Predicting mortality in novel environments: tests and sensitivity of a behaviour-based model

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Summary

1. In order to assess the future impact of a proposed development or evaluate the cost effectiveness of proposed mitigating measures, ecologists must be able to provide accurate predictions under new environmental conditions. The difficulty with predicting to new circumstances is that often there is no way of knowing whether the empirical relationships upon which models are based will hold under the new conditions, and so predictions are of uncertain accuracy.

2. We present a model, based on the optimality approach of behavioural ecology, that is designed to overcome this problem. The model's central assumption is that each individual within a population always behaves in order to maximize its fitness. The model follows the optimal decisions of each individual within a population and predicts population mortality rate from the survival consequences of these decisions. Such *behaviour-based* models should provide a reliable means of predicting to new circumstances because, even if conditions change greatly, the basis of predictions – fitness maximization – will not.

3. The model was parameterized and tested for a shorebird, the oystercatcher *Haematopus ostralegus*. Development aimed to minimize the difference between predicted and observed overwinter starvation rates of juveniles, immatures and adults during the model calibration years of 1976–80. The model was tested by comparing its predicted starvation rates with the observed rates for another sample of years during 1980–91, when the oystercatcher population was larger than in the model calibration years. It predicted the observed density-dependent increase in mortality rate in these years, outside the conditions for which it was parameterized.

4. The predicted overwinter mortality rate was based on generally realistic behaviour of oystercatchers within the model population. The two submodels that predicted the interference-free intake rates and the numbers and densities of birds on the different mussel *Mytilus edulis* beds at low water did so with good precision. The model also predicted reasonably well (i) the stage of the winter at which the birds starved; (ii) the relative mass of birds using different feeding methods; (iii) the number of minutes birds spent feeding on mussels at low water during both the night and day; and (iv) the dates at which birds supplemented their low tide intake of mussels by also feeding on supplementary prey in fields while mussel beds were unavailable over the high water period.

5. A sensitivity analysis showed that the model's predictive ability depended on virtually all of its parameters. However, the importance of different parameters varied considerably. In particular, variation in gross energetic parameters had a greater influence on predictions than variations in behavioural parameters. In accord with this, much of the model's predictive power was retained when a detailed foraging submodel was replaced with a simple functional response relating intake rate to

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mussel biomass. The behavioural parameters were not irrelevant, however, as these were the basis of predictions.

6. Although we applied the model to oystercatchers, the general principle on which it is based applies widely. We list the key parameters that need to be measured in order to apply the model to other systems, estimate the time scales involved and describe the types of environmental changes that can be modelled. For example, in the case of estuaries, the model can be used to predict the impact of habitat loss, changes in the intensity or method of shellfishing, or changes in the frequency of human disturbance.

7. We conclude that behaviour-based models provide a good basis for predicting how demographic parameters, and thus population size, would be affected by novel environments. The key reason for this is that, by being based on optimal decision rules, animals in these models are likely to respond to environmental changes in the same way as real ones would.

Introduction

Much applied ecological research is concerned with acquiring the understanding needed to devise ways to decrease the abundance of organisms regarded as pests or to increase the abundance of those that are viewed as having become too scarce. Often only a qualitative level of understanding is required to achieve these goals. For example, in the case of reversing a population decline, we may need only to identify the factors responsible in order to devise remedial action (Green 1995). Although policy makers are still asking rather broad qualitative questions about potential ecological impacts, there is an increasing need to provide quantitative predictions. For example, when a development proposal is being considered that would remove some of the intertidal feeding grounds of shorebirds overwintering on an estuary, policy makers often ask for predictions on how many extra birds would die of starvation than do at present, were the development to go ahead. Furthermore, quantitative predictions are also required for evaluating the cost effectiveness of proposed mitigating measures. Again using shorebirds as an example, the loss of existing intertidal feeding areas can be offset by providing new mudflats by breaching the present sea wall and allowing new high-level flats to develop on land that may previously have been fields. But this can be costly. The expenditure might be justified if large numbers of a comparatively scarce species of bird were thereby to be saved, but not if only very small numbers of an already abundant species were to benefit. In order to answer such questions, ecologists must be able to provide quantitative predictions using a tested methodology. Despite these demands, research that provides such 'what-if' predictions is still unusual in ecology.

While it is sometimes true that one constraint on making quantitative prediction is the complexity of ecological systems, the difficulty often lies in the fact that the present-day range of environmental conditions does not encompass the circumstances for which predictions are required. In these circumstances, simple 'top-down' regression and phenomenological descriptive models, as advocated by Peters (1991), may be unreliable. Rather, we must develop ways not only to predict how the organisms will respond to the environmental changes but also to forecast the effect that their responses will have on their chances of surviving and reproducing. In doing this, we must be able to predict the quantitative relationship between the demographic rates and population size because – as in any system – the precise form of these population feedback functions has a crucial influence on system dynamics and response (May 1981).

Many responses to new environments, particularly of higher animals, will be behavioural. In these cases, the game theoretic and optimality approaches developed by behavioural ecologists (Maynard-Smith 1982; Krebs & Davies 1997) provide a promising basis for prediction (Goss-Custard & Sutherland 1997). In line with the now well-established interest in understanding the dynamics of animal populations from the behaviour of their constituent individuals (Łomnicki 1988; Sutherland 1996), population dynamics can then be viewed as the population consequences of the fitness-maximizing decisions made by each individual (Goss-Custard & Sutherland 1997) and population ecology becomes based on a general theory, evolution through natural selection, which it otherwise lacks (Sutherland 1996). Robust population predictions should then be possible because, even if conditions change, the

basis of predictions – fitness maximization – will not (Goss-Custard 1996; Goss-Custard & Sutherland 1997).

Up to now, the models based on this approach have been either rather abstract (Sutherland & Dolman 1994) or empirical but incompletely parameterized, with their most important demographic predictions, which they are designed to produce, being untested (Goss-Custard *et al.* 1995a,b,c). This article describes the first fully parameterized empirical behaviour-based model the principal demographic rate predictions of which have been successfully field-tested. Using as our model system a shorebird, the oystercatcher *Haematopus ostralegus* L., feeding in the Exe estuary, UK, on a shellfish, the blue mussel *Mytilus edulis* L., during the non-breeding season, we developed and tested a behaviour-based model to predict by how much a bird's mortality rate would be affected by environmental changes that affected its overwinter feeding conditions. The model was restricted to the non-breeding season because oystercatchers do not breed on this site but migrate to a range of breeding areas in northern Britain, the Netherlands and Scandinavia (Goss-Custard *et al.* 1980). It did not consider movement between estuaries because the majority of individuals within the oystercatchers' population remain on the Exe throughout winter (Goss-Custard *et al.* 1980). Earlier versions of the model highlighted the potential of the behaviour-based approach, but were part of the development process and had limitations. The first version (Goss-Custard *et al.* 1995a,c) did not include prey depletion and so could not predict starvation rates, the key population-level output of the model. The second version (Goss-Custard *et al.* 1995b, 1996c; Clarke & Goss-Custard 1996) included only one food supply, the mussel *M. edulis*, and so greatly overestimated oystercatcher mortality. The new model removes this limitation by incorporating all major feeding areas. Importantly, it also includes several much-refined parameter estimates and additional aspects of the system, which allowed its main prediction to be field-tested.

Most European oystercatchers that die have starved, often in late winter during severe weather (Goss-Custard *et al.* 1996c). The model's principal determinant is therefore the numbers starving between September, when most birds have arrived from the breeding grounds, and March, when most adults have returned to their breeding areas. Its key prediction is the quantitative dependence of winter starvation rates on the numbers of birds settling on the estuary the previous autumn. We report in this paper that the model satisfactorily predicted the density-dependent function relating starvation rate to population density even though, at the time the prediction was made, the dependence of that mortality rate on population density was not known.

Simulations with a separate demographic population model have illustrated how being able to predict this feedback function is vital to both understanding the population's behaviour and to predicting its response to novel environmental change (Goss-Custard *et al.* 1995b,c, 1996a,b).
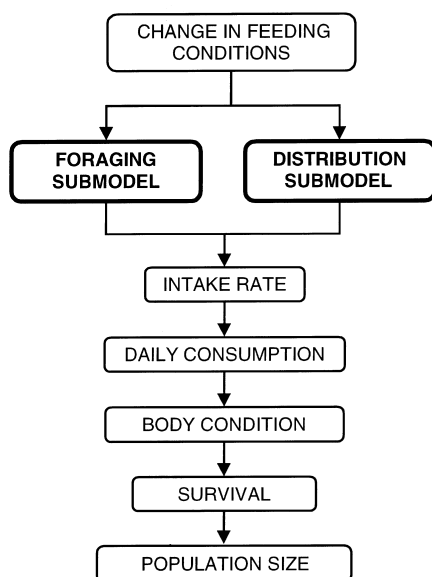
The model

CONSTRUCTION STRATEGY

The model is only concerned with the non-breeding season and so its development was guided by its accuracy of predicting the overwinter mortality rates of different oystercatcher age classes. Exe oystercatcher mortality rates were first measured between September 1976 and March 1980 (Goss-Custard *et al.* 1982b) and the model was calibrated for these years. To achieve our objective of high predictive power while keeping the model as simple as possible, the model was developed by adding new components to reduce the discrepancy between observed and model-calculated mortality rates for those five winters. Based on our current understanding of the system, components were added in order of their probable importance in closing the remaining gap between predicted and observed rates. All parameter values added to the model were derived empirically. The model's ability to predict starvation rates in a sample of subsequent years from 1980 to 1991 was used as its main test.

GENERAL STRUCTURE

The model's general structure is very simple and applicable to many other systems. It follows the location, behaviour and body condition of each individual oystercatcher. Each has a unique combination of age, feeding method, interference-free intake rate and dominance. The model uses a game theoretic approach to determine where each individual feeds at each stage of the tidal cycle, the body reserve levels and survival consequences of these decisions for the individual and for all others in the population. Although all individuals base their decisions on the same principle, intake rate maximization, the actual decisions made by each differ and depend on their own particular characteristics.

The model includes two behavioural submodels that predict the response of birds to their food supply (Fig. 1). The rate-maximizing prey choice submodel predicts how the low tide consumption rate of each individual would be affected by changes in the density and age structure, and thus size class structure, of the mussel population. The ideal free distribution submodel predicts where each bird will feed during each stage of the tide and the change in each bird's consumption rate that arises when birds redistribute because the area or quality of some or

Fig. 1. Flow chart showing how the model predicts the effect of the winter mussel food supply on the body condition of individual oystercatchers and on the starvation rates of the population. The two behaviour submodels are outlined with heavy lines.

all feeding areas has been changed, either temporarily or permanently. By combining these two outputs, the model calculates the consequences for the energy reserves of each bird of the change in its consumption rate arising from its responses to the change in its food supply.

Whether an individual survives is determined by the balance between its daily rates of energy expenditure and acquisition. Energy expenditure depends on the cost of general metabolism plus any cost of thermoregulation at low temperatures. Energy acquisition depends on both the time available for feeding and instantaneous intake rate. Intake rate depends on two parameters that vary between individuals: *interference-free intake rate* is the rate at which an individual feeds in the absence of competition from others, given the food supply available, while *susceptibility to interference* is the effect of competitors on its intake rate. When daily energy acquisition exceeds daily expenditure, individuals add to their energy reserves or maintain them if a maximum level has already been reached. When daily requirements exceed daily acquisition, individuals draw on their energy reserves. If energy reserves fall to zero, an individual dies of starvation, the only source of mortality in the model, and the main source of mortality in the wild (Goss-Custard *et al.* 1996b).

MODEL DESCRIPTION

As the new model differs greatly from previous versions, we describe it in full but, for brevity, restrict

parameter values and sources to the Appendix. The model contains many parameters and so, again for brevity, we do not describe how each parameter value was estimated or discuss the precision with which it was done. In many cases, we refer in the Appendix to publications where further details of the methods used and parameter precision can be obtained. However, the model occasionally uses data from as yet unpublished studies, and here we either indicate how data were obtained or, more usually, refer to publications where the methodology used is described. In these cases, the standard errors of the parameters used in the model will not yet have been published. Furthermore, the methods used for estimating a number of parameters did not allow the standard errors to be calculated. However, we suggest that the aggregate precision of all the parameter values in the model can be gauged by the success with which the model as a whole predicted its most important behavioural outputs, particularly intake rate, and the winter starvation rate.

