Population growth rate and its determinants: An overview

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Population growth rate and its determinants: an overview

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We argue that population growth rate is the key unifying variable linking the various facets of population ecology. The importance of population growth rate lies partly in its central role in forecasting future population trends; indeed if the form of density dependence were constant and known, then the future population dynamics could to some degree be predicted. We argue that population growth rate is also central to our understanding of environmental stress: environmental stressors should be defined as factors which when first applied to a population reduce population growth rate. The joint action of such stressors determines an organism's ecological niche, which should be defined as the set of environmental conditions where population growth rate is greater than zero (where population growth rate $= r = \log_e(N_{t+1}/N_t)$). While environmental stressors have negative effects on population growth rate, the same is true of population density, the case of negative linear effects corresponding to the well-known logistic equation. Following Sinclair, we recognize population regulation as occurring when population growth rate is negatively density dependent. Surprisingly, given its fundamental importance in population ecology, only 25 studies were discovered in the literature in which population growth rate has been plotted against population density. In 12 of these the effects of density were linear; in all but two of the remainder the relationship was concave viewed from above.

Alternative approaches to establishing the determinants of population growth rate are reviewed, paying special attention to the demographic and mechanistic approaches. The effects of population density on population growth rate may act through their effects on food availability and associated effects on somatic growth, fecundity and survival, according to a 'numerical response', the evidence for which is briefly reviewed. Alternatively, there may be effects on population growth rate of population density in addition to those that arise through the partitioning of food between competitors; this is 'interference competition'. The distinction is illustrated using a replicated laboratory experiment on a marine copepod, *Tisbe battagliae*. Application of these approaches in conservation biology, ecotoxicology and human demography is briefly considered. We conclude that population regulation, density dependence, resource and interference competition, the effects of environmental stress and the form of the ecological niche, are all best defined and analysed in terms of population growth rate.

Keywords: demography; niche; population growth rate; population regulation

1. INTRODUCTION

With the persistent increase of the human population—now exceeding six billion—all species face increased pressure on resources. Understanding the factors responsible for limiting populations or causing species' extinctions therefore has increased urgency. Recent developments in population analysis, described below, have refined our understanding of the determinants of population growth rate and linked the theory to field data, and there is increasing interest in applying methods of this kind in conservation, wildlife management and ecotoxicology. This paper emphasizes the central role of population growth rate and reviews the use of data to test relevant theory and models primarily for wildlife populations. In this section

we consider the definition and importance of population growth rate and briefly examine its historical background.

(a) *Definitions and estimation of population growth rate*

Population growth rate is the summary parameter of trends in population density or abundance. It tells us whether density and abundance are increasing, stable or decreasing, and how fast they are changing. Population growth rate describes the per capita rate of growth of a population, either as the factor by which population size increases per year, conventionally given the symbol λ $(= N_{t+1}/N_t)$, or as $r = \log_e\lambda$. Generally here, population growth rate will refer to r. λ is referred to variously as 'finite growth rate', 'finite rate of increase', 'net reproductive rate' or 'population multiplication rate'. r is known as 'rate of natural increase', 'instantaneous growth rate', 'exponential rate of increase' or 'fitness'. In the simplest population model all individuals in the population are assumed equivalent, with the same death rates and birth

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rates, and there is no migration in or out of the population, so exponential growth occurs; in this model, population growth rate = r = instantaneous birth rate − instantaneous death rate.

Population growth rate is typically estimated using either census data over time or from demographic (fecundity and survival) data. Census data are analysed by the linear regression of the natural logarithms of abundance over time, and demographic data using the Euler–Lotka equation (Caughley 1977) and population projection matrices (Caswell 2001). The two methods of estimation can give similar values, as shown in studies of the northern spotted owl, *Strix occidentalis caurina* (Lande 1988; Burnham *et al.* 1996), greater flamingo, *Phoenicopterus ruber roseus* (Johnson *et al.* 1991), and pea aphids, *Acyrthosiphon pisum* (Walthall & Stark 1997). The census method has greater statistical power to detect a population decline than the demographic method when applied to high-density populations and the reverse occurs with low-density populations (Taylor & Gerrodette 1993). The estimation of the finite population growth rate (λ) may be biased by several factors: the manner of analysing census data with zeros, by the existence of spatial variance and spatial–temporal covariance, and by the scale of the area studied (Steen & Haydon 2000).

r varies from a minimum value of $-\infty$ to a value of 0.0 for a stable population, to a maximum value (r_{max}) when the population increases at the maximum possible rate, when food is abundant and there are no predators, pathogens and competitors. The corresponding values of λ are 0.0, 1.0 and λ_{max}. The frequency distribution of λ of a population persisting through time and space is positively skewed, with the maximum value further to the right of the mode than the minimum value. The frequency distribution of r is generally closer to a normal distribution (Hone 1999).

(b) *Importance in projection of future population sizes*

The importance of population growth rate is that it allows qualified projection of future population sizes. If there were no density dependence then population growth would be exponential, at a rate calculable from the Euler–Lotka equation using demographic data from the existing population. However, in a finite world the resources needed to support exponential growth must eventually become inadequate, and population growth rate then declines, giving density dependence of population growth rate as discussed in § 3. If the form of density dependence were constant and known, then the future population dynamics could to some degree be predicted. To what extent this can be realized in practice is discussed below; here we wish only to emphasize the central role of population growth rate in the projection of future population sizes.

Negative feedback between population growth rate and population density is a necessary condition for population regulation (Turchin 1999), and Sinclair (1996) has suggested that we recognize population regulation as occurring when population growth rate is negatively density dependent. According to this view, density dependence is seen as providing an explicit negative feedback mechanism which regulates the population. When density is below

carrying capacity, population growth rate is positive and the population increases towards carrying capacity; conversely when density is above carrying capacity, population growth rate is negative and the population declines. In this way population density is controlled by the mechanism of the negative density dependence of population growth rate, and in the absence of environmental changes or time-lags, population density remains in the vicinity of carrying capacity.

(c) *Historical background*

The pivotal importance of population growth rate has been recognized for a long time. The historical background has been described by Cole (1958) and Hutchinson (1978), on which some of the following outline is based. The idea of geometric population growth restrained at higher densities by the carrying capacity of the environment was put forward in a book by Botero (1588), and was famously elaborated and brought to general attention by Malthus (1798). Detailed interest in tables of mortality began in the late seventeenth century, with mathematical analyses by Huygens and later Buffon among others. Interestingly, Cole suggests that Newton notably 'failed to grasp the basic concept that life expectancy is a function of age'. Euler (1760), in deriving the equation that bears his name, established the mathematical dependence of population growth rate on age-specific birth rates and death rates, and commented that 'it always comes back to these two principles, that of mortality and that of fertility, which, once they have been established for a certain place, make it easy to resolve all the questions which one could propose...'. The proposal that population growth rate declines linearly with population density, known as the logistic equation, was put forward by Verhulst (1838). Population growth rate is central to the work of the modern founding fathers of ecology (Lotka 1925; Fisher 1930; Nicholson 1933; Andrewartha & Birch 1954), but the complexities of its dependence on age-specific birth and death rates have until recently prevented thorough examination of the role of population growth rate. With the advent of modern computing and the development of matrix methods for the analysis of life tables, the importance of population growth rate in the study of population ecology is becoming more widely appreciated (Caswell 2001).

(d) *Scope and layout of paper*

In attempting to establish the central role of population growth rate in population ecology, we first consider how it should be used in the definition of basic concepts such as environmental stress and ecological niche, and then consider its role in population dynamics, examining in particular the form of the relationship between population growth rate and population density. Using these as foundations we then attempt to characterize recent studies in terms of three approaches to the identification of the determinants of population growth rate.

In practice, this means studying the causes of variation in population growth rate, attributing observed variation to known sources of variation, while bearing in mind that the specific sources of variation may change over time and in space. We make no attempt to review the extensive related literature on theoretical population dynamics and
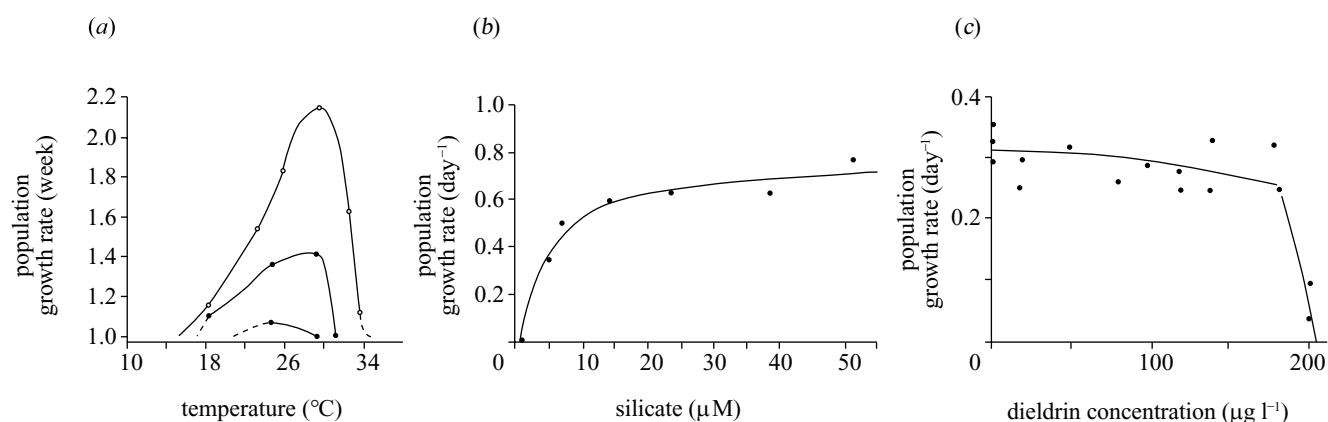
Figure 1. Examples of the effects of environmental stressors. (*a*) Effects of temperature on population growth rate = λ of the grain beetle *Calandra oryzae* (Birch 1953). The different lines represent different moisture contents. (*b*) Effects of the availability of silicon on population growth rate = *r* of the diatom *Asterionella formosa* (Tilman *et al.* 1981). (*c*) Effects of dieldrin on population growth rate = *r* of the cladoceran *Daphnia pulex*. (After Daniels & Allan (1981).)

food webs; for an introduction to these see Berryman *et al.* (1995) and Rees *et al.* (1996). We conclude with an example illustrating our ideas in practice, and some consideration of applications to conservation biology and other fields of wildlife management, and ecotoxicology.

