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The concept of carrying capacity and shorebirds

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SUMMARY

This paper discusses the term 'carrying capacity', defined in terms of the 'one-in, one-out rule'. On this definition, capacity is reached when, for every additional bird that arrives, another one either dies or emigrates, so that numbers in a locality cannot increase and the habitat is fully occupied. Simulations with an individuals-based and physiologically structured model showed that this definition is appropriate for wintering oystercatchers eating mussels, a system in which interference between foraging birds occurs; as the numbers of recruits settling on the mussel beds in September increased to very high levels, the number remaining by spring reached a plateau. Whether birds were assumed to remain on the estuary until they died at some point during the winter or whether they emigrated before they starved made no difference to the predicted capacity of the mussel beds. Carrying capacity in this system could also be defined in terms of the total bird-days per winter because this quantity likewise tended to plateau as the numbers of recruits settling in September increased. However, the plateau was less clearly defined and it took a very much higher number of September recruits for capacity defined this way to be reached.

Further simulations showed that, without interference, the numbers of autumn recruits could be increased to the point at which no birds remained on the mussel beds by spring because food density had been depleted to below the levels required for even the most efficient birds to balance their energy budget. The relationship between numbers remaining by March and the numbers settling the previous September was thus dome-shaped. In systems with little or no interference, therefore, carrying capacity may only be measured as the total number of bird-days per winter. However, without interference, the carrying capacity measured in bird-days per winter depends critically on the numbers of birds that arrive in September. Defining carrying capacity in terms of bird-days per winter rather than in terms of the numbers remaining in March does not solve the difficulties of defining and measuring capacity in systems without interference. In such systems, measuring capacity in bird-days per winter – as is so often done – provides a poor prediction because the total number of bird-days depends on the numbers that arrive in autumn.

Whether carrying capacity is actually reached depends on there being a sufficiently large number of potential recruits to the estuary in autumn; in the oystercatcher–mussel system, it required 8000 recruits in September for the carrying capacity of *ca* 3200 to be achieved. In many species and localities, there may not normally be enough recruits for the capacity of a locality to be reached. However, this should not be taken to mean that a reduction in food supplies through habitat loss or change would not affect local numbers. If competition for food is sufficiently intense for the rates of emigration and/or mortality to be density-dependent, a reduction in the food supply would lead to increased rates of emigration and/or mortality, and so to a reduction in local bird numbers. This was confirmed by simulations which showed that winter habitat loss caused local mortality or emigration to increase in oystercatchers long before carrying capacity was reached.

INTRODUCTION

No other concept in our area of science seems to provoke as much ambivalence as to its use as does the notion of 'carrying capacity'. Some authors put the term inside quotes, as if they are uncertain about the wisdom of using it but are unable to find another notion that encompasses as adequately what it is they want to say.

Others use the term without defining it, as if its meaning was understood and accepted by everyone, but then draw implications that many others would not accept. A particularly unfortunate tendency is for some authors to imply that habitat loss will only affect population size if the carrying capacity of the area has already been reached. It is this dangerous misunderstanding in particular

which makes it timely once again to discuss the definition of the concept, how capacity might be measured and the implications of its use for managing wetland birds.

The useful idea that the term 'carrying capacity' incorporates is that there must be a limit to the numbers of birds that an area can support, given the abundance of resources and enemies that are present. But – as with the term 'carrying capacity' itself – the word 'limit' brings with it connotations that can differ between scientists. In population equilibrium theory, it means that something, such as disease or accidents, reduces the rate of increase of the population and thus lowers the equilibrium population size – at which, on average, birth and death rates are equal – to a level below that at which it would otherwise have been (Sinclair 1989; Goss-Custard 1993; Sutherland 1996a). A limiting factor also affects the rate with which the population returns to equilibrium after it has been perturbed. Used in this sense, a limiting factor can be exerting its downward pressure on numbers even though the population is still increasing. In the context of carrying capacity, however, the word 'limit' implies that no further increase in numbers is possible. Another way of saying this is that capacity is reached when, for every additional bird that arrives, one bird either emigrates or dies (Goss-Custard 1985) – the so-called 'one-in, one-out' definition of carrying capacity. An example is when all the available breeding territories are occupied because, under the prevailing levels of competition, territory size cannot be squeezed any further.