TIME AND ENVIRONMENTAL CONDITIONS

Time

The model simulates a period between 1 September and 15 March. Time progresses by a series of discrete, variable length, time intervals. During each interval environmental conditions remain constant and oystercatchers do not change their location.

Tidal and spring–neap cycles

The major factor influencing the availability of feeding patches is their successive covering and exposure through the tidal cycle. In the model, tidal cycles last for 12·44 h and are divided into four stages, during which the tidal height remains constant: high water, receding tide, low water and advancing tide. The tidal stage is the finest division of time in the model and defines the length of each successive time interval.

Although the duration of tidal cycles remains constant, the tidal range of each successive cycle and the duration of each stage within a tidal cycle vary through the spring–neap cycle. Tidal range is at a maximum on spring tides and a minimum on neaps. The amplitude of the spring–neap cycle is described by a sine curve with a maximum (full spring) on the first day of winter and a constant period of 14 days. Changes in the duration of each tidal stage are incorporated by defining their length on both full spring and full neap tides. The duration of a tidal stage at a given point in the spring–neap cycle is then found by linear interpolation between these two extremes. The spring–neap cycle therefore influences the area and exposure time of intertidal patches.

Day length, diurnal cycles and temperature

Day length is described by a sine curve ranging between 18 h on 21 June and 9 h on 21 December. The model assumes that the hours of light are equally divided either side of midday, and finds the proportion of each tidal stage that falls within the hours of daylight. Daily temperature declines through winter from 17 °C in September to 5 °C in February.

PREY

Most mussel-feeding Exe oystercatchers feed on 10 middle- to low-shore mussel beds. Supplementary feeding occurs on other intertidal areas at a higher shore level, and fields near the estuary. There are 12 feeding patches of three types in the model: 10 mussel beds, one upshore area and one field. The single upshore area and field represent a number of such areas in the real system. The different patches vary in their tidal exposure patterns and in their prey populations.

Patch exposure

Each patch has a maximum area when fully exposed at low water on spring tides. Exposure through the tidal cycle is modelled from the proportion of this area exposed at each tidal stage on both full spring and full neap tides. For intermediate tides, the model calculates the area of a patch exposed by linear interpolation between the spring and neap extremes. Mussel beds are exposed only at low water, upshore areas on the receding tide, low water and the advancing tide, and fields during all tidal stages.

Prey populations

Mussel populations on each bed are divided into 10 size classes, each having, at the start of winter, a particular bed-specific density. The mussel population is divided into size classes for compatibility with the oystercatcher optimal diet model (see below). The density of each size class declines during winter due to oystercatcher predation and other mortality sources, the latter removing mussels at a constant proportional daily rate. Mussel flesh content, which determines their food value to oystercatchers, is size class and bed specific, and declines at a constant linear rate during winter. As mussels located high on the shore contain less flesh than equivalent sized mussels further down, in the model average flesh content is related to the proportion of the bed exposed; when only the high shore levels of the bed are exposed on neap tides, average flesh content is decreased. The foraging of oystercatchers on upshore areas and fields is modelled quite simply

and so the model does not store details of these prey populations. The energy density of prey flesh on all patch types remains constant throughout winter.

OYSTERCATCHERS

Population size and structure

The model is run with a population of 1550 oystercatchers, the average winter population on the main mussel beds during 1976–80, in three age classes: juveniles (first winter), immatures (second winter) and adults. The proportions in each age class are those feeding on Exe mussel beds: 2% juveniles, 7% immatures and 91% adults. Juveniles and immatures tend to be of lower dominance than adults and hence more susceptible to interference. Each bird either stabs open gaping mussels (stabbers) or breaks the shell by hammering (hammerers) (Hulscher 1996). All juveniles, 80% of immatures and 43% of adults are stabbers. On average, hammerers have both a higher interference-free intake rate and susceptibility to interference than stabbers. Within an age-feeding method class, individuals differ in their feeding efficiency on all three patch types and their dominance, and hence susceptibility to interference on mussel beds. The feeding efficiency (E) of each individual on each patch type is drawn from a normal distribution, with unit mean and fixed coefficient of variation, and its dominance from a uniform distribution. It is assumed that the feeding efficiencies of an individual on each patch type are unrelated and that dominance is unrelated to feeding efficiency. The age, feeding method, feeding efficiencies and dominance of each individual are fixed throughout winter.

Feeding times and locations

Birds may move between time intervals but, during each interval, each remains on one of the 12 feeding patches or on a roost, which is always available but on which no feeding is possible. Mussel beds and the upshore can only be used when exposed by the tide, but the field and roost may be used at any time. The model finds the location of each individual throughout the tidal cycle using an iterative game theoretic procedure that is an extension of that used in previous versions of the model (Goss-Custard *et al.* 1995a,b,c; Clarke & Goss-Custard 1996). An iterative process is needed because the decisions made by each bird depend on the locations and relative dominance of all others. In reality, oystercatchers do not feed constantly but roost during periods when their food is unavailable because they balance their energy budgets over a relatively long period, estimated as two tidal cycles (24·9 h) by Kersten & Visser (1996a). Therefore, for each pair of tidal cycles, the model calculates each bird's energy

requirements and then finds the feeding locations and time intervals that allow it to meet its requirements in as short a time as possible. During time intervals in which the bird does not need to feed it moves to the roost. Birds base their patch-choice decisions purely on the intake rates achievable on each patch, with the limitation that they cannot distinguish between intake rates that differ by less than 3% (Goss-Custard *et al.* 1995a). The model attempts to find the stable distribution of birds by repeating this process three times (the model did not stabilize any more with further iterations), processing birds in a different random order during each iteration. The model then recalculates the intake rate of each bird on its final set of patches.

Intake rate on mussel beds

Intake rate is found by calculating interference-free intake rate, and then subtracting the loss due to interference. Interference-free intake rate is calculated by an optimal diet model (similar to Meire & Ervynck 1986) that was parameterized for stabbers and hammerers using field observations of Exe oystercatchers foraging at low competitor densities (J. D. Goss-Custard, unpublished data). The model finds the range of size classes that maximizes, within a 3% intake rate discrimination ability (Goss-Custard *et al.* 1995a), interference-free intake rate given the food supply.

$$\overline{IFIR} = \frac{\sum \lambda_i p_i m_i}{1 + \sum \lambda_i (p_i h_i + (1 - p_i)w_i + I)} \qquad \text{eqn 1}$$

where $\overline{IFIR}$ = the interference-free intake rate of a stabber or hammerer of average feeding efficiency, feeding on average quality mussels during daylight; i = mussel size class; λ = encounter rate; m = ash-free dry mass; p = probability of consuming a mussel after it is attacked; h = handling time of mussels that are attacked and consumed; w = waste handling time of mussels that are attacked but not consumed; I = time wasted inspecting mussels that are subsequently not attacked. Our model extends the original by including the parameter I, as oystercatchers often spend time inspecting mussels that are not attacked and cannot be attributed to a size class.

Encounter rate is calculated in a different way to Meire & Ervynck (1986). First, it is assumed that oystercatchers search visually for mussels by walking at constant speed along a fixed width search path, and attack a certain proportion of the mussels that are visible.

$$\lambda_i = p_{attack} s r v_i D_i \qquad \text{eqn 2}$$

where p_{attack} = probability of attacking a visible mussel within the search path; s = search speed; r = search path width; v = proportion of mussels that is visible; D = mussel density. Secondly, based on empirical data (J. D. Goss-Custard, unpublished data), p_{attack} decreases as the density of mussels longer than 45 mm (D_{45}, i.e. within the size range usually consumed) increases.

$$p_{attack} = \frac{1}{(a + bD_{45})^2} \qquad \text{eqn 3}$$

This differs from most diet selection models, which assume that the proportion of prey attacked is unrelated to prey density. The reason for the decline in P_{attack} is unclear but possible explanations are that (i) birds become more selective as prey density increases; (ii) birds cannot inspect every mussel at high densities; (iii) prey availability decreases as density increases.

Equation 1 calculates the intake rate of an average stabber or hammerer, feeding on average quality mussels during daylight. The interference-free intake rate actually achieved by an individual in the model also depends on (i) its foraging efficiency relative to an average bird (E); (ii) the proportion of the time spent feeding during the day (P_{day}) and night (P_{night}); (iii) its intake rate at night relative to that during the day (E_{night}); (iv) the proportion of mussels not stolen from it by crows *Corvus corone* L. during the day (P_{keep}) (no crows are present at night); (v) the proportion of flesh that can be removed from the mussel shell (P_{remove}); (vi) the flesh content of mussels consumed relative to the average on a mussel bed (Q).

$$IFIR = E(P_{day}P_{keep}P_{remove}Q\overline{IFIR}$$
$$+ P_{night}E_{night}P_{remove}Q\overline{IFIR}) \qquad \text{eqn 4}$$

Interference is incorporated using a variation of the model developed by Stillman *et al.* (1996).

$$IR = IFIR \qquad \text{if } C \le C_0 \qquad \text{eqn 5}$$

$$IR = IFIR\left(\frac{C + 1}{C_0 + 1}\right)^{-m} \quad \text{if } C > C_0$$

where C = density of competitors; C_0 = density of competitors above which interference occurs; m = interference coefficient. This model assumes that interference is absent, or has a negligible effect on intake rate, below a threshold competitor density where birds have a constant interference-free intake rate. Above the threshold, intake rate decreases as competitor density increases at a rate determined by m. Stillman *et al.* (1996) expressed m as a function of a bird's local dominance, measured as the proportion of encounters won (L). The new model extends this by also making m depend on the number of days since 1 September (N).

$$m = a + bL + cN \qquad \text{eqn 6}$$

The parameter values in equations 5 and 6 were estimated using the same methods and from the same data sets used by Stillman *et al.* (1996). In both feeding methods, interference only occurs at competitor densities above 50 birds ha^{-1} and is more severe in birds of low dominance and later in the winter. This interference threshold differs from that estimated by Stillman *et al.* (1996) because equation 6 incorporates both stage of the season and dominance, while the equivalent equation in Stillman *et al.* (1996) only incorporated dominance.

In the model the density of competitors is calculated in two stages. Initially, the overall density of birds is calculated by dividing the number of birds on the bed by the area of the bed exposed by the tide. This approach assumes that birds are uniformly distributed over a mussel bed, whereas in reality they concentrate in areas of high food availability, or away from disturbed areas, or feed at the start or end of the exposure period when densities are particularly high. The density of competitors actually experienced by birds is therefore calculated by multiplying the overall density by a fixed value. This aggregation factor was determined empirically on the Exe as 8 for stabbers, which feed throughout the exposure period, and 4 for hammerers, which avoid the extremes of the exposure period.

Intake rate on upshore areas and fields

Intake rate on supplementary feeding areas is modelled in a much more simple way than on mussel beds because (i) supplementary feeding is less frequent than feeding on mussel beds; (ii) prey in supplementary areas are not depleted significantly during the course of winter (J. D. Goss-Custard, unpublished data); (iii) intake rate in supplementary areas does not change throughout the course of winter (J. D. Goss-Custard, unpublished data); (iv) oystercatcher densities in supplementary areas are generally low, indicating that interference will be absent or negligible. The model assumes that birds have a fixed intake rate on the upshore and field, irrespective of both the food supply and the density of competitors (i.e. no prey depletion or interference occur). However, even though it has not been measured yet, the model does assume that individuals vary in their feeding efficiency on these patches (the amount of individual variation on both patch types is assumed to be the average of that between mussel-feeding stabbers and hammerers). Intake rate on the field is related to temperature, falling to zero at 0 °C (Goss-Custard & Durell, 1987). Oystercatchers on the Exe do not feed in fields at night and so the model assumes that no intake occurs on the field at night. On the Exe, oystercatchers mostly consume cockles on the upshore, and so the night time feed-

ing efficiency on the upshore is that for cockles (Hulscher 1996) and hence lower than during the day.

