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Population growth rates: Determining factors and role in population regulation

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The numerical response function: rate of increase and food limitation in herbivores and predators

Peter Bayliss

Abstract

Animal populations vary in abundance over time. Some populations have declined towards extinction and others have increased dramatically. The patterns of, and reasons for, such variation have been topics of active research for decades. Recent developments in the field, such as more detailed case studies and refined mathematical analysis, allow greater exploration of why populations vary in abundance. The Royal Society held a discussion meeting in London between 6–7 February 2002 on ‘Population Growth Rates: Determining Factors and Role in Population Regulation’ which examined the recent developments for animal populations around the world and provided directions for future research and wildlife management. I presented a seminar on one theme: ‘The numerical response function: rate of increase and food limitation in herbivores and predators’ with colleague Dr David Choquenot. All papers at this conference were published in the *Philosophical Transactions of the Royal Society* (London B)(2002) issue 357. Subsequently all papers were published by the Royal Society separately in a book. Details of the conference, the paper, book and seminar are outlined in this Internal Report.

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The numerical response: rate of increase and food limitation in herbivores and predators

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Two types of numerical response functions have evolved since Solomon first introduced the term to generalize features of Lotka–Volterra predator–prey models: (i) the demographic numerical response, which links change in consumer demographic rates to food availability; and (ii) the isocline numerical response, which links consumer abundance *per se* to food availability. These numerical responses are interchangeable because both recognize negative feedback loops between consumer and food abundance resulting in population regulation. We review how demographic and isocline numerical responses have been used to enhance our understanding of population regulation of kangaroos and possums, and argue that their utility may be increased by explicitly accounting for non-equilibrium dynamics (due to environmental variability and/or biological interactions) and the existence of multiple limiting factors. Interferential numerical response functions may help bridge three major historical dichotomies in population ecology (equilibrium versus non-equilibrium dynamics, extrinsic versus intrinsic regulation and demographic versus isocline numerical responses).

Keywords: numerical response; population growth rate; regulation; herbivores; predators; non-equilibrium

1. INTRODUCTION

(a) *Herbivores and predators: types of consumer–resource systems*

The resources used by animal populations are either non-consumable or consumable (Caughley & Sinclair 1994). While the absolute level of non-consumable resources is generally not influenced through its use (e.g. shelter), the level of consumable resources is (e.g. food). The most comprehensive classification of the relationship between resources and animals is that developed for grazing systems by Caughley & Lawton (1981). They accounted for the degree to which herbivores interact with their food resources and interfere with each others capacity to access those resources. Interactive grazing systems are those in which herbivore consumption influences the rate of renewal of food plants, which in turn influences the dynamics of the herbivore population itself. Interactive grazing systems are further differentiated into interferential systems in which herbivores can affect each others capacity to assimilate food plants, and laissez-faire systems in which they do not. Non-interactive grazing systems are those in which herbivore feeding has no influence on the rate of renewal of food plants and, hence, no reciprocal influence on the dynamics of the herbivore population. Non-interactive grazing systems are differentiated between reactive systems in which rate of change in herbivore abundance is a function of food plants, and non-reactive systems in which herbivore population dynamics are largely independent of food availability. We argue that this classification encompasses the range of mechanisms that link most animal consumer systems to their food resources and so is applicable to both herbivores and predators. Any food resource available to an animal population has the potential to elevate average reproduction and/or survival. The availability of food resources to an animal population will be potentially reduced through the use of those resources by the animal population itself (i.e. the negative feedback loop).

(b) *Food availability and consumer abundance (a short history)*

Solomon (1949) recognized that an increase in food availability would generally elicit two responses in a consumer population limited by those food resources; a ‘functional response’ which elevates the per capita rate of food intake, and a consequent ‘numerical response’ which increases consumer abundance through enhanced reproduction, survival or both. By directly linking food availability and consumer population demography and abundance through the numerical response, Solomon (1949) was generalizing features of more specific models of trophic interaction (primarily Lotka–Volterra predator–prey models) to his central theme of animal population regulation. These models assume that both prey (food) mortality due to predation and predator (consumer) survival are proportional to the product of food (H) and con-

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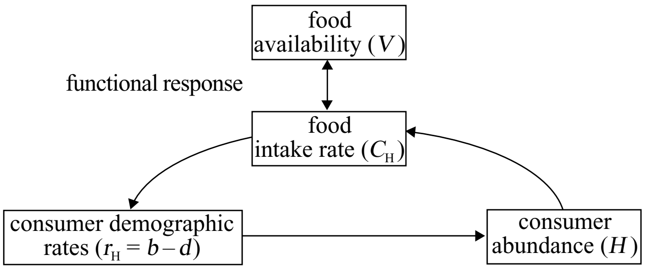

Figure 1. A diagram describing a Lotka–Volterra model of interaction between a predator (consumer) and its prey (food). Symbols are those used in equations (2.3) and (2.4): food availability (V); food intake (C_H); consumer demographic rates (annual rate of increase r_H = births − deaths or $b - d$); and consumer abundance (H).

sumer (P) abundance (i.e. bHP and cHP respectively). In effect, this implies that both the functional response of consumers to variation in food availability and the consequent change in consumer demographic rates are linear, indicating that the transfer of biomass from the food to consumer populations is conserved. Perhaps more importantly, the structure of the model drives changes in consumer abundance according to the direct effect that food intake rate has on consumer demography (figure 1).

Since Solomon's original definition, two types of numerical response have been defined and used to help elaborate the broad interactive dynamics between consumer populations and their food. These are: (i) a 'demographic' numerical response that links rate of change in consumer abundance to food availability (Caughley 1976; May 1981*a*); and (ii) an 'isocline' numerical response that links consumer abundance *per se* to food availability (see Holling (1965, 1966) for total predator responses).

In this paper, we review how both approaches to the numerical response have been used to enhance understanding of herbivore and predator population regulation, and attempt to increase their realism and utility by explicitly accounting for the existence of non-equilibrium dynamics due to environmental variability, biological interactions and situations where multiple factors simultaneously limit rates of change in population abundance. The different approaches to describing numerical responses have also been recently reviewed by Sibly & Hone (2002).

2. DEMOGRAPHIC NUMERICAL RESPONSES

(a) *Single-species logistic models of population growth*

The dominant paradigm in large herbivore ecology proposed that density-dependent mortality regulates population density through food shortage (i.e. the so-called 'food hypothesis' (Sinclair *et al.* 1985)). Most tests of the relevance of this hypothesis to large herbivores have either reduced herbivore population density (or allowed a natural catastrophe to do so), and assessed whether the population returns to its pre-reduction level (Houston 1982; Sinclair *et al.* 1985), or looked for density dependence in r or some valid demographic correlate of r (i.e. growth, body condition, fecundity or survival) (O'Roke & Hammerston 1948; Woodgerd 1963; Boyd & Jewell 1974; Sinclair 1977; Sauer & Boyce 1983; Skogland 1983, 1985; Messier & Crête 1984; Clutton-Brock *et al.* 1985; Eberhardt 1987; Fryxell 1987; Choquenot 1991; Messier 1991). Both of these approaches focus on the dynamics of the herbivore population, interpreting any decline in r or its index as the population moves towards its hypothetical equilibrium as the effect of declining per capita food availability. Because these tests do not consider food explicitly, they are either implicitly or directly underpinned by single-species models of interaction between herbivores and their food resources (Caughley 1976). The simplest model that is generally applied to herbivore populations is the generalized logistic which has the form:

$$r = r_m\left(1 - \frac{N}{K}\right)^z, \qquad (2.1)$$

where r_m is the maximum rate of increase, K is the density of the herbivore population where the rate of renewal in food resources is just sufficient to balance reproduction and survival (where $r = 0$), N is prevailing population size and z is a coefficient describing the degree to which the density-dependent decline in r with N is delayed until higher levels of N are attained (Fowler 1981, 1987; figure 2*a*). The value of z reflects the degree to which the amount of food currently available to herbivores is determined by the number of herbivores currently consuming that food ($z = 1$), or the number that have fed on the food in the past ($z > 1$). Eberhardt (1987) used a fairly high value of $z = 11$ in fitting equation (2.2)●●2●● to population census data for elk (*Cervus elaphus*) in Yellowstone National Park in the western United States, implying that current food availability was heavily dependent on past elk density. Delayed effects of density on r mean that most density dependence is observed at densities near K (figure 2*b*).

The most pressing limitation of single-species models for large herbivores (and hence on tests of the food hypothesis based on single-species models), is that K must be assumed to be relatively constant if the relationship between population density and r is to be consistent (and hence detectable) (Caughley 1976; Choquenot 1998). The importance of this assumption can be illustrated by contrasting the growth trajectories for elk projected from Eberhardt's (1987) model, where K is alternatively stable (1% year-to-year variation in K; figure 3*a*) or unstable (5% year-to-year variation in K; figure 3*b*). While growth towards equilibrium follows a clearly density-dependent trajectory where K is relatively stable, density-dependent population growth is not evident where K is less stable.

(b) *Interactive consumer–resource models*

The more explicit demographic numerical response links change in consumer demographic rates to food availability. In contrast to the single-species density-dependent approach above, consumer–resource models are by nature multi-species models, but only in the sense that separate predator and prey components are explicitly modelled and linked. Additionally, whilst only one predator species is usually modelled, prey may involve all food species lumped on one axis or a subset of most important food species. As a step in formulating an interactive plant–herbivore system, Caughley (1976) described a demographic

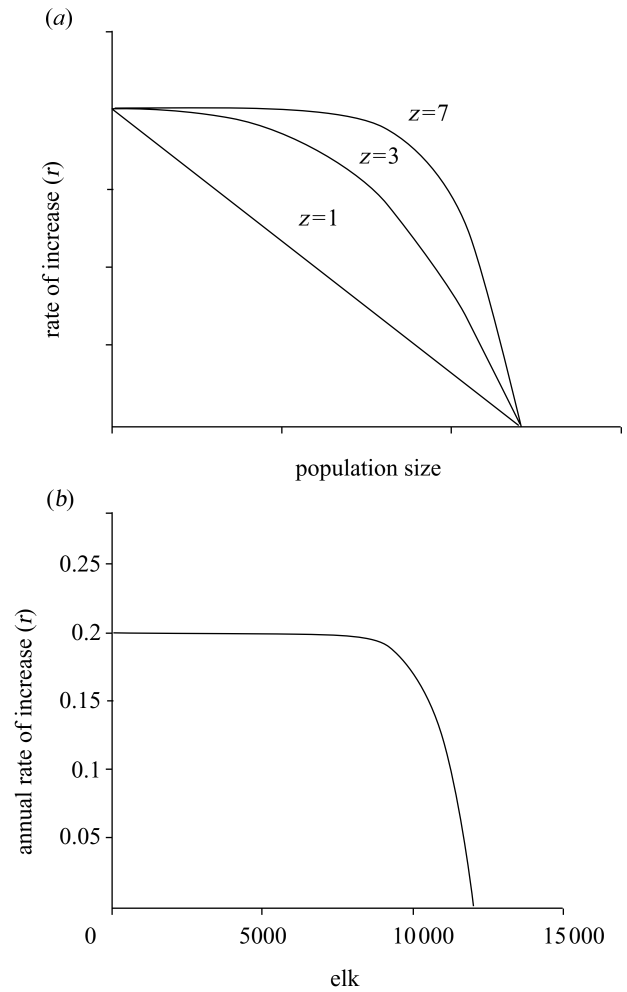

Figure 2. Hypothetical relationships between (*a*) rate of population increase (*r*) and population size predicted from the generalized logistic model in which *z* is varied from 1 to 3 (see lines on graph), and (*b*) the generalized logistic model for Yellowstone elk estimated from population census data (Eberhardt 1987). The parameter values estimated for elk are $r_m = 0.2$ p.a., carrying capacity $K = 12\ 000$ and $z = 11$.

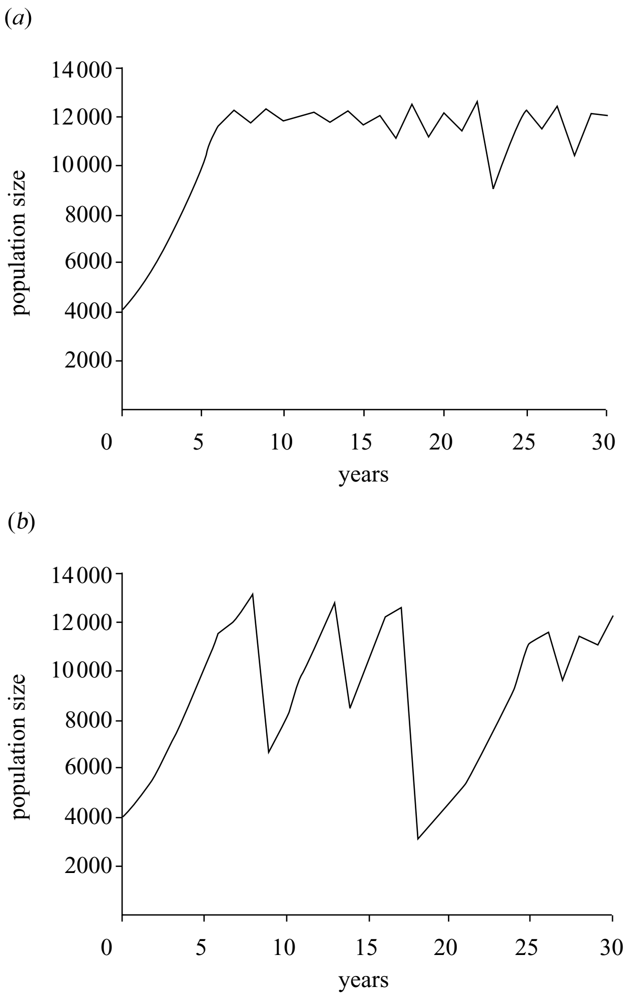

Figure 3. Trajectories of growth for elk populations predicted from a generalized logistic model estimated by Eberhardt (1987), with stochastic variation in *K* equivalent to (*a*) 1% of the mean, and (*b*) 5% of the mean value of *K*.

numerical response (after May 1981*a*) that linked variation in herbivore demographic rates (summarized by the instantaneous rate of population increase, r_H), to the biomass of available food (V):

$$r_H = -a + c_1(1 - e^{-Vd_1}), \tag{2.2}$$

where a is the maximum rate at which the population declines in the absence of food, c_1 is a constant describing the difference between the maximum rate at which the population can increase (r_{mH}) and a (i.e. $r_m = c_1 - a$), and d_1 is the demographic efficiency of the population indexing how quickly r changes from being negative to positive as vegetation biomass increases. The general form of the response and a diagram of the full interactive model are shown in figure 4*a*,*b*.

The other components of Caughley's interactive model were the growth of ungrazed vegetation and the herbivore functional response. Vegetation growth in the absence of grazing was modelled using a simple density-dependent logistic function to link the instantaneous rate of change in vegetation biomass (r_V) to standing biomass (V):

$$r_V = r_{mV}\left(1 - \frac{V}{K}\right), \tag{2.3}$$

where r_{mV} is the maximum rate of increase in vegetation biomass and K is vegetation biomass where shading or competition for water or nutrients limits further plant growth. The herbivore functional response, which describes the increase in per capita vegetation offtake by herbivores (C_H) with increasing vegetation biomass, was modelled using the same exponential form as the numerical response:

$$C_H = c_2(1 - e^{-(V-V_g)d_2}), \tag{2.4}$$

where c_2 is the maximum rate of vegetation intake by each herbivore, V_g is the vegetation biomass where intake by herbivores falls to 0 (i.e. the value of V_g determines whether or not the curve goes through the origin (May 1981*a*, table 5)), and d_2 is the efficiency of the functional response describing how rapidly vegetation intake increases to its maximum rate with increasing vegetation biomass.

The important differences in the model developed by Caughley and the Lotka–Volterra model described above are: (i) the curvilinear functional and numerical responses (equations (2.1) and (2.3)); and (ii) the fact that Caugh-

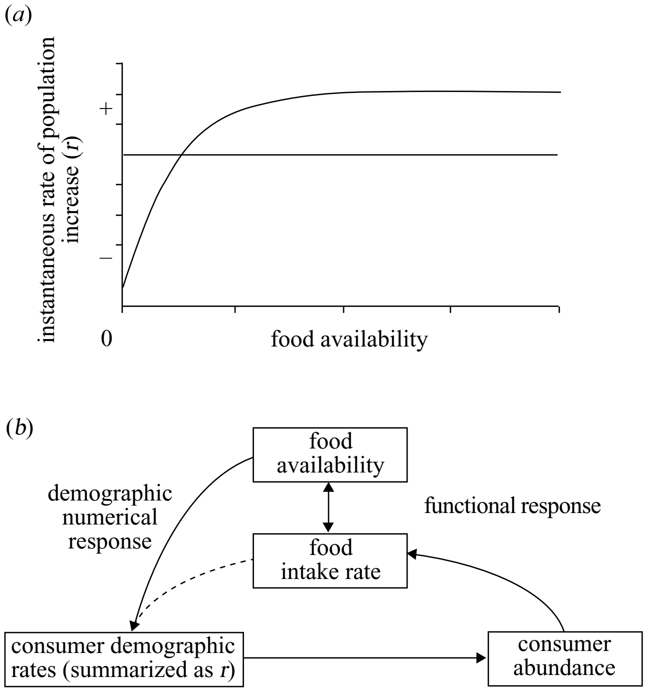

Figure 4. (*a*) The general form of a demographic numerical response described by Caughley (1976), and (*b*) the structure of the interactive model within which the response was used. The dashed line in (*b*) indicates a relationship that is explicit in Lotka–Volterra models but is subsumed by the demographic numerical response in Caughley's interactive model.

ley's numerical response links consumer demography directly to food availability rather than food intake rate. The more complex form of the functional response used in Caughley's model accommodates more sophisticated ideas on how food availability and other environmental factors influence animal foraging behaviour (e.g. Watt 1959; Ivlev 1961; Allden 1962; Holling 1966). In applying the same general form to the demographic numerical response, Caughley's model simply allows the possibility that transfer of biomass between adjacent trophic levels is conserved in the same way as is assumed in Lotka–Volterra models (i.e. maximum reproduction and survival is dependent entirely on the rate of food acquisition). Under these conditions the functional and numerical responses can be parameterized so that maximum rates of increase (r_m) are approached at levels of food availability that produce maximum rates of food intake (C). This would reproduce the linear relationship between the rate of food intake and rate of change in predator abundance used in Lotka–Volterra models. Of course, other forms of this relationship are possible. Crawley (1983) argued that the relationship between food intake rate and r would be curvilinear where: (i) maximum reproduction or survival was limited by factors other than food intake; or (ii) a threshold rate of food intake was required before reproduction was possible. Different forms for the numerical response would need to be considered if these alternatives were to be accommodated.

While the demographic numerical response used in the interactive model subsumes the direct link between food intake and animal demography, it provides a very powerful summary of the indirect effect that food availability, as a limiting factor, has on an animal population. Demographic numerical responses to food availability have been estimated for a range of herbivores including kangaroos (Bayliss 1987), brush-tailed possums (Bayliss & Choquenot 1998), wild pigs (Choquenot 1998) and wild house mice (Pech *et al.* 1999). The primary use to which these numerical responses have been put is in the development of simulation models that explore dynamic interactions between herbivore populations and their limiting food resources (Caughley 1976, 1987; Caughley & Gunn 1993; Bayliss & Choquenot 1998; Choquenot 1998).

