THE ROYAL
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Two complementary paradigms for analysing population dynamics

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To understand why population growth rate is sometimes positive and sometimes negative, ecologists have adopted two main approaches. The most common approach is through the density paradigm by plotting population growth rate against population density. The second approach is through the mechanistic paradigm by plotting population growth rate against the relevant ecological processes affecting the population. The density paradigm is applied *a posteriori*, works sometimes but not always and is remarkably useless in solving management problems or in providing an understanding of why populations change in size. The mechanistic paradigm investigates the factors that supposedly drive density changes and is identical to Caughley's declining population paradigm of conservation biology. The assumption that we can uncover invariant relationships between population growth rate and some other variables is an article of faith. Numerous commercial fishery applications have failed to find the invariant relationships between stock and recruitment that are predicted by the density paradigm. Environmental variation is the rule, and non-equilibrial dynamics should force us to look for the mechanisms of population change. If multiple factors determine changes in population density, there can be no predictability in either of these paradigms and we will become environmental historians rather than scientists with useful generalizations for the population problems of this century. Defining our questions clearly and adopting an experimental approach with crisp alternative hypotheses and adequate controls will be essential to building useful generalizations for solving the practical problems of population management in fisheries, wildlife and conservation.

Keywords: population regulation; density dependence; population limitation; experimental approach; carrying capacity; equilibrium

1. INTRODUCTION

For more than 100 years, ecologists have been estimating populations of animals, beginning with those of economic value, and have tried to make sense of the resulting data. How to make sense of quantitative population data is not immediately clear. Once an ecologist has two successive estimates of population size, he or she follows the first law of quantitative ecology, which is to divide one number by the other, producing the finite population growth rate (λ) that Sibly & Hone (2002) described. However, what to do next?

This is the critical step. Being good scientists, most ecologists would wish to predict the size of the population growth rate and would proceed in one of two directions to do this. First, they could adopt the density paradigm of Sibly & Hone (2002) and plot population growth rate against population density. (The concept of a paradigm as promulgated by Thomas Kuhn (1970) has been used in many ways, and one might argue that the paradigms discussed here are better labelled as 'conceptual approaches'. I have no quarrel with this comment and I use the term 'paradigm' as shorthand for what ecologists do (cf. den Boer & Reddingius (1996).) Alternatively, they could adopt the mechanistic paradigm and plot population growth rate against an ecological factor, such as the amount of food available per capita, which may explain the change. What are the problems and what are the advantages of going in one direction rather than another?

However, let us drop back for a moment to consider a whole set of assumptions that we have already made about our population. Many of these assumptions are discussed in other papers of this issue.

(i) We assume that we can define a population unambiguously. This can be a problem with open populations.
(ii) We assume that we can measure population size accurately and can convert this to absolute population density. This is more difficult than many ecologists think.
(iii) We assume that we have defined a biologically relevant time-step over which to measure the population growth rate. The time-step is not always obvious (Lewellen & Vessey 1998).
(iv) We assume, at least initially, that all of the individuals in the population have equal impact, regardless of sex, age and genetic composition. We can relax this assumption later.
(v) We assume a uniformity of nature, such that whatever variable we can find to predict population growth rate will be the critical variable at other times and in other places. This assumption of repeatability is rarely tested.

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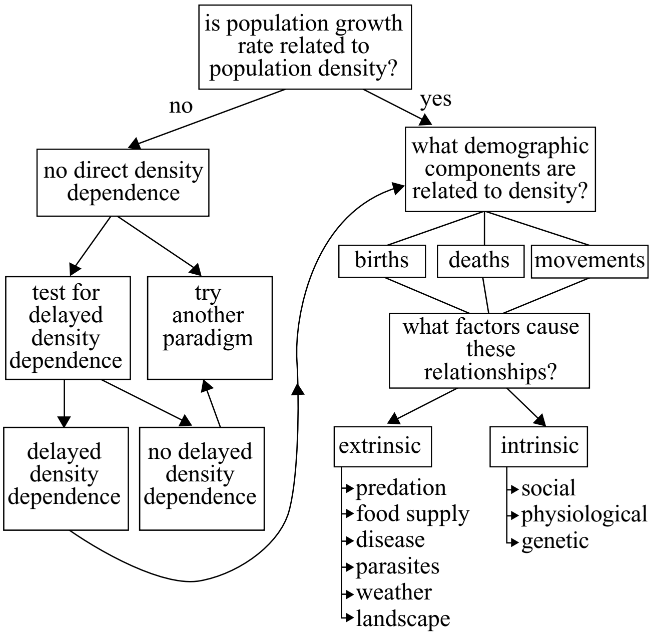

Figure 1. Decision tree for the density paradigm of population regulation.

(vi) We assume that we can substitute time for space, or space for time, so that there is a uniform predictive function.