Energy assimilation

Energy assimilation is calculated from prey digestion. Digestion is incorporated because it is a significant bottleneck limiting the amount that can be consumed by oystercatchers within a tidal cycle (Kersten & Visser 1996b; Zwarts *et al.* 1996b). It is modelled from the food storage capacity of the gut and the rates at which food is passed into and out of the gut (Kersten & Visser 1996b). Gut storage capacity and processing rate are assumed to be fixed (Kersten & Visser 1996b) whereas the rate of food entry depends on intake rate. If a bird's intake rate exceeds the gut processing rate the gut may fill to capacity and limit the amount of time the bird can spend feeding and the total amount consumed during a tidal stage. The amount of energy assimilated (E_{assim}) is calculated from the length of the tidal stage (S), the intake rate while feeding (IR), the proportion of the tidal stage spent feeding (p_{feed}), and the prey energy density (d_{prey}) and assimilation efficiency (a_{assim}).

$$E_{assin} = a_{assin} d_{prey} p_{feed} S\ IR \qquad \text{eqn 7}$$

Energy expenditure

Energy expenditure is modelled from the results of experiments on oystercatchers in outdoor averies (Kersten & Piersma 1987) and an extrapolation to field conditions (Zwarts *et al.* 1996a). Daily energy expenditure (E_{tot}) is divided into general expenditure (E_{gen}) on activity, digestion and other body functions, and thermoregulatory expenditure, which increases at a constant rate (E_{therm}) per degree reduction in temperature (T) below a critical temperature (T_{crit}).

$$E_{tot} = E_{gen} \qquad\qquad \text{if } T > T_{crit} \qquad \text{eqn 8}$$

$$E_{tot} = E_{gen} + E_{therm}\,(T_{crit} - T) \ \text{ if } T \le T_{crit}$$

Energy storage

Whenever energy acquisition exceeds expenditure, the excess is converted into storage tissues and the mass of the bird increases. When the reverse occurs, storage tissues are converted back to energy and the bird loses mass. The mass gain (M_{gain}) and loss (M_{loss}) during energy storage and release are calculated as below.

$$M_{gain} = \frac{a_{store} E_{excess}}{d_{store}} \qquad \text{eqn 9}$$

$$M_{loss} = \frac{E_{deficit}}{a_{release} d_{store}} \qquad \text{eqn 10}$$

where E_{excess} = energy to be stored; $E_{deficit}$ = energy required from stores; a_{store} = energy storage efficiency; $a_{release}$ = energy release efficiency; d_{store} = energy density of storage tissues.

In the model, birds of each type have a maximum, empirically determined, body mass at each stage of winter, which they attempt to achieve. When a bird is at its maximum mass it regulates its intake (by reducing the proportion of time spent feeding) to prevent any further mass increase. If expenditure exceeds intake, birds lose mass and die of starvation if their weight falls to a minimum value.

CALCULATING SIMULATION RESULTS

The characteristics of each individual were randomly generated at the start of each simulation. As a result, some predictions varied slightly between replicate simulations using the same parameter values. Therefore, model tests were based on the average predictions of 10 replicate simulations.

Results

MODEL DEVELOPMENT

The model's development was guided by the accuracy with which it predicted mortality rates during 1976–80, and so the accuracy of these predictions does not provide a test of the model. Mortality rates were measured each winter by repeatedly checking the whole population for the presence of individually colour-ringed birds (Goss-Custard *et al.* 1982b); the details of the method of calculation used in the present paper and evidence that it provides a reliable measure of mortality rate are given in Durell *et al.* (2000) and Goss-Custard *et al.* (1982b). Many of the birds that disappeared were found dead and, often, their emaciated state suggested they had died of starvation. Others, however, had clearly died from other causes, such as becoming entangled in fishing line on the mussel bed and drowning when the tide came in. These birds were not included in the estimates of observed mortality rates in order to get the best measure possible of the proportion of birds that starved each winter.

By the end of development, the predicted mortality rates from the model for immatures and adults were only 7% below those observed, averaged over the 5 years, but that of juveniles was 31% below those observed (Fig. 2). However, the predicted mortality of juveniles was highly variable because very few juveniles were included in each simulation and the range of juvenile mortalities predicted by the model overlapped the observed mortality. We judged that the relationship between predicted and observed mortality rates in the years for which the
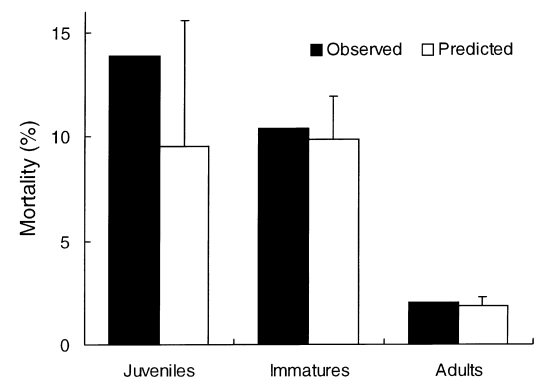
Fig. 2. Predicted (mean +SD) and observed overwinter mortality rates of oystercatchers on the Exe estuary during 1976–80. Observed mortality rates are from Goss-Custard *et al.* (1982b) and Goss-Custard & Durell (1984) but exclude the 18·8% of adult deaths caused by accidents (S.E.A. le V. dit Durell, unpublished data) because this mortality source was not modelled.

model was parameterized was sufficiently close for no further development to be necessary.

TEST OF MAIN PREDICTION, WINTER STARVATION RATE

A further seven estimates of overwinter starvation rates were obtained for adults, although not younger birds, between the winters 1980/81 and 1990/91 (Durell *et al.* 2000). Model simulations were run for each of these winters using the oystercatcher population sizes recorded in the year in question in September. For the main food supply, we used the size of the population of the adult mussels exploited by oystercatchers in those years in which it was measured but the mean adult mussel population size in years in which it was not: the adult mussel population varies between years by so little (McGrorty *et al.* 1990) that the mean value could be used quite safely. The observed oystercatcher winter mortality rate on the Exe during 1976–91 was not related to temperature (Durell *et al.* 2000) and so overwinter temperature was assumed to be the same as during 1976–80. No other parameter values were changed between years.

Plotting the model-predicted and observed winter starvation rates against the density of oystercatchers on the mussel beds in September revealed unexpected density-dependent overwinter mortality rates in both (Fig. 3). Although the close agreement between observed and predicted rates for the model calibration years of 1976–80 is, of course, to be expected, the close agreement for the subsequent years, when both the oystercatcher population size and starvation rate had increased, is a very powerful test of the model's ability to predict quantitatively the factor which it was built to forecast. The model

(a) Grouped years

(b) Individual years
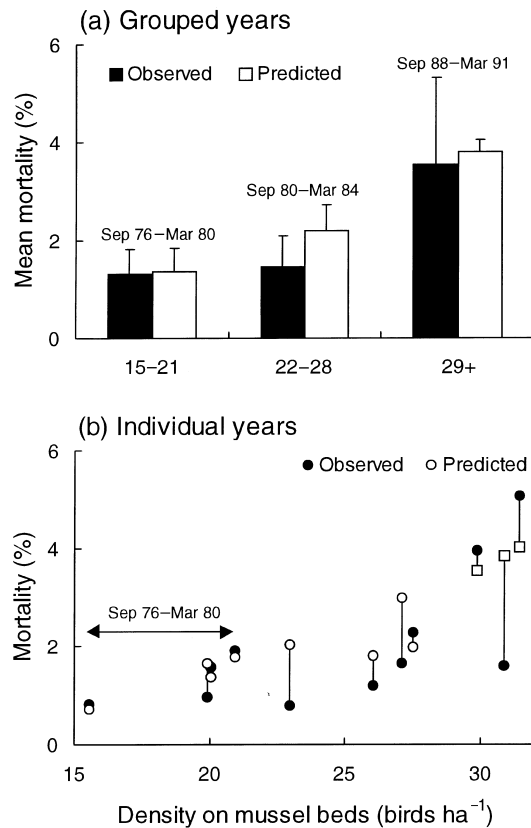
Fig. 3. Predicted and observed (Durell *et al.* (2000), but excluding accidents) overwinter mortality rates of adult oystercatchers on the Exe estuary over 11 winters during 1976–91: (a) mean (+ SD) mortality within groups of years; (b) mortality within each year. Predictions were based on (i) the observed numbers of oystercatchers present in September each year and (ii) either the density of mussels present in September each year [left and middle bars in (a), circles in (b)] or, in winters in which it was not measured, average mussel density in September of all other years [right bars in (a), squares in (b)]. The model development years were 1976–80. Two-thirds of the variation between predicted and observed are explained by annual variation in the combination of winter temperature ($t = -2.53$; $P < 0.05$) and gale frequency ($t = 3.76$; $P < 0.01$), two factors known to affect oystercatcher mortality (Goss-Custard *et al.* 1996b).

therefore accurately predicted the overwinter starvation rate outside the range of conditions for which it was parameterized.

TESTS OF COMPONENT PREDICTIONS

While it is encouraging that the model predicted well the values of winter starvation rate, it may have done so for the wrong reasons. One way to examine this possibility is to test whether the model accurately predicted the seasonal changes in mortality rate, body reserves and behaviour that are thought to reflect the increasing chance of starvation in oystercatchers on the Exe as the winter progresses (Goss-Custard *et al.* 1996b). To inspire confidence,

the model should successfully predict the seasonal changes in these responses of the birds to the changing feeding conditions through autumn and winter.

Timing of starvation

The observed timing of starvation was estimated from the dates on which colour-ringed oystercatchers were last seen on the Exe. Determining the timing of starvation using this approach is problematic because individuals that disappeared may actually have died a considerable time after they had last been seen. An estimate of this 'mortality lag' was obtained from 18 individuals whose recently dead bodies were found. On average, the birds had last been seen alive 23·1 (SE = 4·02) days before their corpses were recovered. The observed time of starvation was therefore calculated by assuming that the average bird died 23 days after it had been last seen alive.

The model predicted that, as winter progressed, birds had increasing difficulty meeting their energy demands so that starvation in all age classes was restricted to the second half of winter (Fig. 4). The observed oystercatcher starvation rate also increased through winter (Fig. 4) although, in adults, it was not as restricted to the end of winter. While this suggests that, in comparison with real birds, those in the model may have rather less difficulty meeting their requirements at the start of winter but more difficulty at the end, the concentration of both observed and predicted deaths towards the end of winter raises confidence in the model.

Body mass

Oystercatchers increase their fat reserves through autumn and winter, to draw on them if the feeding conditions deteriorate (Goss-Custard *et al.* 1996b). In the model, the birds were given as their target mass the observed mean body mass of surviving oystercatchers as determined on the Exe. As the winter progressed, some individuals in the model could not meet their requirements, and so drew on their energy reserves and lost mass. But as most birds were able to achieve their target mass throughout winter, and as the target mass was made the same as the observed mass, the predicted masses of immatures and adults (insufficient field data were available for juveniles) were, inevitably, close on average to the observed (Fig. 5).