Perhaps one the best examples of how demographic numerical responses can be applied to help understand interactions between animal populations and their food resources is the work of Caughley (1987) and his co-workers. They estimated the components of the interactive model described by equations (2.2), (2.3) and (2.4) for the grazing system comprising red kangaroos and native pastures in Australia's eastern rangelands. This grazing system is highly stochastic, being driven by the vagaries of rainfall which varies up to 47% from year to year, with low correlation between years and between seasons within years. This highly stochastic variation leads to wide, seemingly random fluctuations in the abundance of kangaroos and the pastures they feed on. Between 1977 and 1985, Caughley and his co-workers exploited these natural fluctuations to estimate the form of density-dependent pasture responses to rainfall (Robertson 1987*a*,*b*), and the numerical response of kangaroos to pasture biomass (Bayliss 1985*a*,*b*, 1987). During that time, the functional response describing pasture intake by kangaroos to changes in pasture biomass was also estimated in a series of graze-down trials using captive kangaroos held in semi-natural enclosures (Short 1985, 1987).

The vegetation response obtained was modified from that described in equation (2.3) to account for empirically estimated effects of variation in rainfall on pasture growth and die-back, over and above the density-dependent effects of pasture biomass. The modelled vegetation response was:

$$\Delta V = -55.12 - 0.01535V - 0.00056V^2 + 3.946R, \tag{2.5}$$

where ΔV is the pasture growth increment over three months in the absence of grazing, V is pasture biomass at the start of those three months and R is the rainfall in mm over that period. The pasture growth increment was taken as a random draw from a normal distribution with mean equal to the solution of equation (2.5) and a standard deviation of 52 kg ha^{-1}, equivalent to the variation in pasture growth not accounted for by rainfall and standing biomass (Robertson 1987*b*). The functional response of red kangaroos (Short 1985) was estimated as:

$$C = 86(1 - e^{-V/34}), \tag{2.6}$$

(assuming an average body weight of 35 kg), and their demographic numerical response as:

$$r_H = -1.6 + 2(1 - e^{-0.007V}). \tag{2.7}$$

The dynamics of the grazing system were simulated over 100 years, with seasonal rainfall drawn from normal distributions with means and standard deviations estimated from long-term records. Successive pasture growth

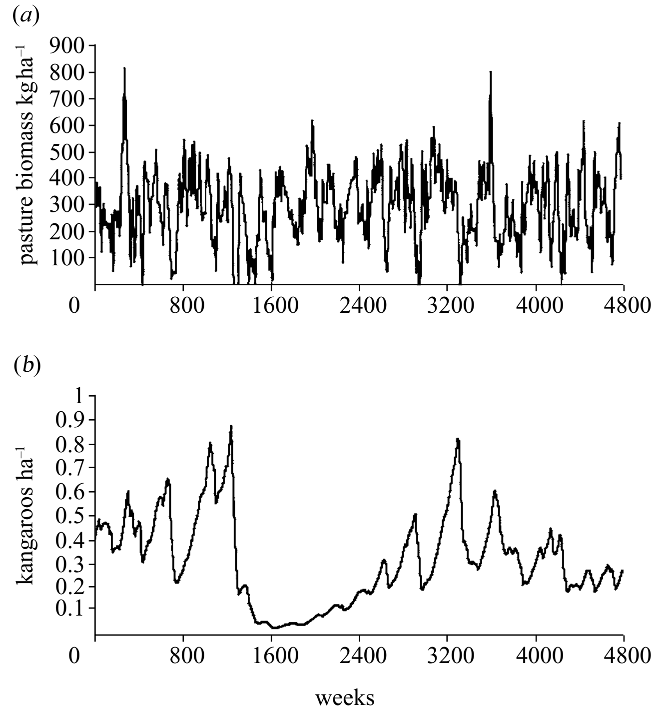

Figure 5. Temporal variation in (*a*) pasture biomass and (*b*) kangaroo density, predicted from a model of interaction between kangaroos and pasture, developed by Caughley (1987).

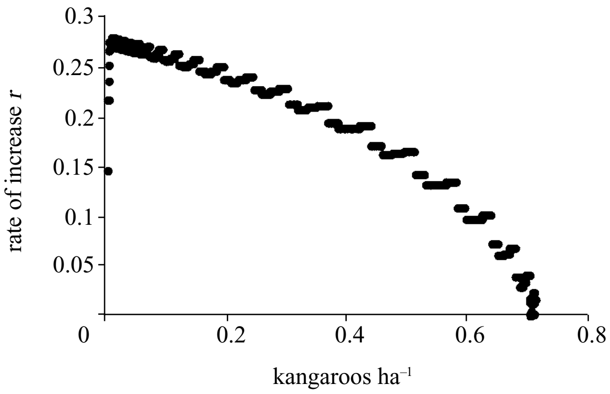

Figure 6. Relationship between density and rate of increase for kangaroos in the absence of stochastic variation in rainfall and pasture growth, predicted from a model of interaction between kangaroos and pasture developed by Caughley (1987).

increments were estimated from equation (2.5), and changes in the per capita rate of pasture consumption and kangaroo density from equations (2.6) and (2.7). Changes in pasture biomass and kangaroo density were accounted weekly. Figure 5*a*,*b* shows changes in pasture biomass and kangaroo density, respectively, from a typical run of the model.

Caughley (1987) found that despite high season to season variation in pasture biomass, and year to year variation in kangaroo density, kangaroos persisted indefinitely in the modelled grazing system, neither crashing to extinction nor increasing without limit. Stochastic rainfall variation led to dramatic fluctuations in pasture biomass that were largely independent of kangaroo density. These fluctuations constantly buffeted the grazing system away from its potential equilibrium, creating the rapid oscillation in pasture biomass and large swings in kangaroo density evident in figure 5*a*,*b*. However, despite this constant buffeting, the reciprocal influence kangaroos and pasture exerted over each others abundance, imparted a sufficiently strong tendency towards equilibrium (i.e. 'centripetality'), that kangaroos persisted indefinitely. The tendency that the grazing system has towards equilibrium is driven essentially by density-dependent competition amongst kangaroos for available pasture. The fact that kangaroos compete for pasture is evident in the 43% increase in average predicted pasture biomass that occurs when kangaroos are removed from the model. This indicates that the grazing system achieves centripetality through the same trophic processes that are represented implicitly by the density dependence of single-species models of other herbivore populations (Sinclair 1989). For example, in the absence of density-independent fluctuations in pasture biomass, the pattern of variation in r for kangaroos with density conforms to that of a generalized logistic model (figure 6). Hence, the interactive model is the general case for vegetation–herbivore systems, single-species models being a 'short-hand' or 'contracted' version that represents the statistical association of herbivore density and rate of increase that emerges when density-independent perturbation of these systems is low or uncommon.

(c) *Consonance with observation*

(i) *Non-equilibrium dynamics (including multiple equilibria)*

Environmental variability and kangaroos

Bayliss (1987) developed numerical response models for red and western grey kangaroos in two locations (a national park and a sheep station). Caughley (1987) used a slightly modified version of these functions to simulate overall grazing system dynamics. An Ivlev (1961) function was fitted (figure 7*a*) to the rate of increase versus food availability data for red kangaroos using maximum likelihood estimation. Results here are for red kangaroos on a national park. Similar patterns were found for both kangaroo species in all locations. The *a priori* model assumes that food is the major proximate factor that regulates kangaroo population dynamics. Two post-drought outliers were hence excluded from the original analysis because they did not fit the *a priori* assumption (figure 7*a*). However, a time-trace of the rate of increase data (figure 7*b*) show that the population dynamics of kangaroos entering a drought from conditions of high food abundance is quite different to that for populations recovering from a drought from conditions of low food abundance. For populations recovering from drought, rates of increase remain negative despite high levels of food (pasture biomass). This 'hysteresis' or 'lens' pattern (resulting in two equilibria where $r = 0$) may reflect the existence of two alternate system states over a drought cycle, where the transition between each is across a threshold or break point.

A density-dependent (isocline) numerical response model demonstrates the non-equilibrium system properties more clearly (figure 7*c*). Results are for western grey kangaroos on Kinchega National Park, however similar patterns were found for both species in all locations. A time-trace of rate of increase with a six month time-lag

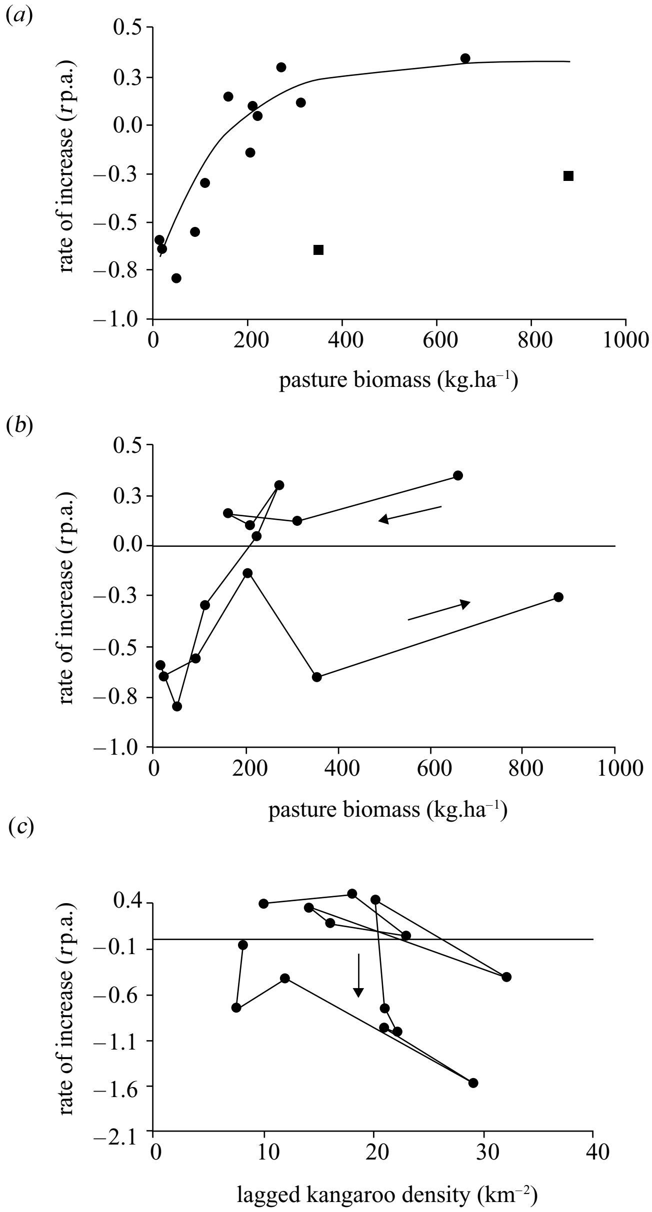

Figure 7. (*a*) Demographic numerical response (r p.a.) for red kangaroos and their food availability (pasture biomass V, kg.ha^{-1}●●12●●). The fitted function is $r = -0.8 + 1.14$ $(1 - e^{-0.007V})$ which excludes two post-drought data (square symbols, Bayliss (1987)); (*b*) time-trace of the same rate of increase data including previously discarded outliers (solid line, high density populations entering a drought; dotted line, low density populations leaving a drought●●11●●); and (*c*) time-trace of western grey kangaroo rate of increase versus lagged density (km^{-2}, six month time-lag), showing the break point transition between two domains of attraction (drought and non-drought conditions).

shows clearly the break point or hysteresis between two postulated 'domains of attraction', reflecting drought and non-drought conditions. Although lagged density may confound both extrinsic (pasture food) and intrinsic (spacing behaviour) regulation processes, P. Bayliss and D. Choquenot (unpublished data) argue that the two parallel and negative linear correlations may simply reflect the high and low phases of a stable limit cycle (i.e. an open-ended ellipse). Once again, this graphical analysis points to the existence of two equilibria (where $r = 0$), one at high

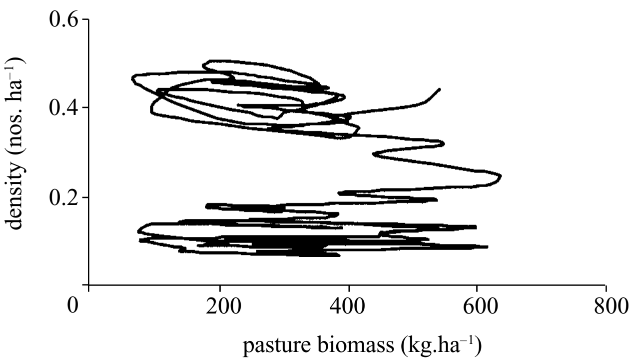

Figure 8. Phase plane trajectory plotting isoclines of pasture food (V, kg.ha^{-1}●●12●●) and kangaroo density (D, nos.ha^{-1}●●3●●) using a demographic numerical response model. Note the apparent existence of two domains of attraction at high (H) and low (L) densities. Each domain is locally stable (centripetal) but globally unstable because of unpredictable changes in rainfall-driven pasture biomass.

density and high pasture biomass, the other at low density and low pasture biomass. Both equilibria may be locally stable but globally unstable because pasture biomass is driven largely by stochastic rainfall events (Robertson 1987*a*,*b*).

Hence, globally, the kangaroo grazing system is a non-equilibrium system but with two postulated local 'domains of attraction' towards stability. The trajectories and positions within this binary system depend critically on initial conditions of pasture biomass (food) and kangaroo density. Populations at high density entering a drought exhibit different population dynamics to low density populations emerging from a drought (e.g. different sex and age structures, response time-lags and reproductive condition (see Bayliss 1980; Cairns & Grigg 1993)). The phase plane trajectory (figure 8), or time-trace of zero isoclines of kangaroo density (H, nos.ha^{-1}●●3●●) and food abundance (V, kg.ha^{-1}●●3●●), clearly illustrate the dynamics between alternate periods of very high and low to medium kangaroo densities.

This result is surprising given that the numerical response model is in fact an equilibrium model applied to a stochastic environment. A probable cause may be the asymmetrical relationship between rate of increase and the availability of food which is in itself driven largely by stochastic rainfall events; for the same amount of rainfall about the annual mean (where $r = 0$), a much greater rate of decrease occurs than a rate of increase. Hence, rainfall variance reduces long-term mean density (Caughley 1987), but may also create a 'two-state' system (a run of high density periods followed by a run of low density periods; see figure 5*b*).

Although not incorporated into the Caughley (1987) 'structural' interactive grazing model, the composition of pastures is also likely to differ between pre- and post drought domains, which should add yet another dimension of complexity and stability. Pastures of course respond in two ways to grazing (see McNaughton (1979) for grassland–herbivore dynamics in the Serengeti), either through changes in biomass and productivity (modelled here), or shifts in pasture composition (not modelled here). Surprisingly, even eastern grey kangaroo popu-

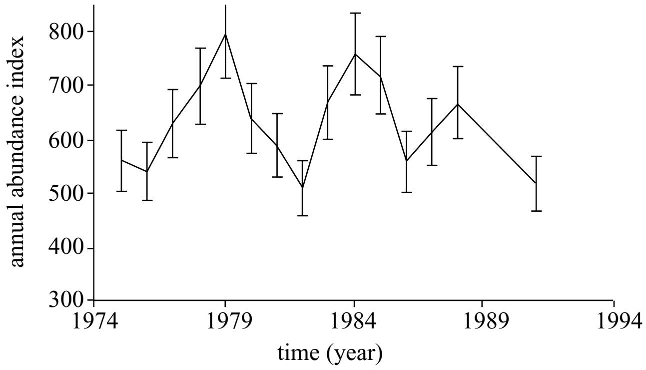

Figure 9. Annual trends in an index of abundance (numbers observed km^{-1} ± s.e.) of eastern grey kangaroos on Tidbinbilla Nature Reserve (ACT, Australia), showing apparent 4–5 year stable limit 'cycles' between 1975–1991 ($n = 17$ years). Kangaroos were counted at night by spotlight along fixed transects across the reserve.

lations living in more stable seasonal, temperate environments of eastern Australia exhibit non-equilibrium behaviour. Figure 9 shows an apparent 4–5 year stable limit cycle for eastern grey kangaroos on Tidbinbilla Nature Reserve, ACT, Australia (P. Bayliss, unpublished data). Although we do not know what causes these apparent cycles (fox predation, competition with rabbits and/or other macropods, disease, el nino, seasonality effects or a combination of causes), or if in fact they are cycles (coincidence), the system is definitely not an equilibrium system as we would predict from the Caughley (1976, 1987) interactive kangaroo grazing model applied to more stable environments. Hence, kangaroos appear to be very good examples of non-equilibrium systems because their numbers over time are characteristically unstable; the abundance of all censused populations of kangaroos varies widely.

Biological interactions and possums in New Zealand

Caughley & Krebs (1983) identified two categories of regulation in order to explain the apparent dichotomy studies of small and large mammal population dynamics. One is intrinsic (self) regulation, where rate of increase (r) is suppressed by some form of spacing behaviour (or physiological process) as density increases. This type of regulation is generally expressed in terms of the negative prediction between r and instantaneous density (e.g. single-species logistic models). The other is extrinsic regulation, where r is governed by the relationship between the consumer and an external factor (food availability, predation, disease, weather or a combination of factors). However, Erb *et al.* (2001) found that patterns of population dynamics in small versus large mammals contradict those predicted by the Caughley & Krebs (1983) hypothesis. Nevertheless, their distinction between intrinsic and extrinsic regulatory mechanisms remains an important distinction and is retained here. The term 'density dependent' generally refers to a prediction between r and density, and density independent a lack thereof. However, density per head of population may index a limiting resource (extrinsic regulation) and/or spacing behaviour (intrinsic regulation). Because the population regulatory mechanisms are not explicitly defined, single-species 'density-dependent' models often subsume or hide biological process rather than expose them.

Although extrinsic and intrinsic regulation are not mutually exclusive they are generally modelled as such. However, some populations may be regulated by both mechanisms (e.g. grazing interference or facilitation may attenuate the numerical response to food availability (see Vessey-Fitzgerald 1968)). A theoretical framework for such combined regulatory influences on a species population dynamics already exists (e.g. Caughley & Lawton 1981; Caughley & Krebs 1983), and is encapsulated in a class of numerical response models called interferential models (Caughley & Lawton 1981; Caughley & Krebs 1983; Barlow 1985). Caughley & Lawton (1981) examined a common form of the interferential numerical response, such that:

$$r_{\mathrm{H}} = r_{\mathrm{m}}\left(1 - \frac{JH}{V}\right), \qquad (2.8)$$

where r_{H} and V are as defined previously, and J is a proportionality constant related to the availability of food needed to sustain consumer H at equilibrium. However, Barlow (1985) argued that, despite its widespread use, this particular type of interferential numerical response model is biologically meaningless. Nevertheless, the addition of an intrinsic density dependent factor which is unrelated to the extrinsic availability of food is easily expressed by including a density term in laisez-faire numerical response models exemplified by equation (2.2). A good example is that provided by Tanner (1975) and explored by Caughley & Krebs (1983), such that:

$$r_{\mathrm{H}} = a + c_1(1 - \mathrm{e}^{-Vd_1}) - gD, \qquad (2.9)$$

where r_{H}, a, c_1, V and d_1 are as previously defined, with D being instantaneous density and g a coefficient depending on the magnitude of the effect. Ginzburg (1998) suggests that it is preferable to keep separate any terms in the numerical response function which reflect unrelated biological phenomena, and this is the approach adopted by Caughley & Krebs (1983), Bayliss & Choquenot (1998) and Pech *et al.* (1999). This is a more realistic and explicit model of interference or aggregation effects than the model proposed by Caughley & Lawton (1981), as it separates the food intake and self-regulation terms in the consumer numerical response whilst leaving the nature of the self-regulation unspecified, as highlighted by Barlow (1985).