All of these assumptions operate within the equilibrium paradigm, and all of them are, potentially, hazardous if we assume a non-equilibrium world view in which transient dynamics are the rule rather than the exception. In this paper, I discuss primarily assumptions (iv)–(vi).

Given that population ecologists must start somewhere, we admit to these assumptions for the moment and ask which direction to follow.

2. DENSITY PARADIGM

The density paradigm instructs our ecologist to plot population growth rate against population density. At this point, our ecologist might become suspicious because the same variable appears in both the x- and the y-axis. However, we are assured by some biometricians that this is not a problem (Griffiths 1998) so we disregard this potential problem. If the density data are a time-series of one or more plots, much now depends on the trend shown by the data. If density is monotonically falling (or rising), it will not be possible to estimate the equilibrium point, except by extrapolation. If the population does not vary much in density, the relationship may well look like a shotgun pattern.

The decision tree (figure 1) illustrates how to proceed. If there is a negative relationship between population growth rate and density, the next question is, which of the demographic components drive this relationship? Given that data are available to answer this question, the next step is to find out which factors, or combinations of factors, cause these changes in births, deaths or movements (if the population is not closed). All of this is what I will call the standard analysis procedure of the density paradigm. What happens if there is no pattern in the plot of growth rate against density?

We are assured by both theoreticians and empiricists (e.g. Nicholson 1933; Sinclair 1989; Turchin 1999) that there must be a negative relationship between population growth rate and density. If this is true, it raises an interesting question in respect of the relationship of theory in ecology to empirical data. If there must be a relationship, the problem of the field ecologist is to describe this relationship in terms of its slope and intercept. The problem is not to ask if indeed such a relationship exists (Murray 1999, 2000). There is no alternative hypothesis to test.

The first strategy that is adopted after finding that there is no relationship between population growth rate and population density is to invoke delayed density dependence (Turchin 1990). This is a reasonable strategy because virtually every interaction in population ecology involves some time delays. However, this strategy opens a Pandora's Box because data analysis begins to take on the form of data dredging since we have no *a priori* way of knowing what the critical time delays might be. There are elegant methods of time-series analysis that can be applied to population data to estimate the integrated time-lags in a series of density estimates (Stenseth *et al.* 1998), but it is far from clear how to translate these estimated time-lags into ecological understanding. Do predators respond to changes in prey abundance instantly, via movements (e.g. Korpimäki 1994) or more slowly via recruitment processes (e.g. O'Donoghue *et al.* 1997; Eberhardt & Peterson 1999)?

If delayed density dependence can be identified in a time-series of population densities, we can proceed in the same manner as the standard analysis procedure of the density paradigm and try to determine what causes these time-lags. The remaining problem is what to do with cases in which no direct or delayed density dependence can be identified in a time-series. In theory, this situation cannot occur, but it seems to arise frequently enough to cause endless arguments in the literature about the means of testing for direct and delayed density dependence (den Boer & Reddingius 1989; Dennis & Taper 1994). Most ecologists in this situation would not give up studying population regulation, but would switch to the second paradigm discussed by Sibly & Hone (2002), the mechanistic paradigm.

3. MECHANISTIC PARADIGM

The mechanistic paradigm can be viewed in two ways. Sibly & Hone (2002) consider it an elaboration of the density paradigm, as shown in figure 1, and indicate that one can proceed to this level of analysis for populations that are well studied in a reductionist manner. Krebs (1995), by contrast, viewed the mechanistic paradigm as an alternative to the conventional approach through the density paradigm. The mechanistic paradigm short-circuited the search for density dependence, on the assumption that no predictive science of population dynamics could be founded on describing relationships between vital rates and population density without specifying the ecological mechanisms driving these rates.

The key question seems to be whether any density-dependent relationship is repeatable in time or space. I

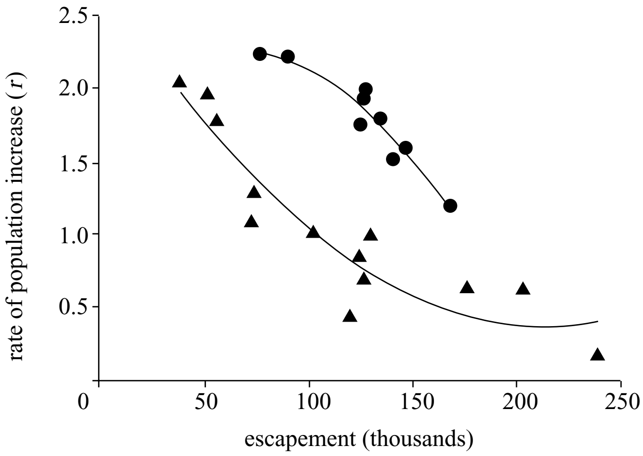

Figure 2. Non-repeatability of the relationship between population density and rate of population growth for Columbia River chinook salmon (*Oncorynchus tshawytscha*) over time. You could not manage this fishery in the 1950s using the relationship from the 1940s; this was because both oceanic and freshwater environments had changed. Upper curve illustrates data for the period 1938–1946; lower curve illustrates data for the period 1947–1959. (Data from Van Hyning 1974.)