2. ENVIRONMENTAL STRESS AND THE ECOLOGICAL NICHE

Environmental stressors can be defined as factors that, when first applied to a population, reduce population growth rate (Sibly & Calow 1989; Hoffmann & Parsons 1991). Examples of stressors may be climatic conditions, toxicants, food quality, pathogens and so on. The advantages of explicit operational definitions of the terms 'stress' and 'stressor' are obvious, and it is encouraging that identical definitions are now used from the population level down to that of molecular responses (e.g. animal welfare (Broom & Johnson 1993) and stress proteins (Hengge-Aronis 1999)). Some examples of the effects of stressors on population growth rate are shown in figure 1.

At the individual and population level the effects of environmental stressors are commonly measured using life table response experiments (Levin *et al.* 1987; Caswell 1989, 2001). The first true example of this approach was Birch's (1953) classic study of the effects of temperature and wheat moisture content on two species of grain beetles (figures 1*a* and 2*a*). The approach has been much developed by the elaboration of matrix population models (Caswell 2001), and in recent years, increasing concern about the environment has led to numerous studies of the population growth rate effects of pollutants (Forbes & Calow 1999).

The combined action of environmental stressors can be thought of as defining an organism's ecological niche. Although textbooks often treat the concept of an organism's ecological niche historically, in terms of Hutchinson's (1957) rectilinear definition of the niche, a more straightforward approach is to define an organism's niche as the set of points in 'niche space' where the population growth rate is greater than zero (Maguire 1973; Hutchinson 1978; figure 2*b*). The axes of niche space are physical or chemical variables such as temperature, food size or

pH. When the niche is characterized at low population density and in the absence of predators, parasites and interspecific competitors, it is referred to as the 'fundamental niche'. In the presence of predators, parasites and interspecific competitors the set of points for which the population growth rate is greater than zero is reduced, and this set of points defines the 'realized niche' (Maguire 1973).

Birch's (1953) summary of his experimental results depicting the effects of environmental stressors on population growth rate (figure 2*a*) looks very similar to figure 2*b*, and it is curious that while Birch's work is generally referred to in discussions of the ecological niche, the explicit link is rarely made. Birch (1953) concluded: 'the significance of this information [i.e. figure 2*a*] is that it provides background experimental data for studies on distribution and abundance. The limits of distribution of the beetles are determined, so far as temperature and moisture are concerned, by the combination of temperature and moisture beyond which the finite rate of increase (λ) is less than 1'. He also showed that the known geographical distribution of the two beetle species conformed to the predictions of the laboratory work. A very similar interpretation of species distribution in terms of population growth rate is described by Caughley *et al.* (1988), in which the edge of distribution is identified as occurring where the maximum value of population growth rate is zero. Populations can however persist with a population growth rate greater than zero if they are maintained by immigration ('sink' populations; Pulliam 1988).

An example of how the niche concept can be used in practice is given in figure 2*c*. The fundamental niches of the trees shown overlap in the central region of figure 2*c* (Ellenberg 1988) but in nature, competition between tree species restricts the occurrence of individual species as illustrated.

3. THE FORM OF THE RELATIONSHIP BETWEEN POPULATION GROWTH RATE AND POPULATION DENSITY

As we have seen, environmental stressors have negative effects on population growth rate, and the same is true
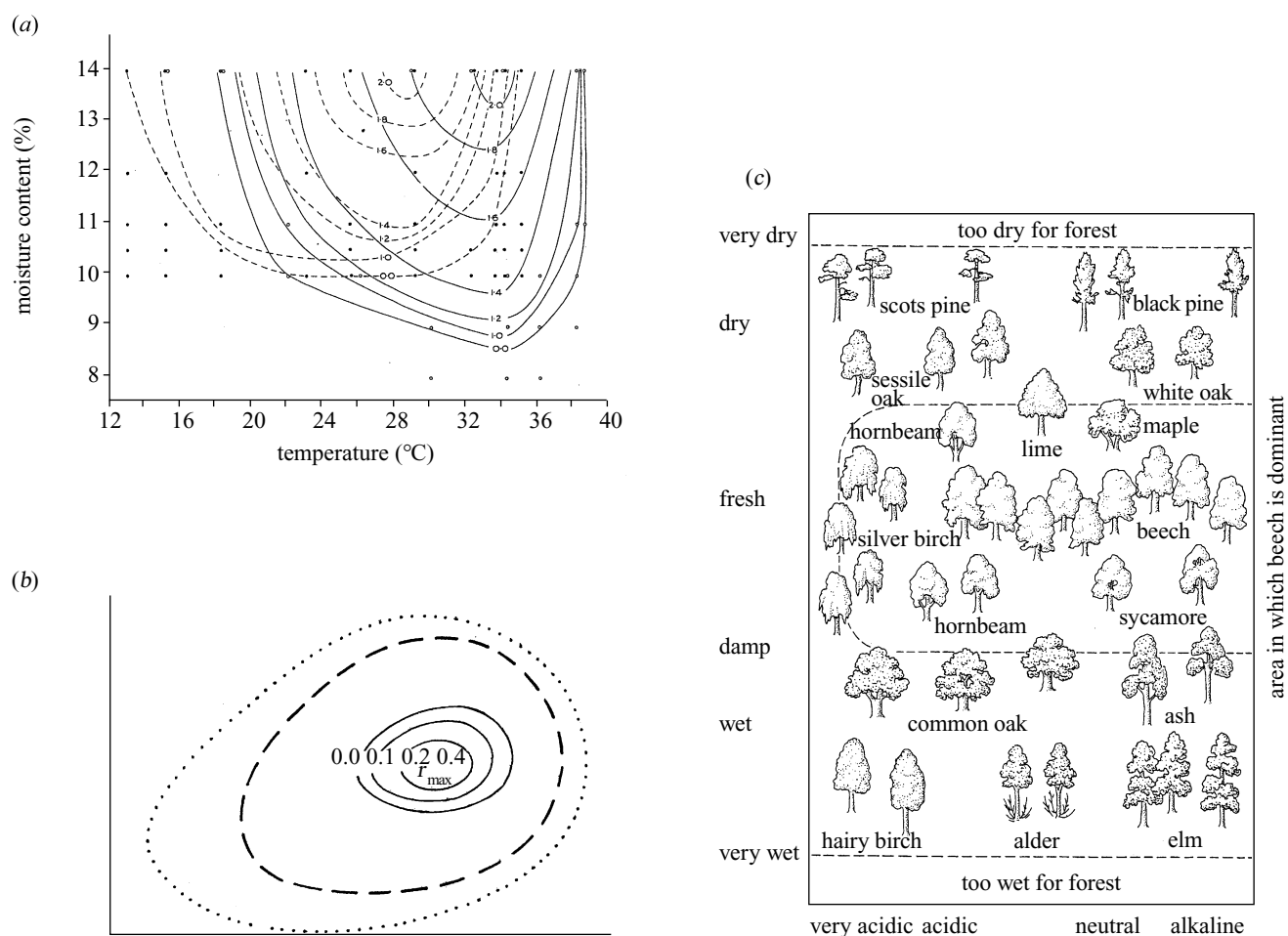
(a)

(b)

(c)

Figure 2. The ecological niche defined by population growth rate contours. (*a*) The study by Birch (1953) of the effects of temperature and wheat moisture content on population growth rate = λ of two species of grain beetle: dotted lines, *Calandra oryzae*; solid lines, *Rhizopertha dominica*. The points on the graph show conditions at which measurements were made. (*b*) Maguire's (1973) definition of the ecological niche in terms of population growth rate = *r* contours (after Hutchinson 1978). Axes are environmental variables as described in the text. (*c*) Niches of the major northern European trees. (From Polunin & Walters (1985), copyright owned by Ellenberg (1988).)

of population density. Indeed the nature of the negative relationship between population density and population growth rate is at the heart of population ecology. If the relationship is linear, the describing equation is the logistic, and many theoretical analyses are built on this assumption. Fowler (1981, 1987) has argued on theoretical and some empirical grounds that relationships between population growth rate and density are expected to be concave, viewed from above, for species with life histories like those of insects, convex for large mammals and similar species, and linear for intermediate species (see figure 3 for examples of concave and convex). Concave and convex correspond to values less or greater than one respectively for the shape parameter θ in the generalized logistic equation (Eberhardt 1987).

