THE ROYAL SOCIETY

Behavioural models of population growth rates: implications for conservation and prediction

William J. Sutherland[1]* and Ken Norris[2]

[1]*Centre for Ecology, Evolution and Conservation, University of East Anglia, Norwich NR4 7TJ, UK*
[2]*School of Animal & Microbial Sciences, University of Reading, Whiteknights, PO Box 228, Reading, RG6 6AJ, UK*

Conservation biologists often wish to predict how vertebrate populations will respond to local or global changes in conditions such as those resulting from sea-level rise, deforestation, exploitation, genetically modified crops, global warming, human disturbance or from conservation activities. Predicting the consequences of such changes almost always requires understanding the population growth rate and the density dependence. Traditional means of directly measuring density dependence are often extremely difficult and have the problem that if the environment changes then it is necessary to remeasure the density dependence. We describe an alternative approach that does not require such long datasets and can be used to predict the density dependence under novel conditions. Game theory can be used to describe behavioural decisions that individuals make in response to interference, prey depletion, territorial behaviour or social dominance, and the resultant fitness consequences. It is then possible to predict how survival or reproductive output changes with population size. From this we can then make predictions about the responses of populations to environmental changes. We will illustrate how this can be applied to a range of species and a range of applied problems.

Keywords: population growth rate; density dependence; game theory; predictive models

1. INTRODUCTION

A common justification of ecological research is that it allows predictions of the consequences of environmental change. There is a considerable need to be able to make realistic and justifiable predictions. With many environmental issues, such as genetically modified (GM) crops, climate change, habitat loss and exploitation, there is an urgent need to be able to produce quantified predictions. Such quantified predictions are essential for policy-makers if they are to consider ecological consequences within their framework of social and economic costs and benefits (Sutherland & Watkinson 2001).

Conservation biologists regularly carry out analyses (usually referred to as population-viability analyses) to evaluate the likelihood of a population persisting in the presence of existing or novel conditions (for reviews see Beissinger & Westphal (1998); Norris & Stillman (2002)). These are then often used to determine the conservation measures required to maintain the population, such as the release of additional individuals, a reduction in exploitation levels or the expansion of the available habitat (see Beissinger (1995); Green *et al.* (1996); Hiraldo *et al.* (1996); Root (1998) for a range of avian examples that illustrate these applications).

The basic elements of all population models are the population growth rate in the absence of interspecific competition, the extent of density dependence and the

level of stochasticity (Burgman *et al.* 1992). However, in practice, population-viability analyses very rarely use measured parameters for density dependence, particularly when models are applied to the management of endangered species due to the paucity of data (see Green & Hirons (1991)). We shall also argue that the frequently used methods for estimating population growth have serious problems associated with them.

In this paper we shall review the importance of density dependence in answering conservation questions, describe the problems associated with conventional methods of studying density dependence and then review the potential of using behaviour-based models of population ecology to answer ecological and conservation questions.

2. DENSITY-DEPENDENT POPULATION GROWTH— ITS MEASUREMENT AND USE IN CONSERVATION

(a) *Importance of density dependence*

Density dependence is obviously central to any understanding of population ecology. It thus follows that it is essential for predicting the consequences of environmental change (Sibly *et al.* 2000). For a population showing no consistent increase or decrease over time, if density dependence is absent then any reduction in the population growth rate results in eventual extinction while any increase leads to an infinite population.

The importance of density dependence is most straightforward when considering the consequences of a density-independent change in vital rates, such as a change in the levels of exploitation, mortality due to pollution, or breeding output resulting from predators or natural disasters. It

1273

is then conceptually straightforward to consider the change in population size resulting from a change in the vital rate assuming that the density-dependent responses stay constant.

The population response to habitat loss (Sutherland 1996*a*), habitat deterioration (Sutherland 1998) or human disturbance (Gill *et al.* 1996) depends critically upon the density dependence. In the absence of any density dependence, individuals would just move out of the lost–deteriorated–disturbed patches and occur at higher densities within the remaining–unaffected–undisturbed patches. There will only be population-level effects if the density dependence operates and the higher population densities in the unaffected patches result in increased mortality or reduced reproductive output. Thus Sutherland (1996*a*) showed how the extent to which habitat loss for migratory birds resulted in population declines (as usually stated by conservation lobbying groups objecting to the change in land use) or birds simply being accommodated elsewhere (as usually stated by those favouring some alternative use of the disputed land) depends upon the relative strengths of density dependence in the breeding and wintering grounds. By estimating these strengths it is then possible to estimate the relative importance of these two processes and thus show how quantitative predictions can replace verbal arguments.

Density dependence is similarly central to the understanding of exploitation. In the absence of any density dependence any increase in mortality due to increased exploitation inexorably leads to extinction. Thus, the essence of exploitation is that it reduces population size and as a result of density dependence the population grows and it is this growth that can be exploited.

(b) Problems in measuring density dependence
There are three mains ways of studying how population growth rate changes with density, each of which has associated problems.

The first way is the most common and analyses a time-series of population estimates. As has been realized for some time, a serious problem that undermines such techniques results from the fact that populations are usually estimated with some level of measurement error (Bulmer 1975; Royama 1981). As a year with an atypically high level of measurement error is likely to be followed by a year with a more typical measurement error, then the analysis of rate of population change (N_{t+1}/N_t) plotted against population size (N_t) can result in inflated measures of density dependence. Although this phenomenon has been appreciated and there are a range of suggested solutions, it is still extremely difficult to overcome this problem if the measurement error is unknown (Shenk *et al.* 1998).

A second way of studying density dependence is to correlate some aspect of fitness (such as mortality or fecundity) against population size (e.g. Paradis *et al.* 2002). This has the considerable advantage of overcoming the statistical problems associated with measurement error of time-series as described above. A problem is that vertebrate populations usually show little variation in abundance over the study period, unlike many insect populations. Even if abundance does vary over time, the range of variation may be insufficient to reveal the under-

lying density-dependent function. One problem, especially with relatively short datasets, is that the population is often either increasing or decreasing over time and the correlation with a similar change in some component of the demography may be an artefact and not causal. Another problem is that the population changes are driven by changes in demography, which may be due to changes in the weather, food supply, predation level and other unknown factors. Thus periods of, say high food abundance, may result in both a high survival rate and high population size. Correlating the survival rate and population size will then provide underestimates of the strength of density dependence.

The third way of studying density dependence is to carry out field experiments. This is an excellent means, but it is rarely feasible to carry out well designed replicated experiments on vertebrate populations (but see Smith *et al.* (2000)).

(c) Problems in measuring population growth
The intrinsic rate of population increase r_{max} (or R_{max} in the finite form) is an important measure. It determines the ability of a population to survive stochastic events or respond to environmental change or exploitation.

In the absence of an assessment of the level of density dependence, it is often impossible to assess the intrinsic growth rate. A common method is to measure life-history parameters, such as age-specific mortality and fecundity, and use these with a population matrix to determine the population growth rate (e.g. Lande 1988; Hiraldo *et al.* 1996). For populations near an equilibrium level, the value of population growth must inevitably be close to 1— and for plant populations this is typically the case even though the actual values are likely to be considerably higher (R. Freckleton and A. R. Watkinson, personal communication).

As we shall describe in § 3, a problem with applying the conventional means of population ecology to conservation issues is that even if it is possible to quantify the values of the intrinsic rate of population growth and of density dependence under existing conditions, these are likely to alter as a result of the conservation issue under consideration. Indeed, it is often these precise alterations that bring about the resulting changes in population size.

The problems of estimating the population growth rate are probably clearest in the determination of sustainable levels of exploitation. As a rough approximation, a proportion of individuals equivalent to the population growth rate can be removed each year in a sustainable manner. For a population at its natural equilibrium there will be no population growth and thus no exploitation is possible (Caughley 1977). However, it is common to calculate the population growth for an unexploited population at naturally occurring levels and then use this to calculate the response to exploitation. As the growth is negligible in unexploited populations at natural levels this inevitably leads to the conclusion that the population is sensitive to very small levels of exploitation, even though this may not be the case.