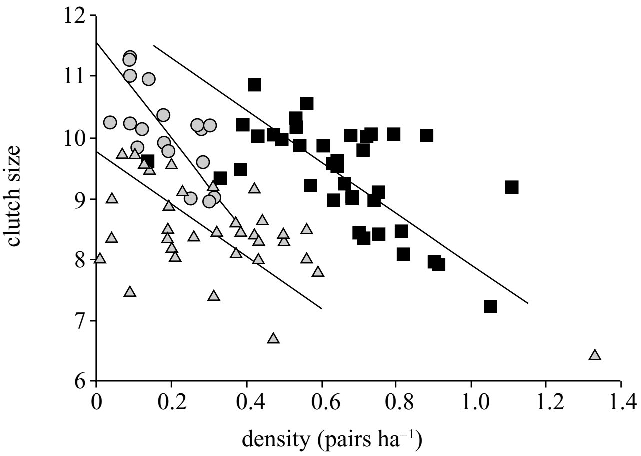

Figure 3. Non-repeatability of the density-dependent relationship between clutch size and population density for great tits (*Parus major*) in three woodlands in the Netherlands. You cannot use the density-dependent relationship from one area to predict clutch size in another area. Circles, Hoge Velue A; triangles, Vlieland; squares, Hoge Velue B. (Data courtesy of Both 1998.)

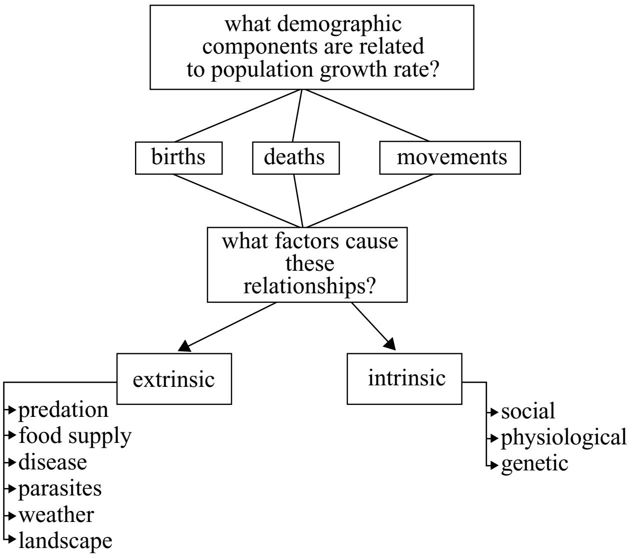

Figure 4. Decision tree for the mechanistic paradigm of population regulation. The key difference from figure 1 is that we ask what demographic factors are related to population growth rate, not population density.

have been able to find few ecologists who have asked this question. The most well-studied groups in this regard might be commercial fishes, birds and large mammals. The Pacific salmon fisheries of western North America are managed partly on the basis of Ricker curves, which plot stock versus recruitment and are another form of a plot for density dependence. The clear conclusion from much research work is that these Ricker curves cannot be specified as a fixed relationship either temporally, in the same river system, or spatially, between different rivers (Walters 1987). Figure 2 gives one illustration for a Chinook salmon stock from the Columbia River system. The Ricker curve for this salmon stock has changed over time, which is not surprising since there has been so much human influence on this river system that many extrinsic environmental factors, as well as intrinsic factors (Ricker 1982), have changed over time.

Considerable work on bird populations allows us to test whether density-dependent relationships are repeatable over time and space. Both (2000) reviewed studies on density dependence in clutch size in passerine birds and found that, for the great tit (*Parus major*) in Europe, only 12 out of 24 long-term studies showed significant density dependence in clutch size. So even within the same species, there is no consistency of density dependence among different populations. Moreover, even in those areas with density-dependent clutch size, no consistent relationship applied to all areas (figure 3). This means that one cannot use the data from one area to predict what to expect in another area—density dependence is area-specific. The conclusion is that density-dependent relationships occur often but are not repeatable and are an unreliable basis for a predictive ecology.

Figure 4 illustrates the flow diagram for the mechanistic paradigm. It looks identical to figure 1, but has one very significant difference: instead of asking what demographic components are related to population density, it asks which are related to population growth rate. In cases in which density is closely related to population growth rate, there will be no difference between these two approaches. However, in every non-equilibrial system, the differences can be very large. The critical assumption again depends on whether there is an equilibrium point for the system under study. The mechanistic paradigm is best adapted to short-term considerations in which questions about ultimate equilibrium states are not particularly relevant. It is closely related to the approach to population dynamics typified by the Leslie matrix (Caswell 1989).