Given its fundamental importance in population ecology, it is surprising that data on the form of the dependence of population growth rate on density have only rarely been plotted out and analysed, though Berryman (1999) and Turchin (1999) give examples. No doubt this is partly because the relationship cannot be seen without adequate variation in density in a fairly constant environment; thus the best evidence may come from population recoveries after experimental perturbations (Sinclair

1996). Of the 25 cases we found (examples in figure 3), 12 relationships are linear, and in all but two of the remainder the relationship was concave viewed from above (table 1). Note, however, that there is considerable scatter about each relationship (e.g. figure 3), indicating that other factors besides density affect population growth rate. Interestingly, there does seem to be some support for Fowler's hypothesis, but the data are not conclusive, and there are counter-examples (e.g. elk and sparrowhawk are linear not convex). Further support has recently been provided by studies of birds (Sæther *et al.* 2002). There are also studies of the relationship between λ and density, in for example the dipper *Cinclus cinclus* (Sæther *et al.* 2000), but to relate these to the logistic equation, λ has to be $\log_e$ transformed.

Although a priori density dependence can be expected in real populations that persist long term (Sinclair 1996), recognizing the operation of density dependence in real datasets has been the subject of much controversy. A number of meta-analyses have been performed applying these methods to data from different taxa, including birds and insects (Hassell *et al.* 1989; Greenwood & Baillie 1991; Woiwod & Hanski 1992). The largest such study is that of Woiwod & Hanski (1992), which analysed 5715
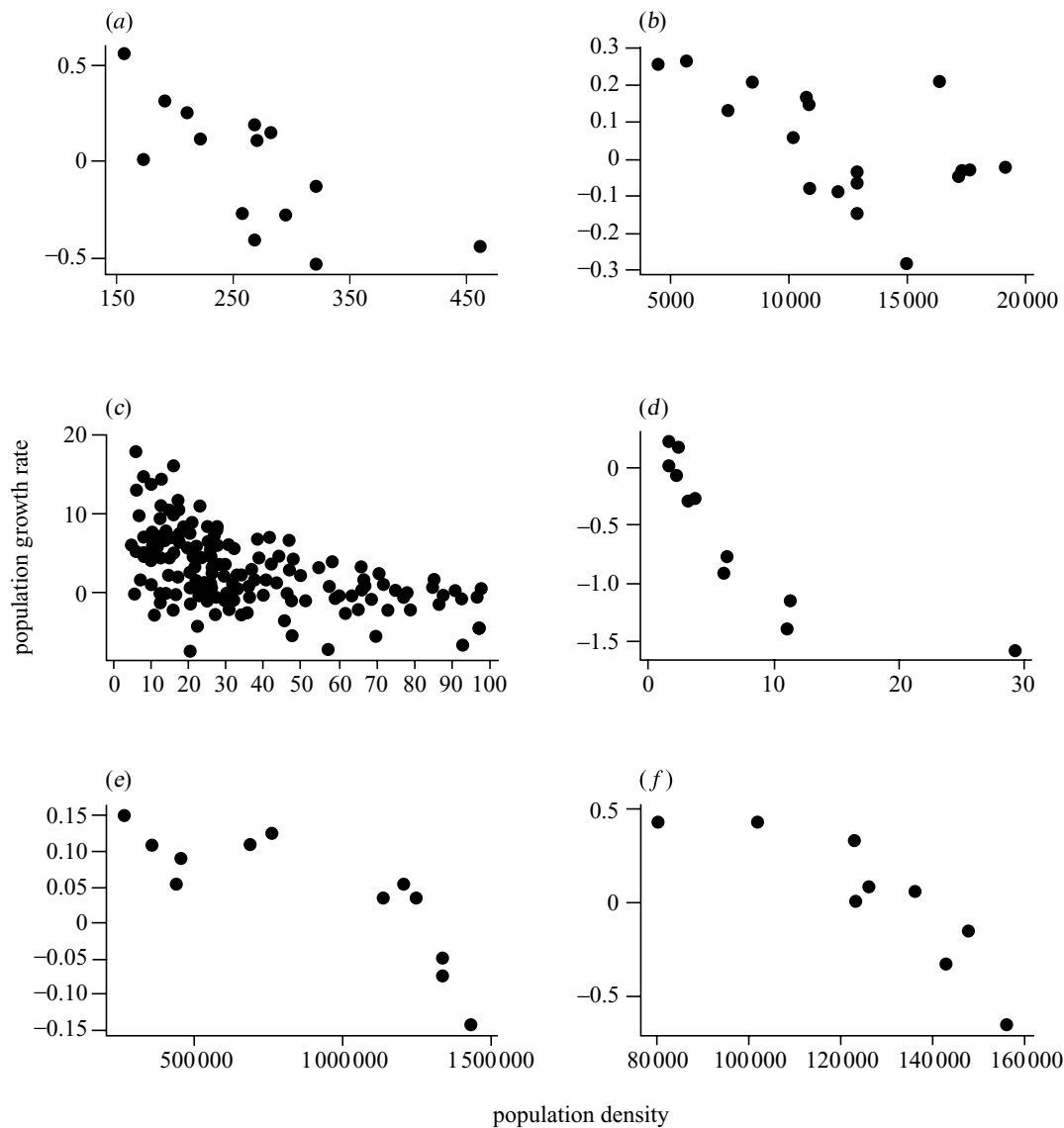
Figure 3. Examples of the form of the relationship between population growth rate (r) and population density. Linear relationships in (a) magpie goose and (b) elk; concave viewed from above in (c) meadow vole and (d) arctic ground squirrel; convex viewed from above in (e) wildebeest and (f) sandhill crane. Sources in table 1.

time-series of 447 species of moths and aphids in the UK, and found good agreement between three analytical methods which differ in their assumptions about the form of density dependence, namely those of Bulmer (1975); Pollard *et al.* (1987) and simple regression of $\log_e(N_{t+1}/N_t)$ against N_t.

The general conclusion of these meta-analyses is that the existence of density dependence can be established from census data provided sufficient data are available. The objective in analysing density dependence should therefore be the discovery of the form of density dependence, and the effect, if any, of time-lags. The existence of time-lags can be investigated by adding terms such as N_{t-1} into the regression of $\log_e(N_{t+1}/N_t)$ against N_t (Turchin 1990; Woiwod & Hanski 1992; Berryman 1999; Erb *et al.* 2001).

Despite the successes of the meta-analyses, worries remain about the effects of measurement errors and of fluctuations in environmental variables. None of the existing methods allows for the effects of measurement errors, which may exaggerate the effects of density dependence,

and could produce the illusion of density dependence in invariant populations (Woiwod & Hanski 1992). Some authors recommend Bulmer's test but all methods have strengths and weaknesses (Lebreton & Clobert 1991; Fox & Ridsdill-Smith 1996). An additional serious concern is that fluctuations in environmental variables may obscure density effects and make it difficult to locate the positions of equilibrium densities ('density vagueness'; Strong 1986; Murdoch 1994; Krebs 2002).

4. CONTRASTING APPROACHES TO IDENTIFYING THE DETERMINANTS OF POPULATION GROWTH RATE

Because so many factors affect population growth rate, it is never going to be easy to separate their effects when they operate simultaneously. Ecologists have used a variety of methods to study the combined and relative effects on population growth rate of determining factors. Here, we compare and contrast the three main approaches that have been used to identify the determinants of population

Table 1. Examples of linear and nonlinear density dependence in the relationship between population growth rate and population density.

(Our classification is in some cases provisional and original references should be consulted. Some more complicated cases involving time-lags can be found in Berryman (1999) and Turchin (1999).)

species	reference
linear	
cladoderan *Daphnia pulex*	Frank *et al.* (1957)
treehole mosquito *Aedes triseriatus*	Livdahl (1982) and Edgerley & Livdahl (1992)
annual plant *Salicornia brachystachys*	Crawley (1990)
guppy *Poecilia reticulata*	Barlow (1992)
magpie goose *Anseranas semipalmata*	Bayliss (1989)
Yellowstone elk *Cervus elaphus*	Coughenour & Singer (1996)
European rabbit *Oryctolagus cuniculus*	Barlow & Kean (1998)
lake whitefish *Coregonus clupeaformis*	Berryman (1999)
red pine cone beetle *Conophthorus resinosae*	Berryman (1999)
mountain pine beetle *Dendroctonus ponderosae*	Berryman (1999)
sparrowhawk *Accipter nisus*	Sibly *et al.* (2000c)
field vole *Microtus agrestis*	Klemola *et al.* (2002)
concave viewed from above	
cladoceran *Daphnia magna*	Smith (1963)
wood mouse *Apodemus sylvaticus*	Montgomery (1989)
fruitfly *Drosophila melanogaster*	Turchin (1991)
winter moth *Operophtera brumata*	Roland (1994)
grey-sided vole *Chlethrionomys rufocanus*	Saitoh *et al.* (1997)
meadow vole *Microtus pennsylvanicus*	Turchin & Ostfeld (1997)
leaf-eared mouse *Phyllotis darwini*	Lima & Jaksic (1999)
cowpea weevil *Callosobruchus maculatus*	Berryman (1999)
marine copepod *Tisbe battagliai*	Sibly *et al.* (2000b); cf. figure 7a
brushtail possum *Trichosurus vulpecula*	Efford (2000)
Arctic ground squirrel *Spermophilus parryii plesius*	Karels & Boonstra (2000)
convex viewed from above	
wildebeest *Connochaetes taurinus*	Sinclair (1996)
sandhill crane *Grus canadensis*	Berryman (1999)