There will be maximum population growth at very low population levels (unless an Allee effect operates (Courchamp *et al.* 1999; Stephens & Sutherland 1999)), yet this value is sometimes recommended for calculating

sustainable exploitation (Robinson & Redford 1991). An extreme version of this problem arises from measuring the population growth rate under optimal conditions (Robinson & Redford 1991). For example, measures of reproductive output from zoos, such as age of first breeding, age of last breeding, number of young produced per attempt, have been used to estimate the possible breeding success. Such estimates may well overestimate the breeding success of typical individuals in natural conditions. The measure that is required for sensible sustainable exploitation is the population growth rate at the exploited population size. It is often assumed that the highest sustainable growth will occur at *ca.* 60% of the unexploited population size (e.g. Caughley & Gunn 1995; Robinson & Redford 1991).

3. EVEN PERFECT KNOWLEDGE OF THE DEMOGRAPHY MAY BE INSUFFICIENT

As described in § 2, there are a range of problems associated with measuring population growth rate and density dependence. What if these problems could be overcome and there was a complete knowledge of population growth rate and density dependence? In this section we shall argue that even this rarely achievable ideal is insufficient.

In order to describe density-dependent processes adequately in wild populations, the ideal would be to follow populations that are changing in size over time from very low abundances to abundance levels at which there is evidence of regulation such that the population no longer grows. Ironically, conservation biology often offers such opportunities when populations are restored to areas from which they have been extirpated. For example, the Mauritius kestrel (*Falco punctatus*) population was reduced to only four known individuals in the wild in 1974 (Temple 1977) due to a combination of pollution and habitat loss. A recovery programme was initiated in the early 1970s, and in the late 1980s captive-reared individuals were released into the Bambous mountains in the east of Mauritius, a former part of the kestrels' range from which the last wild individual was recorded in 1955 (Jones *et al.* 2002). Since its initiation, this population has been intensively monitored using colour-marked individuals, and the complete life histories of virtually every bird that has existed in the population are known. A recent analysis indicated that very few (i.e. less than 10) nesting attempts in the history of the population have been missed (Groombridge *et al.* 2001), indicating that the demographic information available for this population is perhaps more complete than for any other vertebrate.

There is evidence that this kestrel population is now showing signs of regulation (figure 1). This means that it is possible to examine density dependence in particular vital rates as the population has grown in size. For example, the annual survival probability of wild-bred kestrels in their first year of life has declined dramatically as the population size has increased (figure 1*a*). Similar analyses could be repeated for other aspects of the birds' life history, and the relative importance of different density-dependent processes in regulating abundance assessed. This would permit us to model, in an extraordinary degree of detail, the dynamics of this population, at
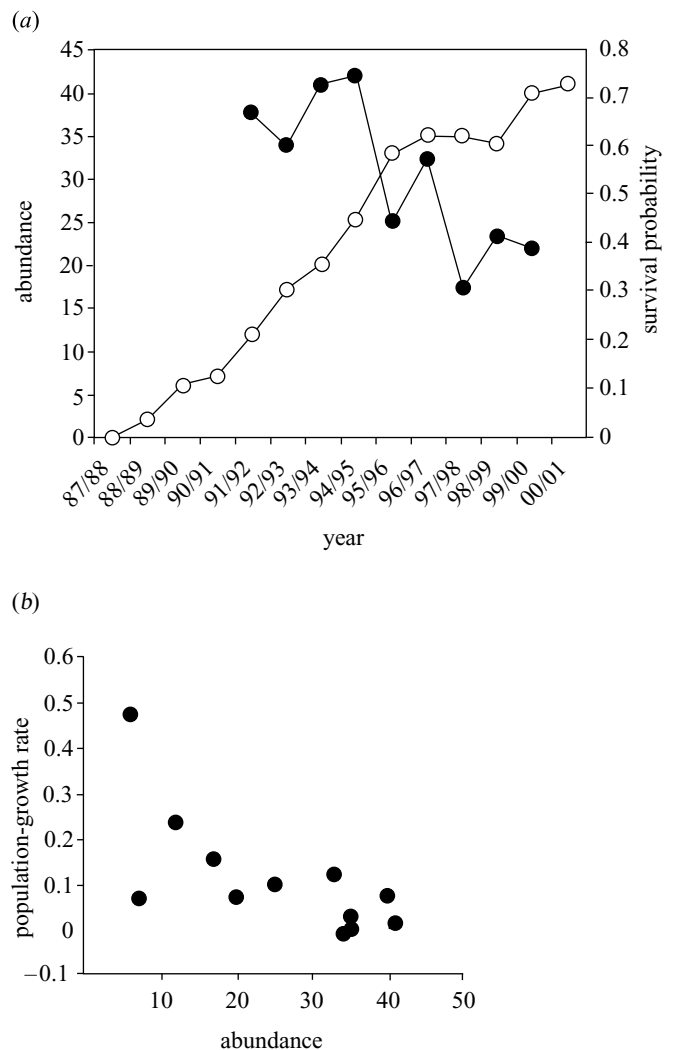

Figure 1. Time-series trends in the abundance and survival of a reintroduced population of Mauritius kestrels. (*a*) The population increase in the Bambous region of Mauritius and the juvenile survival probability rate (estimated using a mark-resighting analysis). White circles show abundance and black circles show juvenile survival rate. (*b*) The density-dependent population-growth rate with $r = -0.694$ and $p = 0.012$. Note that censuses were complete, so there is no sampling error in the abundance estimates (M. Nicoll and C. G. Jones, unpublished data).

least in terms of regulatory processes. What insights might such a demographic model provide?

Conservation biologists use demographic models for two broad purposes—risk assessment and designing effective conservation management. The former aims to quantify the risk faced by a population as a result of a particular environmental change, whereas the latter concerns quantifying the potential benefits of planned changes to the environment. The question then becomes, how useful would our demographic model be for reliably predicting the impact of environmental change? The answer is that it depends on the extent to which environmental changes influence density-dependent processes. For example, one potential future threat to the persistence of the kestrel population at Bambous is an increase in the frequency or severity of cyclones. This is essentially a stochastic process, and one that could, at least in principle, act in a

density-independent way. Heavy rain associated with cyclones can flood nest sites, destroying the nesting attempt and thereby reducing fledgling output. Our demographic model could then be used to estimate the rate at which population size is likely to recover following a cyclone, and examine how population persistence might be affected by the frequency and severity (in terms of nest mortality) of cyclonic events.

By contrast, it is also conceivable that cyclones could interact with density-dependent processes. For example, imagine that the negative density dependence in juvenile survival (figure 1a) is driven by competition for food, such that vulnerable juveniles are more likely to starve when competing for food at relatively high population size. Further, imagine that during the heavy rain and wind associated with cyclones hunting efficiency is severely reduced, exacerbating the starvation risk of vulnerable juveniles, particularly at relatively high population sizes. This mechanism would mean that the form of density-dependent juvenile survival varied with respect to cyclonic conditions. Although a hypothetical example, data from long-term population studies are beginning to document such interactions between the environment and density-dependent processes (e.g. Soay sheep, *Ovis aries*; Coulson *et al.* 2001). The consequence of such a process in the kestrel population would be that the observed density dependence in juvenile survival would represent the interactive effects of both population density and cyclone frequency–severity on survival, the exact survival rates observed in the wild being determined by the frequency and severity of cyclones, and the form of density dependence under different cyclone conditions. If in the future cyclone frequency and severity increases, then the negative effects of population size on juvenile survival would become more severe, but in a way that is unlikely be predictable from past population behaviour because the new combinations of environmental (cyclone frequency and severity) and population density experienced by the population are likely to be unique. Therefore, without detailed data that allow us to describe interactions between density-dependent processes and the environment, the predictive ability of any demographic model, even based on a very complete dataset describing the current population, would become compromised when applied to novel future conditions. This lack of data is the general rule for demographic information on endangered or threatened species, even in well-studied taxa such as birds (Green & Hirons 1991).