The mechanistic paradigm asks how individual animals are influenced by the factors affecting density and recognizes that individuals vary in their responses to predators, food supplies, parasites and weather, as well as in their

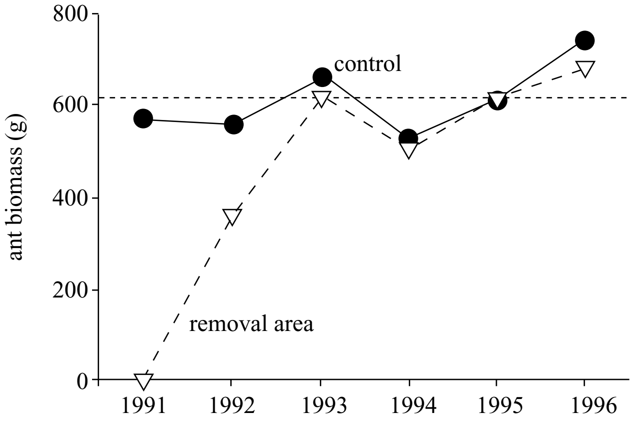

Figure 5. Density convergence experiment on the monogynous (territorial) form of the fire ant *Solenopsis invicta* in Florida. All colonies in core areas of 1018 m^2 were removed from six plots in the spring of 1991. Recolonization was followed by measuring spring biomass of ants in each of the next five years. Convergence was 60% after one year and complete after two years, demonstrating density regulation back to the average control density of 613 g per 1018 m^2 measured on six unmanipulated plots. The dotted line shows the average control ant biomass. Control biomass showed a coefficient of variation of 13%. (Data from Adams & Tschinkel 2001.)

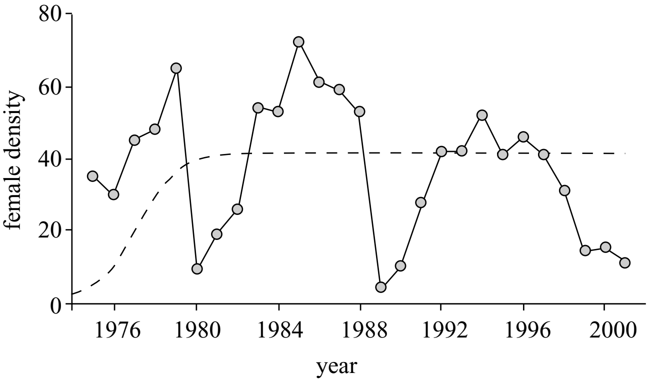

Figure 6. Density of song sparrow (*Melospiza melodia*) females on Mandarte Island, British Columbia, 1975–2001. Data courtesy of J. N. M. Smith and P. Arcese. The dashed line is the logistic equation fitted to these data by Sæther *et al.* (2000) and is clearly a very poor descriptor of the population trace. Female density is given per 6 ha.

social standing within the population. Behavioural ecology has made a particularly strong contribution to our understanding of individual differences and is pushing strongly to utilize this understanding to enrich population dynamics.

Let us consider four case studies in order to contrast the density paradigm with the mechanistic paradigm.

(a) *Fire ants*

The fire ant (*Solenopsis invicta*) is an introduced pest in the southern United States. It occurs in two forms, a monogyne form with a single queen and a polygyne form with multiple queens per nest. Monogyne fire ants are territorial, whereas polygyne fire ants are non-territorial and reach much higher average densities (Tschinkel 1998). Adams & Tschinkel (2001) carried out a removal experiment in an area of Florida occupied by the monogyne form. They removed all fire ant colonies from a circular core area with a radius of 18 m and then followed the recolonization for a period of five years (figure 5). Recolonization was rapid and ant biomass returned to control (equilibrium) values within two years, illustrating a density compensation driven by territoriality. Adjacent ant colonies expanded and new colonies arose from the dispersal of new queens. Population biomass in this area varied slightly from year to year (coefficient of variation of density 13%), but was on average quite stable. This experiment illustrates very well the standard analysis procedure of the density paradigm, which works well in this fire ant system. It also illustrates the mechanistic paradigm because the population carrying capacity was set by territoriality among colonies.