growth rate in wildlife populations with overlapping generations and with, usually, no explicit spatial elements. For convenience we label these three approaches the 'density paradigm', the 'demographic paradigm' and the 'mechanistic paradigm'. These are best understood as different simplifications of a rather complicated reality. Intuitively it is clear that population growth rate is fully determined by the complete record of age-specific birth and death rates, and mathematically the link is made by the Euler–Lotka equation. Exploration of the link between population growth rate and the age-specific life table gives the demographic paradigm. Age-specific birth and death rates depend causally on such factors as food supply per individual, parasite burdens, predation, environmental stressors and interference competition, and some of these depend directly or indirectly on population density. Looking directly at the link between these causal factors and population growth rate gives the mechanistic paradigm, and focusing on the link between population growth rate and population density gives the density paradigm; these two paradigms were identified and contrasted by Krebs (1995). Any or all of these approaches can be undertaken using observational, experimental and modelling studies. In this section we first consider use of these approaches on their own, and then how they have been used in combination.

The density paradigm, discussed in § 3 and illustrated in figure 3, aims primarily to describe density effects on population growth rate, and is used to make predictions taking account of population density, where detailed mechanistic understanding may be unnecessary or impossible because of lack of appropriate data. It assumes, however, constancy of important features of the environment such as population food supply; where such assumptions are untenable, as occurs in most populations of wild animals, the mechanistic approach is preferable (see § 4b).

(a) The demographic paradigm

The demographic paradigm focuses on the relationship between population growth rate and age-specific fecundity and survival. Population growth rate is increased by an increase in fecundity or survival, or by breeding earlier. Detailed examination of the link between population growth rate and demographic parameters is often made using population projection matrices as described by Caswell (2001), although other methods are also available employing the classical Euler–Lotka equation (e.g. Lande 1988; Burnham *et al.* 1996; Calow *et al.* 1997). Because stable age structure is necessary to the derivation of this equation it is often supposed that population growth rate cannot be estimated without stable age structure. However, Sibly & Smith (1998) have argued that even when the age structure is not stable and the various age classes are growing at different rates, population growth rate

Table 2. *Examples of wildlife population dynamics, analysed to study determinants of population growth rate, using one or more of the density, demographic and mechanistic analyses, and their combinations.*
(The yes/no classification refers to whether an analysis was or was not used.)

demographic analysis	mechanistic analysis	density analysis	
		no	yes
no	no	exponential; large mammals (Eberhardt 1987)	logistic; magpie goose (Bayliss 1989), sparrowhawk (Sibly et al. 2000c)
no	yes	numerical response; red kangaroo (Bayliss 1987), barn owl (Taylor 1994)	ratio; wolf (Eberhardt & Peterson 1999), modified numerical response; house mouse (Pech et al. 1999)
yes	no	modified Lotka; northern spotted owl (Lande 1988)	modified logistic; white-tailed deer (Hobbs et al. 2000)
yes	yes	modified Lotka; red fox (Pech et al. 1997)	modified logistic; kit fox (White & Garrott 1999)

defined as the solution of the Euler–Lotka equation still provides a useful index of population growth, because it represents an appropriate weighted average of the growth rates of the different age classes.

Many examples of work within the demographic paradigm are described by Caswell (2001), and this approach has also been important in studies of the northern spotted owl (*Strix occidentalis caurina*), in which λ is related to estimates of fecundity and survival obtained in mark–recapture studies (Lande 1988; Lahaye *et al.* 1994; Burnham *et al.* 1996; Franklin *et al.* 2000; Seamans *et al.* 2001).

The relative effects on population growth rate (λ) of proportional changes in fecundity and survival rates have been examined in elasticity analysis, which was reviewed in a series of recent studies (e.g. Caswell 2000; De Kroon *et al.* 2000; Easterling *et al.* 2000; Grant & Benton 2000; Heppell *et al.* 2000; Sæther & Bakke 2000; Van Tienderen 2000; Wisdom *et al.* 2000). These studies compared the contributions of fecundity and survival to population growth in species with differing life histories; in short-lived species fecundity can make a greater proportional contribution than survival, and the reverse in longer-lived species. Elasticity analysis is used alongside observation of actual levels of variation in demographic parameters (Gaillard *et al.* 1998) to determine which demographic factors have most effect on population growth rate. In a similar vein Sibly & Smith (1998) have argued that traditional 'key factor' analysis should be redesigned to identify the life-history trait whose variation has most effect on population growth rate.

Spatial elements have also been incorporated into efforts to explain variation in population growth rate. The contributions to population growth rate of *in situ* recruitment, survival and immigration can be estimated from mark–recapture studies, as described for meadow voles (*Microtus pennsylvanicus*) by Nichols *et al.* (2000). Populations for which emigration exceeds immigration are referred to as source populations; where the reverse obtains, we have sinks (Pulliam 1988). Thomas & Kunin (1999) have demonstrated a graphical method of representing the concepts.

(b) *The mechanistic paradigm*

The mechanistic paradigm focuses on the relationship between population growth rate and variables such as climate, food availability, predator abundance, pathogens and parasites, and competitors ('extrinsic factors'). Turchin (1999) provides an excellent discussion of what we can treat as variables: ideally one might keep track of the fates of all relevant individuals, but apart from the impossibility of this, there is often more heuristic value in using summary variables such as 'numbers in each age class' and so on. Historically, the mechanistic paradigm was followed in early models of the effects of competition by Lotka and Volterra in the 1920s, of predation (Lotka 1925; Volterra 1926), and of pathogens (Kermack & McKendrick 1927). Monod (1950) considered the relationship between population growth rate and resource availability in populations of bacteria, and in an influential experiment Tilman *et al.* (1981) related population growth rate of the diatom *Asterionella formosa* to the availability of silicon, which diatoms need to secrete their silicate 'shells' (figure 1b). Later, in a theoretical synthesis, Tilman (1982) considered more generally the relationship between population growth rate and the availability of resources. These ideas are very similar to the formulations of ecological niche theory and stressors discussed earlier.

In the simplest case, the effect of population density on population growth rate is replaced, in the mechanistic paradigm, by resource availability. A collation of the results of many studies of mammals (table 2; Sinclair 1996) showed that food is very often a cause of density dependence. In these cases density may have no effects other than those on food availability. We shall refer to the relationship between population growth rate and food availability as the 'numerical response' (table 2), although it is important to note that not all authors use the term this way, as there has been an evolution in its meaning since Solomon (1949) first used it to describe the increase in numbers of animals as their resources increased. Application to the relationship between population growth rate and food availability came later, via an intermediate step of May (1974, p. 83) who used the term to describe the effect of food availability on fecundity, and Caughley
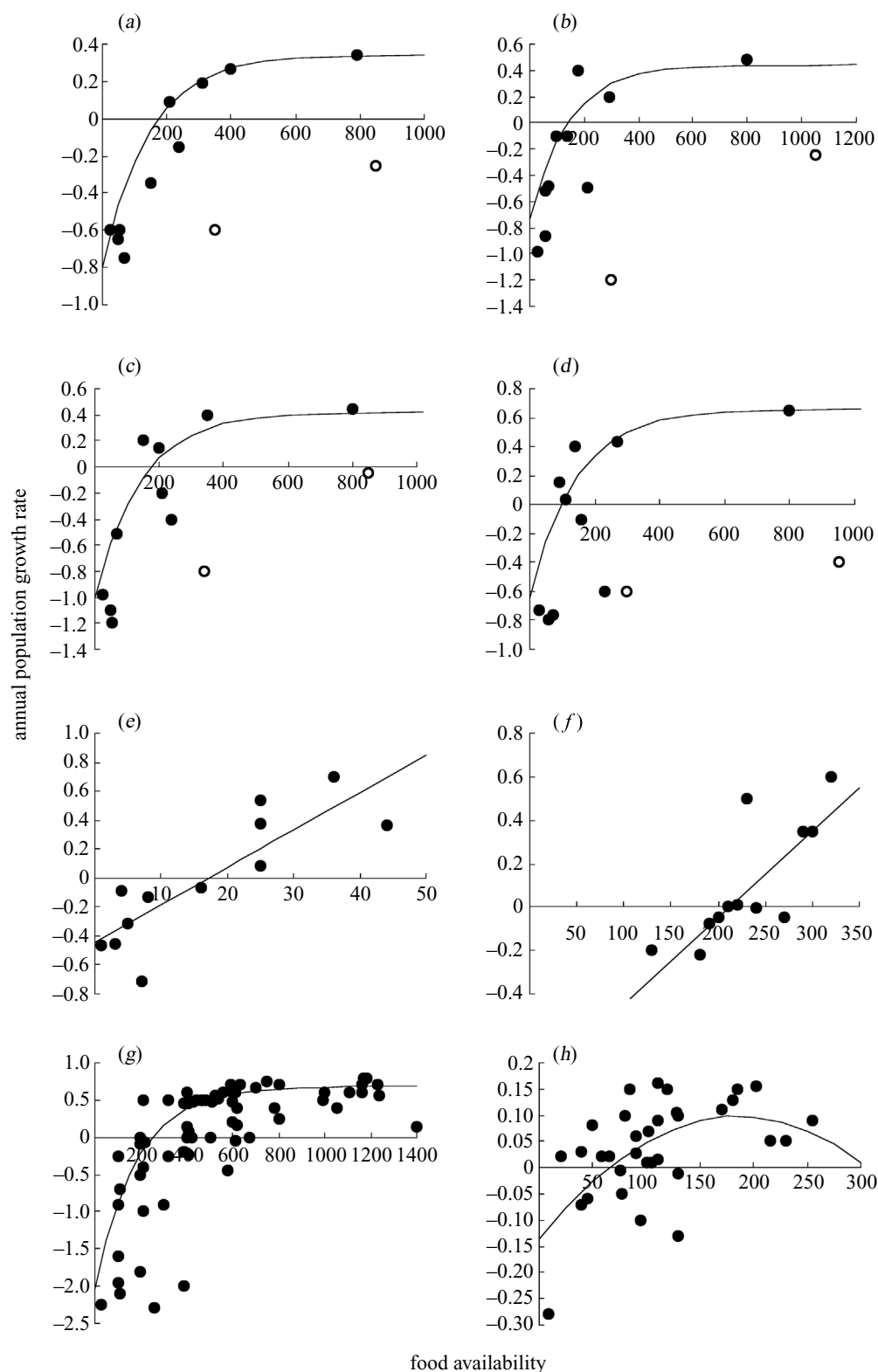
Figure 4. Examples of the numerical response of populations to food availability, plotting annual population growth rate (r) against pasture biomass (kg ha^{-1}), except in (e) the x-axis is vole abundance and in (h) the x-axis is per capita food availability. (a) Red kangaroo in Kinchega National Park (Bayliss 1987); (b) red kangaroo next to Kinchega National Park (Bayliss 1987); (c) western grey kangaroo in Kinchega National Park (Bayliss 1987); (d) western grey kangaroo next to Kinchega National Park (Bayliss 1987); (e) barn owl (*Tyto alba*) (modified from Taylor (1994); $r^2 = 0.72$, $p < 0.01$); (f) feral goat (Maas 1997); (g) feral pig (*Sus scrofa*) (Choquenot 1998); (h) wildebeest (*Connochaetes taurinus*) (Krebs *et al.* 1999). (a–d) Open circles represent data not used in the estimation.