When used in this sense, the concept of carrying capacity is best applied in migratory birds to the maximum numbers that can live in a particular locality at a particular time of year; for example, the numbers of territorial breeding pairs. It is not appropriate to apply the term to the equilibrium size of the 'global' (or 'greater' or 'meta') population. Were this to be done, we would find ourselves arguing that the capacity of the wintering grounds was influenced by processes on the breeding grounds, and *vice versa*, because global equilibrium population size in migratory. populations depends on processes operating during both the breeding and non-breeding

seasons (Fretwell 1972; Goss-Custard 1993; Sutherland 1996b). Were it to be applied at this scale, much of the useful commonsense value of the concept would be lost (Goss-Custard 1993). In any case, it seems most unlikely that capacity can actually be reached everywhere throughout the global range. The increasing density-dependent resistance to further population increase would prevent the population from ever reaching the size at which, throughout a species' range, one animal dies for every additional one that is born (Goss-Custard 1993; Goss-Custard *et al.* 1997; Sutherland 1996a). As model simulations below will demonstrate, the supply of recruits must be very high indeed if capacity is to be reached, and this seems likely only to arise at the local scale (Goss-Custard 1993).

This article, therefore, discusses the concept of carrying capacity in the context of the numbers of birds that can be supported in a particular locality at a particular time of year. By simulations with a model describing an intensively studied system, the article explores some of the factors and processes that determine capacity and discusses how it might be measured. It also re-emphasises the frequently misunderstood, yet vital, point that habitat loss can reduce local bird numbers even before the capacity of the area has been reached. When predicting the effect of habitat loss, the key issue is whether density-dependent processes are already operating, or will operate after the habitat is lost, and not whether the area is already at capacity (Goss-Custard *et al.* 1995).

FACTORS AND PROCESSES DETERMINING OVERWINTER CARRYING CAPACITY

The simulation model was constructed to capture what we believe to be the important features of the interaction between populations of oystercatchers (*Haematopus ostralegus*) and mussels (*Mytilus edulis*); here, we use simulations from version 2 of the model, as detailed by Clarke and Goss-Custard (1996).

Model of the Exe estuary mussel beds
The model is individuals-based and physiologically structured. It uses empirically determined responses of individual oystercatchers to each other and

to their common food supply obtained on the Exe estuary, SW England. It calculates the biomass of mussels consumed each day by every individual oystercatcher in the model population and works out the resulting depletion through the winter of the mussel food supply on each of 12 mussel beds. Overwinter mussel losses due to other mortality agents and the weather-related decline in the flesh content of individual mussels are also included. The model therefore tracks daily through the winter the changing biomass density of the food supply on each mussel bed.

Individual oystercatchers in the model open mussels either by stabbing or hammering, because birds using the two methods have different average foraging efficiencies and are subject to different levels of interference (Goss-Custard & Durell 1988). Age-related changes in feeding method and dominance – which affect a bird's susceptibility to interference – are included in the age-structured model. In order to calculate the mussel bed on which each individual bird feeds over each low-water period, the model first calculates, from a functional response relating intake rate to the biomass density of large (>30 mm long) mussels, the interference-free intake rate of a bird of average efficiency for each of the mussel beds. The rate a particular individual would actually achieve on each bed then depends on its own foraging efficiency and dominance – two components of competitive ability which vary between birds independently of each other – and on the current density of oystercatchers on the bed. Next, each individual is selected each day in random order to choose, within its empirically determined ability to discriminate, the mussel bed where it achieves the highest gross intake rate at that time. The model is therefore based on game theory in that the choices made by one competing individual as to where to feed over a low-tide period are contingent on those made by its competitors. Many birds – particularly the subdominant ones – continually change their feeding site as the relative quality of the mussel beds changes over the winter through differential rates of prey depletion and as other birds change their foraging location, or die. Changes in

bed area associated with the fortnightly neaps/springs cycle are included because oystercatcher densities, and thus interference competition, are much higher on neaps. It is assumed the rates of feeding are the same during night and day low-water periods.

The model tracks the feeding location and intake rate of each bird on each day from September to March. It also tracks their body condition. Each bird is given fat reserves in September drawn at random from the empirically determined distribution of weights for each age class. Energy requirements for each day are calculated from Kersten and Piersma (1987), using the average air temperature for that day on the Exe. The birds are assumed to be inactive at roosts for 12 hours each day; this is the only time when additional thermo-regulation costs below the thermo-neutral temperature are likely to be incurred. Once an individual has assimilated its daily existence energy requirements, any surplus energy consumed is stored as fat, deposited with an empirically determined efficiency (Kersten & Piersma 1987), up to a maximum rate of 5% of current body weight per day (Zwarts et al. 1990). Each bird attempts during autumn and winter to accumulate fat at the mean rate observed by its age class on the Exe. The reserves maintain the bird on days when it fails through foraging to meet its current daily requirements. An individual dies if its fat reserves fall to zero for one day.