(b) *Song sparrows*

The song sparrow (*Melospiza melodia*) on Mandarte Island, British Columbia, has been the subject of a long-term study since 1962 and has been reported by Smith & Arcese (1986), Arcese & Smith (1988), Smith (1988) and many others. Figure 6 illustrates the population density changes in the song sparrow on this 6 ha island since 1975. The population trend consists of periods of three to four years of population growth followed by a catastrophic 1-year decline, and this has been repeated three times in the last 25 years. The first two of these population declines were correlated with severe winter weather; the third was not. Arcese & Smith (1988) showed that fledgling production declines at high density in this population, and these demographic symptoms could be relieved by adding food to territories. This population shows a clear difference between the density and the mechanistic paradigms. If we ask what prevents population increase, we answer that reproductive output is reduced as density increases and the mechanism limiting reproductive output is food shortage. If we ask what causes the largest changes in population growth rates, we answer that the major or key factor is severe winter mortality. The population trace of this species is the net result of negative feedback of high density on reproductive output and occasional major winter mortality. Does this population have an equilibrium density? We can ask what would happen to this population if there were no winter losses. The answer to this question is hypothetical and problematic because none of the identified density-dependent relationships does more than slow down the rate of population increase; they do not set it to zero (Arcese & Smith 1988). To complicate the matter more, this island is part of a metapopulation of song sparrows in the general region and while immigration is rare, it is critical for the maintenance of genetic diversity and for recovery from low numbers (Smith *et al.* 1996). Recent analyses (P. Arcese and J. N. M. Smith, personal communication) suggest that immigrants strongly affect the population growth rate because their outbred offspring have much higher survival and reproductive rates compared with birds with no immigrant genes in their lineage. The key to winter losses seems to be the genetic quality of individual birds. To summarize, the song sparrow on Mandarte Island is a very well-studied bird population and we have a good understanding of its population dynamics,

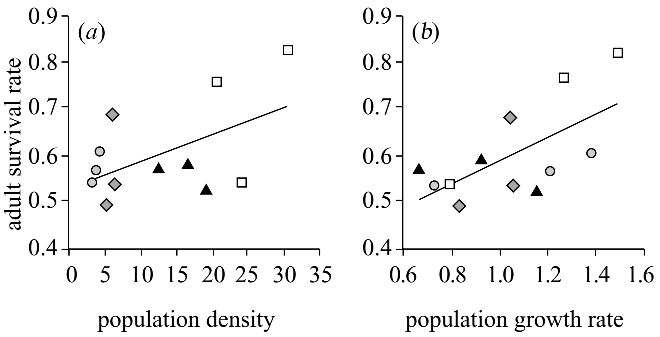

Figure 7. Relationship of annual adult survival rate to (*a*) population density and (*b*) population growth rate (λ) for house sparrows (*Passer domesticus*) on four islands in Hegeland, north Norway, 1993–1996 (circles, Gjærøy; squares, Infre Kvarøy; triangles, Ytre Kvarøy; diamonds, Hestmannøy). The density paradigm would expect adult survival rate to fall as population density rose. However, the opposite was observed. (Data from Sæther *et al.* 1999.)

which can be well described by both the density and the mechanistic paradigms. If, for some reason, we had to manage this population, we would try to manipulate the level of outbreeding to maintain high individual quality. Density dependence in this population does not prevent instability.

(c) *House sparrow*

Sæther *et al.* (1999) have analysed the demography of the house sparrow (*Passer domesticus*) on four islands off north Norway over a period of four years. They were particularly interested in metapopulation dynamics, but their detailed studies allow us to ask how well we can understand their results with the approach suggested by the density paradigm. Sæther *et al.* (1999) measured breeding population density by direct enumeration, and, from 1993 to 1996, estimated reproductive success (number of offspring fledged per female), juvenile survival over the first year and annual adult survival rates. None of these vital rates was negatively related to population density (figure 7). All three variables—reproductive success ($r = 0.40$), juvenile survival rate ($r = 0.51$) and adult survival ($r = 0.65$)—were positively related to population growth rates, and jointly determined whether or not a particular island was a source or a sink population in any given year. There was no correlation between population density and population growth rate. Sæther *et al.* (1999) suggested that the large year-to-year variations in the rates of increase on the different islands were associated with weather variation, but it is not clear if the impact of weather was direct or through changes in food supplies. Thus, the exact mechanisms causing change are not known for these populations. The suggestion for these house sparrow populations is that the density paradigm does not work, and the mechanistic paradigm is not sufficiently evaluated to show whether a predictive model based on particular mechanisms could be defined.

(d) *Large mammals*

The density paradigm is particularly well defined for large mammals (Gaillard *et al.* 1998). Figure 8 illustrates the curvilinear pattern of density dependence postulated for large mammals by Fowler (1987). Juvenile survival is predicted to be most sensitive to population density, while adult survival and reproductive rates are predicted to begin to decline only at high densities. This paradigm is well accepted by many large-mammal ecologists (Huff & Varley 1999) and we can use the extensive data from North American elk to test this paradigm.