This is a very specific example, but illustrates two crucially important general principles. First, even a demographic model based on a complete set of data such as those available for the Bambous kestrel population would only provide reliable predictions about how the population (in terms of changes in abundance over time) would respond to future environmental change if the change influenced vital rates via a mechanism that acted completely independently of any density-dependent processes operating in the population. If the environmental change alters the form of density dependence in a way that is unpredictable from past population behaviour (and this is likely to be the general rule), then the model is no longer reliable. Second, it is clear from the hypothetical example that understanding how the environmental change is likely to impact on demography depends on developing an understanding of the mechanisms driving density dependence in particular vital rates. How can this be done in a way that provides insights for conservation?

4. A ROLE FOR BEHAVIOUR-BASED MODELS?

Behaviour-based models have been largely developed by behavioural ecologists interested in understanding decisions taken by animals competing for resources (e.g. Sutherland 1996b; Goss-Custard & Sutherland 1997; Pettifor *et al.* 2000a). These models examine the fitness consequences of various alternative decisions animals can take, and determine evolutionarily stable strategies (ESSs) that individuals within a population should adopt in order to maximize their fitness. When the 'optimal' decision for one individual is affected by decisions taken by others in the population, game theoretical approaches have been used to determine the ESSs. Perhaps the most influential and widely used theoretical frameworks employed to date are the ideal-free and ideal-despotic models originally formulated by Fretwell & Lucas (1970).

Behaviour-based models are linked to density dependence in demography because they describe the behavioural mechanisms underlying density-dependent processes. They can be used to derive density-dependent processes directly by including in a particular model a relationship that describes how fitness components such as survival or fecundity vary in relation to the resources acquired by individuals in the population. For example, simple prey depletion models of competition for food resources assume that individuals starve or emigrate if they fail to achieve a threshold rate of food intake (Sutherland & Anderson 1993; Pettifor *et al.* 2000a). In this way, density dependence in survival or fecundity can be derived from a behaviour-based model simply by re-running the model for variable numbers of competitors (e.g. Stillman *et al.* 2000).

Why is this approach potentially more useful for understanding the impact of environmental change than the more classical approach of measuring density dependence directly? We have already shown that the classical approach suffers from the problem that the form of density-dependent processes are likely to change in the future if environmental change affects habitat quality, and by implication resource availability. Behaviour-based models are robust in that models can be re-run for any plausible future environmental change scenarios because the principle that individuals attempt to maximize their fitness does not change. The environment provides the stage on which behavioural games designed to maximize an individual's fitness (by acquiring resources) are played out between individuals. If the stage changes, the individuals still 'play' by the same fitness maximization rule, although the demographic outcome of the game may be different. What insights might understanding such games provide to the conservation biologist? To answer this question we illustrate the approaches taken to address a range of specific conservation problems using behaviour-based models.

(a) *Mortality, sustainable population sizes and competition for food resources*

Shorebirds overwinter in vast numbers on the coasts of northwest Europe. These habitats provide essential food

resources that permit birds to survive the winter, and fuel their spring and autumn migrations to and from their high-latitude breeding grounds. The large numbers of birds means that many coastal sites are recognized as being of international importance for particular shorebird populations, and so are regarded as being habitats of high conservation value. Man also exploits these coastal habitats. Intertidal land is reclaimed to support development projects and so habitat is permanently lost. Habitat change also occurs because of a range of activities that include the dredging of sediment, the commercial exploitation of intertidal invertebrates and recreation.

As these habitats have high conservation value, conservationists often want to assess whether particular human activities are potentially damaging to particular bird populations. The ecological impact of habitat loss and habitat change occurs via a reduction in food availability. If food availability is limiting, then such changes might reduce the number of birds an area could support over a given time-period, or increase the mortality rate. Risk assessment, therefore, requires predictions about the magnitude of such changes in sustainable numbers or demography following habitat loss or change. We illustrate using two particular examples how behaviour-based models can be used to make such an assessment.

Oystercatchers (*Haematopus ostralegus*) spend the winter on predominantly sandy estuaries, where they are specialist consumers of bivalve molluscs, such as the edible cockle (*Cerastoderma edule*) and blue mussel (*Mytilus edulis*) (Goss-Custard 1996). The behavioural dynamics of competition between oystercatchers for food have been studied in detail in the Exe Estuary in southwestern England over the last 20 years. This work has produced a behaviour-based model that describes mechanisms of competition in this population, and derives estimates of mortality resulting from the impact competition has on the energy budgets of individual birds (Stillman *et al.* 2000). The model includes the effects of spatial and temporal variation in food availability, kleptoparasitism, feeding method, foraging efficiency, prey depletion and a range of other environmental factors on food intake, and has provided relatively accurate estimates of density-dependent mortality (figure 2). It is worth noting that the behaviour-based model was constructed using data collected prior to 1980, when the oystercatcher population size on the Exe Estuary was low and relatively stable (see figure 2). Subsequently, the number of birds wintering on the Exe increased, and the behaviour-based model predicted relatively accurately the resultant increase in mortality, even though the model was constructed with data prior to the population increase. A classical description of density-dependent mortality of the same initial period would have been inadequate to predict how mortality would have responded as population size increased. This highlights the potential importance of explicitly considering behavioural mechanisms in studying density-dependent processes.

The bivalve molluscs consumed by oystercatchers are also harvested commercially for human consumption by fishermen. Stillman *et al.* (2001) used the behaviour-based model described in the previous paragraph to examine various aspects of fishery management on the mortality of oystercatchers exploiting the same prey population. Fish-
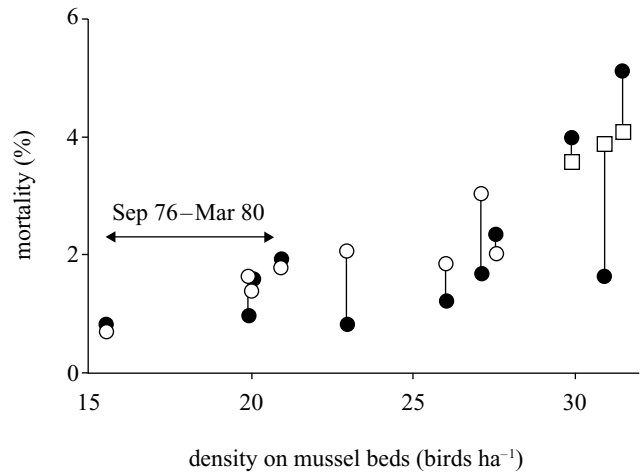
Figure 2. The predicted and observed density-dependent survival rates for oystercatchers on the Exe Estuary. Note that the model was created using data from the low densities occurring in 1976–80 but explains the subsequent response reasonably well. The black circles indicate observed rates and the white circles and squares indicate model predictions, but different estimates of food availability. (From Stillman *et al.* 2000.)

ermen reduce food availability to the birds and so can exacerbate any density-dependent mortality by potentially increasing the risk of density-dependent starvation. Such interactions could be complex, and so would be virtually impossible to predict using previous observations of mortality rate in relation to population density and the activities of fishermen. Furthermore, risk assessment often involves asking how the population might respond to novel future conditions, such as an increase in fishing effort or a change in fishing methods. Such questions cannot be addressed using empirical data of population behaviour in the past. Figure 3a gives examples of some of the specific predictions that can be generated from the behaviour-based model when applied to fishery management issues such as fishing effort and fishing methods. Furthermore, the model can also be used to examine interactions between density-dependent mortality (due to starvation) and environmental conditions. For example, density-dependent mortality is likely to be more severe in oystercatchers in cold winters because competition for food resources at high population densities would lead to a greater number of birds failing to acquire sufficient resources and starving than would be the case in a mild winter. This has implications for assessing the impact of fishing because an increase in fishing effort, for example, would be more severe in a cold winter than in a mild one. Assessing such an impact using observations of past population behaviour is made difficult because the population may not have experienced the precise range of density, environmental and fishery management conditions that need to be assessed. However, the behaviour-based model can be used to generate predictions for a range of conditions, irrespective of whether these have been experienced by the population previously (e.g. figure 3b).