Bayliss & Choquenot (1998) suggested that interferential numerical response models of equation (2.9) may provide a more useful framework for understanding population dynamics because the combination of extrinsic (consumer–resource) and intrinsic (animal–density) regulation processes may embody the much broader spectrum of population regulation mechanisms that most probably exist in species. They examined this proposition for the introduced possum in New Zealand forests, which is summarized below.

Population models developed for possums *per se* have curiously been entirely single-species logistic models (e.g. Barlow & Clout 1983) and, hence, ignore plant–herbivore interactions despite the marked impact that possums have on native forests (although Barlow (1991) and Barlow *et* *al.* (1997) developed comprehensive multi-species possum-disease models as extensions of the earlier single-species logistic model). Hinau (*Elaeocarpus dentatus*) is an endemic New Zealand hardwood tree that lives up to 400 years and is known to mast; fruit production alternates between periods of low and super abundance in cycles of two plus years. Possums are primarily folivorous, but also feed extensively on fruits, flowers and buds of many native trees such as hinau. Hinau fruit is a critical winter food source and may even index all winter food sources (Bell 1981). Bell found that the birth date of possums, the percentage of females with pouch young and body weight all were positively correlated to the annual crop of hinau fruit. Cowan & Waddington (1990) found that hinau fruit production increased dramatically when possums were eradicated, and that fruit production was suppressed again with subsequent recolonization. The ecological relationships between possums and food availability were examined in greater detail in two stages, using hinau fruit to index food availability. First, the physiological relationships between possums and hinau abundance were examined and used to underpin the population-level analyses. Second, an interferential numerical response model was then developed using the availability of hinau fruit as an index of food supply overall and ‘instantaneous density’ to index possible spacing behaviour effects (e.g. feeding interference and/or competition for nest sites) which may be independent of the effects of food. We argue that behavioural density-dependent effects are likely to be instantaneous (i.e. no time-lag) and, by contrast, additional extrinsic effects unrelated to food (e.g. predation or disease) are more likely to be indexed by lagged density effects. Nevertheless, the exact cause of any instantaneous density-dependent effect is unknown and, therefore, additional extrinsic effects (in interaction or in combination) cannot be ruled out.

Possum reproductive and body condition (weights and fat storage) were collected during a long-term trap–kill study of possums in the Pararaki Valley ($n = 32$ years; 1965–1997), New Zealand (M. Thomas and J. Coleman, unpublished data.). Female body fat increased with increasing availability of hinau fruit at Orongorongo Valley (20 km distance from Pararaki Valley; figure 10*a*). The trend is mostly linear although overall significantly nonlinear (quadratic, concave down) due to one point. The proportion of female possums with pouch young increased with increasing body fat condition up to a maximum level (figure 10*b*). An Ivlev curve was fitted by maximum likelihood estimation, explaining a high proportion of variance ($r^2 = 89\%$). The proportion of females with pouch young increased with increasing food availability up to a maximum level (figure 10*c*). A logistic curve was fitted by maximum likelihood estimation explaining a high proportion of variance ($r^2 = 99.5\%$). There was a negative linear correlation between birth date (arbitrary estimated as days since the 1st January on a logarithmic scale) and hinau food availability (figure 10*d*). More possums were born early when food levels were high compared with more possums being born late when food levels were low. However, only a low proportion of variance was explained ($r^2 = 15\%$) by this relationship.

Long-term ($n = 31$ years; 1966–1997 (Efford 1998, 2000)) population level data were collected at Orongorongo Valley by mark–recapture and contemporaneously with estimates of the annual crop of hinau fruit (via seedfall traps (Cowan & Waddington 1991; P. E. Cowan *et al.* unpublished data●●4●●). A classic Ivlev curve was fitted *a priori* by maximum likelihood estimation to the numerical response between rate of increase and food (figure 11*a*), explaining 40% of observed values ($r_{\mathrm{poss}} = -0.60 + 0.85(1.0 - \mathrm{e}^{-0.037V})$. The estimate of r_{m} is 0.25 p.a. which compares favourably with the range of estimates (0.22–0.25 p.a.) derived by Hickling & Pekelharing (1989). There was a significant and negative linear correlation between rate of increase and instantaneous density (figure 11*b*), explaining 35% of observed values ($r_{\mathrm{poss}} = 0.65–0.084D$). Backwards extrapolation to the *y*-axis ($D = 0$) predicts a r_{m} value of 0.65 p.a., significantly higher than that estimated by the demographic numerical response above. However, the linear extrapolation is well outside the range of observed data, and may be an overestimate if the relationship between *r* and density is nonlinear as expected (because of the interaction between limiting food resources).

The dynamics of hinau fruit production as impacted on by possums, and of possums as influenced by intrinsic and extrinsic regulatory mechanisms, are characterized by a family of curves or relationships and, hence, multiple equilibria (figure 12*a*,*b*). Bayliss & Choquenot (1998) developed an interferential numerical response function for possums by statistically combining both extrinsic (r_{poss} versus hinau, V) and intrinsic (r_{poss} versus density, $D_{\mathrm{poss}}\,\mathrm{ha}^{-1}$) numerical responses (figure 12*b*) into a joint multiple regression equation ($r_{\mathrm{poss}} = \{[-0.60 + 0.85(1 - \mathrm{e}^{-0.037V})] - 0.01D_{\mathrm{poss}}\}$). Both variables were statistically significant entries into the overall regression equation, which explained 69% of observed values. These two numerical response models are a good example of the contrasting paradigms described by Sibly & Hone (2002).

The dynamics of hinau fruit production in the presence of consumption by possums is best described by a logistic model with an independent term for the negative impact of possum density (figure 12*a*). The high intrinsic rate of increase of annual hinau fruit production ($r_{\mathrm{hin(m)}} > 2.0$) produces stable limit cycles with a periodicity of 2.0 years (see years 1–20; figure 12*c*). Without the impact of possums hinau would mast every two years (i.e. low one year and high the next), although environmental variability (P. E. Cowan *et al.* unpublished data●●4●●) may mask detection of any regular cycles. Figure 12*c* shows a simulated trend in hinau and possum abundance after a liberation of 0.1 possums ha^{-1}. The modelled stable limit cycle of hinau fruit is flattened out after 20 years because the increasing abundance of possums and associated absolute consumption of hinau has an equilibriating effect. The abundance of hinau fruit eventually stabilizes at a level of 44 (cf. an observed mean value of 47). Similarly, possum densities are predicted to equilibriate at 8.4 ha^{-1} in contrast to mean observed densities of 8.2 ha^{-1} (and mean $r_{\mathrm{poss}} = 0$, as predicted by the joint regression model). Although this close fit is not an independent test of the model, the outcomes at least concord with observed data. Without the density effect in the possum numerical response function, the model predicts an equilibrium possum density of 10.7 ha^{-1}, 30% above the observed mean,

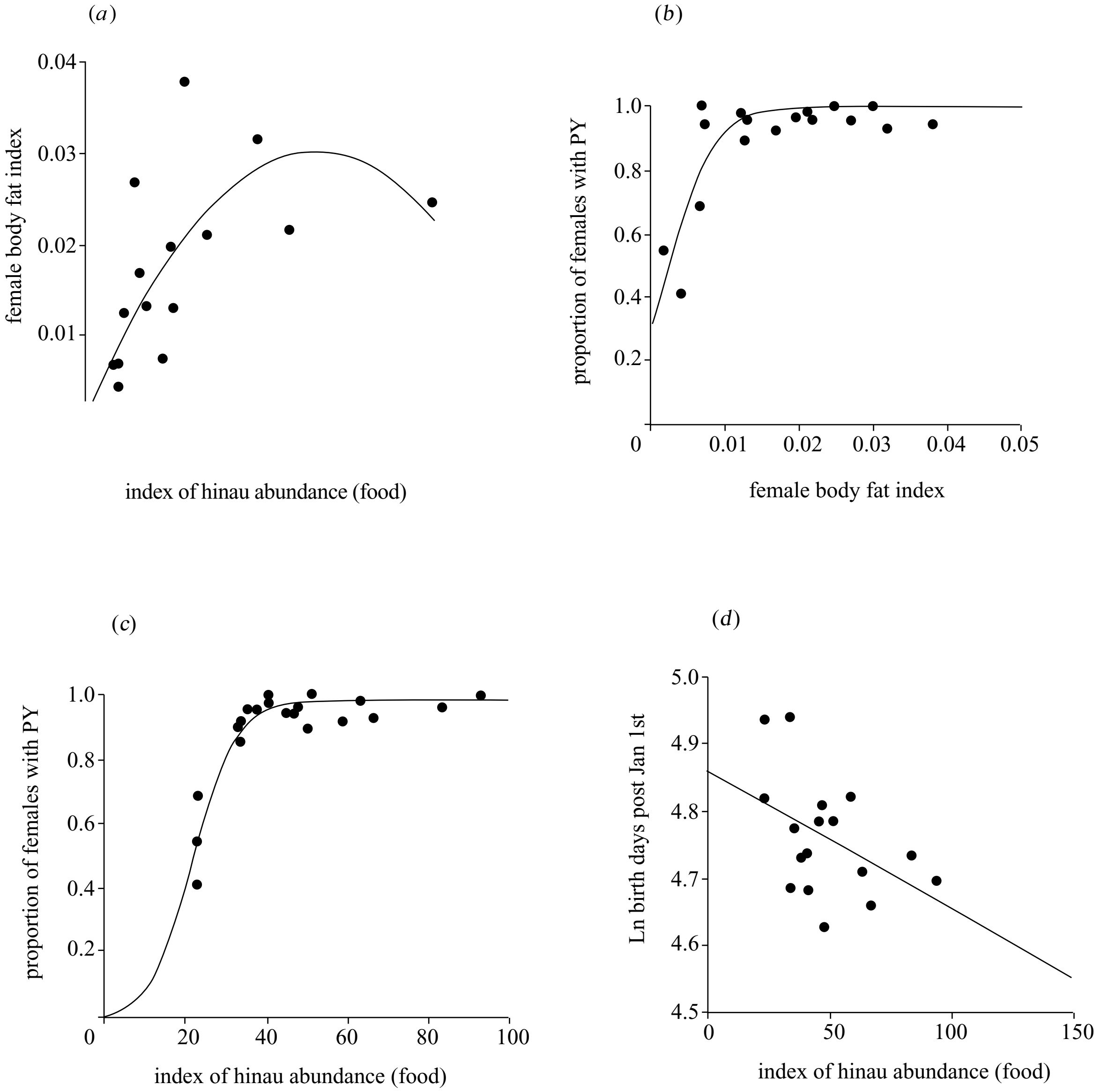

Figure 10. Physiological responses of possums in the Pararaki Valley (New Zealand) to winter food supply as indexed by the availability of hinau fruit in the Orongorongo Valley 20 km away (trap–kill data, 1965–1997) for: (*a*) female body fat index versus food (hinau fruit) availability (quadratic polynomial regression: $r^2 = 48\%$, d.f. $= 2/13$, $p < 0.01$); (*b*) proportion of females with PY versus female body fat index ($r^2 = 89\%$, $n = 17$, $p < 0.01$); (*c*) proportion of females with PY versus food (hinau fruit) availability (logistic model: $r^2 = 99.5\%$, $n = 20$, $p < 0.001$); and (*d*) timing of births (natural logarithm of arbitrary number days since 1 January) versus food (hinau fruit) availability (negative linear correlation, $r^2 = 15\%$, $n = 17$, $p < 0.05$). All nonlinear functions were fitted using maximum likelihood estimation.

whilst hinau fruit abundance decreases to 33% less than the observed mean.

3. ISOCLINE NUMERICAL RESPONSES

(a) *Underlying assumptions*

An isocline numerical response links changes in the abundance of a consumer population *per se* directly to the availability of its food resources (figure 13*a*). Isocline numerical responses are generally formulated as an asymptotic increase in consumer abundance, indicating that the upper limit to consumer abundance is imposed by some factor which is independent of food availability (e.g. available territories, nest sites or some socially mediated crowding effect). Isocline numerical responses subsume both the effect that food availability has on the rate of food intake through the functional response, and the influence food intake has on demographic rates of the consumer population (figure 13*b*). While the isocline approach greatly simplifies the way in which interaction between food and consumer abundance can be represented, it also assumes that territorial behaviour or interference competition regulates populations at high density, and the accessibility or availability of limiting resources at low density (Choquenot & Parkes 2000●●13●●).

(b) *Stability properties of the wolf–moose system: graphical analyses*

Probably the best known application of isocline numerical responses is in the graphical analysis of the stability properties of consumer–resource systems (Rosenzweig & MacArthur 1963; Noy-Meir 1975; Messier 1994; Caugh-

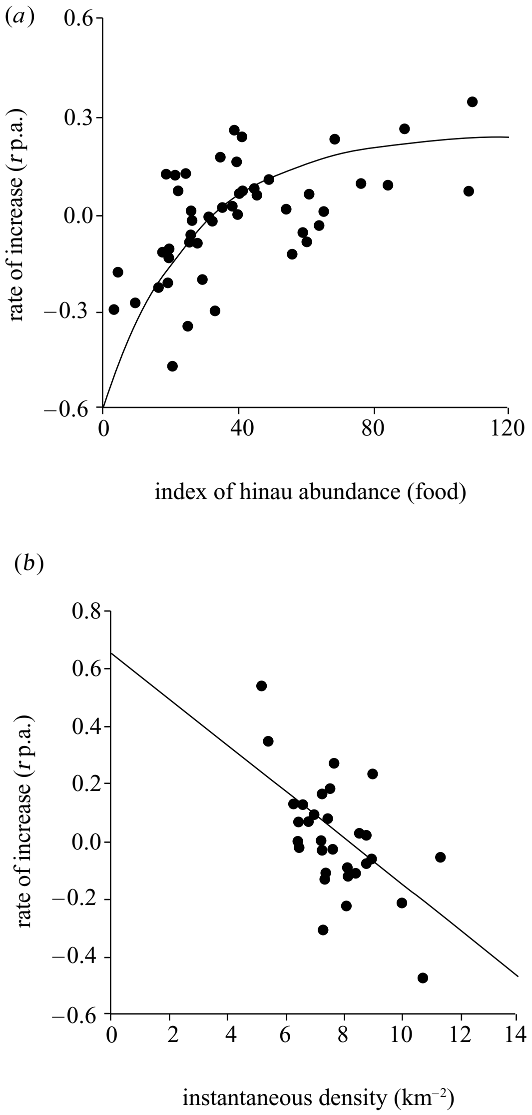

Figure 11. The (*a*) extrinsic numerical response (*r* p.a. versus index of food availability *V*: Ivlev curve fitted *a priori* is $r_{\text{poss}} = -0.60 + 0.85(1.0 - e^{-0.037V})$ where $r^2 = 40\%$, $n = 50$, $p < 0.001$) and (*b*) intrinsic numerical response (*r* p.a. versus instantaneous density *D*, nos.ha^{-1}:●●3●● $r_{\text{poss}} = 0.65–0.084D$ where $r^2 = 35\%$, $n = 31$, $p < 0.001$) of possums in Orongorongo Valley, New Zealand (see Bayliss & Choquenot (1998) for methods). Data are winter and summer annual exponential rates of increase (*r* p.a.), and the index of food availability (hinau seedfall) has a six month time-lag. The parameters of the Ivlev curve fitted to (*a*) were estimated by maximum likelihood estimation; r_m was estimated at 0.25 p.a.

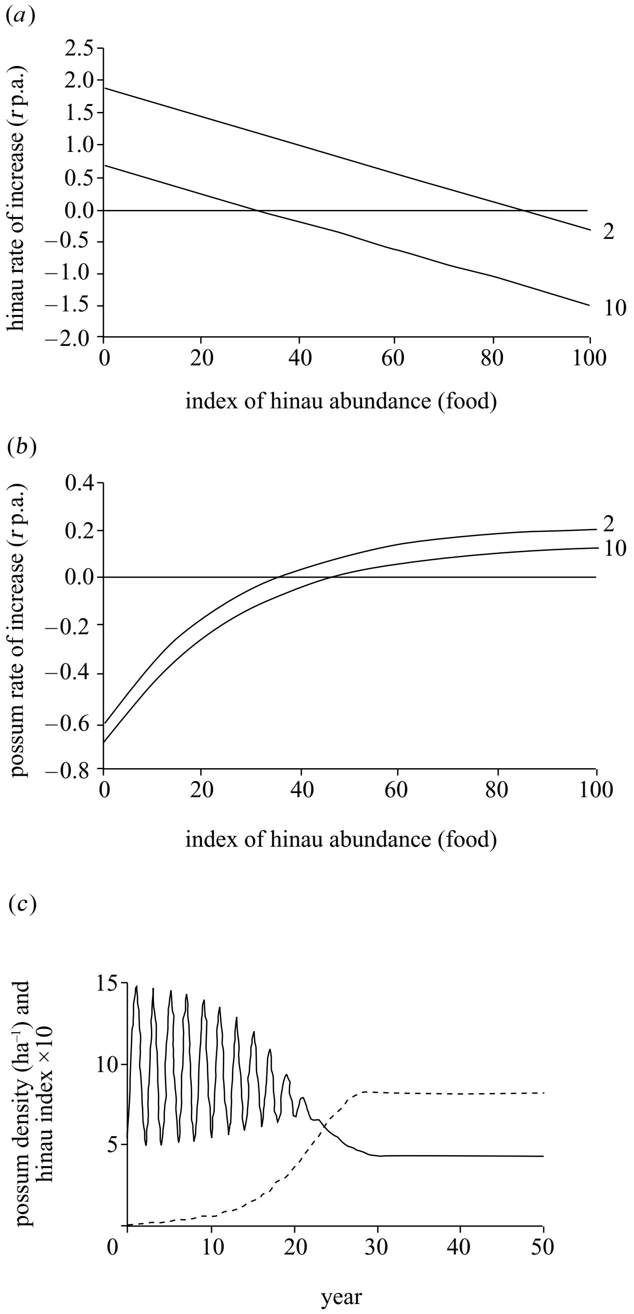

Figure 12. Plant–herbivore model for possums. The numerical response (r_{hin} p.a.) of (*a*) hinau fruit production as combined negative functions of the previous years production *V* (via a logistics model) and possum density (D_{poss}, nos.ha^{-1})●●3●●, $r_{\text{hin}} = 2.2(1 - V/100) - 0.15D_{\text{poss}}$, ($r^2 = 68\%$, $p < 0.001$, d.f. = 1/47); and (*b*) possums (r_{poss} p.a.) as functions of hinau (food) availability (*V*) and possum density (D_{poss}, nos.ha^{-1})●●3●●, $r_{\text{poss}} = \{[-0.60 + 0.85(1 - e^{-0.037V})] - 0.01D_{\text{poss}}\}$, ($r^2 = 69\%$, d.f. = 1/47). A family of numerical response curves exist for both hinau and possums depending on possum density, and are here illustrated with 2 and 10 possums ha^{-1}. (*c*) Simulated equilibriation between hinau fruit production (solid line) and possums (dashed line) 50 years after liberation predicting extinction of the hinau 'masting' cycle.

ley & Sinclair 1994). In these analyses, proportional gains and losses to the food population are contrasted over the full range of its potential abundance in order to identify levels of food availability which are relatively stable. Potential increases in the abundance of the food population are usually represented by a generalized-logistic model similar to that shown in figure 2*a*. This model assumes that in the absence of the consumer population, the upper limit to food population abundance is imposed by interspecific competition for some limiting resource or through social regulation. Potential losses from the food population are the product of consumer population's abundance (estimated from its isocline numerical response to food availability; figure 14*a*) and per capita food intake (estimated from its functional response). When potential loss is expressed as a proportion of the food population it

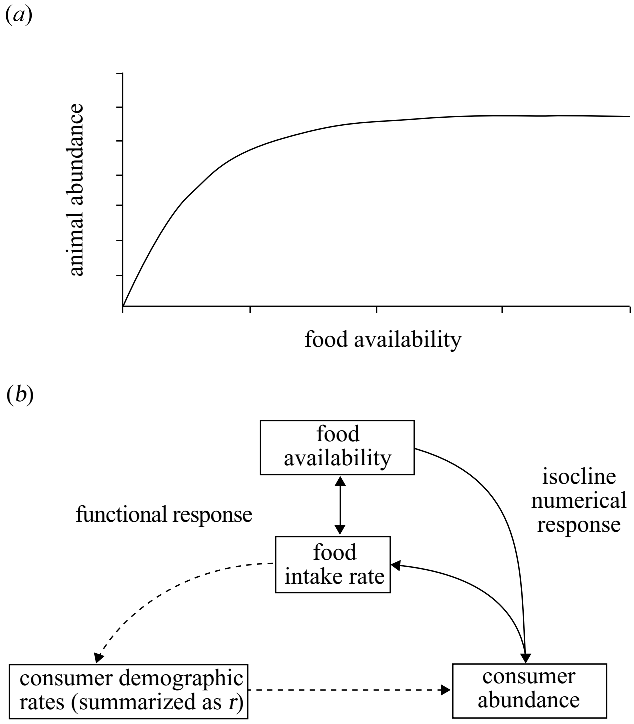

Figure 13. (*a*) The general form of an isocline numerical response derived by Rosenzweig & MacArthur (1963), and (*b*) the structure of the predator–prey model within which the response was used. The dashed lines in (*b*) indicate relationships that are explicit in Lotka–Volterra models but subsumed by the isocline numerical response used in Rosenzweig & MacArthur's model.

is generally termed the consumer total response. Figure 14*b* shows an example of a graphical analysis of the stability properties for a wolf–moose system in North America using predator–prey population parameters estimated by Messier (1994). Our graphical derivation of an equilibrium point between wolves and moose agree with the conclusion by Eberhardt & Petersen (1999) that a two-state system need not apply. The isocline numerical response underpins calculation of the proportion of the moose population that would be consumed by wolves at given moose densities. These isocline curves are essentially the same as those shown by Sinclair *et al.* (1998) for predation in general.