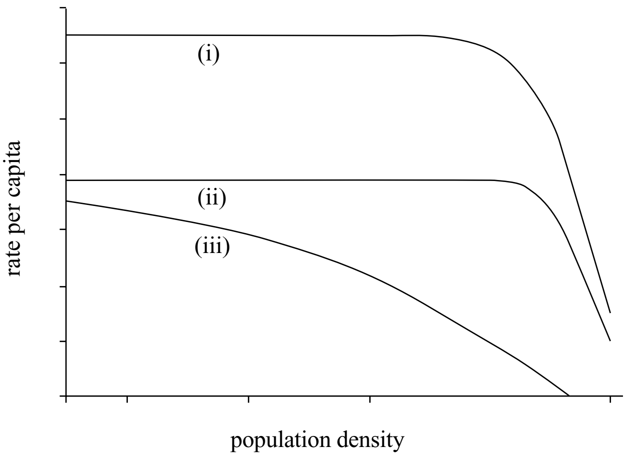

Figure 8. The density paradigm model for large mammals as articulated by Fowler (1987). In this model reproductive output and adult survival rates are not affected by density until the population almost reaches carrying capacity. Graph (i) represents reproduction; graph (ii) represents adult survival and graph (iii) juvenile survival.

Native ungulates in North American national parks have been subjected to a variety of management policies during the last 100 years (Houston 1982). In 1968, Yellowstone National Park instituted a new management policy, (‘natural-regulation’ management) which was a hands-off policy that permitted ungulates to reach an unmanipulated population level. The natural-regulation management policy assumes first that density-dependent changes in birth and death rates will occur as ungulates increase and reach a dynamic stable equilibrium and second, that this equilibrium will be reached without extensive impacts on vegetation, soils or other species of animals in the community (Singer *et al.* 1998). The Northern Yellowstone elk population has been particularly well studied (Houston 1982). As elk populations increased after control by shooting in the Park was stopped in 1968, Houston (1982) found a slight reduction in pregnancy rates and an increase in the age at sexual maturity at high elk densities, as well as a major density-dependent decline in calf survival during the first year of life. These density-dependent processes would tend to move the elk population toward an equilibrium density.

Wolves, a major predator until Europeans arrived, were missing from the Yellowstone ecosystem after the 1920s until they were reintroduced in the early 1990s. Mechanisms of population limitation for large mammals are simplified if major predators are missing from a system and the major candidate mechanisms remaining are disease, food shortage, weather and social factors. Ungulates are rarely candidates for social regulation (Wolff 1997) and we are left with only three potential factors to consider. Brucellosis is of minor importance to this elk herd

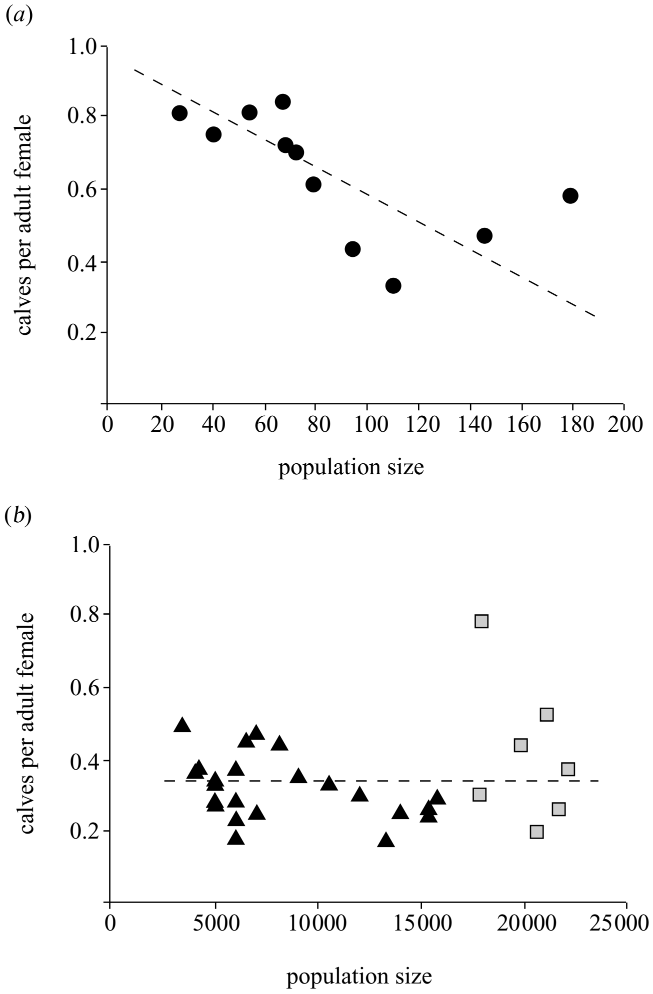

Figure 9. Non-repeatability of density-dependent relationships in North American elk from (*a*) Eastern Washington ($r^2 = 0.44$) and (*b*) Northern Yellowstone ($r^2 = 0.03$; squares represent 1985–1991, triangles represent 1951–1979). The ratio of calves per adult female measures the combination of natality and juvenile survival during the first six months of life. Data from Eberhardt *et al.* 1996; Singer *et al.* 1997; Houston 1982. The results are not consistent with the density paradigm model for large mammals (Fowler 1987).