Carrying capacity and the departure decision rules used

When oystercatchers arrive on the estuary in autumn from the breeding grounds, the carrying capacity of the mussel beds could be achieved almost immediately, by one bird leaving for every additional one that arrives, or later, by one bird starving at some point during the winter, or by both. As we do not know the relative contribution played by emigration and mortality in determining how many birds overwinter successfully, we ran simulations using a number of alternative decision rules which birds may use. Having arrived on the Exe in autumn, each individual was assumed to:

• remain until spring, unless it died first

because its fat reserves fell to zero;

- emigrate if, at any time before March, its fat reserves fell to a level equivalent to 8% of its body weight, the point at which oystercatchers leave the Wadden Sea in severe weather (Hulscher 1989, 1990); or
- emigrate if its weight fell for five days in succession at any time before 31 December, it being assumed that it would be too risky to seek a new wintering area any later in the winter.

Birds of all ages and feeding methods were assumed in these simulations to make any of these three decisions. However, as birds may only be flexible in their choice of wintering estuary during their immaturity, a fourth series of simulations were run in which only the immature birds were allowed to leave the estuary if their weight fell for five days in succession.

In order to determine the carrying capacity of the mussel beds, the numbers of oystercatcher recruits to the estuary in autumn was varied between ca 0.1 and five times the numbers that overwinter on the Exe at present. In the first instance, each simulation was run for one winter. Plotting the numbers of oystercatchers remaining the

following March as a function of the number of recruits the previous September revealed that the number of 'survivors' levelled off at ca 3200 birds when the number of recruits had reached ca 8000 (Figure 1). From then on, one bird emigrated or died for every additional recruit that arrived in autumn. The numbers remaining in March could not rise any higher so carrying capacity had been reached. This shows that the 'one-in, one-out' definition of carrying capacity is applicable to the oystercatcher–mussel system, at least over the range in the numbers of September recruits employed.

Predicted capacity was the same for all four decision rules employed (Figure 1). The reason is that, when large numbers of recruits arrived in autumn, the interference competition was so intense that many birds could not feed fast enough to survive, let alone to increase their body weight, even at this time of year when food was abundant and the birds' temperature-related energy requirements were rather low. It did not matter whether model birds opted to emigrate or remained until they died because a bird that lost weight for five days in succession was destined to die shortly anyway. Many birds disappeared more-or-less immediately, irrespective of the decision rule they used (Figure 2). Accordingly, much of the strongly density-dependent overwinter decrease in bird numbers (inset to Figure 2) - which was, of course, the demographic process responsible for capacity being achieved – occurred early on, when large numbers of recruits arrived. In contrast, when smaller numbers of recruits arrived in September, rather few birds lost weight before the end of December so that many of the losses occurred late in the winter with all four decision rules. It thus made little difference to the predicted value of carrying capacity whether we assumed that capacity was achieved through starvation or emigration.
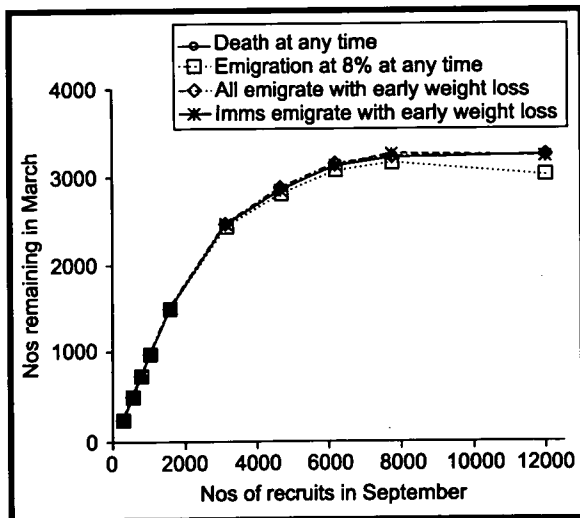

Figure 1. Model predictions for the numbers of oystercatchers remaining on the Exe estuary mussel beds at the end of winter (March) as a function of the numbers settling there during the previous September. Four decision rules were used to eliminate individual birds: a bird of any age (i) died if its fat reserves fell to zero at any time during the winter, (ii) emigrated if its fat reserves fell at any time to 8% of its body mass, or (iii) emigrated if its fat reserves fell for five successive days at any time before 31 December, after which it remained on the estuary and may have died. In (iv), only immature birds (1st–4th winter) emigrated if their fat reserves fell for five successive days before 31 December, after which they remained on the estuary and may have died