(1976, p. 207) who described it as the effect of food availability on the rate of amelioration of population decline. Later, the term was commonly used to describe the relationship between population growth rate and food availability (May 1981). The divergence is well illustrated by Caughley & Sinclair (1994): in ch. 10, p. 172 they use

the Solomon definition and in ch. 6, p. 75 they use the population growth rate definition. The relationship between these concepts is considered by Sinclair & Krebs (2002). Methods of analysis of the numerical response were developed in particular by Caughley (e.g. Caughley 1976, 1987; Caughley & Lawton 1981; Caughley & Krebs 1983), and prior to and subsequent to his death in 1994 his work has much influenced the development of mammalian ecology, especially in Australia and New Zealand.

Examples of the numerical response, plotting population growth rate against food availability, are shown in figure 4. Note that as food availability increases, population growth rate generally increases to a maximum. Availability is availability to individuals, and is not always best measured by the population food supply (Abrams & Ginzburg 2000). If the population is food limited, for instance, it may be more appropriate to divide the population food supply by population density (see § 4d and § 5). In addition to the examples in figure 4, positive generally nonlinear relationships between population growth rate and food availability have been reported for European rabbit (*Oryctolagus cuniculus*; Pech & Hood 1998), red fox (*Vulpes vulpes*; Pech & Hood 1998) and house mouse (*Mus domesticus*; Pech *et al.* 1999). A positive linear relationship between the annual percentage population growth of a barn owl (*Tyto alba*) population and abundance of voles (*Microtus agrestis*), their main food, was reported by Taylor (1994) and this is converted in figure 4*e* to a relationship between population growth rate and vole abundance. In these examples of the mechanistic paradigm, density, previously seen as a surrogate of resource availability, has been replaced by a direct measure of the availability of food.

In other studies of the numerical response, food availability is replaced by a surrogate, such as rainfall. Examples have been reported for red kangaroo (Caughley *et al.* 1984; Bayliss 1985; Cairns & Grigg 1993; McCarthy 1996), Pacific black duck (*Anas superciliosa*) and maned duck (*Chenonetta jubata*; Briggs & Holmes 1988), magpie goose (Bayliss 1989), feral buffalo (*Bubalus bubalis*) (Freeland & Boulton 1990; Skeat 1990) and feral cattle (*Bos taurus*) (Skeat 1990), feral pig (Caley 1993) and house mouse (Brown & Singleton 1999). Lebreton & Clobert (1991) urge caution in simple regression analysis of the effects of environmental variables, because although estimates of slope are not biased, their variances are, and this leads to problems in significance testing.

The above examples of the mechanistic paradigm have been observational or correlative studies. Stronger inferences of cause and effect can be obtained using experiments. The effects on population dynamics of extrinsic factors have been studied in field-based experiments, such as adding food or removing predators (the snowshoe hare (*Lepus americanus*) studies of Krebs *et al.* (1995)) or controlling pathogens (the red grouse (*Lagopus lagopus*) and nematode (*Trichostrongylus tenuis*) studies of Hudson *et al.* (1998)). There is considerable scope for further testing of the cause and effect basis of relationships in the mechanistic paradigm with such experimental studies, especially the relationship between population growth rate and food availability (Eberhardt 1988).

Controversy between the supporters of the density and mechanistic paradigms dominated population ecology for decades during the middle 1900s, as described by Sinclair (1989, 1996), Krebs (1995) and Kingsland (1996). The debate was partly about approaches and partly about differences in terminology and understanding, especially limitation versus regulation (Sinclair 1989, 1996). The more recent emphasis on biological mechanisms has shed new light on population dynamics (Bjornstad & Grenfell 2001).

(c) *Analyses of demography and density*

Density and demography are linked in studies of density dependence operating on mortality, survival or fecundity; *k*-value analyses fall into this category as *k*-values are measures of mortality rates (see Sinclair (1989, 1996) for reviews of *k*-value analyses). Density dependence of fecundity is studied within *k*-value analysis by positing a maximum possible fecundity, and treating observed fecundities as falling short in consequence of 'mortality'. This manoeuvre, while awkward, is of course realistic in the case of abortions. There would seem no reason nowadays not to examine the relationships between life-history traits, density and population growth rate directly (Sibly & Smith 1998). For instance if we write r for population growth rate, x for density and b and m for two independent life-history traits, then

$$\frac{\mathrm{d}r}{\mathrm{d}x} = \frac{\partial r}{\partial b}\frac{\mathrm{d}b}{\mathrm{d}x} + \frac{\partial r}{\partial m}\frac{\mathrm{d}m}{\mathrm{d}x}. \tag{4.1}$$

This shows how changes in density ($\mathrm{d}x$) which change life-history traits (e.g. $\mathrm{d}m$) result in changes in population growth rate ($\mathrm{d}r$). In practice, $\mathrm{d}m/\mathrm{d}x$ would be measured as the regression coefficient in, for example, a *k*-value analysis. The contribution this makes to changing population growth rate is given by the sensitivity of population growth rate to the life-history trait ($\partial r/\partial m$). Formulae for sensitivities are available for many life histories (e.g. Caswell 2001; Sibly *et al.* 2000*a*), calculated by implicit differentiation of appropriate forms of the Euler–Lotka equation. Alternatively, the effect of density on population growth rate acting through demographic parameters can be described in density-dependent Leslie matrix models (Lebreton & Clobert 1991; Caswell 2001).

The life-history stages at which density-dependent effects occur in mammals were reviewed by Sinclair (1996) (table 1). Density was found to affect fecundity in over half the large terrestrial herbivores and large marine mammals, and in some species had effects in the early juvenile phase. By contrast, in small mammals and carnivores the effects of density were felt most in the late juvenile phase.

Demography and density have been linked for white-tailed deer (*Odocoileus virginianus*) in the modified logistic equations (table 2) of Hobbs *et al.* (2000) which assume positive effects of survival and fecundity on finite population growth rate (λ) and a linear negative effect of density on recruitment (the net result of fecundity and survival to first reproduction). Detailed field studies have demonstrated that density affects fecundity and mortality in red deer (*Cervus elaphus*; Clutton-Brock & Albon 1989; Clutton-Brock *et al.* 1997) and Soay sheep (*Ovis aries*; Clutton-Brock *et al.* 1997; Milner *et al.* 1999). Lebreton & Clobert (1991) have argued that it is more efficient to ana-

lyse the effect of density on population growth rate via its effects on demographic parameters.

Demography and density are used in population viability analyses to model the probable dynamics of small populations. In one implementation, in the software program VORTEX (Lacy 1993), there is the option to make the demographic parameters density dependent, and outputs include population growth rate and estimated mean time to extinction. VORTEX has been used to assess the feasibility of reintroducing wild boar (*Sus scrofa*) to Scotland (Howells & Edwards-Jones 1997).