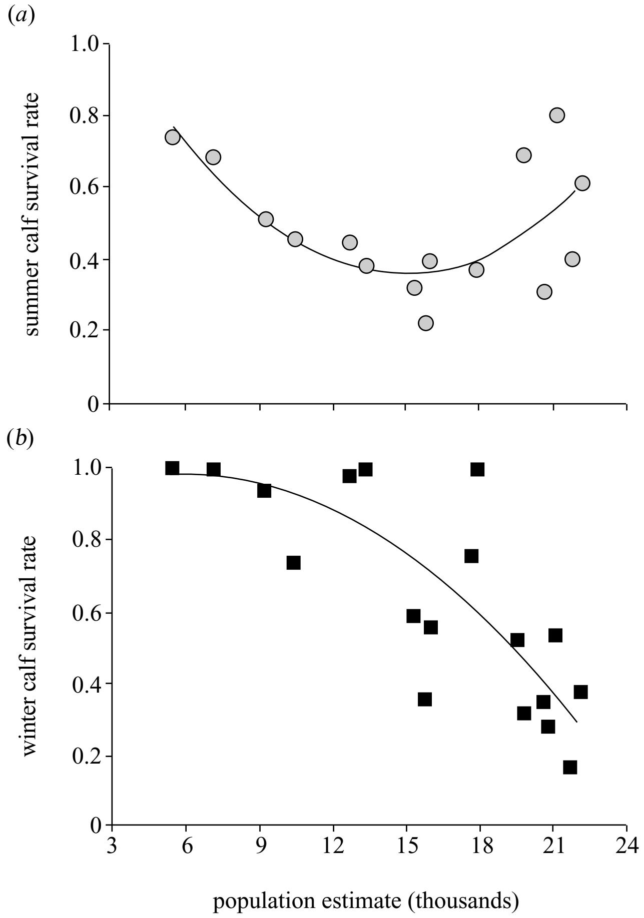

Figure 10. (*a*) Summer and (*b*) winter elk calf survival in the Northern Yellowstone national park, 1968–1990, in relation to the number of elk in the herd. Sample size is 16 years for summer, and 19 years for winter data. (Data from Singer *et al.* 1997.)

(Cheville *et al.* 1998) and we are left with only two potential mechanisms to drive demography.

Can we describe the population dynamics of the Northern Yellowstone elk herd by the density paradigm? Data on elk populations (figure 9) do not fit the simple density-dependent paradigm of Fowler (1987). Eberhardt *et al.* (1996) followed the population growth of an elk population in eastern Washington and found a density-dependent decline in calf recruitment at very low elk densities. This decline was not due to a reproductive failure, since all adult females were pregnant, and they suggested that calf mortality in the first few weeks of life might be the mechanism behind the density-dependent response shown in figure 9*a*. Predation might be the mechanism of loss but no detailed studies were possible to test this speculation. In contrast to this view of elk density dependence, Singer *et al.* (1997) found that summer calf mortality was only loosely related to elk numbers ($r^2 = 0.29$, $n = 17$ years), but winter calf losses were much higher at high densities ($r^2 = 0.65$) (figure 10).

There has been only a vague relationship between population size and rate of population growth in the Northern Yellowstone elk populations for the past 20 years (figure 11). The reason for this is that two climatic variables have a strong influence on demographic parameters (Huff & Varley 1999). Severe winter weather increases calf mortality rates (Houston 1982). A combined regression model with elk density and winter weather severity can explain, statistically, 73% of the variability in winter calf losses (Coughenour & Singer 1996). Summer precipitation has a strong impact on summer plant production and, consequently, on calf summer survival. The overall picture for the North Yellowstone elk population is of a population with vague density dependence buffeted by variable weather conditions that impact on summer grazing conditions and winter snow levels. The recent introduction of wolves to the Yellowstone ecosystem is predicted to reduce elk numbers, but the predicted reduction in equilibrium density varies from *ca.* 10–20% reduction (Mack & Singer 1993), to a 50–66% reduction (Gasaway *et al.* 1992). It is clear that the northern Yellowstone elk population has not yet reached its equilibrium and may never get there because of stochastic variation in weather

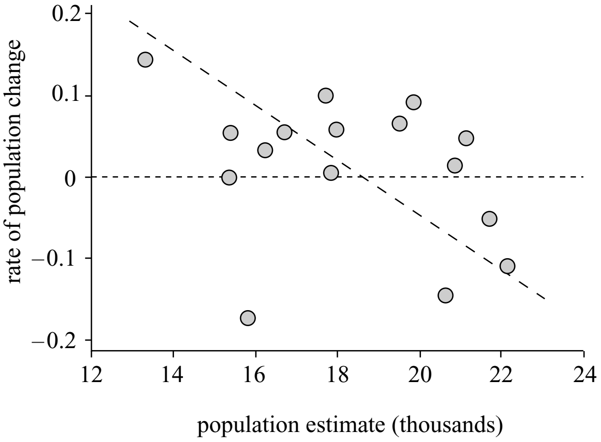

Figure 11. Northern Yellowstone elk population, 1975–1992, rate of population change (r) versus estimated population size, $r^2 = 0.12$, $n = 16$. Data corrected for hunting removals. Data from Cheville *et al.* 1998; Singer *et al.* 1997. The horizontal line divides increasing populations above from declining populations below. A negative trend is apparent but with great variability.

as well as human influences in the areas surrounding Yellowstone.