The only legitimate test of the model's body mass predictions is its ability to predict the extent to which different classes of birds fall short of the common target masses. This was done by testing the model predictions for the relative mass of hammerers and stabbers. Despite having the same target mass, both immature and adult hammerers achieved a higher mass than stabbers in the model, as in rea-

(a) Juveniles and immatures
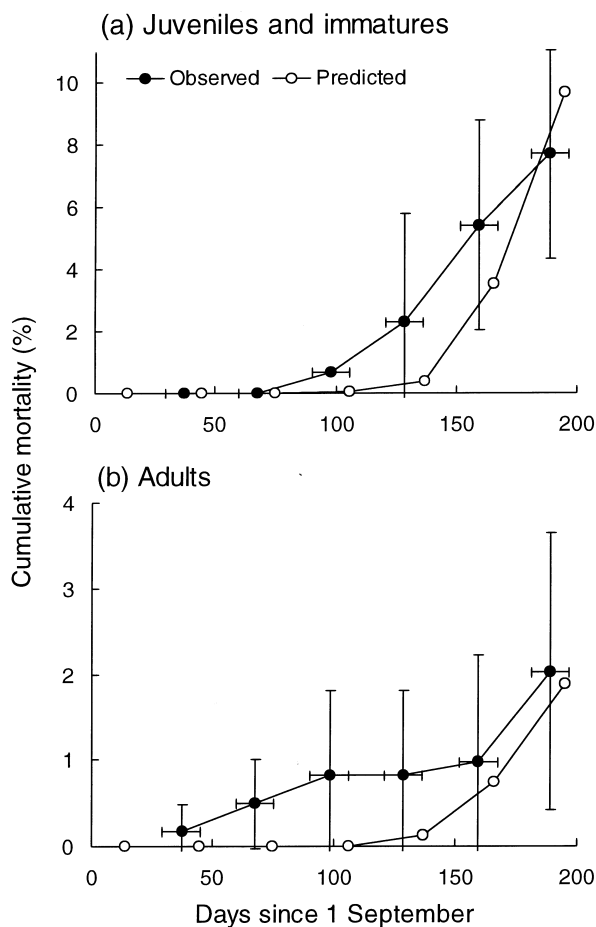
(b) Adults

Fig. 4. Predicted and observed timing of mortality in mussel-feeding (a) juvenile and immature and (b) adult oystercatchers on the Exe estuary. Observed data are based on the dates on which known mussel-feeders were last seen on the Exe plus the 23 days 'mortality lag' between the date of a bird last being seen and its actual date of death; the horizontal error bars show the 95% confidence limits of the lag and the vertical error bars the 95% confidence limits for mortality based on the variation in estimated mortality between years. Observed deaths exclude the 18·8% of adult deaths caused by accidents (S.E.A. le V. dit Durell, unpublished data). Juveniles and immatures are combined as insufficient field data were available.

lity (Fig. 5). As the mean mass of model hammerers was virtually the same as the target mass, nearly all were able to maintain their target mass. In contrast, the mean mass of stabbers, especially by the end of winter, was well below their target and many were failing to meet their requirements. In adults, the model also successfully predicted that stabbers and hammerers maintained a similar mass up to midwinter, after which the mass of stabbers started to fall below target.

Time spent feeding on the mussel beds

Rising energy demands and interference combined with decreasing mussel quality make it increasingly difficult for oystercatchers to meet their energy demands over the low water period as the winter proceeds and, to compensate, they increase the length of time spent in feeding over the low tide period (Goss-Custard *et al.* 1996b). This prediction is difficult to test because oystercatchers do not always move directly between the roost and a single bed as they do in the model. Instead, many feed on high level mussel beds or other upshore areas between the roost and the bed they use at low water. However, a recent radio-tracking study of oystercatchers on the Exe identified precisely when a bird first arrived on a mussel bed as the tide receded and left for the roost as the tide advanced (H. Sitters, personal communication), allowing the duration of the feeding period to be defined. The proportion of that period actually spent feeding by each bird was assumed, as an approximation, to equal the proportion (90%) spent feeding by a large sample of birds on the same mussel beds (numbers 3 and 4) at the same time of year (autumn) on the same tides (springs). The model accurately predicted the number of minutes spent feeding by the average bird in one spring tide exposure period, both at night and during the day (Fig. 6).
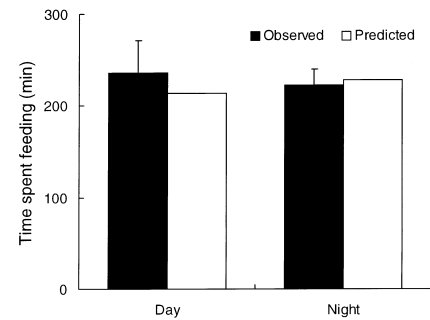
(a) Immatures

(b) Adults
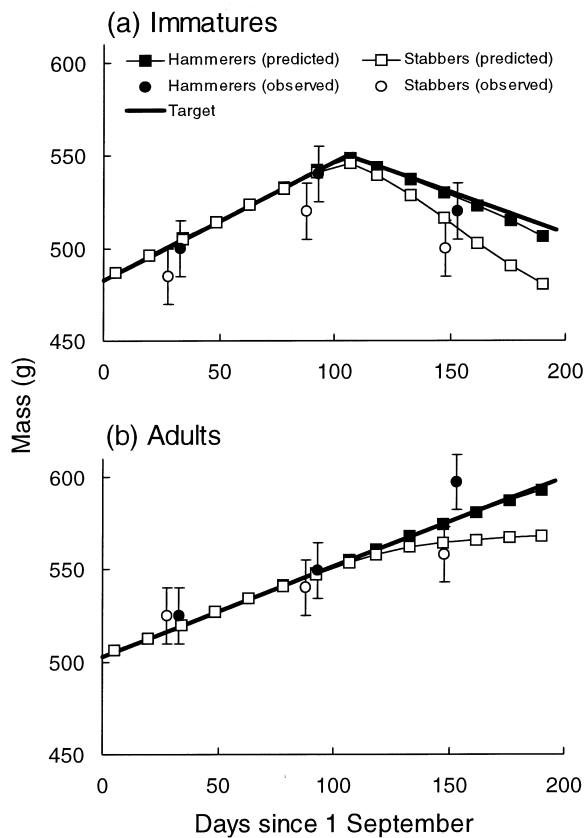
Fig. 5. Predicted and observed body mass (mean ± SE) of immature (a) and adult (b) oystercatchers on the Exe estuary. Thick lines show the age-class specific target masses which both stabbers and hammerers attempted to maintain in the model.

Fig. 6. Predicted and observed (mean ± SD) numbers of minutes spent feeding by oystercatchers on mussel beds on the Exe estuary during an autumn, spring low tide exposure period falling during the day or night. The observed data ($n = 9$ bird days and 5 bird nights) are from a sample of radio-tagged stabbers and hammerers whose arrival and departure times from three of the main mussel beds were known.

Use of supplementary feeding areas

Despite feeding for longer over low tides, many birds still cannot meet their energy requirements from mussel beds alone (Goss-Custard *et al.* 1996b). To compensate for this on the Exe they increasingly use supplementary upshore feeding areas on the advancing and receding tide and fields at high water (Caldow *et al.* 1999). It is not possible to test the model predictions for the numbers of birds feeding on these supplementary food sources as we only counted the total numbers of birds in the fields, and not the numbers feeding; once the autumn arrives many birds go to the fields at high tide and roost. However, the model predicted that birds would start feeding in fields during the last 10 days of October, which coincides well with the observed dates of mid–end of October (Goss-Custard & Durell 1983).

Individual oystercatchers on the Exe vary considerably in the frequency with which they use the upshore and field supplementary feeding areas over high tide, with present evidence suggesting that the most frequent users are those with low foraging efficiency rather than low dominance (Caldow *et al.*

1999). The model prediction for the effect of foraging efficiency on the use of supplementary feeding areas accords well with field data (Fig. 7). In both the model and reality, the most inefficient birds used the fields about 1·5 times as much as an average bird, while the most efficient used them about half as much. However, the field data suggested that an individual's dominance had little effect on its use of the fields (Caldow *et al.* 1999), whereas the model predicted a steady decrease in the use of fields with increased dominance. This suggests that the model overestimates the importance, or strength, of interference, perhaps because real birds in the wild are able to avoid interference from other birds more than our model presently recognizes.

TESTS OF SUBMODEL PREDICTIONS

It is important that the two behaviour submodels produce reasonably accurate predictions of how the birds behave because they predict how the birds would respond to changes in their food supply.

Foraging submodel

The main prediction of the foraging submodel is the instantaneous interference-free intake rate of a bird of average foraging efficiency on each mussel bed, measured as milligrams of ash-free dry mass of mussel flesh consumed per second. The submodel's ability to predict interference-free intake rate was examined in a jack-knife test in which the model was parameterized for all sites but one, whose intake rate was then predicted and compared with the observed rate, measured below the threshold bird densities at which interference begins. As a number of birds were watched in most sites, the observed

(a) Foraging efficiency
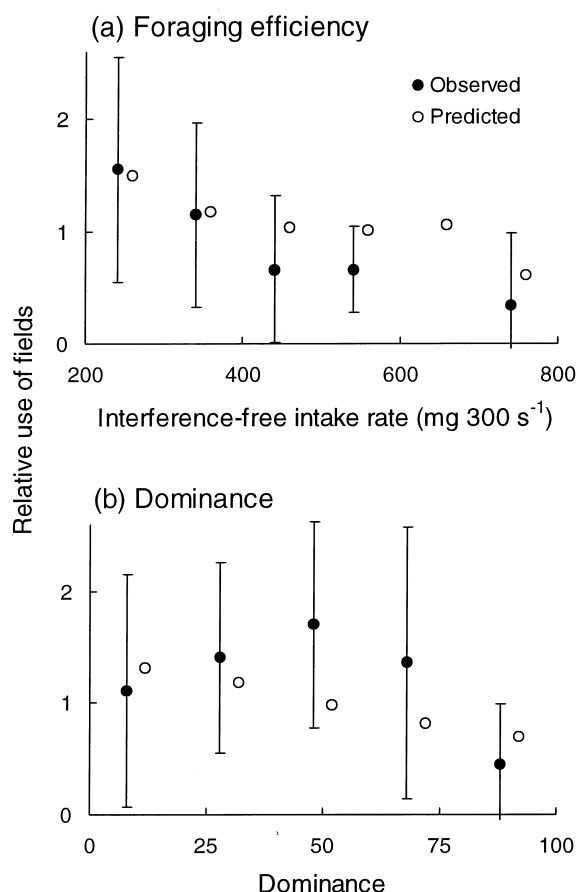
(b) Dominance

Fig. 7. Predicted and observed use of fields for supplementary feeding by birds of different (a) foraging efficiency and (b) dominance. The predicted use for each bird was the proportion of high tides (on full neaps during daylight between September and March) on which it used the fields for supplementary feeding. The observed use for each bird was the proportion of observer visits to the fields (mostly on neap tides, during daylight between September and March) on which it was seen. The use for both model and real birds is expressed relative to the average use of birds of that type because the observed data underestimated field use as birds could not always be identified in the fields even if they were present. The average use of fields is shown (± 95% confidence limits for observed data) within ranges of foraging efficiency and dominance. Observed values were calculated from the data used by Caldow *et al.* (1999).

interference-free intake rate probably approximates that of a bird of average efficiency. The procedure was repeated, dropping out a different site on each occasion and predicting the intake rate recorded there, and comparing it with the observed.

The predictions matched the observed rates quite well but there was a tendency for the submodel to underpredict at high values and to overpredict at low values (Fig. 8). The slope of the relationship between predicted and observed rates is significantly less than unity ($b = 0.72$, SE $= 0.10$, $t = 2.78$, $P < 0.01$) and the intercept is significantly greater than zero ($a = 159$, SE $= 61$, $t = 2.60$, $P = 0.013$). Omitting

the single outlying point at the highest observed rate recorded (Fig. 8) did not convincingly correct the tendency to underpredict at high values, even though the slope was no longer significantly different from unity ($b = 0.82$, SE $= 0.10$, $t = 1.84$, $P > 0.05$) and the intercept was not different from zero ($a = 110$, SE $= 60$, $t = 1.83$, $P > 0.05$). A tendency to underpredict at high values probably reflects the large error terms in the independent variables, such as the measurement of the density of highly clumped mussels, in some of the regression equations that are used in the submodel. When the regression analysis assumption of no errors in the x-axis is strongly violated like this, the calculated slope of the relationship is underestimated, a tendency that cannot yet be corrected in multiple regression analysis (Snedecor & Cochran 1967). Errors in the x-axis alone may thus explain the submodel's tendency to overpredict at low values and underpredict at high ones. On the other hand, in only four of the 38 comparisons did the 95% confidence limits of the observed data not encompass the predicted rate. We conclude that the match between the submodel predicted and observed interference-free intake rates, though not perfect, was sufficiently close to suggest that, over a wide range of values, the submodel predicted intake rates reasonably well.

Distribution submodel

Most mussel-feeding oystercatchers on the Exe feed throughout the autumn and winter on mussel beds at low tide, with only very small numbers feeding on the supplementary upshore and field areas. The model predicted this well: at low tide 99·5% of model birds fed on mussel beds and only 0·5% fed on the upshore area and none used the fields or roosted. This occurred because virtually all oystercatchers achieved their highest intake rates on mussel beds.