An alternative approach to risk assessment when changes in habitat availability affect food resources is to estimate the extent to which sustainable population sizes might decline if habitat is lost or degraded. Behaviour-
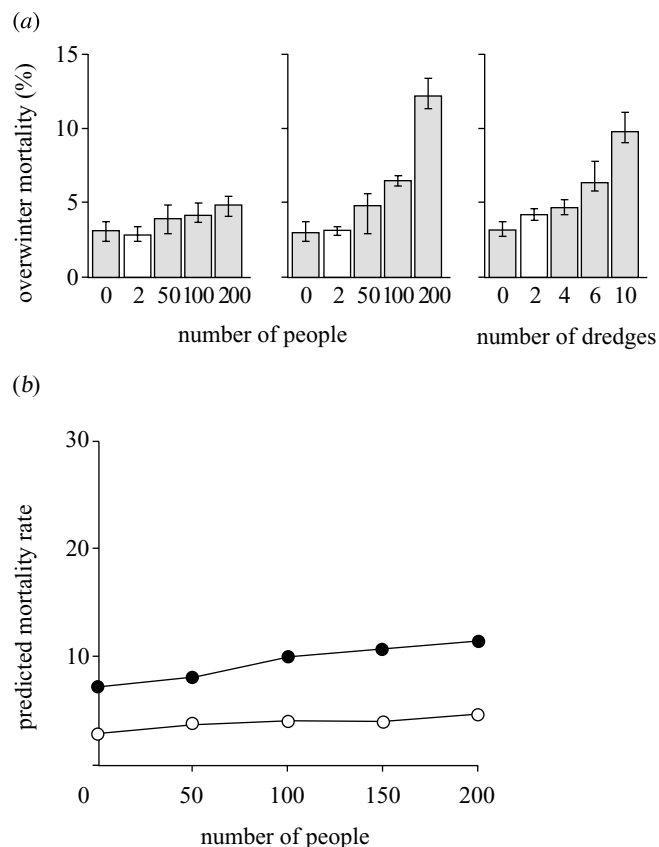
(a)

(b)

Figure 3. (a) The predicted overwinter survival rates of oystercatchers in relation to changes in (from left to right): the number of people hand-picking mussels; the number of people hand-raking mussels; and the number of dredges removing mussels. In each graph the light bar shows the current levels of fishing effort (from Stillman *et al.* 2001). (b) The predicted mortality rate of oystercatchers in relation to the number of people hand-picking mussels under different environmental conditions. The white circles show normal winter weather conditions and the black circles represent cold weather conditions (from Stillman *et al.* 2001).

based models that do this usually describe the process of scramble competition for resources, and to date have been primarily based on the spatial depletion model of Sutherland & Anderson (1993) (e.g. Sutherland & Allport 1994; Percival *et al.* 1996, 1998; Pettifor *et al.* 2000b; Gill *et al.* 2001a). This model is conceptually very simple. Consider an area of habitat, divided into discrete patches which vary in resource availability. At the start of a season (e.g. winter), animals aggregate in the food patch(es) with the highest food availability. As food resources are consumed and prey in the best patches become depleted, food availability in the best patch(es) will eventually reach availabilities that are similar to other patches that were initially less rich in resources. At this point, individuals spread out and occupy these additional patches too. As the season progresses, resources get depleted and a greater range of patches become exploited. If one assumes that there is a threshold food availability below which a patch can no longer be used (e.g. birds would starve), then this model can be used to calculate how many individuals the resources could support for a given period of time. Recent work by Gill *et al.* (2001a) on black-tailed godwits (*Limosa*

limosa islandica) that feed on soft-shelled clams during winter has shown that a simple prey depletion model such as this can be used to predict population sizes at different levels of a spatial scale (figure 4). It is then a relatively simple process to incorporate habitat loss or degradation and re-run the model to predict the extent to which the maximum sustainable population size might decline at various scales.

(b) *Territoriality*

Territorial behaviour is an obvious form of density dependence. At low population sizes individuals typically occupy large, high-quality territories. As the population density increases, territorial behaviour may change in three ways, each with clear implications for fitness. Territories may shrink as a result of the increased costs of territorial defence, poorer quality territories may be occupied or some individuals may decide not to breed (such individuals are usually known as 'floaters'). Thus, as the population increases the reproductive output declines.

Kokko & Sutherland (1998) analysed the question of when individuals should opt not to breed and become floaters. With a given distribution of habitat quality, perfect knowledge and no competition, individuals will obviously start by selecting the highest quality territory. Further individuals will then occupy the highest quality territory that is free. Assuming that searching for new territories and territory occupancy are mutually exclusive, there becomes a threshold territory quality at which it is better not to breed but to wait for a better territory to become available. The game theoretical solution can be derived for the optimal decision of individuals in deciding whether to breed in the best available territory or float. Once the demographic consequences of this decision are determined, it can be shown that the optimal game theoretical solution for deciding when to float is also the one that maximizes the numbers of floaters in the population. If the threshold is at a higher territory quality, then fewer individuals breed and so the total population is lower. If the threshold is at a lower territory quality, then the population is higher as more individuals breed and produce young, but the number of floaters is reduced as individuals that would have otherwise floated now breed in poor quality territories. Pen & Weising (2000) and Kokko *et al.* (2001) expand this result to consider a range of situations and its implications.