My perception is that the density paradigm for large mammals does not work well (Peterson 1999), in spite of the common belief that it does. Bison populations in Yellowstone show no clear evidence of density dependence (Singer *et al.* 1998). The moose–wolf interaction on Isle Royale in Lake Superior has not provided a good fit to the large-mammal paradigm illustrated in figure 8 (Peterson 1999).

(e) *Two contrary views*

There are two points of view, that argue strongly against the mechanistic paradigm. The multiple factor hypothesis of population regulation (Holmes 1995) argues that there are no necessary conditions or predictable relationships between ecological factors like predation and disease and changes in population density. What happens in one population in a given year cannot be predicted from its density, from what happened last year, or from any set of mechanistic relationships. The multiple factor viewpoint, in its extreme form, is not consistent with the density paradigm, which expects population growth rate to fall in a predictable way with population density. If the multiple factor hypothesis is correct, it explains the failure of ecologists to achieve a predictive theory of population dynamics—there can be no such theory. Such a view would appear to condemn ecologists to *a posteriori* descriptions of population changes.

A different type of multiple factor hypothesis suggests that several factors will interact to determine population changes (Lidicker 1994). This view appears to be stated as a polar opposite to the single-factor hypothesis and seems to be based on a confusion of the distinction between necessary and sufficient conditions. Most hypotheses in population regulation do not clearly state whether the proposed mechanism is necessary or sufficient or both, so this confusion is understandable. The problem reduces to what factors are assumed constantly present as background sources of mortality for a population, and this is confounded even more when no distinction is made between additive and compensatory forms of loss.

The multiple factor hypothesis of population regulation is an important viewpoint and we do not yet have enough data on populations of the same species in different environments to know how general our explanations might be. In the bad-case scenario, predictive relationships for one population will not apply to another in a different region. In the worst-case scenario, predictive relationships for one population will not even apply to the same population in later years, so that every population is unique. If this turns out to be correct, ecologists will become environmental historians instead of scientists, charting how populations change with no predictive insights. At the heart of both the density and the mechanistic paradigms is the faith that, although there are many variables that impact on a population, the major controlling variables will show strong signals through the noise of contingent events. We do not know at this time whether this belief is well placed.

A second contrary view is that climate change will invalidate all of the relationships that we ecologists can establish between populations and their ecological agents of control. This view argues that we are now in a state of transient dynamics with no possible predictability of future trends or outcomes. Again, in this case we have no way of determining whether this belief is correct or not, and all we can try to do is falsify it by achieving the goals of the density paradigm and the mechanistic paradigm.

4. CONCLUSIONS

If not all population ecologists can agree that populations are regulated (Murray 2000), we might, at least, hope to find that there are predictive relationships between ecological mechanisms and population growth rates. We can demonstrate these kinds of predictions for only a few population systems, and our goal should be to increase the breadth and variety of case studies of mechanistic population regulation. A first cut can be to distinguish populations whose growth rate is limited top–down by predators and diseases from those whose growth rate is limited bottom–up by nutrients or food supplies (Kay 1998; Power 1992).

My suggestions here are parallel to those of Chitty (1996), who has argued for the view that comparative studies can untangle the Gordian knot of density dependence by searching for mechanistic differences between experimental and control populations. The key here is to use the experimental approach, particularly manipulative experiments where they are possible, and to consider at all times multiple working hypotheses. Our experiments ought to be designed to evaluate several alternative hypotheses, not just our favourite one.

One of the enigmas of the study of population dynamics is how, historically, it has become so entwined with the ideas of density dependence. The major thrust of ecology over the past 50 years has been to show that population density can be decomposed into sets of individuals with variable traits and interesting ecological interactions. This study of individual differences has brought behavioural ecology into the limelight over the past 20 years, and is now doing the same for disease ecology. Not all individuals are the same, as George Orwell told us long ago, and yet we must aggregate these individuals into a density if we are to use density dependence as a central pillar in our theory of population dynamics. My plea here is to concentrate our efforts on finding out in the short-term why population growth rate is positive or negative. In doing this, we can abandon the worries about equilibrium that have caused so much controversy and put more interesting experimental biology into population dynamics. By concentrating on what factors affect population growth rate, we can provide a science that will be useful to decision makers and managers of the diversity of populations on our planet.

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