4. DISCUSSION

(a) *Density dependence and population regulation*

While density-dependent, density-independent and inversely density-dependent factors can all limit population density, only density-dependent factors impart a tendency towards an equilibrium. Hence, while any process that affects population density will be a limiting factor, only density-dependent factors are also regulating factors (Sinclair 1989).

Density dependence can arise from both intrinsic and extrinsic factors operating on a population (Krebs 1985). Changes in the exponential rate of increase (r) of an intrinsically regulated population slows at high density through the effect of some type of spacing behaviour on mortality, fecundity or migration as population density increases. Populations regulated in this way can be thought of as 'self-regulating', with rate of change in their abundance determined instantaneously by their prevailing density (Caughley & Krebs 1983). By contrast, r for an extrinsically regulated population is determined by the availability of some environmental resource such as food or nesting sites, or by the effect of some limiting environmental agent such as predators or disease (Caughley & Krebs 1983). Rate of change in the abundance of an extrinsically regulated population is determined instantaneously or cumulatively by the availability of the critical resource or the effect of the critical agent.

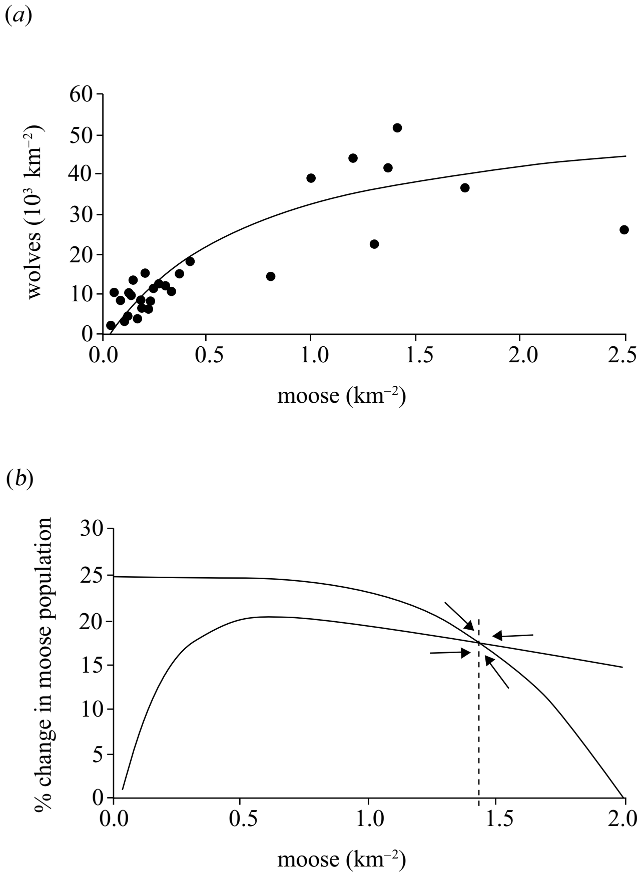

Figure 14. The wolf–moose system in North America showing (*a*) an example of an isocline numerical response linking the density of consumer populations (y, wolves) to the availability of their food resources (x, moose) (Messier 1994) with the fitted function $y = 58.7(x - 0.03)/0.76 + x$ and, (*b*) a graphical stability analysis representing the interaction between moose and wolves based on empirically derived functions in Messier (1994). The lower curve, describing the percentage loss of moose to wolves as a function of prevailing moose density, was calculated from the functional and isocline numerical responses of wolves to moose density (see (*a*)). The upper curve, describing the gain in moose abundance in the absence of wolves, was derived by fitting a generalized-logistic model to data ($r_m = 0.22$ p.a., $K = 2.0$ moose km^{-2} and $z = 4.0$) presented in Messier (1994). The dashed line indicates the equilibrium moose density predicted by the model.

(b) *Population regulation: single-species models*

The abundance of large herbivore populations is widely held to be limited by extrinsic factors, most commonly food supply (Caughley 1970, 1987; Laws *et al.* 1975; Sinclair 1977; Houston 1982; Skogland 1983; Sinclair *et* *al.* 1985; Fryxell 1987; Choquenot 1991, 1998), predation (Bergerud 1980; Gasaway *et al.* 1983; Messier & Crête 1984; Messier 1991, 1994), or both (Caughley 1976, 1977). Factors that limit the size of large herbivore populations may or may not also regulate them, depending on whether they operate in a density-dependent fashion. Sinclair (1989) reviewed studies of regulation in large terrestrial mammals and concluded that the majority (including all ungulates) were regulated by density-dependent mortality related to food shortage. Similar conclusions were reached by Fowler (1987) in a review based on many of the same studies. Sinclair (1989) also found that while predator removal experiments have shown predation to be an important limiting factor for large herbivore populations, there was no empirical evidence that predation could also be a regulating factor for large herbivores. Skogland (1991) and Boutin (1992) concurred with Sinclair (1989), finding no consistent evidence for regulation of ungulate populations by predation. However, Messier (1994) inferred from a comparative study of interaction between moose (*Alces alces*) and wolves (*Canis lupus*) across North America, that moose populations could be regulated by wolf predation. If predation does not commonly regulate the abundance of large herbivore populations, processes that could impart density dependence to their dynamics reduce to intrinsic (socially mediated) mechanisms, the debilitating effects of disease or parasites, or food availability.

Several recent reviews (e.g. Gaillard *et al.* 1998) of empirical evidence for density dependence in large herbivore demography indicate that the role of density-independent variation in the abundance of herbivores and their key food resources has not been fully recognized in tests of the food hypothesis. Caughley & Gunn (1993) argued that in areas with highly variable environments, factors such as unpredictable precipitation could introduce significant degrees of density-independent variation in food availability and herbivore abundance. When combined with lags and overcompensation in vegetation and herbivore responses, density-independent variation can obscure any tendency that herbivore density may have towards equilibrium. Similarly, Putman *et al.* (1996), and Saether (1997) considered that even in temperate grazing systems, stable equilibria between large herbivores and their food resources were unlikely because of the direct effects of environmental variation on herbivore demographic rates and overcompensation in herbivore responses to variation in food availability. If stable K cannot be assumed for large herbivore populations, tests of the food hypothesis which fail to detect density-dependent variation in r (or its correlates) cannot differentiate between perturbation of the system by density-independent limiting factors, and the absence of regulation through density-dependent food shortage. To account for the potential effects density-independent variation in food availability and herbivore abundance have on the tendency of a herbivore population towards equilibrium, interaction between herbivores and their food resources must be considered in a more explicit framework than can be provided by single-species density-dependent models (Choquenot 1998).

(c) *Population regulation: interactive models*

Explicit models of vegetation–herbivore interaction were developed by Noy-Meir (1975) and Caughley (1976), who derived them from the predator–prey models of Rosenzweig & MacArthur (1963) and May (1973). The interactive model described by Caughley (1976) for a deterministic environment is described in detail here as applied to kangaroos in the Australian rangelands, a stochastic environment driven by unpredictable rainfall (Caughley 1987). The three components of the interactive model (growth of ungrazed plants, functional and numerical responses) operate collectively as two negative feedback loops governing the influence that vegetation and herbivores exert over each others abundance. Density-dependent growth of ungrazed vegetation forms a vegetation biomass feedback loop, reducing vegetation growth at high biomass and keeping vegetation in check regardless of how good seasonal conditions may be for plant growth, or how low vegetation offtake by herbivores is. The functional and numerical responses of the herbivore form a vegetation–herbivore feedback loop, increasing the number of herbivores and how much vegetation each consumes at high vegetation biomass, and reducing herbivore abundance and their per capita consumption of vegetation at low vegetation biomass. Caughley (1976) combined these feedback loops in two linked differential equations which predict coincident variation in the abundance of herbivores and the vegetation they feed on.

Herbivores reach a stable equilibrium point that is qualitatively similar to that produced by the generalized logistic model described for elk. However, in the interactive model, equilibrium is achieved through the reciprocal influence vegetation and herbivores exert over each others abundance, while in the generalized logistic model, equilibrium reflects an algebraic limit to herbivore population growth imposed by the existence of K. This does not mean that the herbivore population is not regulated through essentially density-dependent processes.

Regardless of the density from where the herbivore population starts, its density moves back towards equilibrium through the same series of dampening oscillations. While the processes producing the tendency towards equilibrium are essentially density dependent (i.e. the vector of vegetation and herbivores at any point in time is a direct consequence of past grazing activity which is a consequence of past herbivore density), the tendency itself is of more importance to the stability of the grazing system than is the attainment of any specific point equilibrium. To reflect this, Caughley (1987) coined the useful term ‘centripetality’ to describe the tendency that a vector in vegetation and herbivore abundance has towards equilibrium. Centripetality de-emphasises the importance of an equilibrium in the dynamics of vegetation–herbivore systems, focusing instead on the stabilizing properties that the potential existence of an equilibrium imparts.

(i) *Stochastic rangelands grazing systems: kangaroos*

Caughley (1987) demonstrated that stochastic rainfall variation in the rangelands of Australia produced high frequency and high amplitude fluctuations in pasture biomass with wearying monotony and largely independent of kangaroo density. Hence, the kangaroo grazing system is constantly buffeted away from its potential equilibrium.

McLeod (1997) argued that, in this environment, the concept of equilibrium carrying capacity density has no meaning. Nevertheless, the reciprocal influence that kangaroos and pasture exerted over each others dynamics and, ultimately abundance, imparted a strong tendency towards equilibrium (i.e. centripetality). Hence, in this model ecosystem kangaroos were able to persist indefinitely. Interactive models may be the general case for vegetation–herbivore systems (and by extension all consumer–resource systems such as predator–prey systems). By contrast, contracted single-species models are, however, a 'short-hand' proxy, often represented by a statistical negative correlation between herbivore rate of increase and density that manifests when density-independent perturbation of these systems is low or uncommon. By contrast, McCarthy (1996) used variable rainfall as a surrogate for pasture biomass (see Bayliss 1985*a*,*b*) to examine the combined statistical relationships between red kangaroo rate of increase, food availability and past kangaroo density. This approach falls neatly between the single-species and interactive consumer–resource approach, and could be better modelled with an interferential numerical response model.

(ii) *Habitat effects on food limitation*

Like most animals, large herbivores balance their foraging efficiency with exposure to direct sources of mortality or debilitation in order to maximize the rate at which they can utilize their food resources to increase individual fitness (Belovsky 1981, 1984; Stephens & Krebs 1986). Hence, the quality of the various habitats in which large herbivores may elect to spend time will reflect both the availability and quality of food found there, and the degree to which habitat-related constraints effect the rate at which this food can be assimilated to enhance their reproduction or survival. Habitat-related constraints can influence the rate at which herbivores can find and ingest food relative to its availability (foraging constraints), or the degree to which ingested food can be used to enhance reproduction or survival (demographic constraints). For example, increased predation risk in open areas reduces the foraging efficiency of snowshoe hares (*Lepus americanus*) by limiting their access to the food available in these areas (Hik 1995). Alternatively, the demographic efficiency of caribou (*Rangifer tarandus*) is limited by the availability of habitat that affords their calves protection from predators, over and above any effects of food availability (Skogland 1991).

Habitat-related constraints on foraging or demographic efficiency inhibit the potential a herbivore population has to respond demographically to variation in its food resources. Hence, models of how habitat-related foraging and demographic constraints influence large herbivore population dynamics need to be formulated within a framework which explicitly represents interaction between the herbivores and their food resources. Caughley's (1976) interactive model links herbivore foraging efficiency to food availability through a functional response, and herbivore demographic efficiency to food availability through a numerical response. These two responses collectively form a vegetation–herbivore feedback loop that controls the interdependent effects vegetation and herbivores exert over each others abundance. However, the vegetation–herbivore feedback loop implies that variation in food availability effects herbivore demography (summarized as r) independently of its effect on their rate of food intake. While this simplification is of little consequence where constraints on foraging or demographic efficiency are constant, it compromises the usefulness of the interactive model where these constraints vary between habitats. Hence, where habitat quality is in part determined by constraints on herbivore foraging or demographic efficiency, the general form of the interactive model cannot be used to consider how habitat quality influences herbivore population dynamics. For example, Choquenot & Dexter (1996) hypothesized that wild pigs in the rangelands thermoregulate when radiant heat loads are high by seeking refuge under the more or less continuous cover afforded by riverine woodlands. Behavioural thermoregulation when ambient temperatures are high is obligatory for wild pigs inhabiting other arid and semi-arid environments (Van Vuren 1984; Baber & Coblentz 1986). Choquenot & Dexter (1996) suggested that the thermoregulatory needs of wild pigs when temperatures were high could link the spatial accessibility of riverine woodlands to either: (i) their foraging efficiency by restricting the area over which they could forage; or (ii) their demographic efficiency by restricting the area within which they could survive and reproduce. In either case, the quality of any particular location to wild pigs will be determined by both habitat composition of the immediate area around the location (i.e. the accessibility of riverine woodlands), and the availability of food in that area.

(d) *Conclusions*

The two main reasons why we construct ecological models are to predict and to aid understanding of the system (Caughley 1981). Both modelling functions are essential to the development and implementation of population management goals for whatever objective (conservation, control or harvesting). Simulation of population management scenarios to assess their efficacy is becoming increasingly popular if not necessary because of the general lack of experimentation. However, the success of this approach depends entirely on the ability of the model to capture real ecological processes, but progress in understanding ecological systems has been less than spectacular. A little scrutiny shows that most wildlife populations are still managed by trial and error rather than by scientific knowledge, and that most managers still lack tight criteria for the success or failure of their actions (including doing nothing). Nevertheless, the contributions of consumer–resource models to the research and management of over-abundant kangaroos and possums have been substantial. Curiously though, the modelling approaches adopted in Australia and New Zealand have followed two independent paradigms (or multi-species versus single-species models; or mechanistic versus density (Sibly & Hone 2002)). Our re-examination of current kangaroo and possum models, however, indicate that a more useful framework for understanding how marsupial populations work may be obtained by combining the two modelling approaches. A marriage between extreme extrinsic (animal–resource) and intrinsic (animal–density) regulation models could embody the much broader spectrum of population mechanisms that most likely exist within species. Although more complex population interactions may be exposed, the trade-off may be increased predictive power and, hence, utility. This approach increases the realism and predictive power of existing population models for kangaroos and possums at manageable levels of complexity.

We conclude by reinforcing the axiom that in order to manage populations effectively we need to understand their dynamics. However, research costs can be substantial both in terms of time and money. For example, the possum model was developed *a posteriori* (no model in mind) with data collected after 32 years of intensive study of a population more or less in equilibrium. By contrast, the kangaroo model was developed *a priori* (a model in mind) with experimental data collected after 5 years of intensive study of a non-equilibrium grazing system. Hence, one impediment to more widespread use of more useful interactive ecological models is the daunting and costly task of 'parameterizing' such models, especially for populations that exhibit little dynamics within time-scales dictated by funding and career cycles. An adaptive management strategy (Walters 1997), however, may allow a new breed of population models to be developed and tested cost-effectively by integrating focused population-scale management experiments with the modelling process. One such model is the interferential numerical response function, because it may help bridge three major historical dichotomies in population ecology (equilibrium versus non-equilibrium dynamics, extrinsic versus intrinsic regulation and demographic versus isocline numerical responses).