This theoretical abstraction seems to fit well with real world behaviour. Ens *et al.* (1992) described the breeding system of oystercatchers on Schriermonnikoog, The Netherlands, and showed that there were two main types of breeding behaviour (this behaviour is probably typical for many locations). Birds adopting one strategy, known as *residents*, obtain territories adjacent to the mudflats and then move onto the mudflats with their chicks to feed. The alternative strategy, known as *leapfrogs*, involves having a territory inland and flying over the residents to obtain food from the mudflats. As a result of the markedly reduced provisioning efficiency, the annual reproductive success rate of leapfrogs was only one-third of that of residents. Individuals usually cannot both occupy a leapfrog territory and wait for a resident territory to become vacant. Why then did some birds adopt the leapfrog strategy? After examining several explanations, including that the leap-
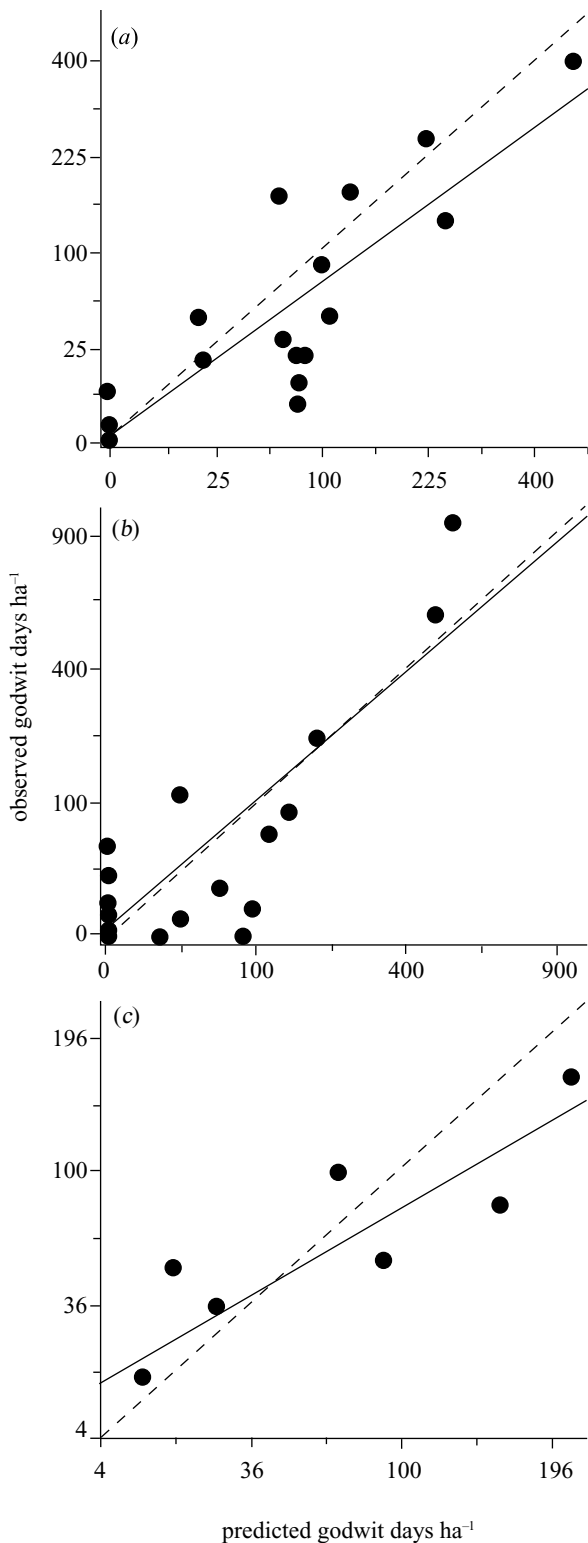
Figure 4. The observed number of bird days plotted against the predicted number for a population of black-tailed godwits wintering on the east coast of England. The model incorporated data on the food abundance, searching efficiency and handling time. The fit seemed good whether for a comparison of different patches on mudflats (*a*), different mudflats on estuaries (*b*) or different estuaries (*c*). Details of the model and the fit to observed data are given in Gill *et al.* (2001*a*).

frogs were making mistakes, leapfrogs were poorer quality or that leapfrogs lived longer, Ens *et al.* (1995) showed that the most probable explanation was that the two strategies are an ESS with similar average lifetime reproductive successes. There is considerable competition to become a resident that results in considerable delays in obtaining a territory, with many individuals dying while waiting for an occupancy. There is very little competition in becoming a leapfrog and so these can obtain a territory immediately. Leapfrogs thus, on average, breed for many more years but with a lower annual success rate.

Sutherland (1996*a*) extended the concepts and data of Ens *et al.* (1992, 1995) to produce a model of the consequences for the breeding output of a game theoretical model of whether individuals should take a leapfrog territory or join a queue to wait to occupy a resident territory. This model predicted the nature of the density-dependent breeding output. By incorporating data on the known survival rate between fledgings and returning to breed as an adult, it was then possible to model the density-dependent production of adult recruits. By adding the known annual mortality, the equilibrium population size was determined which seemed to fit well with the actual population size at Schiermonnikoog. This model can then be used to determine the consequences of changes in mortality on population size and was used to provide parameters for the model of habitat loss of migratory species (Sutherland 1996*a*).

Liley (1999) developed this approach to predict the consequences of human disturbance on populations of ringed plovers (*Charidrius hiaticula*). As with the model of the oystercatchers described in an earlier paragraph, there were empirically quantified differences in territory quality and the plovers showed preferences according to habitat type. From this it was possible to calculate the density-dependent reproductive success. Birds that were colour ringed when breeding at Snettisham were observed in winter across a wide area including France, southwestern Britain with some even heading north to winter in northern England. Thus, although there may be competition and density dependence acting upon ringed plovers in winter, when considering the Snettisham ringed plovers in isolation there is likely to be negligible density dependence— for example, doubling the population at Snettisham will, once the extra birds were spread across northwestern Europe, have a negligible effect on the total competition. Thus, by restricting the analysis to the Snettisham population, we can incorporate winter mortality as being density independent. It is then possible to calculate the equilibrium population size.

The main objective of Liley's study was to predict the consequences of human disturbance. Most papers on the disturbance of breeding birds tend to consider either the consequences on behaviour (e.g. time spent alert or off the nest) or the possible fitness consequences (e.g. number of nests trampled), but these do not determine the consequences for the total population. However, it is the consequences on populations that matter from a decision-making perspective. The model could easily be modified to consider the consequences of removing the quantified effects of humans trampling the eggs. The predicted increase in the population size would be 8%. In addition, as the ringed plovers avoided areas of high human den-

sities, many of which had the characteristics of high-quality territories, the removal of the disturbance would be predicted to increase the ringed plover population by 71.3%. Removing both the effect of trampling and the avoided good territories would increase the population by 84.9%. Using a similar approach, the model was also used to predict the consequences of sea-level rise on the ringed plover population: a 25 cm rise is predicted to reduce the population by 4.3%.

(c) *Social behaviour*

A recent development is to create demographic behaviour-based models incorporating social behaviour. These can be considered as a development of territorial models, but with the complication that individuals differing in rank will differ in reproductive success. Understanding the dispersal between groups, and the resultant mortality costs, is a key component.

Stephens *et al.* (2002) devised models of the alpine marmot *Marmota marmota* based on a 13 year field study within Berchtesgaden National Park (e.g. Arnold 1990*a*,*b*; Hackländer & Arnold 1999) in which about 95% of the study population was captured at least once a year. There were data on the major components of demography such as age of maturity, litter size, sex ratio, summer survival and winter survival.

Stephens *et al.* (2002) compared four models: (i) a population-based matrix model that incorporated environmental stochasticity and density-dependent fecundity; (ii) a group-based matrix model (i.e. similar to (i) but subdivided into groups with density dependence acting within groups); (iii) a spatially and temporally explicit individual-based model using field data to decide the probability of individual fates; and (iv) a behaviour-based model in which the optimization of an individual's residual fitness determined the individual fates. The main behavioural decision was when individuals dispersed, with individuals dispersing at the time that resulted in the highest lifetime fitness. The game theoretical solution thus depends upon factors such as the individual's dominance status and the mortality risk associated with dispersal. Model (iii) led to the most unrealistic results with the greatest deviation from the data (figure 5). As the decisions of individuals were based on fixed probabilities, individuals would often make irrational decisions, such as dispersing from a territory in which they would otherwise be just about to reproduce. This resulted in a lower growth rate than did the other models (figure 5).

The behavioural-based model was reasonably successful in predicting the dispersal behaviour, distribution of groups sizes and rates of turnover of dominant animals (figure 6). An emergent property of this model was the Allee effect, the reduction in reproductive success at lower population sizes.