Individual beds differ in quality, measured as the interference-free intake rates achieved by oystercatchers. Accordingly, beds supported different numbers and densities of oystercatchers. There was a positive relationship between the predicted and observed numbers and densities on the 10 mussel beds (Fig. 9). However, particularly in the case of predicted density, there was again a tendency for the submodel to underpredict at high values and to overpredict at low values. The slope of the relationship between predicted and observed numbers was not significantly different from unity ($b = 0.719$, SE $= 0.230$, $P > 0.05$), but that for density was significantly lower than unity ($b = 0.403$, SE $= 0.257$, $P < 0.05$). The intercept of the relationship between predicted and observed numbers was not significantly different from zero ($a = 43.7$, SE $= 40.6$, $P > 0.05$), whereas that for density was ($a = 15.8$, SE $= 6.9$, $P < 0.05$).
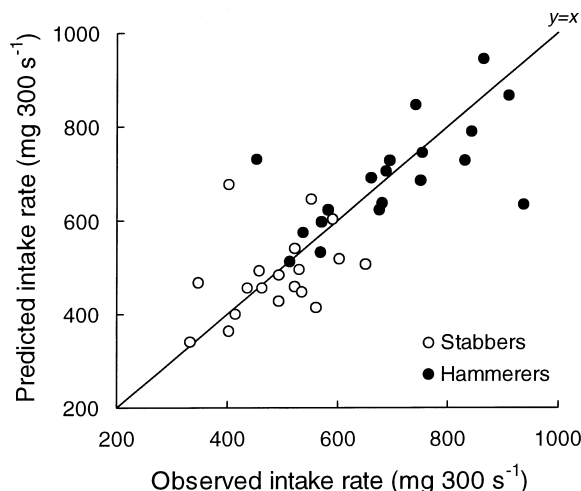
Fig. 8. Jack-knife comparison between the observed interference-free intake rates of stabbers (open symbols) and hammerers (closed symbols) and the rates predicted by the foraging submodel.

Once again, the tendency to overpredict at high values and to underpredict at low values probably reflects the often large error terms in the estimation of independent variables in some of the component regression equations used in the submodel.

MODEL SENSITIVITY TO PARAMETER VALUES

A sensitivity analysis was carried out to identify those parameters, whose values could be varied, that have the greatest influence on model predictions. This is not only interesting in its own right but also identifies the parameters on which research effort should be focused to improve model predictive precision. The output used to measure sensitivity was overwinter starvation rate, which the model was built to predict. Either single parameters (Fig. 10) or groups of related parameters (Fig. 11) were decreased or increased by 25% of their value in standard simulations. Within groups, individual parameters were not necessarily all changed in the same direction, but were changed to have the combined effect of either increasing or decreasing the survival difficulty of oystercatchers. To test whether sensitivity was influenced by population size, simulations were run at the 1976–80 population of 1550 birds, and at a much higher one of 10 000 birds. Predicted mortality was virtually unchanged between replicate simulations, and so only one simulation was run for each set of parameter values.

Mortality was more sensitive to changes in parameter values at the higher population size (Figs 10 and 11), due to the greater difficulty birds had in meeting their energy demands. At the lower population size, most birds met their demands easily, so

very large changes in conditions were needed to increase mortality. As only a few parameters caused such large changes, mortality was insensitive to most parameters. In contrast, at the higher population size most birds had difficulty in meeting their demands. Many either only just survived or died at the very end of winter. Small changes in conditions therefore determined whether these birds survived, and so mortality was more sensitive to variation in parameter values.

Model sensitivity to the different parameters indicates whether it contained the appropriate number of parameters. If sensitive to only a few parameters, the remainder would be redundant. However, changing each individual parameter produced at least one prediction outside of the range of the standard
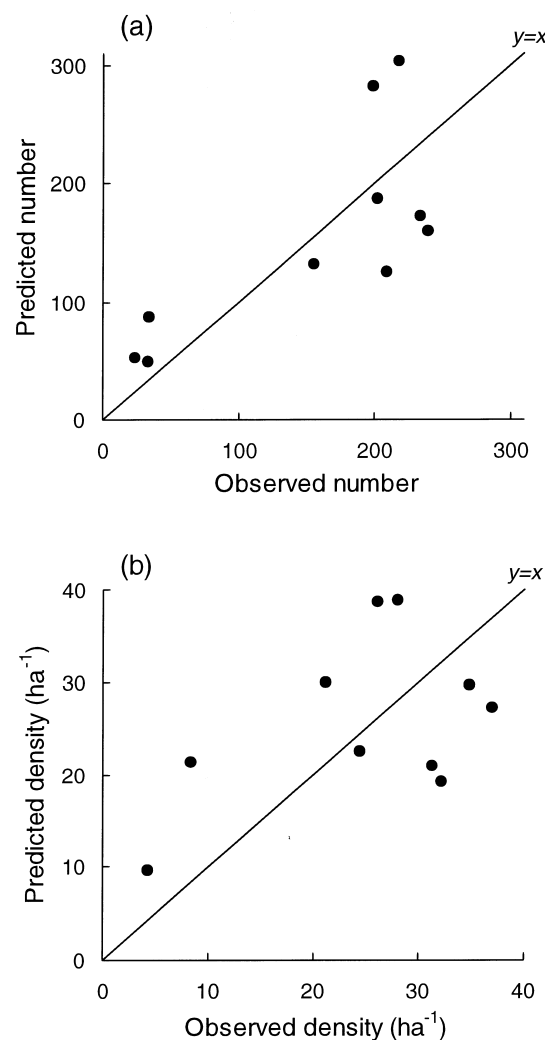
Fig. 9. Predicted and observed distributions of oystercatchers over 10 Exe estuary mussel beds; (a) numbers and (b) densities on each mussel bed. Values are for spring low tides, during the hours of daylight, between 1 September and 31 January, a period when the total population and distribution of oystercatchers on the Exe are particularly stable.
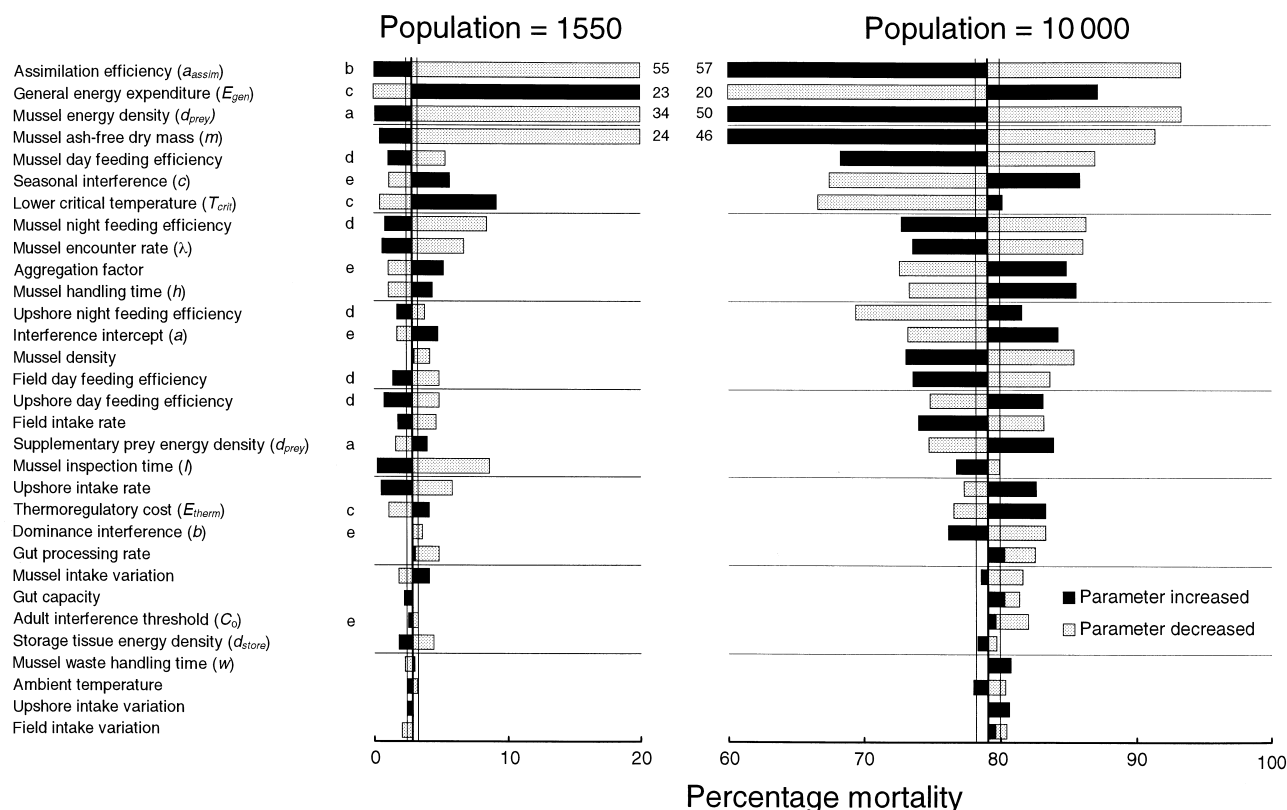
Fig. 10. Sensitivity of predicted overwinter mortality to changes in single parameter values. Vertical lines show the mean (thick line) and range (thin lines) of mortality rates predicted by 10 simulations using the standard parameter values. Bars show the predicted mortality when single parameters were decreased or increased by 25% of their standard value. Numbers against bars show percentage mortality rates outside the range of a plot. Parameters are sorted by their mean influence on mortality at the two population sizes. Letters a–e show parameter groups (Fig. 11).

simulations (Fig. 10). All parameters tested therefore had at least some effect on predictions, although some had a much larger effect than others.
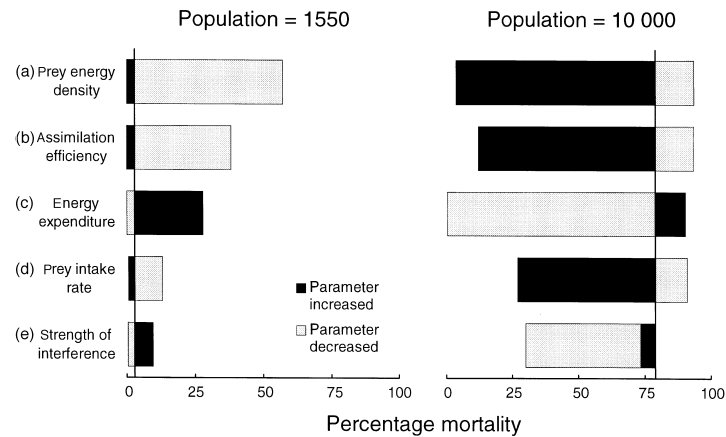
Increased assimilation efficiency, mussel energy density and ash-free dry mass, and decreased energy expenditure and critical temperature, increased the ease with which oystercatchers could meet their energy demands and so fewer died. These gross energetics parameters were some of the most important in the model. They all directly related to oystercatcher energy requirements (equation 7) and the rate at which they obtained energy from their prey (equation 8).

Many behavioural parameters significantly affected percentage mortality, although to a lesser extent than the gross energetic parameters. Perhaps because oystercatcher behaviour was modelled in detail, variation in single parameters had a lesser effect than an equivalent variation in overall intake rate, which these parameters were used to predict. However, even when groups of behavioural parameters were varied together their combined effect was still less than groups of energetic parameters (Fig. 11). Nonetheless, interference clearly played an important role in the model. Increased seasonal interference, aggregation factor and interference intercept (the interference experienced by subdominant birds at the start of winter) were among the most important parameters. The individual foraging efficiency of birds on mussel beds during both day and night was also important, and more so than their efficiency on supplementary prey. Of the parameters used to calculate the intake rate of birds feeding on mussels (equation 1), prey encounter rate was most important, followed in order of importance by handling time, mussel density, inspection time and waste handling time. Changes in intake rate on fields and upshore areas produced equivalent changes in mortality. The extent of individual variation in feeding efficiency on mussels was more important than that on the upshore or field.