(d) *Analyses of mechanisms and density*

The 'numerical response' discussed above in § 4b calculates the effects on population growth rate of food availability, and as noted there, availability may sometimes be best measured by dividing the population food supply by population density. Thus, McCarthy (1996) reported for red kangaroo a positive relationship between population growth rate and the resources/density ratio (a per capita numerical response), and Barlow & Norbury (2001) found in ferrets (*Mustela furo*) a negative relationship between population growth rate and the ferrets/rabbit ratio. These analyses derive ultimately from Leslie's (1948) ratio model of the predator–prey relationship, developed subsequently by May (1974), Caughley & Lawton (1981) and Caughley & Krebs (1983). In similar vein, Pech *et al.* (1999) showed for the house mouse (*M. domesticus*) a positive effect of food availability and a negative effect of density on population growth rate (table 2). The population growth rate of Yellowstone elk was positively related to autumn precipitation and negatively related to density (Coughenour & Singer 1996), and similarly population growth rate of the San Joaquin kit fox (*Vulpes macrotis mutica*) was positively related to annual growing season rainfall and negatively related to density (Dennis & Otten 2000). The analyses of McCarthy (1996) and of Barlow & Norbury (2001) assumed a multiplicative effect of food and the reciprocal of density, and the analyses of Coughenour & Singer (1996) and of Pech *et al.* (1999) assumed an additive effect of food and density. The finite rate of population growth (λ) of wolf (*Canis lupus*) populations has been negatively related to the ratio of wolves per deer (Eberhardt 1998; Eberhardt & Peterson 1999). All these studies corrected for density to produce a measure of food availability relative to abundance. If more animals were competing for the food, less was available to each, so there was competition for the resource. Density may, however, have negative effects on population growth rate additional to those of resource competition, as a result of interference competition. This is discussed further in § 5.

(e) *Analyses of demography and mechanisms*

The demographic and mechanistic approaches are linked by showing that demographic parameters are affected by variables from different trophic levels, e.g. food availability. The population growth rate of red fox has been related to separate effects of rainfall on fecundity and on survival (table 2; Pech *et al.* 1997). In a barn owl population in southern Scotland, Taylor (1994) showed that an increase in vole abundance increased fecundity (figure 5a), decreased adult mortality rate (figure 5b) and decreased juvenile mortality. The net effect of increasing
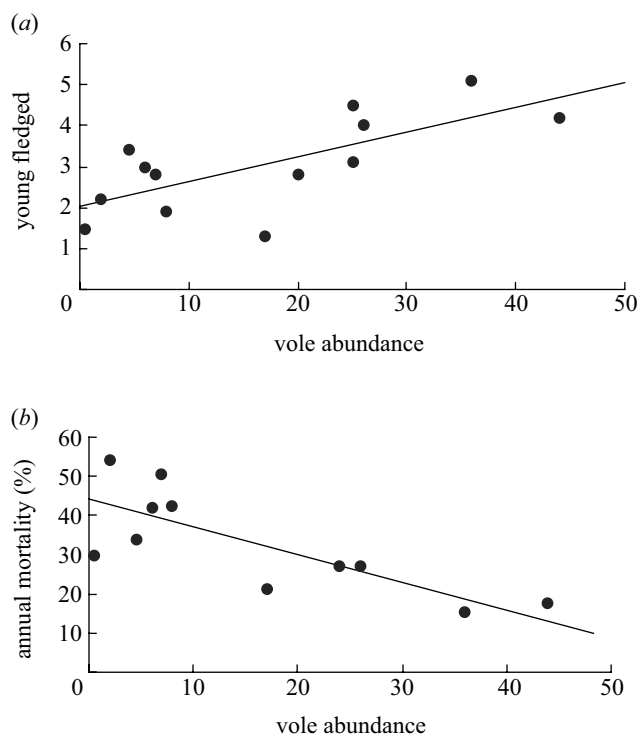

Figure 5. An example of use of the combined demographic and mechanistic paradigm. (*a*) First-brood young barn owls fledged per year per breeding pair plotted against abundance of voles. (*b*) Annual mortality of breeding adult barn owls and vole abundance. (After Taylor (1994).)

food abundance on population growth rate of the owls was positive (figure 4e). In a study of the northern spotted owl the finite population growth rate (λ) was estimated from survival and recruitment rates with these demographic rates influenced by climate and/or habitat features (Franklin *et al.* 2000). Food availability was not estimated.

(f) *Combined analyses of demography, mechanisms and density*

A full analysis shows the effects of trophic factors and density on demography and hence on population growth rate (table 2). For instance the rat, *Mastomys natalensis*, has dynamics determined by the effects of rainfall on fecundity and the effects of rainfall and density on survival (Leirs *et al.* 1997). The population dynamics of the kit fox are determined by demographic rates which are age-structured. White & Garrott (1999) showed that reproductive rates were positively related to food (leporid) availability (figure 6a), which in turn depended on rainfall. Juvenile mortality (figure 6b) was positively density dependent (because of predation by coyotes, *Canis latrans*). Soay sheep (*O. aries*) have population dynamics influenced by demography which in turn depends on weather conditions and density (Coulson *et al.* 2001). Harsh winters kill young and old sheep but only in high-density years (Bjornstad & Grenfell 2001).

The many mathematical models that have been used to describe relationships between population growth rate and demographic parameters, mechanistic and density effects suggest a need for a more detailed comparative evaluation of the fit of the models. Steps have been made in this direction, such as the comparative analysis by assessing
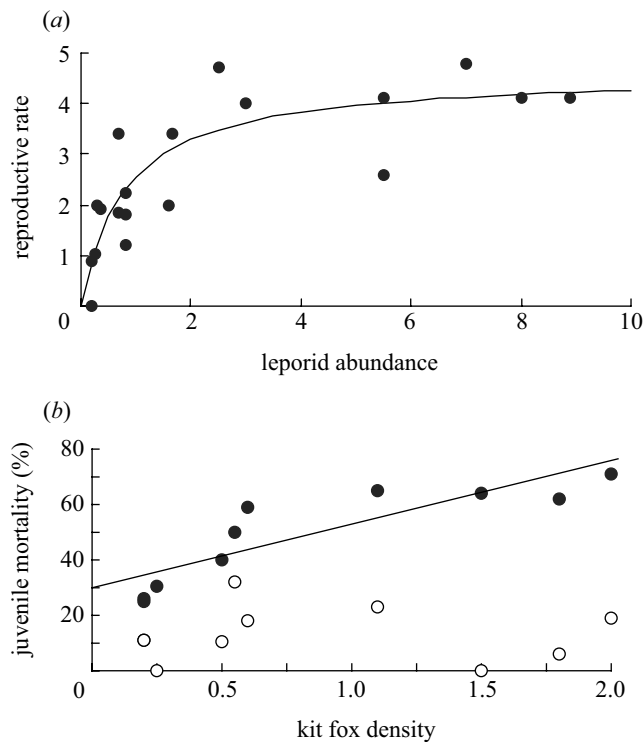
Figure 6. An example of the combined density, demographic and mechanistic paradigm. (*a*) Adult reproductive rate of kit fox and the abundance of leporids, their main food. (*b*) Juvenile mortality (%) of kit fox and kit fox density. The solid line and solid points demonstrate density-dependent mortality caused by predation by coyotes. The open circles show density independence associated with other causes of juvenile mortality. (After White & Garrott (1999).)

goodness of fit using coefficients of determination (r^2) (water buffalo and feral cattle (Skeat 1990), feral goats (*Capra hircus*; Maas 1997), red kangaroo populations (McCarthy 1996), *Mastomys* rat (Leirs *et al.* 1997) and the house mouse (Pech *et al.* 1999)). An alternative is to use an information theoretic model-selection procedure (kit fox; Dennis & Otten 2000).

5. CASE STUDY

The following example illustrates some of the ideas discussed in the paper so far, including density dependence, the numerical response and the action of environmental factors. The case study is based on the results of an experiment into the dynamics of a marine copepod, *Tisbe battagliai*. When the data were presented by Sibly *et al.* (2000*b*) they were analysed solely in terms of density dependence and environmental factors. Here, we analyse the numerical response, and show that some of the negative effects of population density are due to partitioning of food between competitors. It turns out, however, that interference competition further restricts access to resources and produces additional negative effects on population growth rate. The study provides an example of analysis in terms of mechanism and density.

(a) *Methods*
A factorial experimental design was used, comprising two factors (prey species richness and food con-

centration), each applied for 11 weeks to 10 replicate laboratory populations of the marine copepod *T. battagliai*. Food was either the alga *Isochrysis galbana*, which alone will sustain cultures indefinitely, or a mix of two algal species, *I. galbana* and *Rhodomonas reticulata*. Each food was given at two concentrations (1300 and 3250 μg C l^{-1}), replaced daily. Each *Tisbe* population was founded at low density (usually two pairs), and surviving copepods were transferred daily to a duplicate culture plate containing 10 ml of freshly prepared test solution. Population biomass was calculated as the sum of the dry weights of all age classes of copepods. Population growth rate (r) was estimated as the natural logarithm of (biomass in week $t + 1$)/(biomass in week t). Further details are given in Williams (1997) and Sibly *et al.* (2000*b*).