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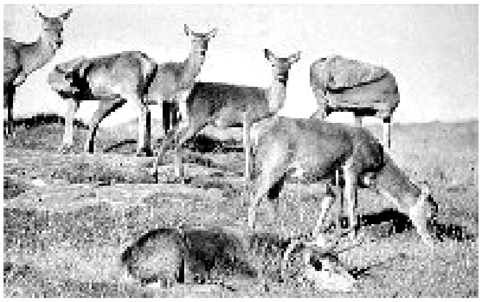
GLOSSARY

PY: pouch young

THE ROYAL SOCIETY

Population growth rate: determining factors and role in population regulation

Compiled and edited by RM Sibly, J Hone and TH Clutton-Brock
Published 29 September 2002



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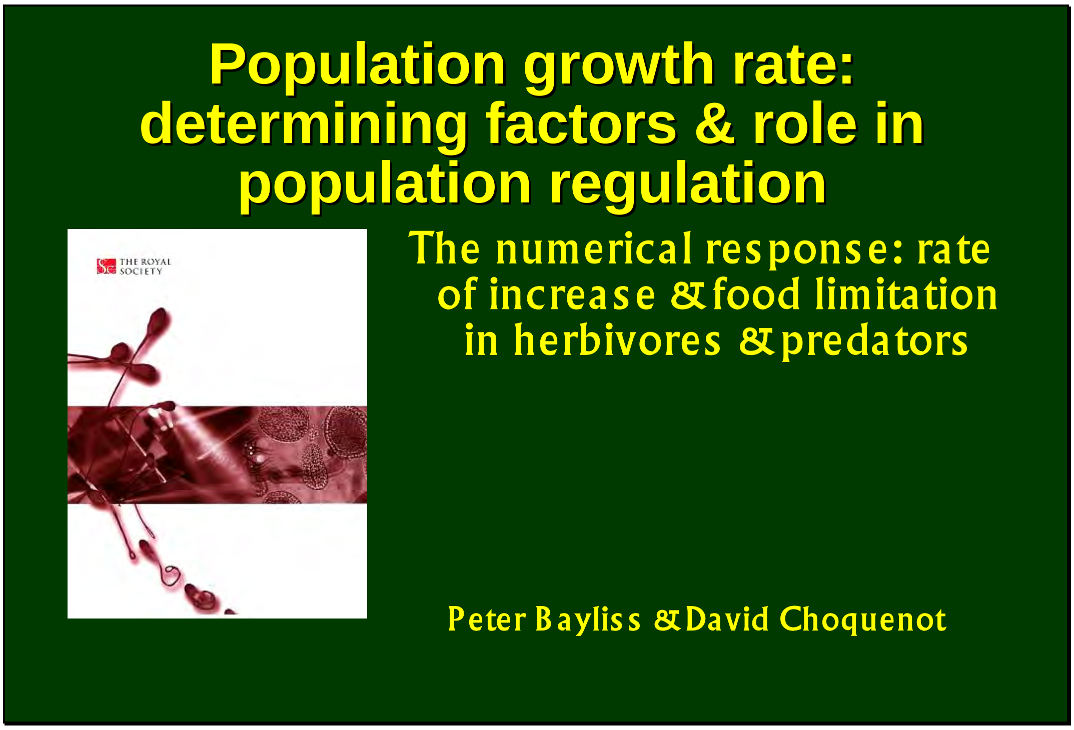
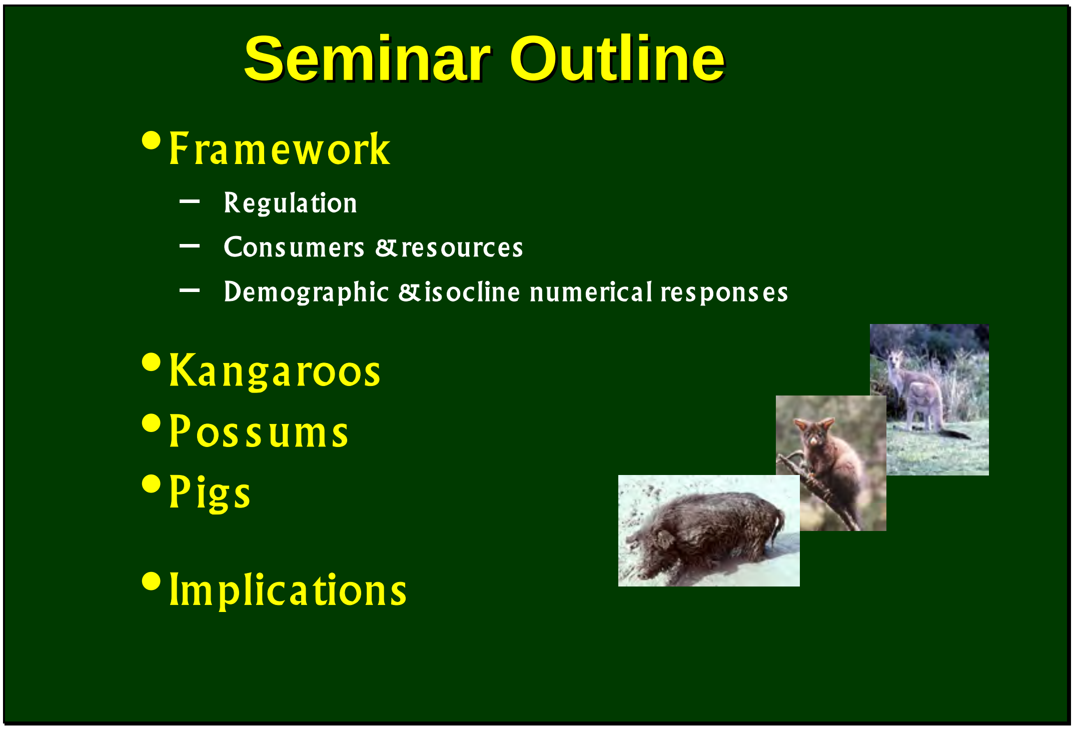


Population growth rate: determining factors & role in population regulation

The numerical response: rate of increase & food limitation in herbivores & predators

Peter Bayliss & David Choquenot



Seminar Outline

- Framework
  - Regulation
  - Consumers & resources
  - Demographic & isocline numerical responses
- Kangaroos
- Possums
- Pigs
- Implications

Types of population regulation

- What regulates population dynamics (or rate of increase)?

  $$r = (b - d) + (i - e)$$

- Caughley & Krebs (1983) identified two categories of regulation which are not mutually exclusive:

  1. *Extrinsic* – external, often multiple factors

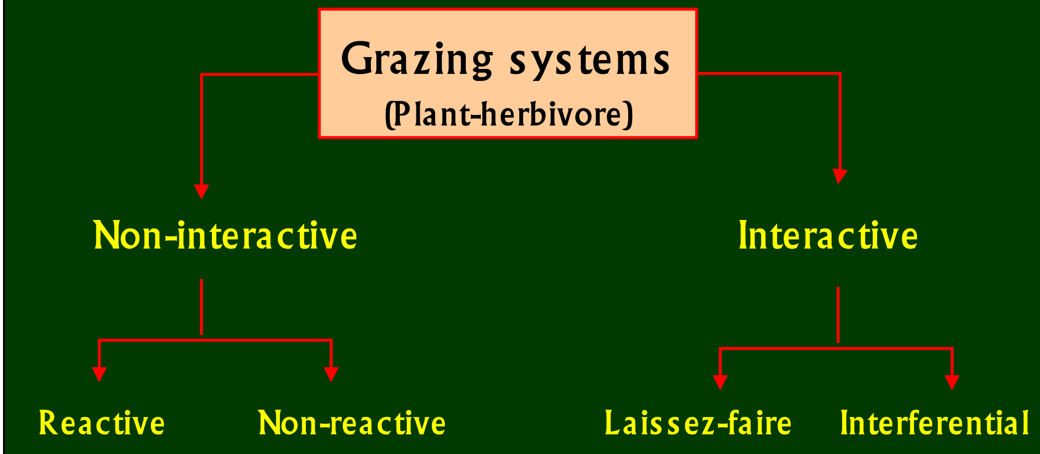
     $$r = f\,(resources, predators, weather)$$

  2. *Intrinsic* (=self regulation) – spacing behaviour &/or physiological constraints; additional to extrinsic factors

     $$r = -g\,(density)$$

Consumers & food resources – types of systems

(after Caughley & Lawton 1981)



Grazing systems

(Plant-herbivore)

Non-interactive

Interactive

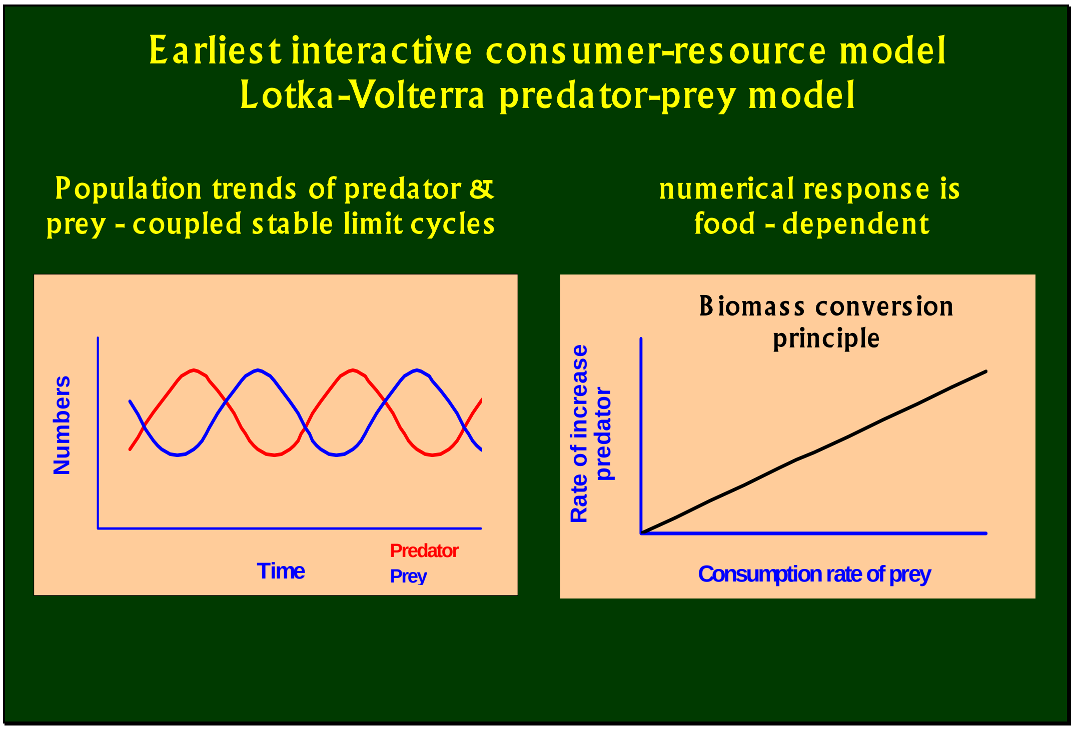
Reactive

Non-reactive

Laissez-faire

Interferential

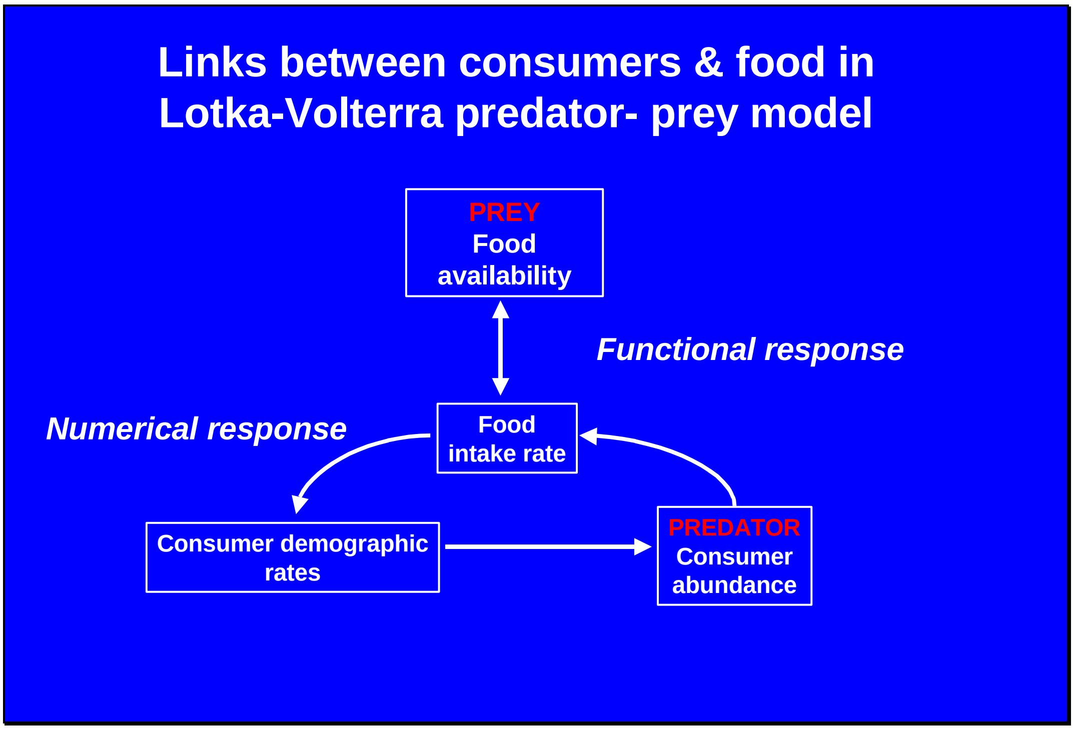
Classification system generic to most consumer-resource systems: e.g. predator-prey & parasite-host



Earliest interactive consumer-resource model
Lotka-Volterra predator-prey model

Population trends of predator & prey - coupled stable limit cycles

numerical response is food - dependent



Links between consumers & food in Lotka-Volterra predator- prey model

PREY
Food availability

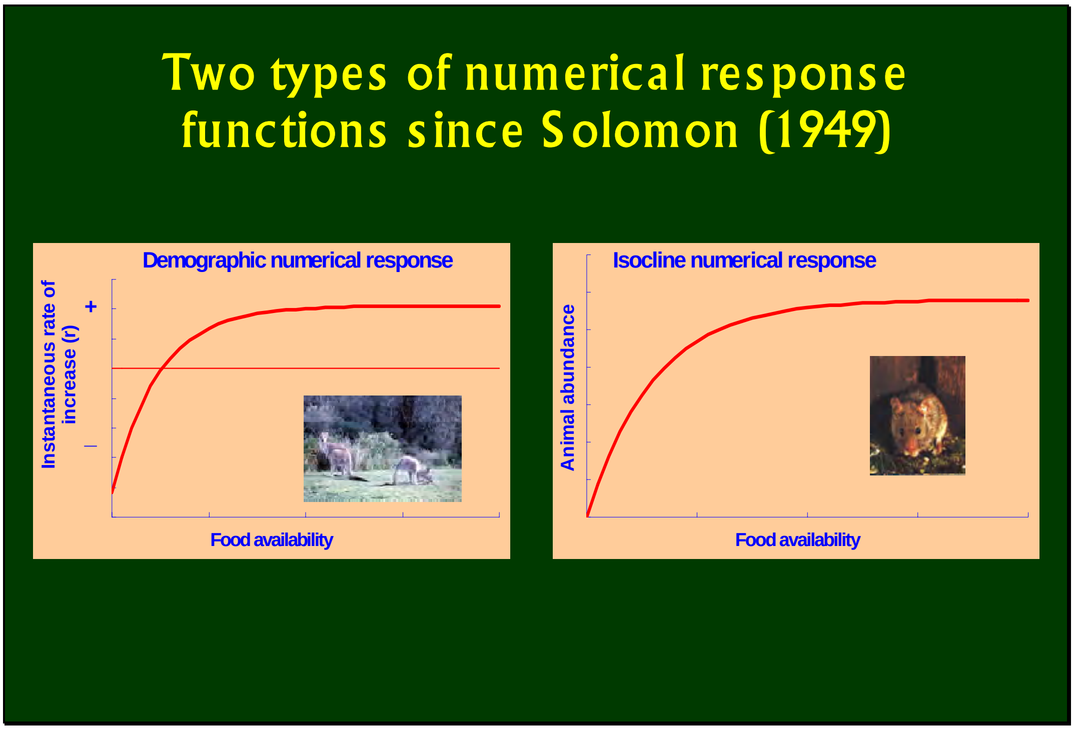
Functional response

Food intake rate

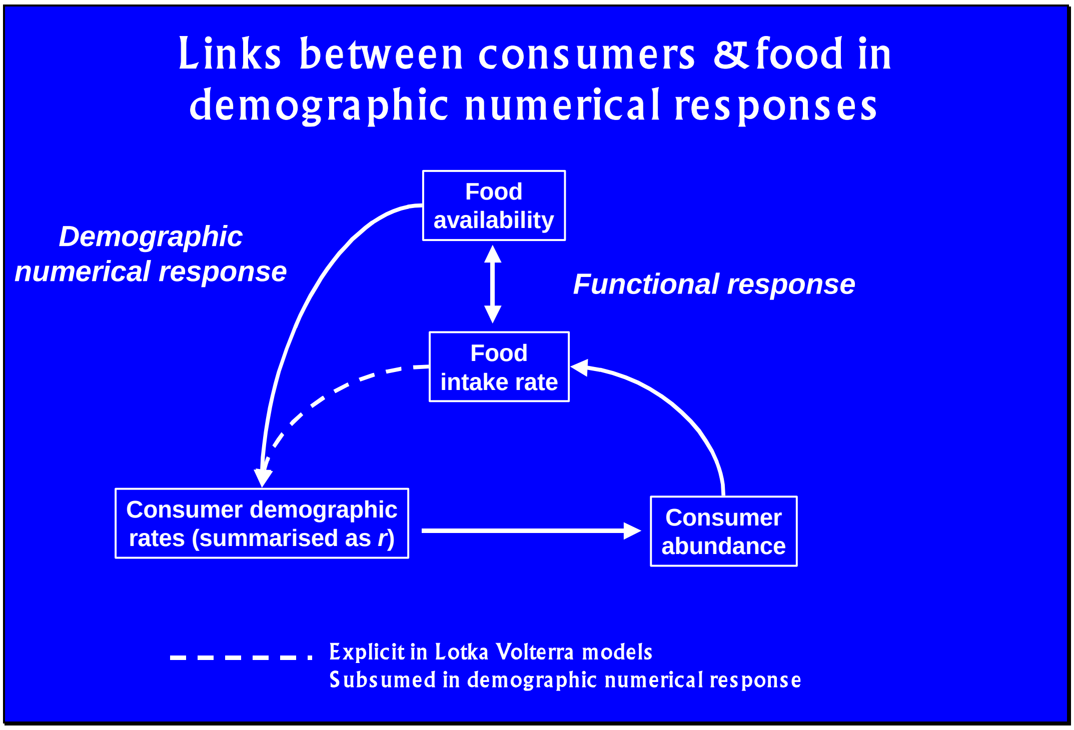
Numerical response

Consumer demographic rates

PREDATOR
Consumer abundance



Two types of numerical response functions since Solomon (1949)



Links between consumers & food in demographic numerical responses

Food availability

Demographic numerical response

Functional response

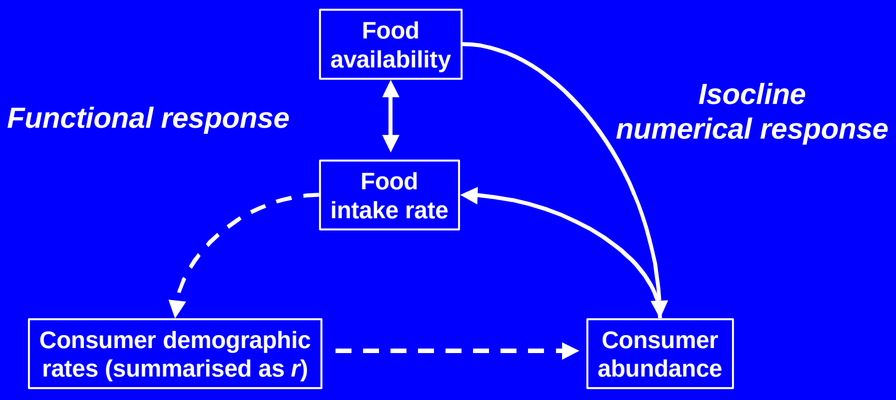
Food intake rate

Consumer demographic rates (summarised as *r*)

Consumer abundance

Explicit in Lotka Volterra models
Subsumed in demographic numerical response

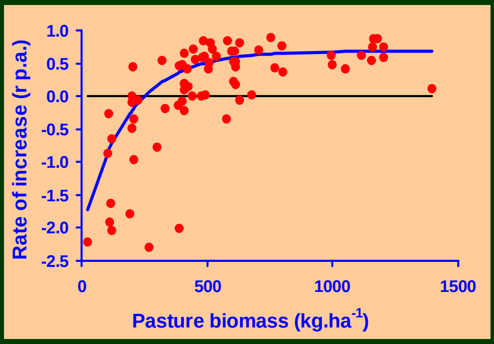
Links between consumer & food in isocline numerical responses



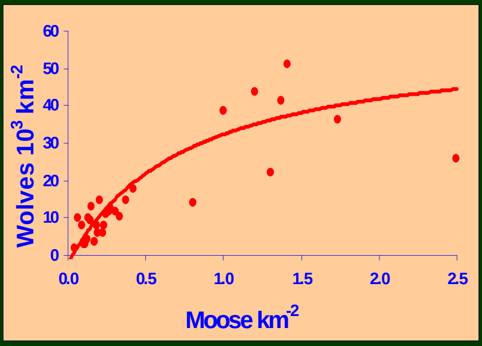
- - - - - - Explicit in Lotka Volterra models
Subsumed in isocline numerical response