MODEL SIMPLIFICATION

Behaviour-based population models are more complex than traditional demographic population models. The birth or death rate demographic functions of traditional models are not expressed directly, but arise from the reproductive and survival decisions of individuals, which are themselves derived from mul-

Population = 1550   Population = 10 000

(a) Prey energy density

(b) Assimilation efficiency

(c) Energy expenditure

(d) Prey intake rate

(e) Strength of interference

■ Parameter increased
□ Parameter decreased

0   25   50   75   100   0   25   50   75   100
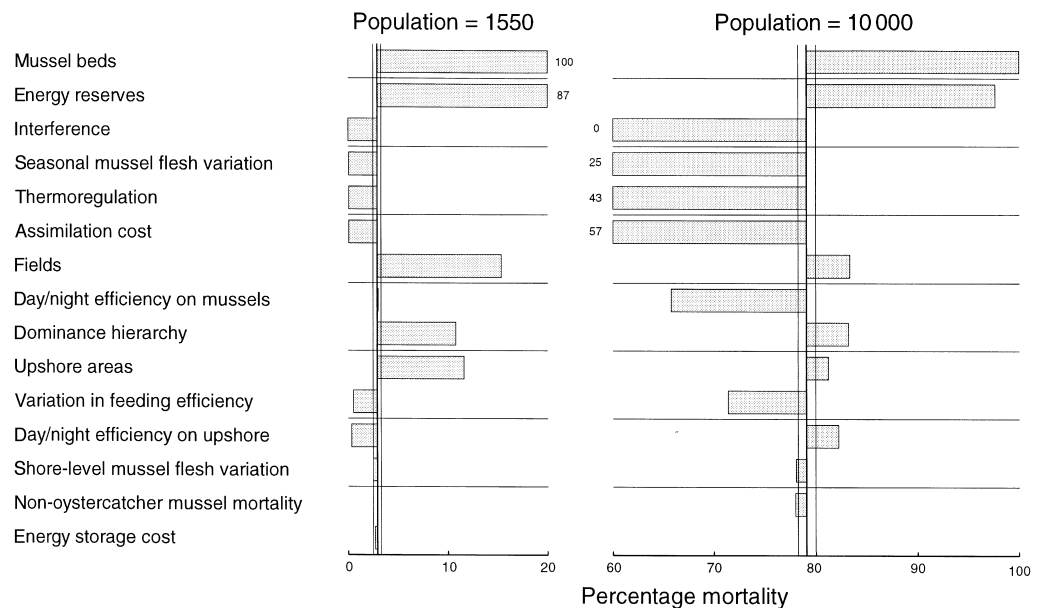
Percentage mortality

Fig. 11. Sensitivity of predicted overwinter mortality to changes in groups of parameter values. The vertical line shows the mean mortality predicted by 10 simulations using the standard parameter values. Bars show predicted mortality when groups of parameters were decreased or increased by 25% of their standard value. Parameters are sorted by their mean influence on mortality at the two population sizes. See Fig. 10 for the individual parameters contained in each parameter group.

tiple behavioural parameters and functions. Complexity may also increase if testable predictions are required for a specific system, as in the present study; high predictive power may depend on multiple components of the system rather than just a few. Finding the right balance between complexity and generality, a key element in all modelling, may be particularly challenging for behaviour-based population models (Goss-Custard & Sutherland 1997). Therefore we explore here the extent to which the model can be simplified by omitting parameters and

replacing complex functions with simpler ones. Again, the outcome is measured in terms of the effect on overwinter starvation rate.

Removal of parameters

Model sensitivity was tested by removing groups of related parameters, assumptions or components, at populations of 1550 and 10 000 birds (Fig. 12). One simulation was run for each set of parameter values.

Population = 1550   Population = 10 000

Mussel beds
Energy reserves
Interference
Seasonal mussel flesh variation
Thermoregulation
Assimilation cost
Fields
Day/night efficiency on mussels
Dominance hierarchy
Upshore areas
Variation in feeding efficiency
Day/night efficiency on upshore
Shore-level mussel flesh variation
Non-oystercatcher mussel mortality
Energy storage cost

100
87
0
25
43
57

0   10   20   60   70   80   90   100

Percentage mortality

Fig. 12. Sensitivity of predicted overwinter mortality to the removal of model components. Vertical lines show the mean (thick line) and range (thin lines) of mortality rates predicted by 10 simulations using the standard parameter values. Bars show predicted mortality when a model component was removed. Numbers against bars show percentage mortality rates outside the range of a plot. Components are sorted by their mean influence on mortality at the two population sizes.

The presence of mussel beds was the most important component of the model. Their total removal caused all birds to die even at the lower population size. None could survive by just feeding on the upshore and field. But even though these areas could not sustain birds on their own, they were still important as supplementary feeding areas. Removal of either caused mortality to increase greatly, indicating that some birds depended on these habitats to supplement their mussel intake. Other components dealing with aspects of the mussel food supply had a range of effects. Mortality was decreased greatly when mussel flesh content remained at its September value rather than declining and, to a lesser extent, when flesh content did not decline at high shore levels. In contrast, the removal of mussel mortality due to factors other than oystercatchers had little effect on the model's predictions because these losses were small.

The oystercatcher energy reserve was the second most important component. Without reserves, birds attempted to maintain their body mass at the starvation mass and starved if their energy requirements were not met during a single day. Most birds had at least one day in which their demands were not met and so almost all of them died when they did not store reserves. Two other energetic components, thermoregulation and assimilation costs, were also important, the presence of either increasing the level of mortality. In contrast, the presence of energy storage costs did not influence predictions.

Interference was the third most important of the components tested. Without interference, no birds died at either population size, indicating that interference was one of the major factors killing birds in the model. In accord with this, the presence of a dominance hierarchy was also important. When all birds were of the same dominance, mortality increased because the average level of interference increased: with a dominance hierarchy only subdominants suffered. Removal of the other source of individual variation, feeding efficiency, meant that all birds were of average efficiency. Under this condition mortality decreased because only birds of below average efficiency died in the standard simulations. Removal of a dominance hierarchy or variation in feeding efficiency produced a similar magnitude of change in mortality, indicating that both sources of individual variation were of similar importance.

Removal of the foraging submodel

A large number of parameter values were required for the foraging submodel (equations 1–3; Appendix). Several parameters were estimated on each of several mussel beds for birds of each feeding method. In addition, the density of the different size classes of mussels was also estimated on each bed. A large part of fieldwork devoted to model parameterization was concerned with this submodel.

A simpler approach would be to replace the foraging submodel with a functional response, a single function in which instantaneous intake rate is related to the biomass density of the mussels of the size range from which oystercatchers obtain most of their intake. This loses the ability of the model as a whole to predict to very different mussel food supplies. For instance, a reduction in nutrient input to the estuary would reduce the food supply to the mussels and thus their rate of growth, and therefore size, and also the flesh-content of a mussel of a given size, and thus its value to the birds. However, this danger can be minimized by describing the functional response over as wide a range of mussel numerical density, size distribution and flesh-content as possible. This was done by recording intake rate and mussel biomass density in small (c. 0·25–1 ha) study sites, using techniques described in Goss-Custard & Durell (1987). Mussel biomass density is measured for mussels exceeding 30 mm in length, as most mussels on the Exe taken by oystercatchers in autumn and winter exceed this length (Cayford & Goss-Custard 1990).

Instantaneous intake rate is quite variable in both stabbing and dorsally hammering oystercatchers but there is no trend across a wide range of mussel biomass density; the functional response is essentially flat down to very low mussel biomass densities (Fig. 13). Some of the variation is related to the change in the flesh content of the mussels over the winter. While the time costs of finding and opening a mussel of a given size remain broadly the same as the winter progresses (J. D. Goss-Custard, unpublished data), the energy return from each mussel declines by up to 40%. Accordingly, in fitting a hyperbolic asymptotic function to the data, which was forced through the origin, the ash-free dry mass of a standard mussel of length 47·5 mm in each site was also included in the analysis. The fitted equation was equation 11.

$$\overline{IFIR} = \frac{(a + bm_{47.5})B_{>30}}{c + B_{>30}} \qquad \text{eqn 11}$$

where $\overline{IFIR}$ = interference-free intake rate of a stabber or hammerer of average feeding efficiency; $m_{47.5}$ = ash-free dry mass of a mussel of length 47·5 mm; $B_{>30}$ = biomass density of mussels in size range consumed by oystercatchers (> 30 mm). Non-linear regression was used to estimate the values of a = 292·7, b = 0·311 and c = 0·379 for stabbers and a = 151·7, b = 0·864 and c = 0 for hammerers.

Simulations were run at a range of September population sizes and the starvation rate plotted against initial population size, using either the foraging submodel or the functional responses to calculate interference-free intake rates (Fig. 14). The
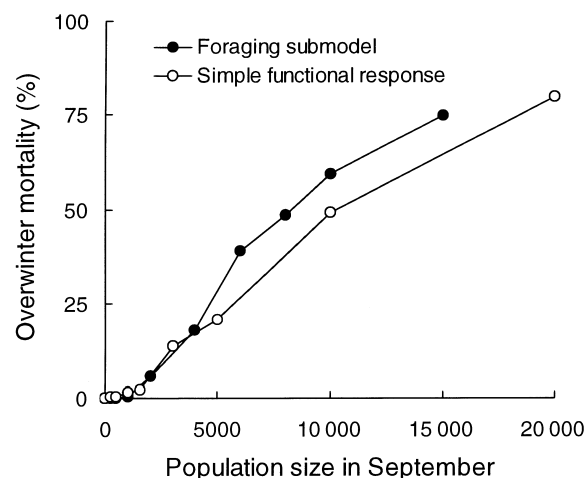
(a) Stabbers

(b) Hammerers
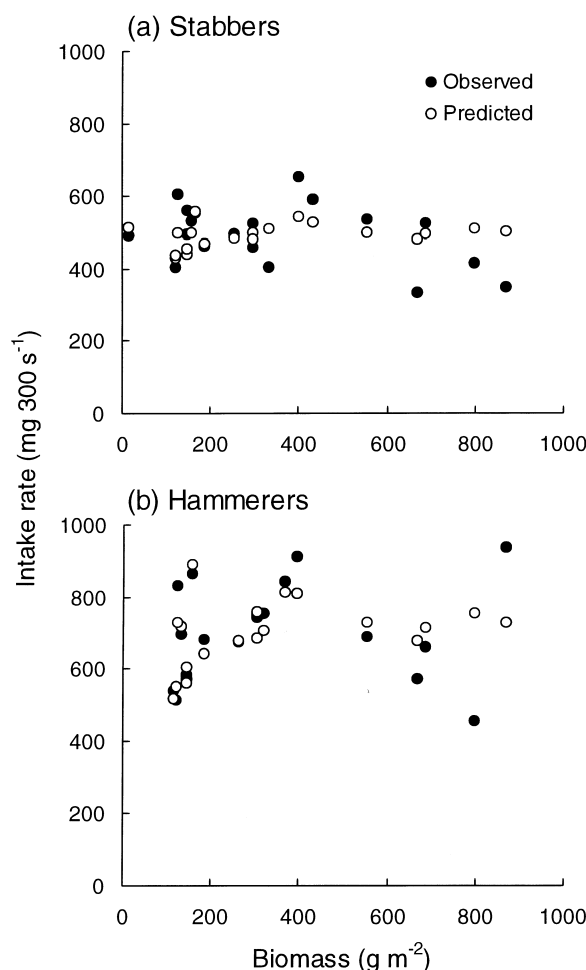
Fig. 13. Observed and predicted functional responses of (a) stabbers and (b) hammering oystercatchers. Predictions were derived by fitting equation 11 to the observed data and incorporate the effect of both the biomass of mussels longer than 30 mm and the ash-free dry mass of a standard 47·5 mm mussel.

Fig. 14. Predicted density-dependent starvation functions in which the interference-free intake rates of the oystercatchers were either calculated from the foraging submodel (solid symbols) or, more simply, from the functional responses shown in Fig. 13 (open symbols).

resulting density-dependent functions were very similar, suggesting that the biomass functional response adequately captures the variation in intake rate within the range of conditions in which the data were obtained.

Discussion

The model was developed to produce quantitative predictions for novel feeding conditions as well as those for which it was parameterized. An ability to predict starvation rates in new circumstances was regarded as the most powerful test of our understanding of the system. But it was also necessary for exploring 'what-if' scenarios; some examples of how the density-dependent starvation functions derived from the model can be incorporated into demographic population models to explore the population consequences of a change in the feeding conditions are given in Goss-Custard *et al.*

(1995a,b,c, 1996a,b). To achieve the level of predictive power required, the model needed to contain many parameters specific to the Exe system. However, the basic principle of the model, that the demographic functions, and thus the dynamics of a population, can be predicted from the optimizing behaviour of its individuals, applies to any system. The model can therefore be used to draw conclusions for behaviour-based population models in general.