(d) *Buffer effects*

A particularly important behavioural process underlying density dependence in survival and fecundity in animal populations is the buffer effect. This term is used to describe the process whereby at relatively low population sizes most animals in the population are able to occupy high-quality habitat, but as the population size increases an increasing fraction of the population is forced to occupy
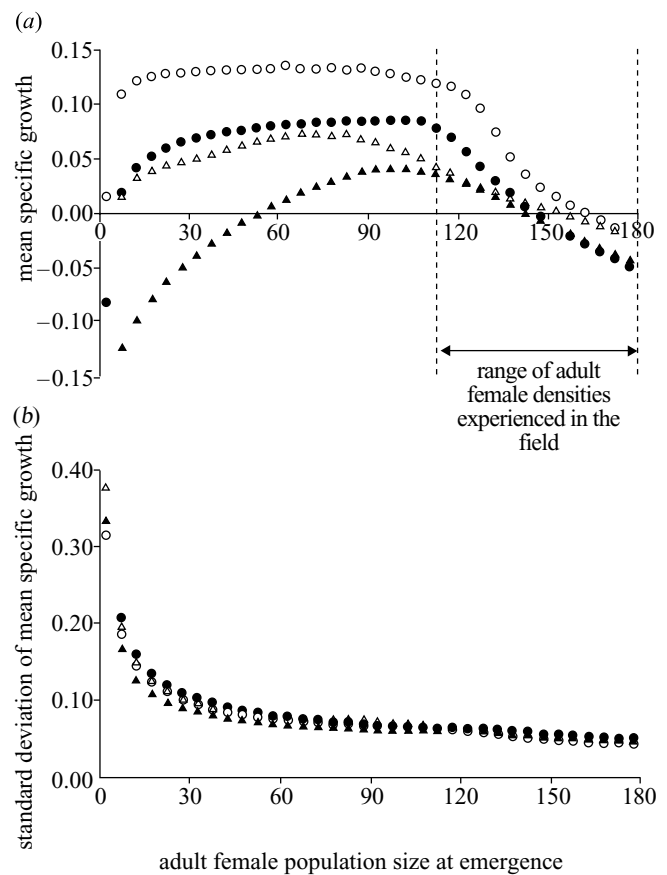

Figure 5. The mean (*a*) and standard deviation (*b*) of population growth of the alpine marmot *Marmota marmota* as predicted for different female emergence population sizes using four different models. Matrix model (white circle), matrix-group model (black circles), individual-based spatial model (black triangles) and behaviour-based model (white triangles) (from Stephens *et al.* 2002).

progressively poorer quality habitat. As this results in a reduction in fitness in animals occupying poor-quality habitat, the buffer effect is an important density-dependent mechanism. Its specific impact on demography is dependent on the stage of the life cycle in which it operates and the components of fitness influenced by habitat quality experienced during that life-cycle stage. It is obvious that the buffer effect can arise in breeding populations in which animals maintain exclusive breeding territories. However, there is also extensive evidence that the buffer effect can operate during the non-breeding period and affect fitness components other than fecundity. Recent work on shorebirds has also shown that the fitness consequences of the buffer effect can be cross-seasonal, in that fitness components outside the season in which the buffer effect is evident can be affected (Gill *et al.* 2001*b*).

Although the simple description of a buffer effect cannot necessarily elucidate the behavioural mechanisms driving it, the description has some qualitative value for conservationists. This is because it permits some ecologically relevant measure of habitat quality to be made by comparing abundance trends within habitat patches to overall changes in population sizes, and examining how such patterns relate to fitness. For example, recent studies on black-tailed godwits (*Limosa limosa*) revealed a buffer effect operating during the non-breeding period when
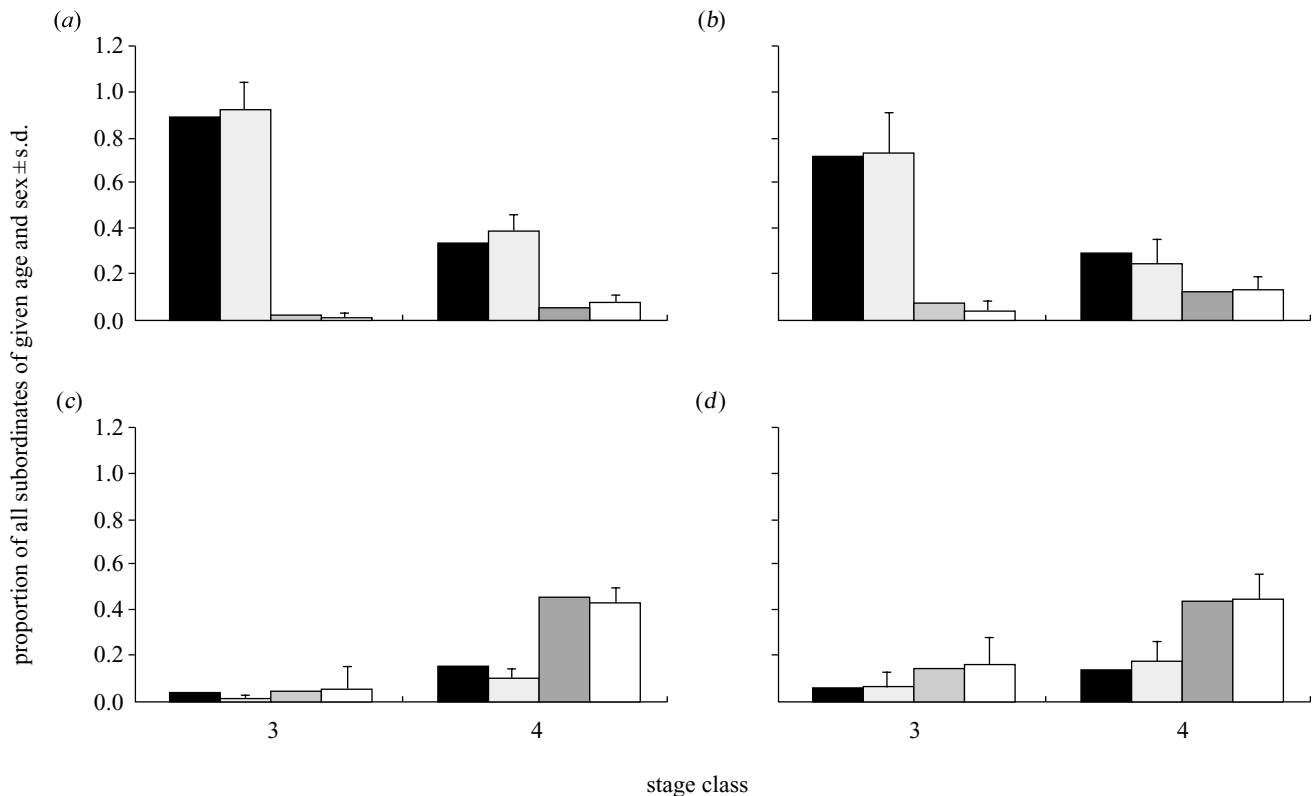
Figure 6. The fates of subordinate alpine marmots *Marmota marmota* as predicted by a behaviour-based model. (*a*) Males and (*b*) females that stayed in the territory. The shading shows those that remained subordinate (empirical, black), those that remained subordinate (model, light grey), those that became territorial (empirical, dark grey) and those that became territorial (model, white). (*c*) Males and (*d*) females that were dispersed from natal territory. The shading shows those that became territorial in the neighbourhood (empirical, black), those that became territorial in the neighbourhood (model, light grey), those that were dispersed beyond the neighbourhood (empirical, dark grey) and those that were dispersed beyond the neighbourhood (model, white) (from Stephens *et al.* 2002).

birds occupy estuarine habitats on the coasts of south and eastern England (Gill *et al.* 2001*b*) (figure 7). The population increase is buffered on the south coast by individuals moving to the east coast. Those godwits wintering on the south coast had higher food intake rates in spring, higher survival rates and earlier arrival dates on their breeding grounds in Iceland, than birds wintering on the east coast. This buffer effect shows that both survival and arrival date are density dependent in this population. These population-level density-dependent processes would be affected by habitat loss, but in different ways depending on whether good (south coast) or poor (east coast) habitat was lost or degraded. If a south coast site was lost, birds would be forced to occupy poorer quality habitat and experience reduced survival and later arrival dates. By contrast, birds occupying poor-quality habitat already have reduced fitness, so the loss of a poor-quality site is likely to have a relatively less severe impact on survival and arrival date.