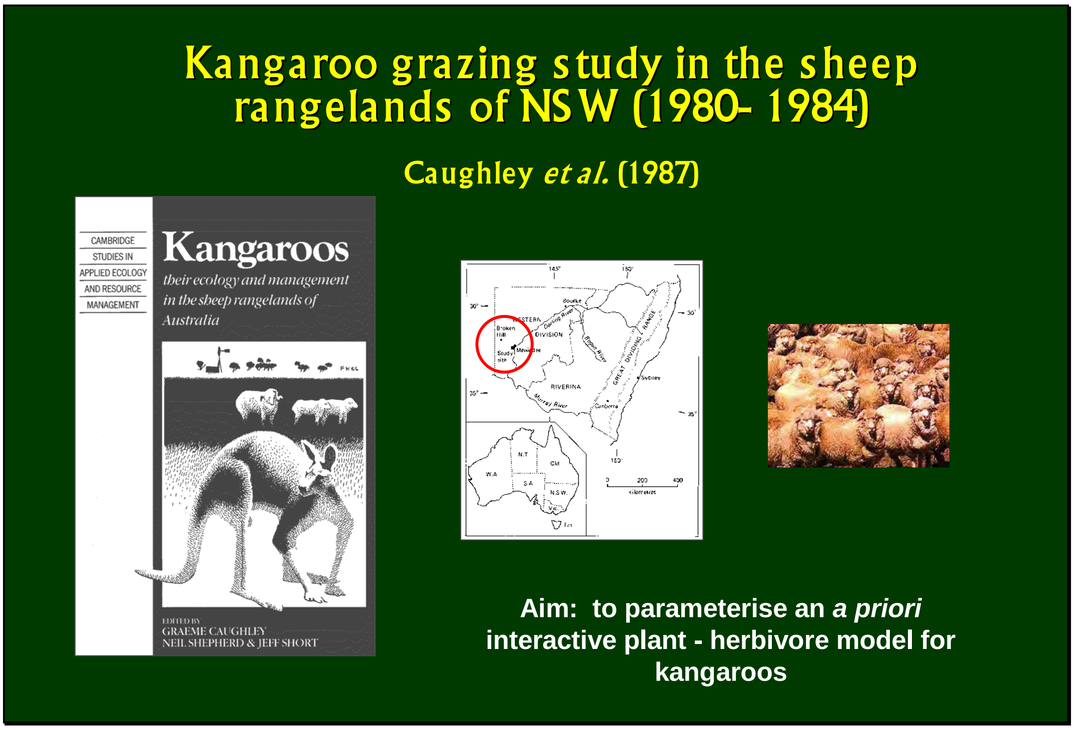
Examples: numerical responses & food

Demographic numerical response for pigs-pasture (Choquenot 1994)



Isocline numerical response for wolf-moose system. After Messier (1994)

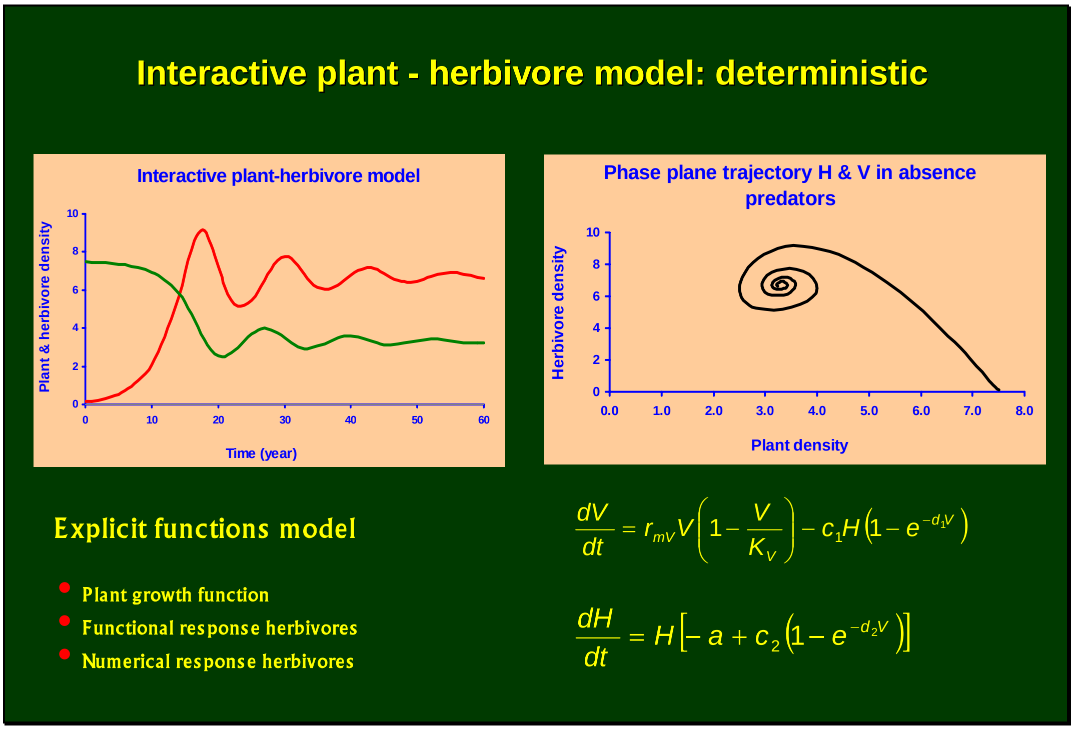




Kangaroo grazing study in the sheep rangelands of NSW (1980- 1984)

Caughley *et al.* (1987)

Aim: to parameterise an *a priori* interactive plant - herbivore model for kangaroos



Interactive plant - herbivore model: deterministic

Interactive plant-herbivore model

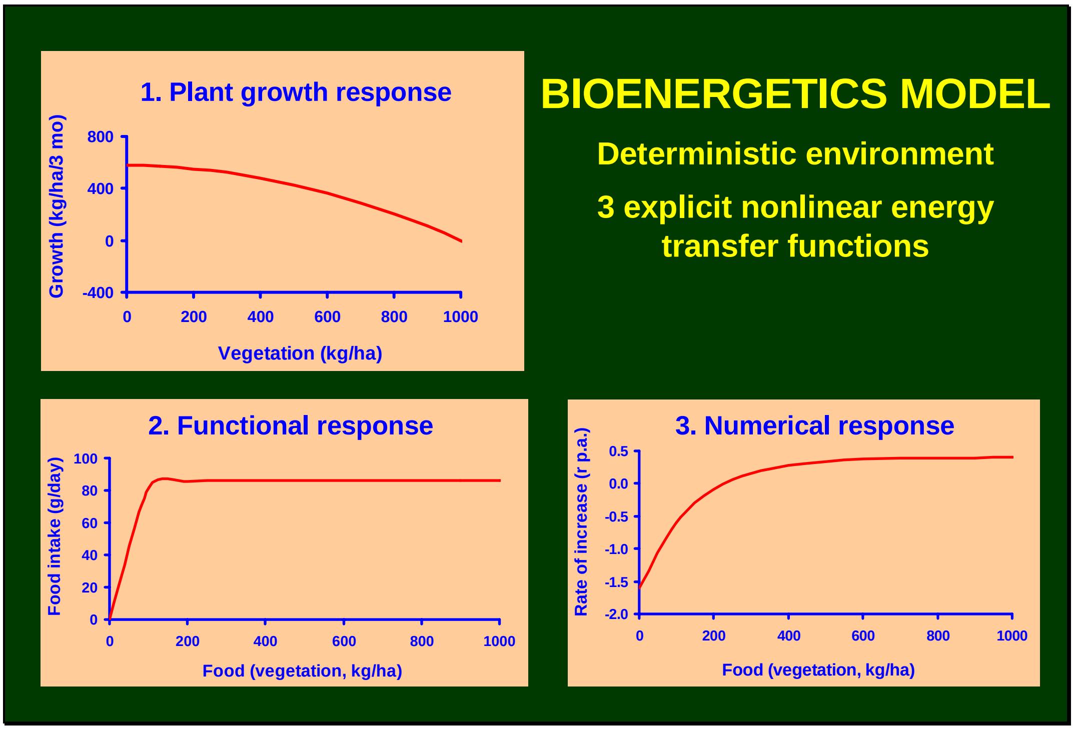
Phase plane trajectory H & V in absence predators

Explicit functions model

- Plant growth function
- Functional response herbivores
- Numerical response herbivores

$$\frac{dV}{dt} = r_{mV} V \left(1 - \frac{V}{K_V}\right) - c_1 H \left(1 - e^{-d_1 V}\right)$$

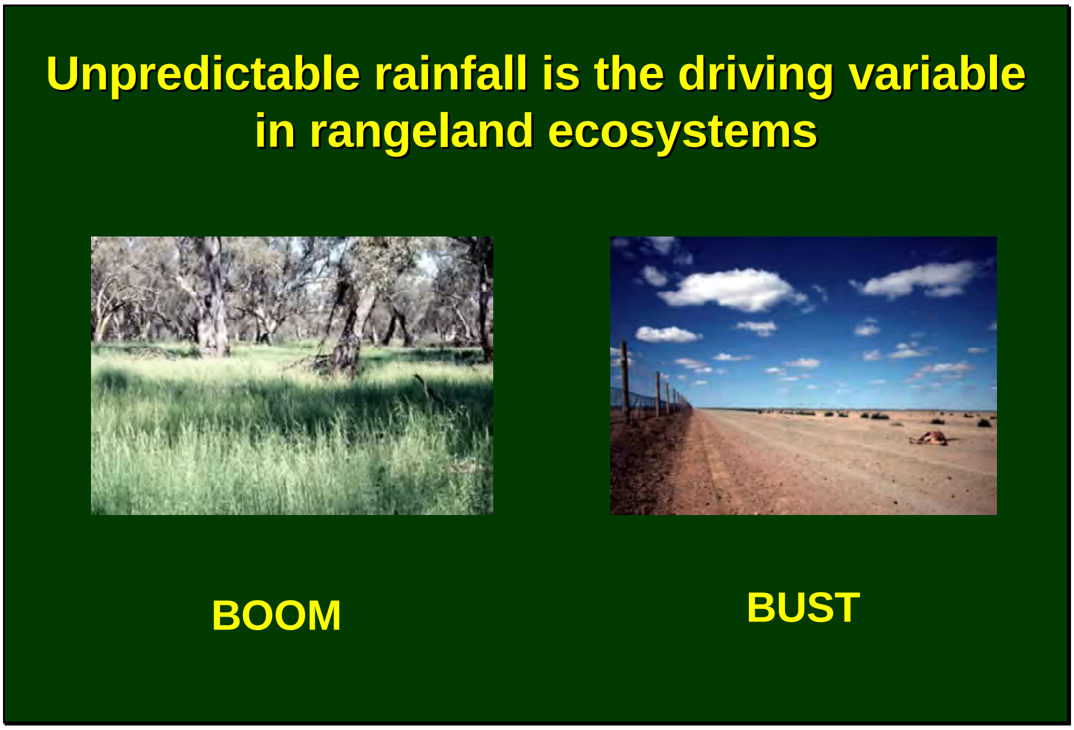
$$\frac{dH}{dt} = H\left[-a + c_2\left(1 - e^{-d_2 V}\right)\right]$$



BIOENERGETICS MODEL

Deterministic environment

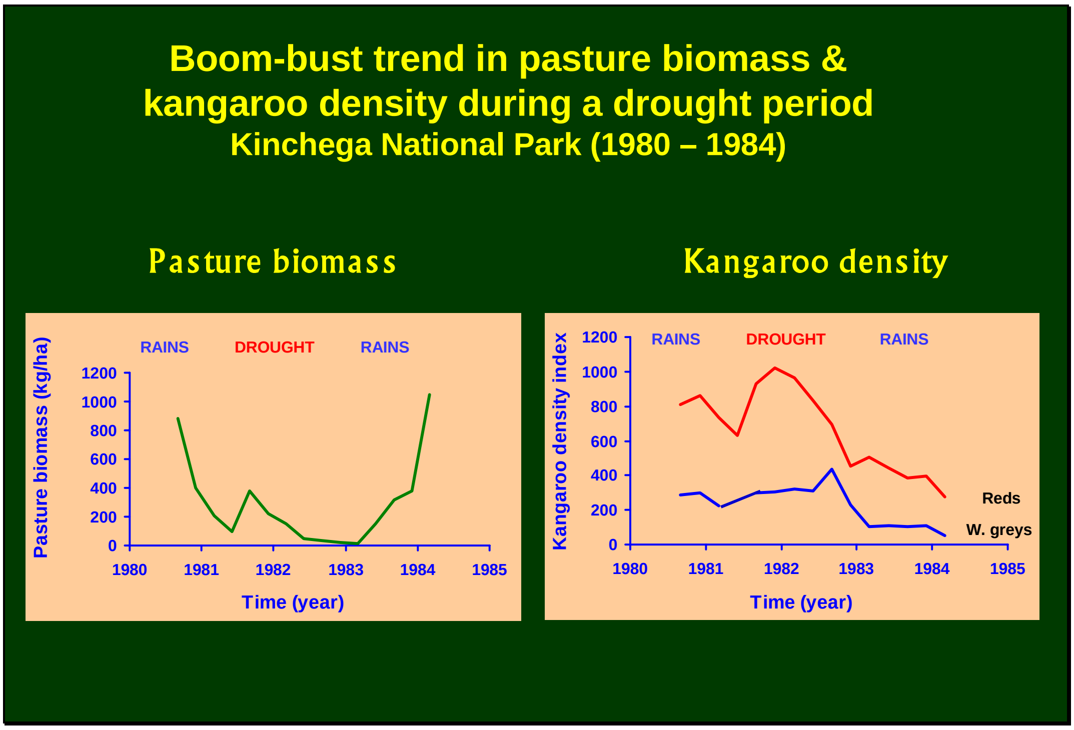
3 explicit nonlinear energy transfer functions



Unpredictable rainfall is the driving variable in rangeland ecosystems

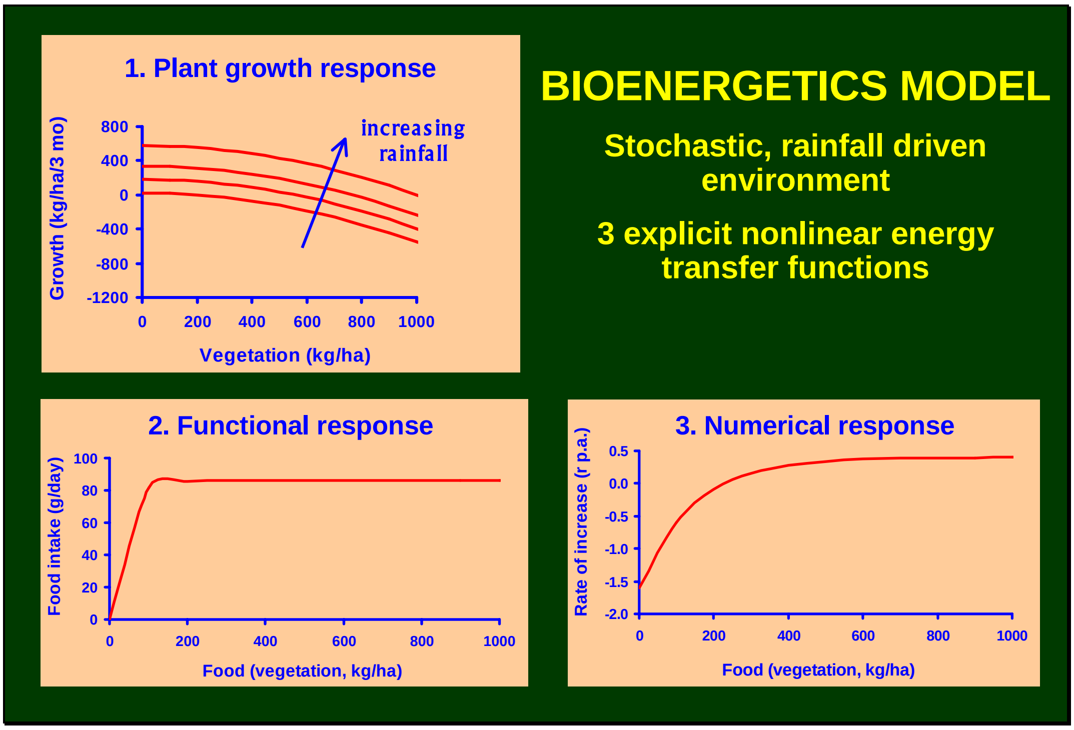
BOOM

BUST



Boom-bust trend in pasture biomass & kangaroo density during a drought period

Kinchega National Park (1980 – 1984)

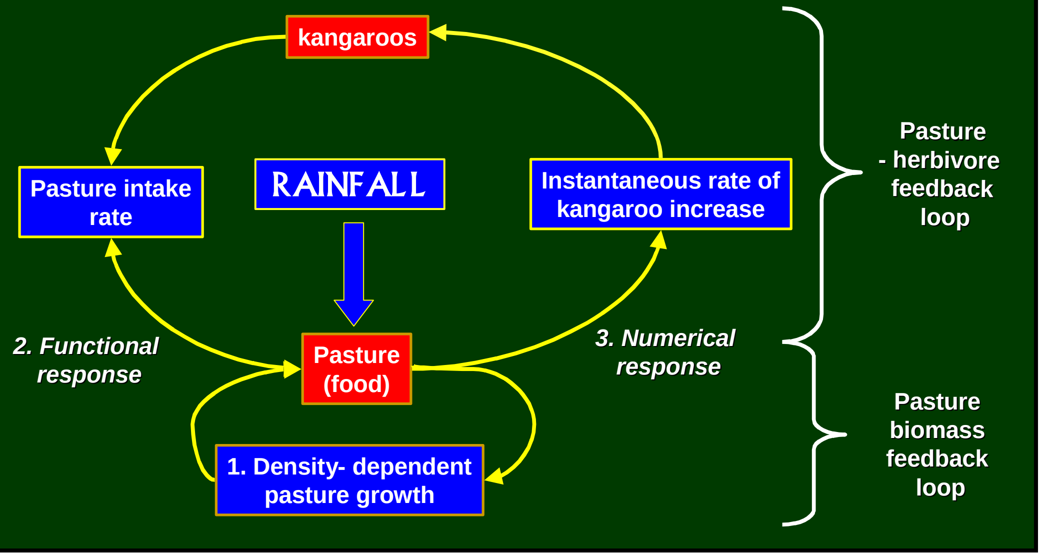


BIOENERGETICS MODEL

Stochastic, rainfall driven environment

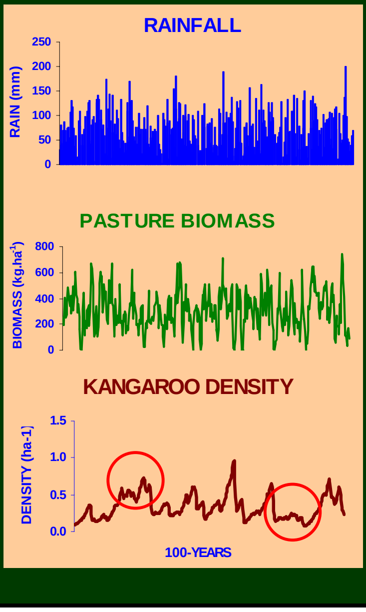
3 explicit nonlinear energy transfer functions

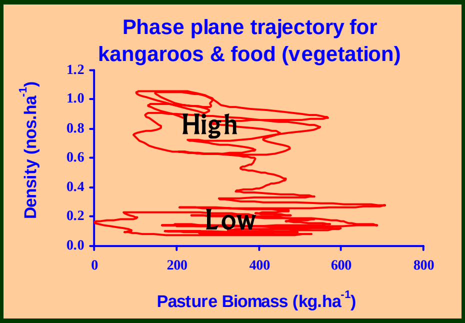
The *a priori* interactive kangaroo grazing model Feedback loops & regulation