The critical test of the model's predictive power was its success in predicting observed adult mortality rates during the years 1980–91 when the Exe population increased above the baseline years 1976–80. The model predicted the density-dependent increase in mortality with a high degree of accuracy, even though both the population sizes and mortality rates were outside the range for which it was parameterized. This is a powerful test because model parameters were derived directly from empirical data; none was chosen to force the model to produce accurate predictions over this period. The ability of the model to predict accurately to new circumstances raises confidence that it provides a realistic description of the system.

The model also predicted quite well other components of the real system. These included the use of mussel beds at low tide in preference to upshore areas or fields, the numbers and densities of birds feeding on the different mussel beds, the interference-free intake rate of birds of average foraging efficiency, the length of time over low water that birds fed during the day and at night, the stage of the winter at which birds started to supplement their mussel intake by feeding in the fields over high tide,

the mass difference between birds of different feeding method and the timing of mortality. This shows that the overall mortality rate predicted by the model was based on realistic behaviour and physiology of oystercatchers within the model population.

Even though the importance of each model component was checked during development, it was still possible that the model had become unnecessarily detailed. The sensitivity analyses suggested that this was not the case. The quantitative predictions were altered by nearly all of the model's parameters. Nonetheless, there was considerable variation in the sensitivity of the model to different parameters. The model's predictive power was based on many parameters, even though it described a relatively simple system of one predator and three prey types. Many other systems are more complicated. Therefore, behaviour-based models intended to produce accurate predictions may need to incorporate many detailed aspects of a system. On the other hand, we showed that the model could be much simplified, while retaining much of its predictive power, by replacing the detailed foraging submodel with a biomass functional response. By doing so, the model loses the ability to predict the sizes of prey taken by the birds, which is important when this model is coupled with a model of prey population dynamics and simulations are run over many prey generations. But for the purposes of predicting how many birds starve within one winter, the functional response is a satisfactory alternative to a parameter-rich foraging submodel, and should make it much easier to apply to other systems.

Ease of application will also be improved when the factors that determine the variation between predator species and prey species in the two parameters of the hyperbolic functional response are better understood. In shorebirds, for example, preliminary work suggests that the plateau of the function varies with the body size of the bird, with prey size and whether the prey are located by sight or touch, while the gradient may vary just with the method of prey location (J. D. Goss-Custard, unpublished data). Once the rules governing the variation in plateau and gradient, both within and between predator species, have been established, it should be possible to parameterize the functional response with new fieldwork only being conducted on components of the system that are easy to study, such as prey size. The same point applies to the rules governing the strength of interference, and in the amount by which it varies between individuals. In the present model, a very extensive field programme was required to parameterize the interference functions. Even then, these functions may not provide a secure basis for forecasting bird behaviour in new conditions because they may only apply to the present-day conditions in which they were determined (Goss-Custard *et al.* 1995b). However, it is likely

that there are rules which govern variation in the shape and parameter values of interference functions. Once discovered, these rules could be used to parameterize the model more easily and, additionally, provide parameters that would apply to new feeding conditions, outside the present-day empirical range. Such rules are currently being pursued with an individual-based model of interference (Stillman, Goss-Custard & Caldow 1997).

The sensitivity analyses showed that most energetic parameters had a larger impact on model predictions than most behavioural parameters. The behavioural parameters were not irrelevant, however, because these were the basis of predictions. All behaviour-based population models that predict mortality rates must in some way express the circumstances under which animals die. When death is by starvation, they must compare the rates of energy expenditure and acquisition. The sensitivity analyses suggest that, although these models are necessarily behaviour-based, the accuracy of predictions also greatly depends on energetic parameters, which must therefore also be well researched.

Sources of individual variation in the model were largely restricted to differences in the foraging performance of individuals, as in previous behaviour-based population models (Sutherland & Dolman 1994, 1995b; Goss-Custard *et al.* 1995a; Sutherland 1996). However, as model predictions were so sensitive to energetic parameters, individual variation in these parameters may be even more important than variation in foraging performance. One source of such variation could be parasite load, which can affect energy expenditure (Booth, Clayton & Block 1993) and digestive efficiency (Connors & Nickol 1991). Future studies need to measure individual variations in energy expenditure and assimilation efficiency, and incorporate these into behaviour-based models to test the relative importance of individual variation in energetic and behaviour parameters.

The sensitivity analyses show that the principal prediction of the model is sensitive to the value of many of its parameters. This increases the chances that the model produced, for the wrong reasons, accurate forecasts of winter starvation rate in the years following those for which it was calibrated. A wide variety of combinations of parameter values could, in principal, produce the same outcome. The only way to ensure that the model accurately captures the most important elements of the system is to explore its properties continually by testing its component predictions in order to detect a quantitative mismatch between prediction and observation. In the present model, most of the component predictions were quantitatively consistent with observation, which does suggest that the model captures the main features of the system. The main discrepancy we have detected so far is the greater importance,

relative to variation in individual foraging efficiency, that the model gives to individual dominance in determining whether a bird must supplement its low-tide mussel consumption by feeding in the fields over high tide. But with so many of the other component predictions supported by observation, we regard this as a stimulus for further investigation of this aspect of the system to understand why this discrepancy has arisen, rather than as being fatal to the approach as a whole.

The model can be used to provide predictions on the effects of shorebird overwinter survival, and thus population size, of a wide range of human activities that have an impact on their feeding environment. By removing part or the whole of a feeding patch, or patches, the model can predict by how much mortality during the non-breeding season will increase at present-day, and possible future, population sizes. This equates to predicting the effect of habitat loss arising from such activities as land-claim for recreation and industrial purposes (Goss-Custard *et al.* 1996c). A particular advantage of the approach is that the quality of the patch that is lost, relative to the quality of the others that remain, is taken into account, as is their shore-level and thus period of availability to the birds during the tidal cycle; the model avoids the need to make the often unreal assumption that only habitat of average quality is removed (Goss-Custard & Sutherland 1997). The model can also predict the effect on the birds of temporary losses of feeding areas arising, for example, from human disturbance. When a bait-digger or dog-walker drives shorebirds away from a feeding area, the birds usually join other birds feeding in currently undisturbed places, thus temporarily intensifying any interference and depletion competition that occurs. But once the source of disturbance has left, or at night when disturbance is often uncommon, the birds are able to return to the previously disturbed areas and continue to exploit the food supplies there. The model can thus predict by how much winter mortality rates are increased, if at all, by different levels of disturbance from people. Similarly, the model can predict the effect on mortality rate of the harvesting of intertidal food resources, such as shellfish. The model not only incorporates the effect of the removal of shellfish prey itself but also takes into account the disturbance, if any, from the people that are doing the harvesting (Goss-Custard *et al.* 2000). The model can also predict by how much mortality will be affected by other changes in the feeding environment, including general increases or decreases in the food supply arising from changes in the nutrient regime of the system, sea level rise or offshore changes in sedimentation.

The essential requirement for using the model to make such predictions is that the food supply, perhaps best expressed as an average over a number of winters, is known in each of the main feeding areas

('patches') and that the length of time for which each patch is exposed during the tidal cycle is also known. Although sometimes this will mean that the food supplies have to be surveyed anew, in many estuaries they have often been sampled before as part of earlier environmental impact and scientific studies or ongoing monitoring programmes. As the functional response is now known to be adequate for predicting shorebird mortality rates, only the biomass density of the main shorebird prey species has to be known; only in special circumstances, such as modelling the long-term interaction between the populations of shorebirds and shellfish, will the numerical densities of particular size-classes of the prey be needed (Goss-Custard *et al.* 2000). When model predictions are required for 'what-if' scenarios that will involve changes in food abundance, predictions are required for prey biomass density in the new scenario. These are often quite easy to obtain because average macro-invertebrate density depends so much on the values of parameters that are themselves predictable, particularly organic content, sediment particle size composition and shore level (Yates *et al.* 1993). Many of the other parameter values needed for parameterizing the model are available in the literature; for example, the daily energy requirements, the main prey species taken and their loss of energy content over the winter. The most important parameter values that are presently not widely available are those measuring the gradient and asymptote of the 'biomass' functional response and the coefficients for the interference functions in each of the 1–20 common shorebird species for which predictions are usually required. Both, however, are being actively researched and it should be possible within 2–3 years to predict their values from characteristics of the birds and their prey organisms (prey size, bird feeding method) that are themselves easy to define in any particular case (Stillman, Goss-Custard & Caldow 1997). Once this has been achieved, it will be possible to apply the model to a particular estuary in a short time period, and certainly within the time usually available in environmental impact studies on estuaries (two to three winters) and, if the food supply is already known, in considerably less.

The main model output is the winter mortality rate under the different scenarios considered. This output can be used by policy-makers considering alternative policy scenarios, including the present-day management plan for the estuary, in two ways. First, any increase in mortality rate that is predicted by the model for a particular policy option or scenario can be used to predict, from the current population size, the extra number of deaths that would be expected to occur; thus the ornithological 'cost' of implementing a given policy or scenario can be measured in terms of the increased number of deaths, if any. Secondly, the model can predict the

parameters of the density-dependent starvation function that would occur under a given scenario (Goss-Custard *et al.* 1996c). This predicted function can then be used in a year-round demographic population model to predict the effect on the long-term equilibrium population size (Goss-Custard *et al.* 1995d,e). Which of the uses to which the mortality predictions are put will, of course, depend on what is thought to be most appropriate by the policy-makers.

That the model predicts the behaviour of the birds well is important because the main feature of this model is that it is behaviour-based. It is also individual-based and physiologically based, but the parameters of neither of these features change in response to environmental change; the characteristics of individuals stay the same and the physiological constants, such as assimilation efficiency, are assumed also to remain the same. However, when the feeding conditions change, the model birds respond behaviourally. Depending on the kind of change envisaged, the birds in the model can alter where, when and for how long they feed, the size of mussels they select and whether to exploit supplementary food supplies. Their choices are based on simple rate-maximization optimization rules, derived from 25 years of research in behavioural ecology. While the present model does not include such potentially important features as state-dependent decision-making, there is no reason in principal why this cannot be added in cases where it seems important to do so. The key point is that, by being based on optimization decision-making rules, the birds in the model are likely to respond to changes in their feeding conditions as real birds would. We view this as the main strength of a modelling approach that may be widely applicable to many systems and which puts our understanding of the system to the rigour of quantitative test and predicts the response of populations to novel environmental change.

Acknowledgements

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Appendix

Parameter values used in the model

TIME AND ENVIRONMENTAL CONDITIONS

Parameter and source	Value		
Duration of winter	1 September–15 March		
Duration of tidal cycle	12·4444 h		
Number of tidal stages	High water, receding tide, low water, advancing tide = 4		
Duration of spring–neap cycle	14 days = 27 tidal cycles		
Time of first high water on full spring tides	6·25 h after midnight		
Duration of tidal stages on full spring tides (methods in McGrorty & Goss-Custard 1991)	High water, 4·74 h; receding tide, 1·00 h; low tide, 5·70 h; advancing tide, 1·00 h		
Duration of tidal stages on full neap tides (methods in McGrorty & Goss-Custard 1991)	High water, 4·14 h; receding tide, 1·00 h; low tide, 6·30 h; advancing tide, 1·00 h		
Duration of longest and shortest days at latitude of Exe estuary (including the hours of twilight)	18·11 h on 21 June, 9·25 h on 21 December		
Mean daily temperature at Exeter airport (the nearest weather station to the Exe) from September 1976 to March 1982 (S.E.A. le V. dit Durell, unpublished data)	1 September, 16·5 °C; 1 October, 12·5 °C; 1 November, 9·2 °C; 1 December, 7·0 °C; 1 January, 5·6 °C; 1 February, 5·3 °C; 1 March, 5·8 °C (intermediate temperatures occur between the dates shown)		