In analysing the numerical response a realistic measure of food availability is needed (§ 4b and § 4d). Here, we use food per copepod because carrying capacity increased linearly with population food supply in this experiment (Sibly *et al.* 2000*b*), suggesting that the copepods ate all the food supplied to them, at least at higher densities. The amount of food available to each copepod ('food per copepod') was therefore calculated as the population food supply divided by the copepod population biomass. This approach to measuring food availability when predators eat all the food supplied was introduced by Leslie (1948).

(b) *Results and discussion*
Population growth rate decreased as density increased, the expected density-dependent response (figure 7*a*). Population density alone did not account for all the observed variation, however, because population growth rate was higher at the higher food concentration (crosses above circles in figure 7*a*). This is readily understood because individuals living at higher food availability are expected to grow and reproduce faster, resulting in higher population growth rate.

The numerical responses of population growth rate to food availability (figure 7*b*) show that populations declined (population growth rate < 0) when food per copepod was low, but increased (population growth rate > 0) when food availability was higher. The increase in population growth rate with food supply was not linear, because as food increased, the copepods showed diminishing ability to transform extra food into further population growth. When the relationship is linearized using a log transformation (figure 7*c*), it appears that while food availability (food per copepod) accounts for a great deal of the variation in population growth rate, there is still some unexplained variation: note the crosses below the circles in figure 7*c*. The combined effects on population growth rate of food availability, prey species richness and population density, the data of figure 7*c*, were analysed by multiple regression, the regression equation being

population growth rate
$$= -2.89 + 1.46\log_{10}(\text{food per copepod})$$
$$+ 0.43 \text{ prey species richness} - 0.24 \text{ density.} \quad (5.1)$$

The multiple regression was highly significant ($F_{3,303} = 128.1$; $p < 0.0001$; $r^2_{adj} = 56\%$). In the regression, prey species richness was 1 or 2, density was $\log_{10}$ (copepod biomass) and other predictors were defined as in figure 7. Statistical significance of regression coefficients
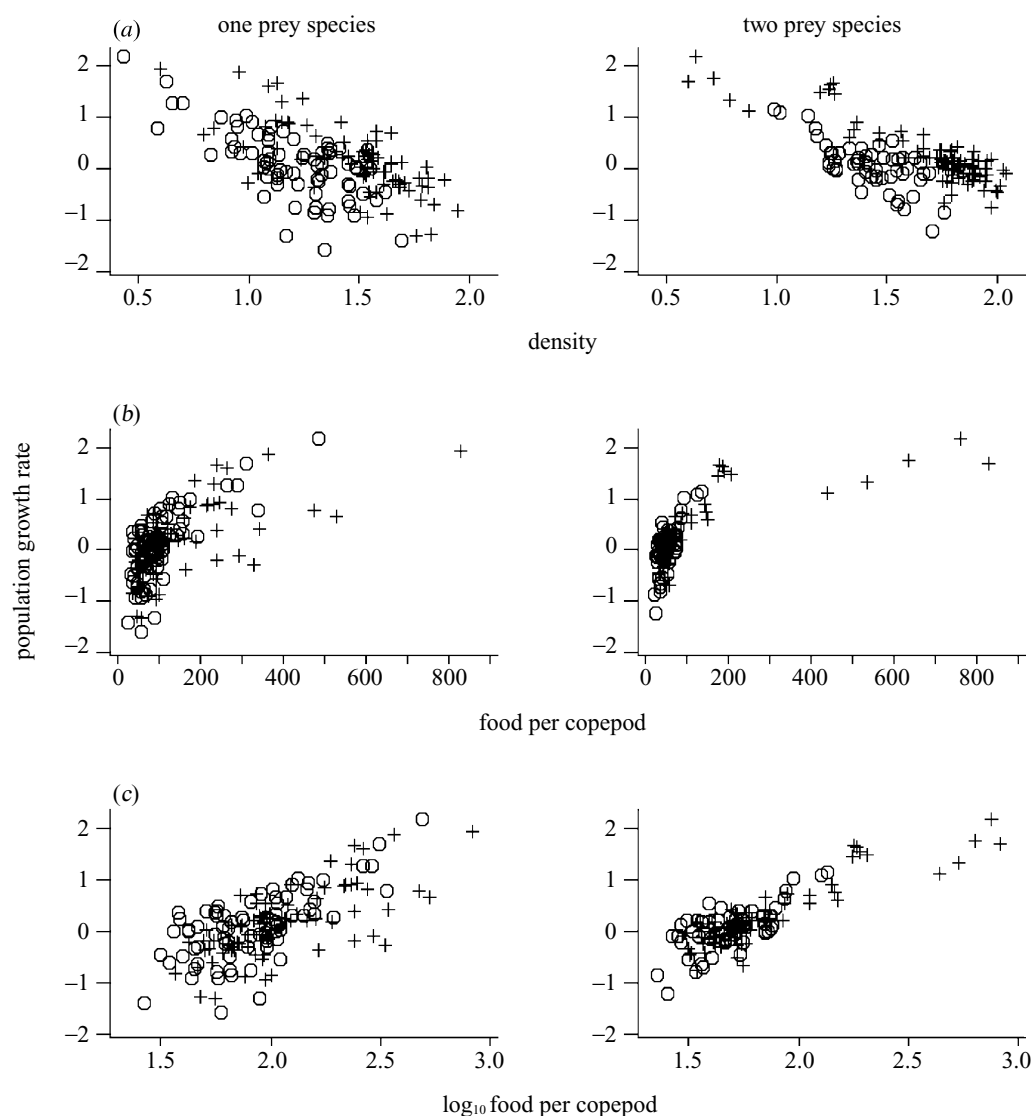
Figure 7. The determinants of population growth rate (r) in *Tisbe battagliai*. Population growth rate per week is plotted in relation to (a) density, measured as $\log_{10}$ copepod population biomass, μg; (b) food availability, measured as food supply per unit biomass of copepod, μg C l^{-1} μg^{-1}; (c) as (b) with food per copepod transformed to $\log_{10}$ on the x-axis. Food was either the alga *Isochrysis galbana* (left-hand panels) or a mix of two algal species (*I. galbana* and *Rhodomonas reticulata*, right-hand panels). Food concentrations were: crosses, 3250 μg C l^{-1}; circles, 1300 μg C l^{-1}.

were food per copepod: $t_{300} = 11.05$, $p < 0.0001$; prey species richness: $t_{300} = 8.46$, $p < 0.0001$; density: $t_{300} = -2.02$, $p < 0.05$. Plots of residuals against predictor variables show no indication of departure from model assumptions and there was no evidence of serial correlation (Durbin–Watson statistic 1.81).

The population's food supply is shared between its members through a process of resource competition. This is why we assess food availability by 'food per copepod'. The additional negative effects of density on population growth rate of *T. battagliai* could occur because of interference competition influencing reproductive performance, survival or somatic growth or foraging efficiency. Crowding is known to increase swimming activity in *T. battagliai*, with an associated increase in energy costs (Gaudy & Guerin 1982) possibly as a result of antagonism between larvae (Brand *et al.* 1985); crowding is also known to reduce reproductive output and depress larval viability (Fava & Crotti 1979; Zhang & Uhlig 1993) and to influence the sex ratio from a female bias at low density

to a male bias at high density in *T. holothuriae* (Hoppenheit 1976; Heath 1994). Negative effects of population density on population growth rate could occur in nature because of density-dependent effects of predators, parasites, pathogens, interspecific competitors and mutualists, but they were excluded in this experiment. We therefore conclude that the negative effects of density, additional to effects through food availability, were caused in this experiment by interference competition.

A graphical model of how food availability, density and prey species richness jointly affect population growth rate in this example is given in figure 8. Note that population growth rate is related to *per capita* food availability in contrast to the numerical responses of figure 4, which were not per capita relationships except in figure 4*h*. The results suggest that the ratio model of Leslie (1948) should be modified to incorporate other trophic effects, such as prey species richness and interference competition. For a given level of per capita food availability in the present study, increasing interference competition reduces population
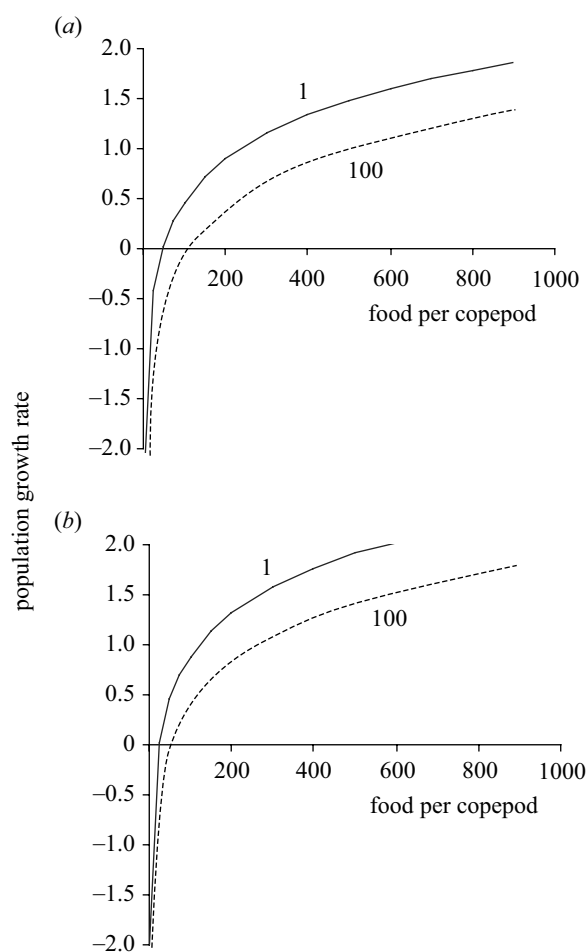
(a)

