearance, the conclusions of Lewontin & Cohen (1969) and the conclusions presented here (equation (2.7)) appear similar—the effect of environmental variability is to reduce the long-term growth rate. However, this is not the case. The arguments used here, to show that the effect of variability in a species primary resource is to reduce the long-term growth rate, hold true only when the numerical response of the population is convex. Interestingly, if it is concave then the same arguments can be used to arrive at the opposite conclusion: the more variable the environment, the higher the long-term growth rate. It is unlikely that any population, herbivore or otherwise, has a concave response to their primary resource, but populations may have a concave response to a climatic variable. For example, the relationship between survival of calves in a population of elk (*Cervus elaphus*) and winter precipitation (R. A. Garrott, unpublished data) is concave. The apparent contradiction is reconciled by realizing that $\bar{\lambda}$ or σ_{λ}^2 , or both of these, may depend on environmental variability, measured as the variance in the species' primary resource, precipitation or some other climatic factor, such that the net effect of increasing variability is to increase the long-term growth rate.

In the model for rabbits, foxes and pasture, the average abundance of the predator in the system declines with increasing variability, while the average abundance of the prey increases. The numerical response of rabbits to pasture is convex, so variability in pasture is expected to reduce the average abundance of rabbits. This is what is observed when foxes are removed, but not when foxes are present. The reason for this reversal is that the equilibrium abundance of rabbits when they are regulated by foxes (0.4) is so low in comparison with their average abundance when they are regulated by their food supply (5–15), that variability provides opportunities for the rabbits to escape predator regulation. The result is the plague dynamics shown in figure 6. The high densities reached during a plague have a large effect on the average abundance of rabbits, as is the case for any skewed distribution. More generally, the net effect of variability in predator–prey systems is likely to vary from one system to another, depending on the maximum rates of increase of predator and prey.

For the more complex model of rainfall-driven pasture, rabbits and foxes, it is not clear whether environmental variability in the form of unreliable rainfall either increases or decreases the likelihood of persistence of the herbivore in the system. The effect of unreliable rainfall is to profoundly change the dynamics at all trophic levels but whether this is to the advantage or disadvantage of the herbivore is difficult to judge, even though average abundance increases. In the presence of foxes, variability in

rainfall increases the frequency of eruptions and eruptive dynamics can allow a species to colonize or recolonize unoccupied habitat. However, particularly in the case of rabbits, eruptions are followed by extremely low densities, providing a route to local extinction.

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