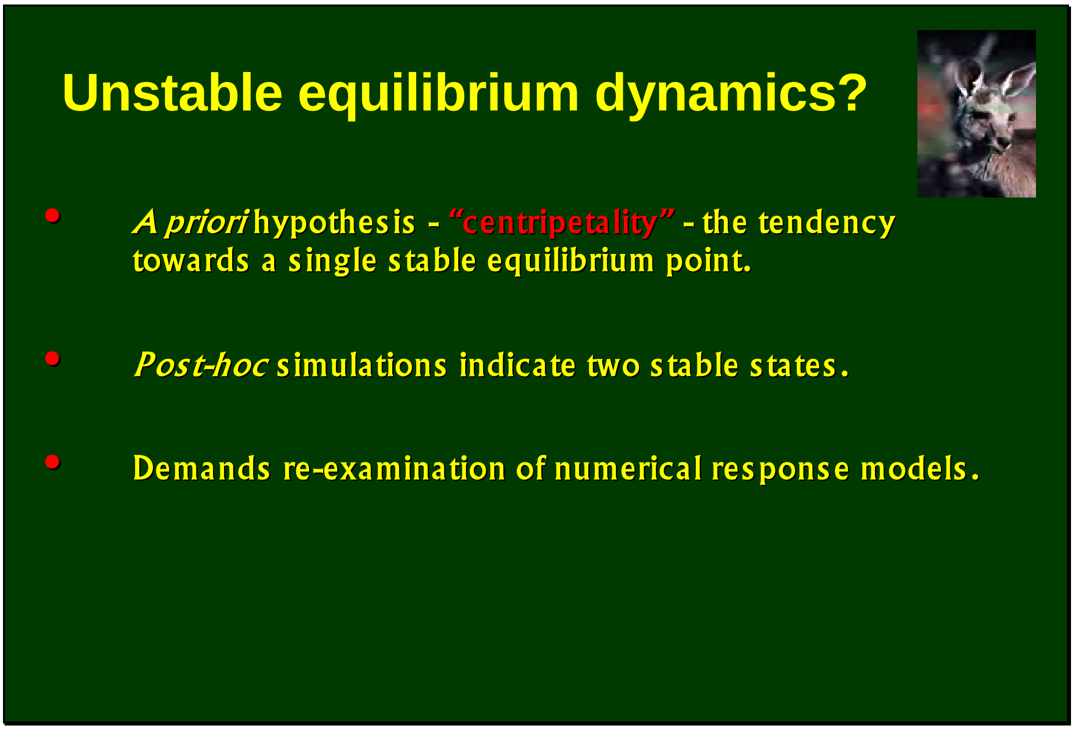


100–year stochastic simulation

The interactive kangaroo grazing model

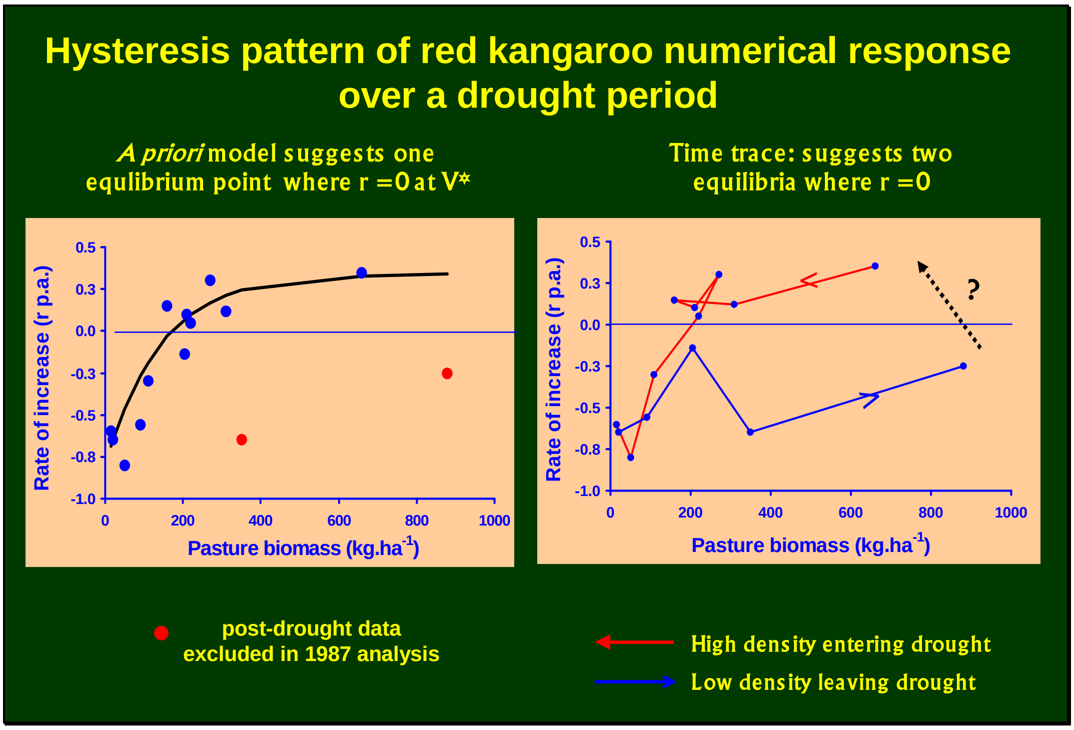






Unstable equilibrium dynamics?

- *A priori* hypothesis - "centripetality" - the tendency towards a single stable equilibrium point.
- *Post-hoc* simulations indicate two stable states.
- Demands re-examination of numerical response models.



Hysteresis pattern of red kangaroo numerical response over a drought period

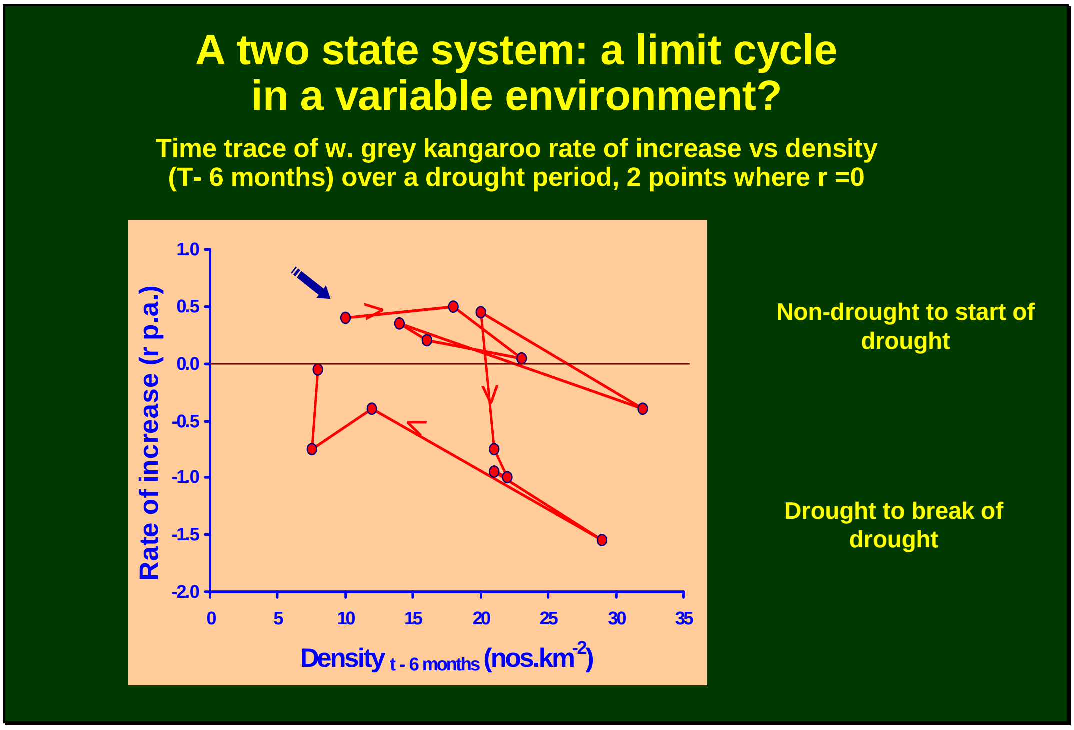
A priori model suggests one equlibrium point where r = 0 at V*

Time trace: suggests two equilibria where r = 0

● post-drought data excluded in 1987 analysis

← High density entering drought

→ Low density leaving drought

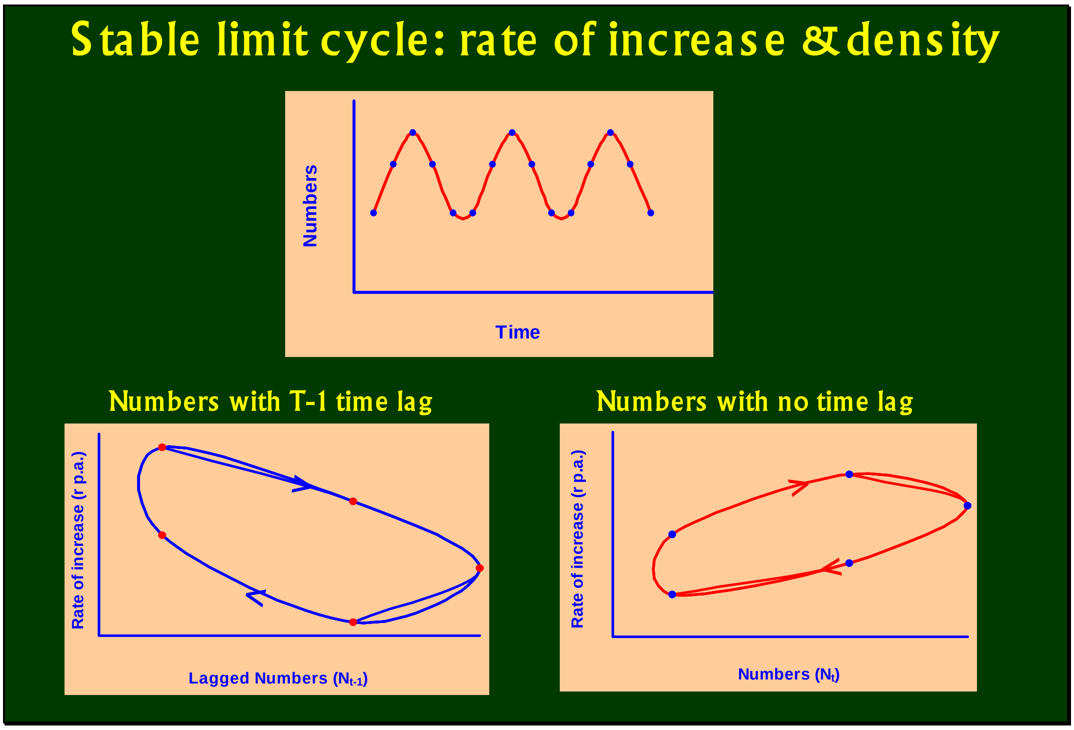


A two state system: a limit cycle in a variable environment?

Time trace of w. grey kangaroo rate of increase vs density (T- 6 months) over a drought period, 2 points where r =0

Non-drought to start of drought

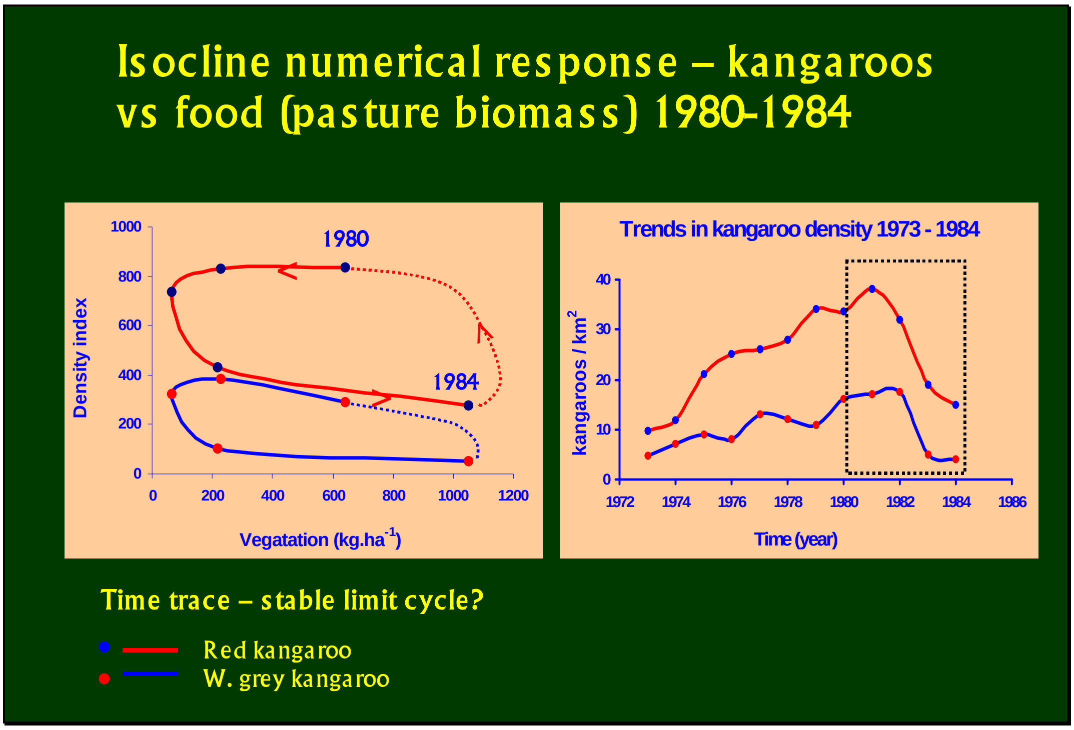
Drought to break of drought



Stable limit cycle: rate of increase & density

Numbers with T-1 time lag

Numbers with no time lag

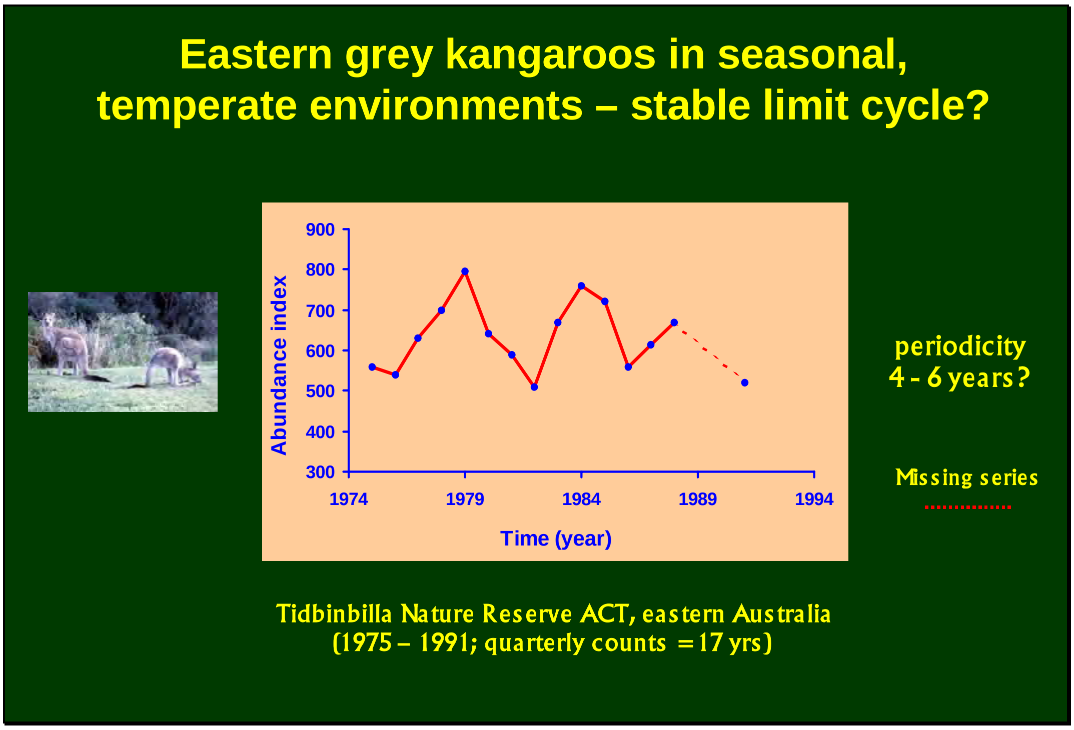


Isocline numerical response – kangaroos vs food (pasture biomass) 1980-1984

Time trace – stable limit cycle?

● ▬ Red kangaroo

● ▬ W. grey kangaroo



Eastern grey kangaroos in seasonal, temperate environments – stable limit cycle?

periodicity
4 - 6 years?

Missing series
……………

Tidbinbilla Nature Reserve ACT, eastern Australia
(1975 – 1991; quarterly counts = 17 yrs)

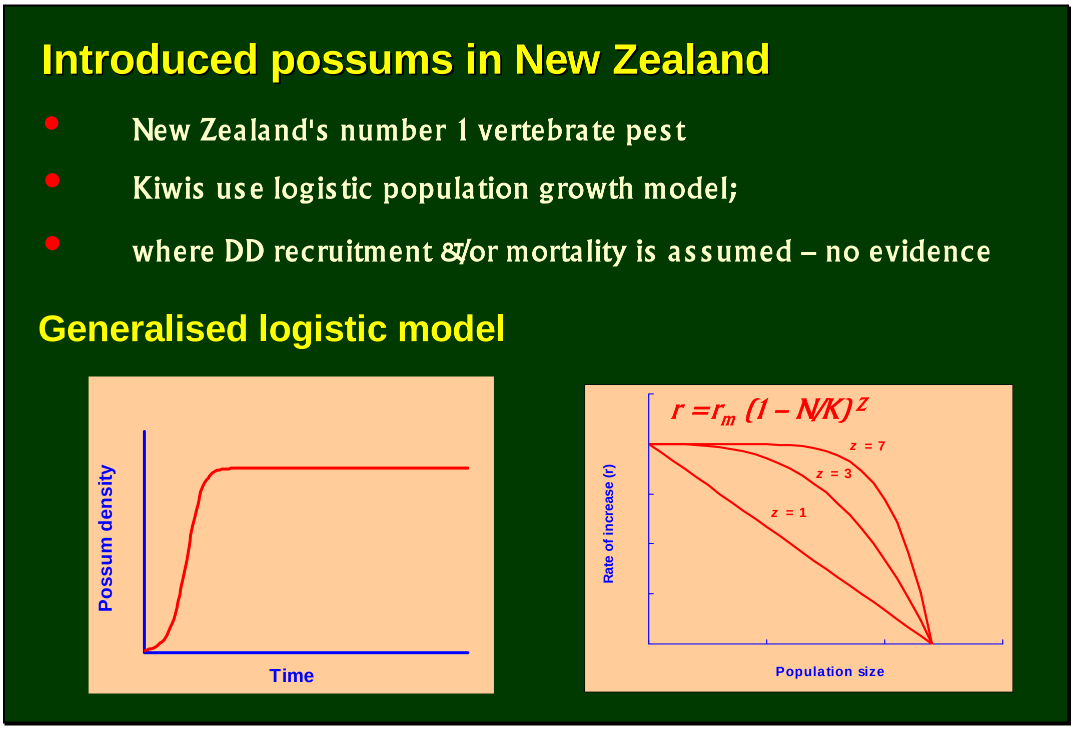
Kangaroo dynamics re-visited

- Rangelands: binary states – droughts & non - droughts.
- States locally stable but globally unstable.
- Kangaroo dynamics different in each state.
- An “unstable” limit cycle in arid rangeleands.
- But stable limit cycle in temperate zone.