The important general issue highlighted by this example is that an understanding of the behavioural mechanisms driving density-dependent processes provides potentially much greater insights than simply describing the population-level processes directly. If survival rates and arrival dates of colour-marked birds had been estimated annually as the godwit population has grown in size over the past 20 years, we could have described density dependence in these life-history variables. However, we would have been

unable to comment on whether the loss of a south or east coast site to development might have had equivalent or disproportionate effects on the population. A simple description of the buffer effect provides such insights; insights that are crucially important if coastal habitats are to be managed in a way that accommodates potentially conflicting (e.g. conservation and development) 'uses'.

5. FUTURE CHALLENGES

The models we have described tend to describe the situation under standard conditions. In reality there are likely to be considerable differences between years. Thus, much of the population regulation may take place under occasional years that are particularly cold, wet, dry or with food shortages. That is, there is likely to be an interaction between environmental conditions and density-dependent processes. Understanding such processes is obviously very important in predicting how populations might respond to future environmental change, given that the change itself is likely to vary in space or time. Certain behaviour-based models deal with the issue explicitly. For example, the model of Stillman *et al.* (2000) of wintering oystercatcher populations includes density-dependent starvation by calculating an energy budget for each individual. Those that lack sufficient resources at any point starve. The resources required to avoid starvation obviously vary temporally depending on weather conditions, so the model includes
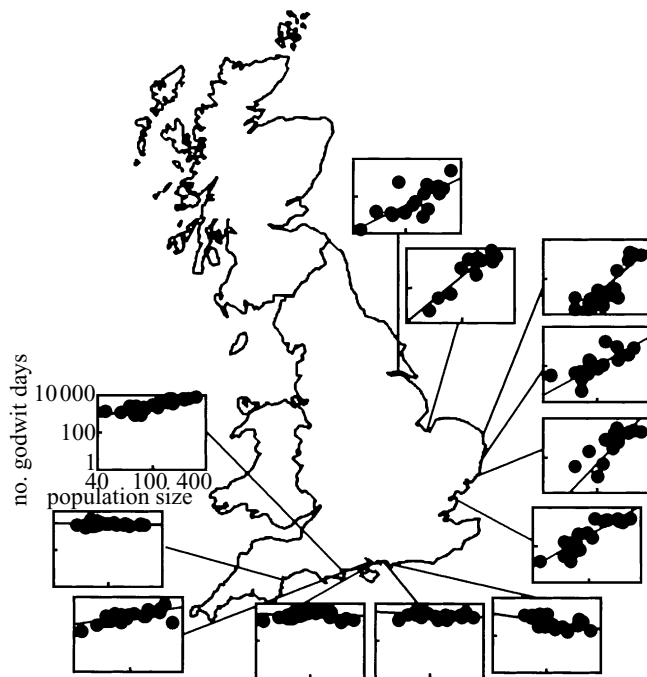
Figure 7. The change in the abundance of black-tailed godwits on different estuaries in Britain. Each graph shows the count (expressed as number of godwit days) on an individual estuary (*y*-axis) plotted against an index of overall population size in the UK (*x*-axis). Those sites with high rates of population increase as the total population has grown are associated with less food, lower intake rate, higher mortality and later arrival in the Icelandic breeding grounds (from Gill *et al*. 2001*b*).

an interaction between weather and density-dependent starvation. This is important because understanding such an interaction is crucial to risk assessment applications of the model (see Stillman *et al.* 2001). It is also worth reiterating that the model is capable of considering the impact on survival of any combination of weather conditions and population density, irrespective of whether the population has experienced similar conditions in the past, due to its mechanistic nature. A wider application of the behaviour-based approach to a range of systems and problems in the future will tell us how well these models cope with similar interactive effects.

6. CONCLUSIONS

We have argued that current demographic models used for conservation purposes are often inadequate due to the lack of data, particularly with respect to the description of density-dependent processes. Even if extremely detailed data exist on the life histories of individuals within a population that has experienced a wide range of population sizes, demographic models based on such data are unlikely to be reliable in the face of future environmental changes that modify density-dependent processes. This is because population responses to such changes are unlikely to be predictable from past population behaviour. Instead, we suggest that studies of the behavioural mechanisms that underlie density-dependent processes are likely to be of more predictive value to conservationists interested in understanding how populations might respond to future

environmental change. This is because such studies require more precise thinking into exactly how environmental change impacts on populations, and behaviour-based models provide tools that can be used to make quantitative predictions about impacts. We have illustrated how this approach might be used for both risk assessment and the design of conservation management for endangered species. This latter application of behaviour-based models is in its infancy but the technique is potentially very valuable because population processes are difficult to describe in small, poorly studied populations, but behavioural mechanisms involved in competition for resources are a much more tractable ecological research problem.

How does a behaviour-based approach relate to the paradigms in population ecology described by Sibly & Hone (2002)? There are obvious parallels with the mechanistic paradigm in that behavioural mechanisms can explain how demography is linked to environmental drivers such as food availability, temperature, etc. However, it is distinct in that all of the existing paradigms can be used to describe how a population has behaved in the past, but only a more mechanistic approach that incorporates decision making by individual animals can provide reliable insights into how populations might behave in the face of future environmental change that modifies density-dependent processes. This is an important progression for population ecologists to make in the sense that it means the subject is moving from being a descriptive science to a more predictive one. This is also of potentially immense practical importance, in that understanding how populations respond to future environmental changes will be pivotal to their effective conservation.

REFERENCES

Arnold, W. 1990*a* The evolution of marmot sociality. I Why disperse late? *Behav. Ecol. Sociobiol.* **27**, 229–237.

Arnold, W. 1990*b* The evolution of marmot sociality. II Costs and benefits of joint hibernation. *Behav. Ecol. Sociobiol.* **27**, 239–246.

Beissinger, S. R. 1995 Modelling extinction in periodic environments: Everglades water levels and snail kite population viability. *Ecol. Applic.* **5**, 618–631.

Beissinger, S. R. & Westphal, M. I. 1998 On the use of demographic models of population viability in endangered species management. *J. Wildl. Mngmt* **62**, 821–841.

Bulmer, M. 1975 The statistical analysis of density dependence. *Biometrics* **31**, 901–911.

Burgman, M., Ferson, S. & Akcakaya, H. 1992 *Risk assessment in conservation biology*. London: Chapman & Hall.

Caughley, G. 1977 *Analysis of vertebrate populations*. London: Wiley.

Caughley, G. & Gunn, A. 1995 *Conservation biology in theory and practice*. Oxford: Blackwell Science.

Coulson, T., Catchpole, E. A., Albon, S. D., Morgan, B. J. T., Pemberton, J. M., Clutton-Brock, T. H., Crawley, M. J. & Grenfell, B. T. 2001 Age, sex, density, winter weather, and population crashes in Soay sheep. *Science* **292**, 1528–1531.

Courchamp, F., Grenfell, B. T. & Clutton-Brock, T. H. 1999

Inverse density dependence and the Allee effect. *Trends Ecol. Evol.* **14**, 405–410.

Ens, B. J., Kersten, M., Brenninkmeijer, A. & Hulscher, J. B. 1992 Territory quality, parental effort and reproductive success of oystercatchers (*Haematopus ostralegus*). *J. Anim. Ecol.* **61**, 703–715.

Ens, B. J., Weissing, F. J. & Drent, R. H. 1995 The despotic distribution and deferred maturity: two sides of the same coin. *Am. Nat.* **146**, 625–650.

Fretwell, S. D. & Lucas, J. H. J. 1970 On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoret.* **19**, 16–36.

Gill, J. A., Sutherland, W. J. & Watkinson, A. R. 1996 A method to quantify the effects of human disturbance on animal populations. *J. Appl. Ecol.* **33**, 786–792.

Gill, J. A., Sutherland, W. J. & Norris, K. 2001*a* Depletion models can predict shorebird distribution at different spatial scales. *Proc. R. Soc. Lond.* B **246**, 369–376. (DOI 10.1098/rspb.2000.1386.)