(b)

Figure 8. Graphical model showing how food availability (food per copepod), density and prey richness together determine population growth rate. The curves are derived directly from equation (5.1). Density has an indirect effect via food availability, and a direct negative effect through interference competition, illustrated here by the contrasting solid and dashed lines (solid line, copepod biomass = 1; dashed line, biomass = 100). (a) refers to one and (b) to two prey species.

growth rate (compare solid and dashed lines) and increases the level of food availability needed to support a stable (population growth rate = 0) population. Increasing prey species richness increases population growth rate and lowers the level of per capita food availability needed to support a stable population (figure 8a,b). This graphical model illustrates our results, and shows that the density-dependent and the mechanistic approaches of figures 3 and 4 are not incompatible. Instead, figure 8 shows that the two approaches are complementary and can be combined by joint analysis of the effects of mechanism and density, thus clarifying the mechanistic links that connect density, food availability and population growth rate.

6. APPLICATIONS IN CONSERVATION BIOLOGY, WILDLIFE MANAGEMENT, ECOTOXICOLOGY AND HUMAN DEMOGRAPHY

A better understanding of how to estimate population growth rate, and what determines population growth rate, is fundamental to the application of population growth rate to wildlife management and other topics in population ecology. The three classical applications of conservation, harvesting and pest control aim to increase, maintain and decrease population growth rate, respectively (Caughley 1976, 1977). Each of these applications also affects the frequency distribution of population growth rate (Hone 1999).

Of general concern in conservation biology is population performance at low density, which is the danger zone for endangered species. Population growth rate may be submaximal when density is low because of the difficulty of finding mates (the Allee effect; Courchamp *et al.* 1999; Stephens & Sutherland 1999) or because of an effect of predation on a prey population, wherein the predator has a type III functional response (Sinclair *et al.* 1998). An example of a decline in population growth rate at low density was described for pronghorn antelope (*Antilocapra americana*; Sinclair 1996). It had been thought that an Allee effect might have kept the North Atlantic right whale at low density, but this possibility has recently been eliminated by demographic analysis (Fujiwara & Caswell 2001). Another potentially important issue in conservation biology is the effect of inbreeding on population growth. Although there is debate about the practical significance of inbreeding in wild animal populations (Caughley 1994; Gundersen *et al.* 2001), it is easy to see that it could be important in small isolated populations, because we know from the Euler–Lotka equation that any reductions in fecundity and survival caused by inbreeding would necessarily depress population growth rate. Inbreeding is included as a determinant of population growth rate in population viability analyses such as Vortex (Howells & Edwards-Jones 1997). These topics in conservation biology focus on the small population size being a cause of conservation problems (Caughley 1994). Also of interest are the questions as to why the population is small, why it declined, and what management can do to reverse the decline.

Another common theme in conservation biology is the decline of populations because of high mortality caused by people. The rate of population growth of populations subject to intensive illegal harvest, such as the African elephant (*Loxodonta africana*) and black rhinoceros (*Diceros bicornis*) has been related to the effort expended in reducing or preventing poaching (Leader-Williams & Albon 1988). The dynamics of seabirds, such as the wandering albatross (*Diomedea exulans*), are influenced by fishing activities. For instance, Weimerskirch *et al.* (1997) showed that the rate of population decline depended on the cumulative number of longline fishing hooks set in albatross foraging areas. These studies use the mechanistic approach to identify the causes of population declines.

Also of general interest are the effects of habitat loss, and research here aims to identify the main features of wildlife habitats, and to establish the way they affect distribution and abundance, i.e. to characterize each species' ecological niche. Traditionally such research has involved measuring a large number of habitat features though typically not including food, predators, pathogens and competitors. In an encouraging effort to advance wildlife habitat studies and hence wildlife management in general, Morrison (2001) recommended a change to a focus on resources such as food, and their effects on survival and

reproduction. Such a focus would be a shift to demographic–mechanistic analysis as described above, and if implemented would lead to greater understanding of mechanisms determining population growth rate.

Wildlife management has two other fields of study, harvesting and pest control. These are conceptually similar (Caughley 1976, 1977), being based on ideas of reducing abundance and expecting compensatory responses in one or both of fecundity and survival. The sustainable harvest of a wildlife population growing according to logistic growth is a function of abundance, carrying capacity and the maximum rate of population growth (r_{max}; Caughley 1977). Species at the same abundance having the same carrying capacity have higher sustainable annual harvests if their r_{max} values are higher. When r_{max} is very low, as in long-lived species like whales and elephants, a sustained harvest may not be economic (Clark 1973; Caughley & Sinclair 1994). Variation in the effects of environmental factors lowers the level of sustained harvest (Bayliss 1989) and of course increases the variation of the harvest (Beddington & May 1977). Negative effects of harvesting on population growth rate have been described in white-tailed deer in Ontario (Fryxell *et al.* 1991), mallard (*Anas platyrhynchos*) in North America (Reynolds & Sauer 1991), and moose (*Alces alces*) in Norway (Solberg *et al.* 1999).

Pest control is another field where population growth rate is central (Hone 1994); indeed, several early population ecologists (e.g. Howard, Fiske, Nicholson, Andrewartha and Birch) studied pests. A pest control programme may become a sustained harvest if pest abundance is reduced and kept at low levels. Pest populations may, however, adapt to control, for example, by developing resistance to pesticides. The rate of development of resistance depends on population growth rate and generation interval (Dobson & May 1986).

Population growth rate can also be seen as the key unifying concept in ecotoxicology (Walker *et al.* 2001). Thus, pollutants can be defined as environmental chemicals that exceed normal background levels and have the potential to adversely affect birth, growth or mortality rates, with consequent reduction in population growth rate. Defined in this way, pollutants appear as a particular case of environmental stressors (see § 2). Although the impact of pollutants on organisms is studied within ecotoxicology at different organizational levels, from biochemistry through to communities, each with its own measure of pollutant effect, it can be argued that population growth rate provides the best summary statistic. After reviewing the experimental literature, Forbes & Calow (1999) conclude that population growth rate is a better measure of responses to toxicants than are individual-level effects, because it integrates potentially complex interactions among life-history traits and provides a more relevant measure of ecological impact. By contrast, Sutherland & Norris (2002) suggest that there are advantages in building up from the level of individual behaviour to a population level perspective on population growth rate.

Where complex models of the determinants of population growth rate are used for management purposes, model validation is clearly of crucial importance: how do we know we can believe the model's predictions? For model validation, long-term field datasets are needed,

ideally from independent sites/populations. In this respect it is interesting to revisit the predictions of the classic early paper of Pearl & Reed (1920), in which they rediscovered the logistic equation and applied it to data on the size of the human population of the continental United States. They implied that the logistic equation results from human competition for the means of subsistence, namely food, clothing material and fuel. They calculated the carrying capacity of the continental United States as 197 million, but noted that at the levels of production then obtaining it would be necessary to import about half the food supply. Their projections look a little low now, but this can be attributed to technological advances. There would seem to be a need for more studies of the type initiated by Pearl & Reed (1920) that consider the match between global levels of sustainable resources and individual levels of human consumption (cf. Lutz & Qiang 2002). A recent projection for the global human population based on existing downward trends in fertility indicates that population growth will slow over the coming decades, and peak in *ca.* 2070 at a population size around nine billion (Lutz *et al.* 2001).

Further examples of model validation can be found in the modelling of a *Mastomys* rat (Leirs *et al.* 1997) and of house mouse population dynamics (Pech *et al.* 1999). In each study, observed rodent abundances were compared with predictions from a model of dynamics constructed using data from the same site but at an earlier time period. Model testing and validation are clearly essential wherever possible to increase the reliability of model projections.

7. CONCLUSION

Our central thesis is that population growth rate is the unifying variable linking the various facets of population ecology; thus analyses of population regulation, density dependence, resource and interference competition and the effects of environmental stress are all best undertaken with population growth rate as the response variable. Throughout, we have emphasized the key role of statistical analyses of observational or experimental data, and we hope in the future to see more studies analysed by multiple regression and allied nonlinear techniques to estimate and distinguish the effects on population growth rate of food availability, environmental stressors, density and so on. Effects of time-lags can also, in principle, be treated within this framework. Such analyses are needed not only to improve the quality of the underlying science, but also to increase the realism and accuracy of prediction in key applied areas such as conservation, wildlife management and ecotoxicology. Much practical concern in controlling, managing or conserving populations has to do with limiting, managing or encouraging population growth; one key indicator of effect in such enterprises is population growth rate. There are, however, still many unresolved issues in identifying the causes of variation in population growth rate, stemming largely from the need to distinguish the effects of many causal factors with distinctly limited datasets. Much challenging research remains.

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