PREY PATCHES

General parameters

Parameter and source	Value		
Number of patches	Mussel beds = 10, upshore = 1, fields = 1		
Maximum patch area exposed at low water on full spring tides (McGrorty et al. 1990)	Bed 1	5.49 ha	
	Bed 3	4.45 ha	
	Bed 4	6.31 ha	
	Bed 20	9.41 ha	
	Bed 22	4.06 ha	
	Bed 25	8.30 ha	
	Bed 26	6.52 ha	
	Bed 27	1.27 ha	
	Bed 30	7.64 ha	
	Bed 31	7.79 ha	
	Upshore	10.00 ha	
	Field	10.00 ha	
Proportion of patch exposed at each tidal stage (high water, receding tide, low water, advancing tide) on spring tides (methods in McGrorty & Goss-Custard 1991)	Bed 1	0.0, 0.0, 1.0, 0.0	
	Bed 3	0.0, 0.0, 1.0, 0.0	
	Bed 4	0.0, 0.0, 1.0, 0.0	
	Bed 20	0.0, 0.0, 1.0, 0.0	
	Bed 22	0.0, 0.0, 1.0, 0.0	
	Bed 25	0.0, 0.0, 1.0, 0.0	
	Bed 26	0.0, 0.0, 1.0, 0.0	
	Bed 27	0.0, 0.0, 1.0, 0.0	
	Bed 30	0.0, 0.0, 1.0, 0.0	
	Bed 31	0.0, 0.0, 1.0, 0.0	
	Upshore	0.0, 1.0, 1.0, 1.0	
	Field	1.0, 1.0, 1.0, 1.0	
Proportion of patch exposed at each tidal stage (high water, receding tide, low water, advancing tide) on neap tides (methods in McGrorty & Goss-Custard 1991)	Bed 1	0.0, 0.0, 0.9, 0.0	
	Bed 3	0.0, 0.0, 0.8, 0.0	
	Bed 4	0.0, 0.0, 0.6, 0.0	
	Bed 20	0.0, 0.0, 0.5, 0.0	
	Bed 22	0.0, 0.0, 0.0, 0.0	
	Bed 25	0.0, 0.0, 0.5, 0.0	
	Bed 26	0.0, 0.0, 0.8, 0.0	
	Bed 27	0.0, 0.0, 0.8, 0.0	
	Bed 30	0.0, 0.0, 0.6, 0.0	
	Bed 31	0.0, 0.0, 0.6, 0.0	
	Upshore	0.0, 1.0, 1.0, 1.0	
	Field	1.0, 1.0, 1.0, 1.0	
Energy density of prey flesh (Zwarts et al. 1996a)	$d_{prey} = 22{\cdot}0\ \mathrm{kJ\ g^{-1}}$		

Mussel bed-specific parameters

Parameter and source	Value
Number of size classes	10
Width of size classes (mm)	20–25, 25–30, 30–35, 35–40, 40–45, 45–50, 50–55, 55–60, 60–65, 65–70
Density (m^{-2}) of each size class at start of winter (D_l) (ordered by increasing size) (S. McGrorty, unpublished data)	
Bed 1	78·0, 89·1, 98·0, 81·0, 44·7, 15·8, 4·4, 2·2, 0·3, 0·1
Bed 3	21·8, 27·9, 44·6, 57·7, 66·1, 50·1, 35·4, 13·3, 4·9, 1·2
Bed 4	28·7, 36·3, 50·7, 73·5, 87·2, 69·9, 40·7, 17·8, 12·0, 3·0
Bed 20	17·7, 20·6, 28·8, 40·1, 47·0, 51·3, 37·9, 16·7, 64, 21
Bed 22	5·2, 4·5, 7·0, 8·9, 12·0, 19·5, 25·2, 17·3, 7·2, 2·3
Bed 25	29·5, 38·4, 50·0, 68·6, 84·0, 71·6, 37·9, 18·6, 5·5, 1·1
Bed 26	87·8, 125·1, 156·3, 154·8, 103·8, 53·9, 18·9, 6·9, 1·8, 0·6
Bed 27	88·5, 112·6, 149·6, 163·8, 123·9, 52·3, 14·6, 1·2, 0·0, 0·0
Bed 30	96·6, 106·4, 132·7, 149·9, 131·0, 98·0, 50·8, 19·4, 4·4, 0·9
Bed 31	104·5, 107·4, 107·8, 101·7, 72·5, 44·9, 22·2, 10·7, 1·7, 0·9
Ash-free dry mass (mg) of each size class at start of winter (m_i) (ordered by increasing size) (methods in Goss-Custard, West & Durell 1993)	
Bed 1	73, 150, 251, 369, 494, 618, 734, 839, 930, 1006
Bed 3	63, 149, 278, 443, 630, 825, 1013, 1187, 1339, 1465
Bed 4	80, 157, 267, 409, 580, 777, 993, 1226, 1469 1719
Bed 20	63, 143, 267, 434, 638, 873, 1129, 1399, 1675 1952
Bed 22	72, 161, 295, 473, 686, 927, 1186, 1453 1722, 1985
Bed 25	63, 143, 262, 415, 594, 789, 990, 1187, 1375, 1549
Bed 26	81, 162, 272, 405, 557, 719, 888, 1058, 1225, 1386
Bed 27	81, 161, 265, 385, 514, 643, 768, 886, 994, 1092
Bed 30	73, 160, 286, 442, 614, 786, 949, 1096, 1225, 1336
Bed 31	64, 151, 282, 452, 649, 864, 1085, 1306, 1524 1736
Over winter non-oystercatcher mortality (S. McGrorty, unpublished data)	7% removed at a constant proportional rate each day
Decrease in ash-free dry mass (Goss-Custard, West & Durell 1993)	40% less at end of winter than that at start
Ash-free dry mass of highest level mussels (Goss-Custard, West & Durell 1993)	90% of the average of all mussels on bed

OYSTERCATCHERS
Population structure

Parameter and source	Value
Population (Goss-Custard et al. 1982b)	1550 individuals
Number of age classes (Goss-Custard & Durell 1983)	Juveniles (first years), immatures (second years), adults (3+ years) = 3
Proportion of birds in each age class (Durell & Goss-Custard 1996)	Juveniles, 0·02; immatures, 0·07; adults, 0·91
Number of mussel feeding methods	Stabbers and hammerers
Proportion of each age class in each feeding method (stabbers, hammerers) (Durell & Goss-Custard 1996)	Juveniles, 1·00, 0·00; immatures, 0·80, 0·20; adults, 0·43, 0·57
Range of dominance values within individuals in each age class (Goss-Custard et al. 1995a)	Juveniles, 0–70; immatures, 0–70; adults, 0–100
Range of feeding efficiencies on each patch type (coefficient of variation) (Goss-Custard et al. 1995a)	Mussel beds (stabbers), 15%; mussel beds (hammerers), 10%; upshore, 12·5%; fields, 12·5%

Intake rate on mussel beds

Parameter and source		Value
Proportion of each size class that is visible (v_i) (ordered by increasing size) (Goss-Custard, West & Durell 1993)		0·48, 0·62, 0·74, 0·83, 0·91, 0·96, 0·99, 1·00, 1·00, 1·00
Probability of successfully attacking prey (p_i) (Cayford & Goss-Custard 1990)	Stabbers	0·98 for all size classes
	Hammerers	0·97 for all size classes
Handling time (s) of each size class (h_i) (ordered by increasing size) (Cayford & Goss-Custard 1990)	Stabbers	20·8, 31·5, 42·2, 52·9, 63·5, 74·2, 84·9, 95·5, 106·2, 116·9
	Hammerers	20·4, 37·4, 54·4, 71·4, 88·4, 105·4, 122·4, 139·4, 156·4, 173·4
Waste handling time (s) of each size class (w_i) (ordered by increasing size) (Cayford & Goss-Custard 1990)	Stabbers	17·9, 20·6, 23·2, 25·9, 28·5, 31·1, 33·8, 36·4, 39·1, 41·7
	Hammerers	17·8, 21·3, 24·7, 28·1, 31·6, 35·0, 38·4, 41·9, 45·3, 48·7
Time spent inspecting prey which are not attacked (Cayford & Goss-Custard 1990)	Stabbers	$I = 79·5$ s
	Hammerers	$I = 62·2$ s
Search speed (Cayford & Goss-Custard 1990)	Stabbers	$s = 0·26$ ms^{-1}
	Hammerers	$s = 0·28$ ms^{-1}
Search path width (estimated by eye) (J. D. Goss-Custard, unpublished data)	Stabbers	$r = 10$cm
	Hammerers	$r = 10$cm
Attack probability coefficients (see text for the meaning of coefficients and further details)	Stabbers	$a = 17·03$, $b = 0·134$
	Hammerers	$a = 13·07$, $b = 0·089$
Perception limit (Goss-Custard et al. 1995a)	Stabbers	3%
	Hammerers	3%
Threshold competitor density (ha^{-1}) above which interference occurs (C_0) (re-analysis of data used by Stillman et al. 1996)	Juvenile stabbers	0·0
	Immature stabbers	0·0
	Immature hammerers	0·0
	Adults stabbers	65·4 (SE = 19·9)
	Adult hammerers	51·2 (SE = 7·9)
Interference coefficients (see text for the meaning of coefficients) (re-analysis of data used by Stillman et al. 1996)	Stabbers	$a = 0·151$ (SE = 0·082), $b = −0·535$ (SE = 0·152), $c = 0·0022$ (SE = 0·0009)
	Hammerers	$a = 0·168$ (SE = 0·067), $b = −0·081$ (SE = 0·067), $c = 0·0014$ (SE = 0·0005)
Aggregation factor (density in sample squares (Goss-Custard & Durell 1988) divided by bed-wide density)	Stabbers	8 times overall bed density
	Hammerers	4 times overall bed density
Daytime feeding efficiency (see text for the meaning of coefficients) (Q = Goss-Custard, West & Durell 1993; P_{keep} = Goss-Custard, Durell & Ens 1982a; P_{remove} = Speakman 1984)	Stabbers	$Q = 0·94$, $P_{keep} = 0·97$, $P_{remove} = 0·93$
	Hammerers	$Q = 0·94$, $P_{keep} = 0·97$, $P_{remove} = 0·93$
Night-time feeding efficiency (see text for the meaning of coefficients) (Q = Goss-Custard, West & Durell 1993; P_{remove} = Speakman 1984; E_{night} = H. Sitters unpublished data)	Stabbers	$Q = 0·94$, $P_{remove} = 0·93$, $E_{night} = 1·00$
	Hammerers	$Q = 0·94$, $P_{remove} = 0·93$, $E_{night} = 0·62$

Intake rate on supplementary prey

Parameter and source	Value	
Ash-free dry mass intake rate (measured using standard techniques in several representative sites) (J. D. Goss-Custard, unpublished data)	Upshore	202 mg 300 s^{-1}
	Fields	159 mg 300 s^{-1}
Daytime feeding efficiency	Upshore	1·000
	Fields	1·000
Night-time feeding efficiency (upshore = Hulscher 1996)	Upshore	0·615
	Fields	0·000
Temperature related prey availability on fields (temperature, availability) (Goss-Custard & Durell 1987)	0 °C, 0·0 (availability changes linearly between these temperatures)	
	4 °C, 1·0	
	12 °C, 0·0	

Body mass and energetics

Parameter and source	Value
Mass on 1 September (S. E. A. le V. dit Durell, unpublished data)	Juveniles, 465 g; immatures, 483 g; adults, 503 g
Starvation mass (S. E. A. le V. dit Durell, unpublished data)	Juveniles, 300 g; immatures, 340 g; adults, 350 g
Target mass (days since 1 September, target mass). Target mass changes linearly between the days shown (S. E. A. le V. dit Durell, unpublished data)	Juveniles day 0, 465 g; day 106, 494 g; day 196, 494 g
	Immatures day 0, 483 g; day 106, 550 g; day 196, 510 g
	Adults day 0, 503 g; day 196, 598 g
Energy expenditure (see text for meaning of coefficients) (Kersten & Piersma 1987 as interpreted by Zwarts *et al.* 1996a)	$E_{gen} = 673·2$ kJ
	$T_{crit} = 10 °C$
	$E_{therm} = 31·8$ kJ °C^{-1}
Energy assimilation (Kersten & Visser 1996b)	Prey assimilation efficiency (a_{assim}) = 0·854
	Gut storage capacity = 11·92 g ash-free dry mass
	Gut processing rate = 2·351 g ash-free dry mass h^{-1}
Time period over which energy expenditure and acquisition are balanced (Kersten & Visser 1996a)	2 tidal cycles = 24·8888 h
Energy storage (see text for meaning of coefficients) (Kersten & Piersma 1987)	$d_{store} = 33·4$ kJ g^{-1}
	$a_{store} = 0·884$
	$a_{release} = 1·000$