Model outputs (A D West, unpublished) revealed that the decision rule used made little difference to the other main conclusions reached by Goss-Custard et al. (1996) on the process by which capacity was achieved.
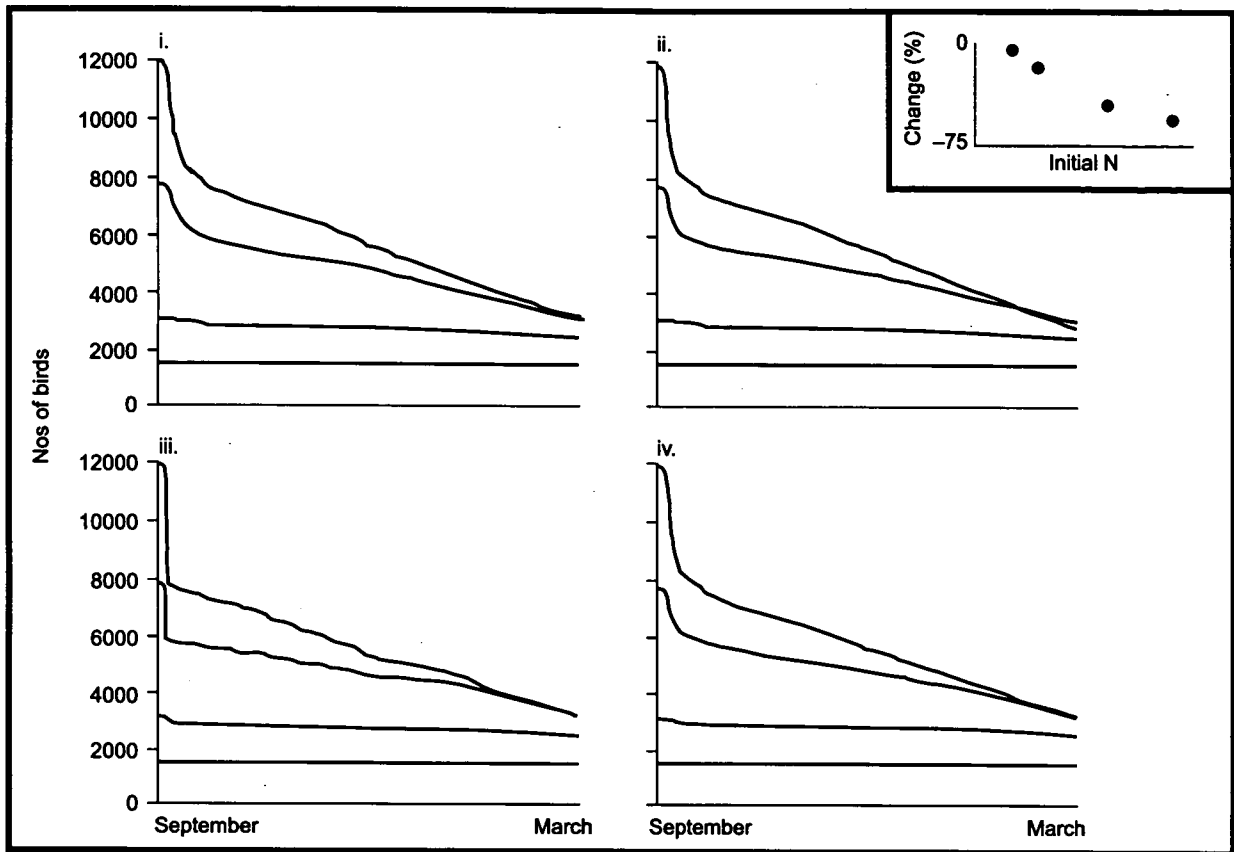
- Although with high numbers of

Figure 2. Model predictions for the numbers of oystercatchers remaining on the mussel beds at each stage of the winter using the four decision rules (i–iv) given in Figure 1. The four lines in each graph show the change in numbers with 12 000, 8000, 3000 or 1750 oystercatchers settling on the mussel beds in September. The inset shows the numbers remaining in March as a percentage of the numbers settling in September in relation to the numbers recruiting in September

September recruits many birds died or emigrated early in autumn, carrying capacity was only finally determined in late winter. It depended on the rate of overwinter mussel loss due to both depletion by oystercatchers and other mortality agents, to the overwinter decline in the flesh content of individual mussels, and to the higher temperature-related energy requirements of the birds.

• The disappearance of birds peaked during neap tides when interference competition was intensified by the reduced area of mussel beds exposed at low tide and, in some simulations, the low flesh content of the upshore mussels exposed on neap tides.

• Whether a bird died or emigrated depended on both its dominance and its foraging efficiency.