The numerical response & multiple limiting factors

- Introduced possums in New Zealand forests

Food +spacing behaviour indexed by instantaneous density

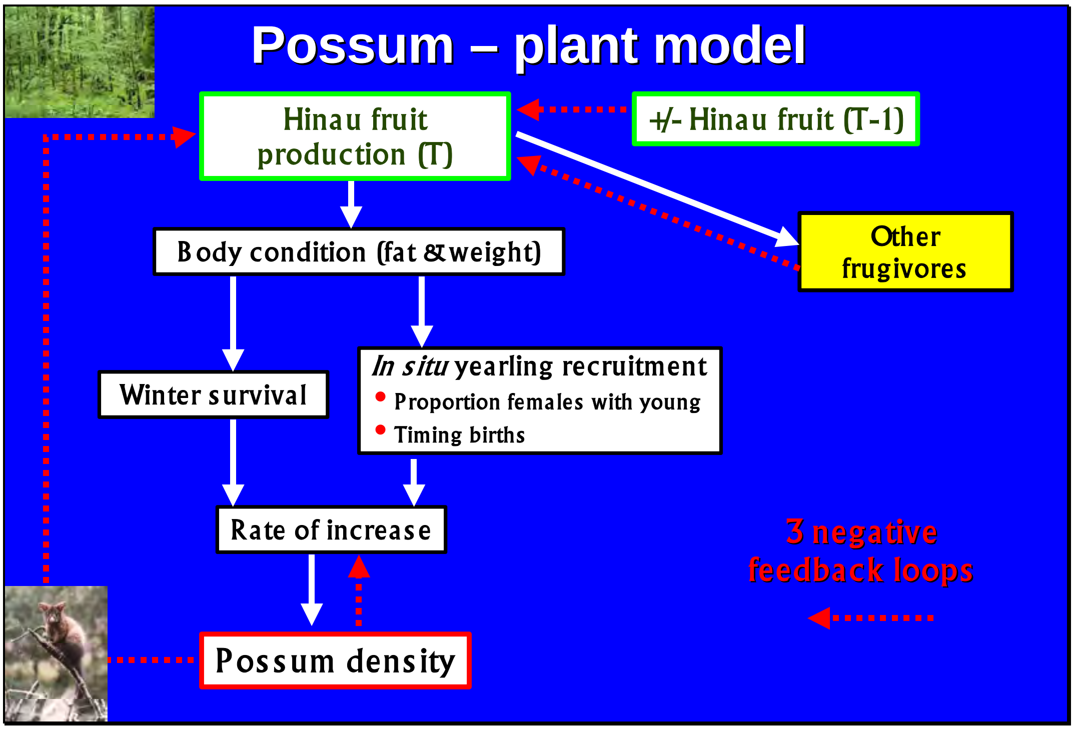


Introduced possums in New Zealand

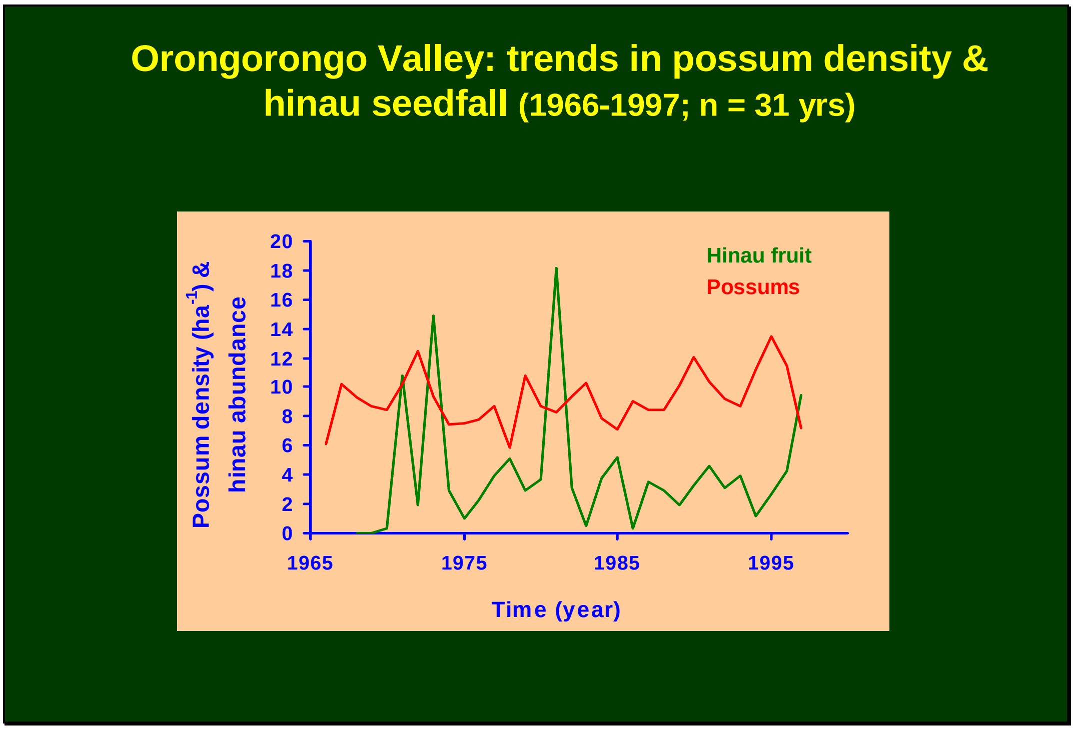
- New Zealand's number 1 vertebrate pest
- Kiwis use logistic population growth model;
- where DD recruitment &/or mortality is assumed – no evidence

Generalised logistic model

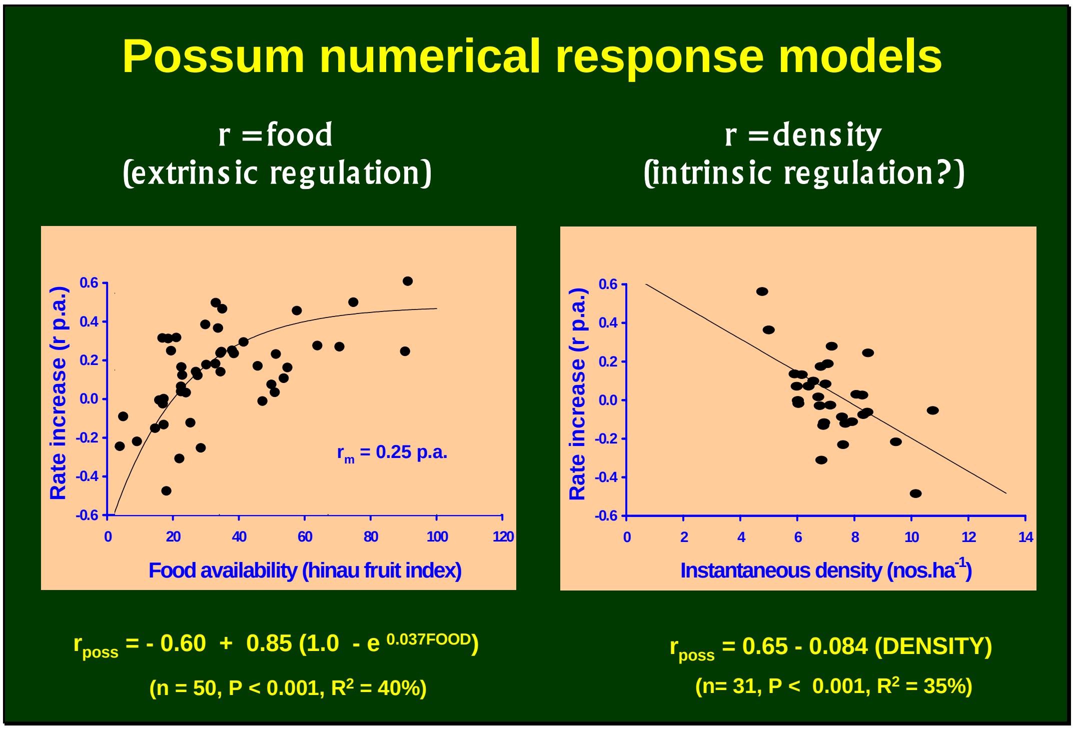
$r = r_m (1 - N/K)^z$



Possum – plant model



Orongorongo Valley: trends in possum density & hinau seedfall (1966-1997; n = 31 yrs)



Possum numerical response models

r =food
(extrinsic regulation)

r =density
(intrinsic regulation?)

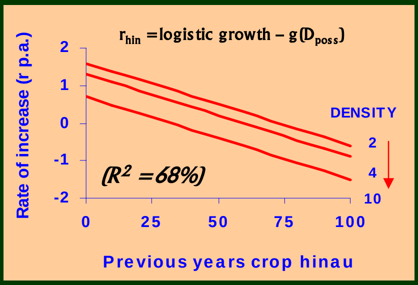
r_{poss} = - 0.60 + 0.85 (1.0 - e $^{0.037FOOD}$)

(n = 50, P < 0.001, R^2 = 40%)

r_{poss} = 0.65 - 0.084 (DENSITY)

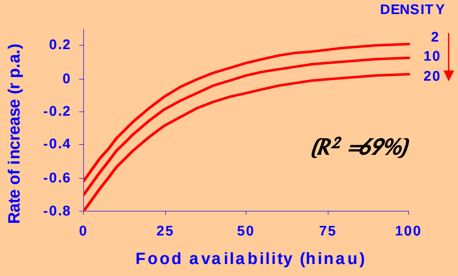
(n= 31, P < 0.001, R^2 = 35%)

1. Numerical response of hinau fruit: logistic growth - possum density



+

2. Possum numerical response: combined regulation model



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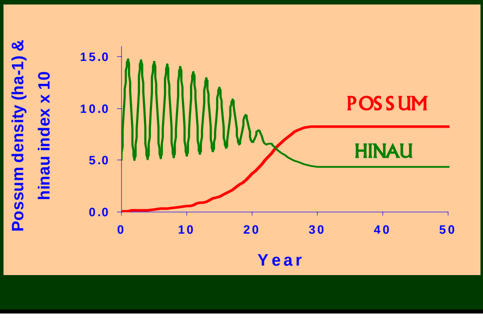


3. Possum - hinau fruit interaction

(Bayliss & Choquenot 1997)

Possums & food – take home messages

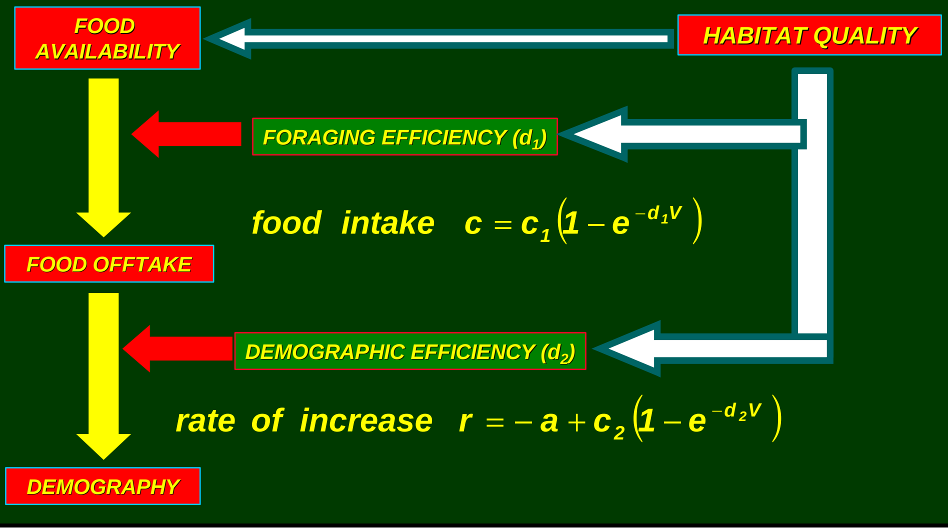
Logistic model:

- OK for possums & bovine Tb
- Inappropriate for complex ecological processes

Pigs - habitat quality & food availability

- Take landscape ecology approach
- Multiple habitat related limiting factors
- Implications for habitat quality & food resources

How does “habitat quality” affect interaction between animal populations and their food resources?



FOOD AVAILABILITY

HABITAT QUALITY

FORAGING EFFICIENCY (d_1)

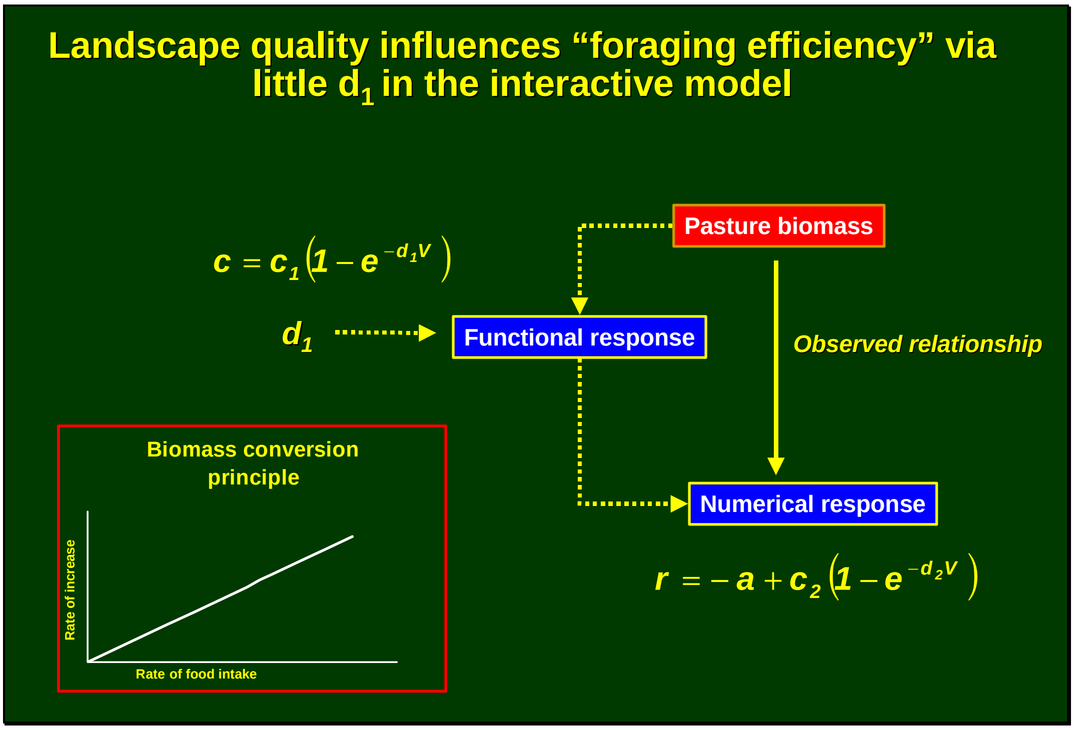
food intake $c = c_1\left(1 - e^{-d_1 V}\right)$

FOOD OFFTAKE

DEMOGRAPHIC EFFICIENCY (d_2)

rate of increase $r = -a + c_2\left(1 - e^{-d_2 V}\right)$

DEMOGRAPHY



Landscape quality influences “foraging efficiency” via little d_1 in the interactive model

$$c = c_1\left(1 - e^{-d_1 V}\right)$$

d_1

Pasture biomass

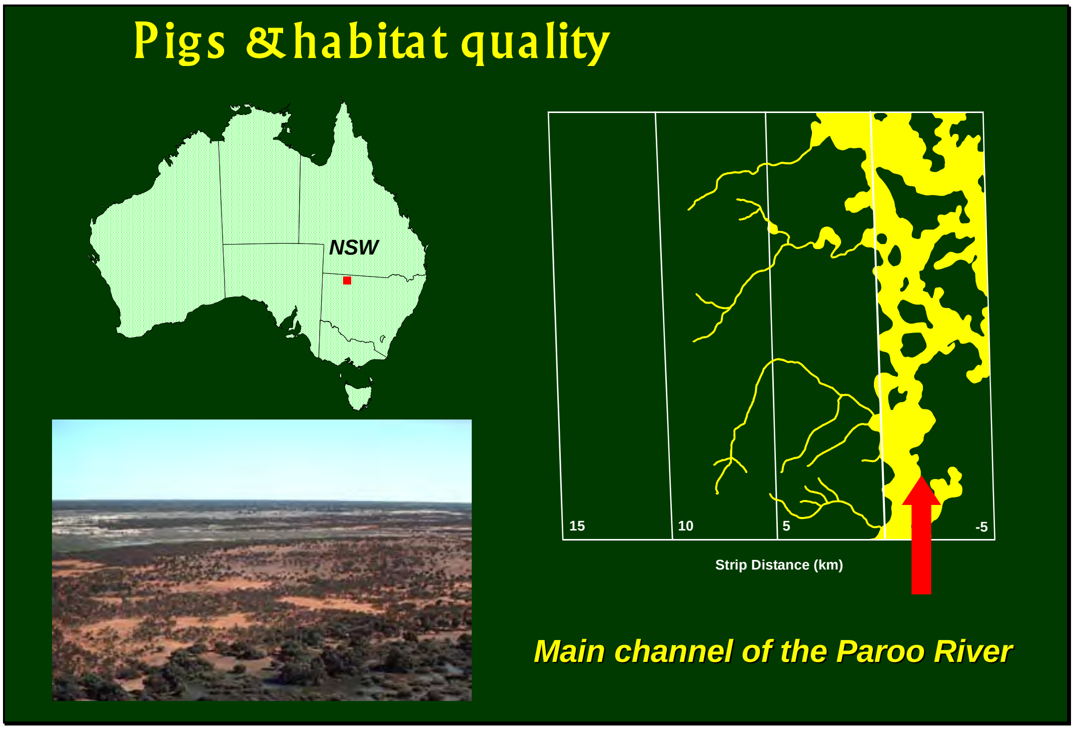
Functional response

Observed relationship

Numerical response

$$r = -a + c_2\left(1 - e^{-d_2 V}\right)$$

Biomass conversion principle



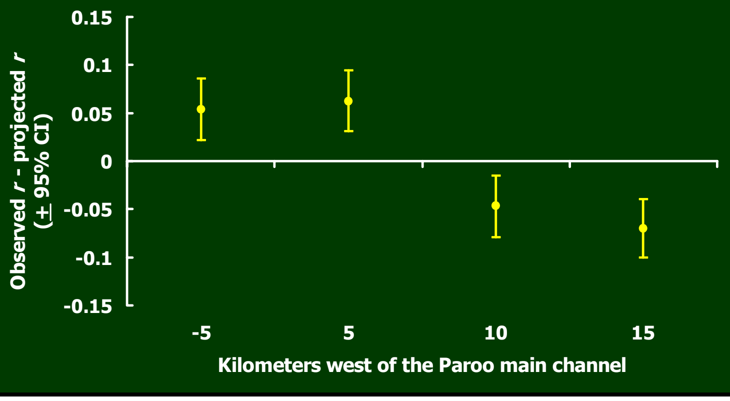
Pigs & habitat quality

Main channel of the Paroo River

Hypothesis

- Does foraging distance influence pig rate of increase because of reduced foraging efficiency?

Result



Summary of pig case study

- Key importance of biomass conversion principle & hence Lotka-Volterra framework
- Landscape approach yields key insights into pig-resource interactions & population dynamics
- Specifically, behavioural tradeoffs & habitat quality (e.g. thermoregulation & foraging)
- Implications for metapopulation analysis & linking population processes to landscape scales.
- Multiple limiting factors supported.

The upshot

- Understanding population dynamics & managing wildlife are tightly coupled.
- Lotka-Volterra model & demographic numerical responses: basic building block for multi-factorial consumer-resource interactions.
- Need to experimentally test *a priori*-multiple-working-hypotheses.
- Great global effort required.
- Critical for conservation, control & harvesting of wildlife.

THE END