Gill, J. A., Norris, K., Potts, P., Gunnarsson, T., Atkinson, P. W. & Sutherland, W. J. 2001*b* The buffer effect and large-scale population regulation in migratory birds. *Nature* **412**, 436–438.

Goss-Custard, J. D. 1996 *The oystercatcher.* Oxford University Press.

Goss-Custard, J. D. & Sutherland, W. J. 1997 Individual behaviour, populations and conservation. In *Behavioural ecology* (ed. J. R. Krebs & N. B. Davies), pp. 373–395. Oxford: Blackwell Science.

Green, R. E. & Hirons, G. J. M. 1991 The relevance of population studies to the conservation of threatened birds. In *Bird population studies* (ed. C. M. Perrins, J.-D. Lebreton & G. J. M. Hirons), pp. 594–633. Oxford University Press.

Green, R. E., Pienkowski, M. W. & Love, J. A. 1996 Long-term viability of the re-introduced population of the white-tailed sea eagle *Haliaeetus albicilla* in Scotland. *J. Appl. Ecol.* **33**, 357–368.

Groombridge, J. J., Jones, C. G., Bruford, M. W. & Nichols, R. A. 2001 Evaluating the severity of the population bottleneck in the Mauritius kestrel *Falco punctatus* from ringing records using MCMC estimation. *J. Anim. Ecol.* **70**, 401–409.

Hackländer, K. & Arnold, W. 1999 Male-caused failure of female reproduction and its adaptive value in alpine marmots (*Marmota marmota*). *Behav. Ecol.* **10**, 592–597.

Hiraldo, F., Negro, J. J., Donazar, J. A. & Gaona, P. 1996 A demographic model for a population of the endangered lesser kestrel in southern Spain. *J. Appl. Ecol.* **33**, 1085–1093.

Jones, C. G., Groombridge, J. J. & Nicoll, M. A. C. 2002 The genetic and population history of the Mauritius kestrel *Falco punctatus*. (In the press.)

Kokko, H. & Sutherland, W. J. 1998 Optimal floating strategies: consequences for density dependence and habitat loss. *Am. Nat.* **152**, 354–366.

Kokko, H., Sutherland, W. J. & Johnstone, R. A. 2001 The logic of territory choice: implications for conservation and source-sink dynamics. *Am. Nat.* **157**, 459–463.

Lande, R. 1988 Demographic models of the northern spotted owl (*Strix occidentalis caurina*). *Oecologia* **75**, 601–607.

Liley, D. 1999 Predicting the consequences of human disturbance, predation and sea-level rise for ringed plover populations. PhD thesis, University of East Anglia, Norwich.

Norris, K. & Stillman, R. 2002 Predicting the impact of environmental change. In *Conserving bird biodiversity* (ed. K. Norris & D. J. Pain), pp. 180–201. Cambridge University Press.

Paradis, E., Baillie, S. R., Sutherland, W. J. & Gregory, R. D. 2002 Exploring density dependence in demographic parameters in populations of birds at a large spatial scale. *Oikos* (In the press.)

Pen, I. & Weising, F. J. 2000 Optimal floating and queuing strategies: the logic of territory choice. *Am. Nat.* **155**, 512–526.

Percival, S. M., Sutherland, W. J. & Evans, P. R. 1996 A spatial depletion model of the responses of grazing wildfowl to changes in availability of intertidal vegetation during the autumn and winter. *J. Appl. Ecol.* **33**, 979–993.

Percival, S. M., Sutherland, W. J. & Evans, P. R. 1998 Intertidal habitat loss and wildfowl numbers: applications of a spatial depletion model. *J. Appl. Ecol.* **35**, 57–63.

Pettifor, R. A., Norris, K. & Rowcliffe, M. 2000*a* Incorporating behaviour in predictive models for conservation. In *Behaviour and conservation* (ed. M. Gosling & W. J. Sutherland), Chap. 12, pp. 198–220. Cambridge University Press.

Pettifor, R. A., Caldow, R. W. G., Rowcliffe, J. M., Goss-Custard, J. D., Black, J. M., Hodder, K. H., Houston, A. I., Lang, A. & Webb, J. 2000*b* Spatially explicit, individual-based, behavioural models of the annual cycle of two migratory goose populations. *J. Appl. Ecol.* **37**, 103–135.

Robinson, P. A. & Redford, K. H. 1991 Sustainable harvest of neotropical forest mammals. In *Neotropical wildlife use and conservation* (ed. J. G. Robinson & K. H. Redford), pp. 415–429. University of Chicago Press.

Root, K. V. 1998 Evaluating the effects of habitat quality, connectivity and catastrophes on a threatened species. *Ecol. Applic.* **8**, 854–865.

Royama, T. 1981 Fundamental concepts and methodology for the analysis of animal population dynamics, with particular reference to univoltine species. *Ecol. Monogr.* **51**, 473–493.

Shenk, T. M., White, G. C. & Burnham, K. P. 1998 Sampling variance effects in detecting density dependence from temporal trends in natural populations. *Ecol. Monogr.* **68**, 445–463.

Sibly, R. M. & Hone, J. 2002 Population growth rate and its determinants: an overview. *Phil. Trans. R. Soc. Lond.* B **357**, 1153–1170. (DOI 10.1098/rstb.2002.1117.)

Sibly, R. M., Williams, T. D. & Jones, M. B. 2000 How environmental stress affects density dependence and carrying capacity in a marine copepod. *J. Appl. Ecol.* **37**, 388–397.

Smith, C., Reynolds, J. D. & Sutherland, W. J. 2000 Population consequences of reproductive decisions. *Proc. R. Soc. Lond.* B **267**, 1327–1334. (DOI 10.1098/rspb.2000.1146.)

Stephens, P. A. & Sutherland, W. J. 1999 Consequences of the Allee effect for ecology and conservation. *Trends Ecol. Evol.* **14**, 401–405.

Stephens, P. A., Frey-Roos, F., Arnold, W. & Sutherland, W. J. 2002 Model complexity and population predictions. The alpine marmot as a case study. *J. Anim. Ecol.* **71**, 343–361.

Stillman, R. A., Goss-Custard, J. D., West, A. D., Durell, S. E. A. le vit de, Caldow, R. W. G., McGrorty, S. & Clarke, R. T. 2000 Predicting mortality in novel environments: tests and sensitivity of a behaviour-based model. *J. Appl. Ecol.* **37**, 564–588.

Stillman, R. A. (and 11 others) 2001 Predicting shorebird mortality and population size under different regimes of shellfishery management. *J. Appl. Ecol.* **38**, 857–868.

Sutherland, W. J. 1996*a* Predicting the consequences of habitat loss for migratory populations. *Proc. R. Soc. Lond.* B **263**, 1325–1327.

Sutherland, W. J. 1996*b* *From individual behaviour to population ecology.* Oxford University Press.

Sutherland, W. J. 1998 The effect of local change in habitat quality on populations of migratory species. *J. Appl. Ecol.* **35**, 418–421.

Sutherland, W. J. & Allport, G. A. 1994 A spatial depletion

model of the interaction between bean geese and wigeon with the consequences for habitat management. *J. Anim. Ecol.* **63**, 51–59.

Sutherland, W. J. & Anderson, C. W. 1993 Predicting the distribution of individuals and the consequences of habitat loss: the role of prey depletion. *J. Theor. Biol.* **160**, 223–230.

Sutherland, W. J. & Watkinson, A. R. 2001 Policy making within ecological uncertainty: lessons from badgers and GM crops. *Trends Ecol. Evol.* **16**, 261–263.

Temple, S. A. 1977 The status and conservation of endemic kestrels on Indian Ocean islands. In *World Conference on Birds of Prey, Report of Proceedings, Vienna 1975* (ed. R. D. Chancellor), pp. 74–82. Basingstoke: Taylor & Francis.

GLOSSARY

ESS: evolutionarily stable strategy
GM: genetically modified