The decision rule used did not make any difference to the distribution of oystercatchers over the 12 mussel beds. These comparisons further confirmed that

uncertainty about the actual decision rule used by oystercatchers when responding to competition for food made little difference to our understanding of the way in which carrying capacity was achieved.

Food supply, interference competition and carrying capacity

The two feedback processes that dictate the carrying capacity of the mussel beds are mussel depletion – in which the more efficient foraging oystercatchers are at an advantage – and interference competition – in which the socially dominant oystercatchers have the advantage. The respective influence of these two processes in determining carrying capacity – measured as the numbers surviving the winter – was explored by independently varying mussel abundance and the intensity of interference competition.

Food abundance was varied by increasing or decreasing the September mussel biomasses on each mussel bed by multiples (range 0.3–1.7) of the average biomass recorded during the eight years of the study, but

retaining the present level of interference. A clear carrying capacity was achieved across a wide range of mussel abundance (Figure 3i). As might have been expected, for capacity to be reached, a greater number of recruits was required in September when food supply was large than when it was small; compared with the number of recruits required at present-day levels of food abundance, some 50% more were required for capacity to be reached with the largest food abundance used. As would also be expected, capacity increased sharply with mussel abundance, but not in proportion to the increase in the food supply (Figure 3ii) because interference competition intensified as numbers increased.

Interference was varied in two ways. First, simulations were run in which it was assumed that all the oystercatchers recruited in September consisted entirely of stabbers,
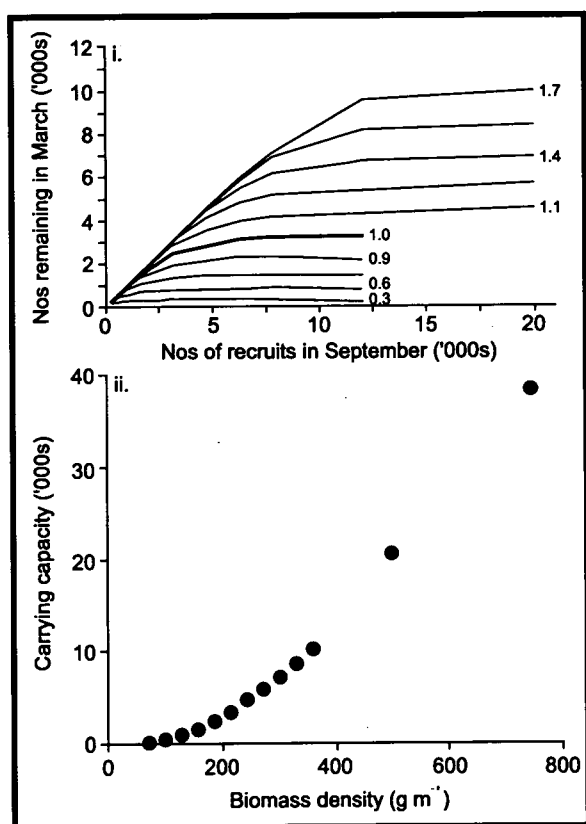

Figure 3. Model predictions for the numbers of oystercatchers remaining on the Exe estuary mussel beds at the end of winter (March) in relation to the abundance of mussels present on the 12 beds in the previous September. Mussel biomass is expressed in multiples of the average mussel biomass recorded on all the beds over eight years. The heavy line represents simulations using the average mussel biomass
i. The numbers of oystercatchers remaining in March as a function of the numbers settling the previous September, with each line referring to one level of mussel abundance
ii. The relationship between carrying capacity – the level of the plateaux in (i) – and food abundance in September

amongst which interference is low, or of hammerers, in which interference is high (Goss-Custard & Durell 1988). Second, the strength of interference experienced by birds of a given social rank in populations containing both stabbers and hammerers was reduced using the procedure detailed in Goss-Custard *et al.* (1995). The intensity of interference was reduced either to half its present level or removed altogether; in the latter case, birds were able to feed together at extremely high densities without the intake rate of the subdominants being affected.

Reducing or removing interference changed the shape of the relationship between the numbers remaining in March and the numbers recruited the previous September from being a curve with a decelerating rise to a clearly identifiable plateau to one which was dome-shaped (Figure 4). Whereas the numbers of birds remaining in March in a population of only interference-prone hammerers remained level across a wide range of numbers of recruits in September – even with 20 times present-day numbers – the numbers remaining in a stabber-only population reached a peak before falling towards zero at high numbers of recruits (Figure 4i). In the simulations in which interference was reduced by half in populations of mixed hammerers and stabbers, the numbers remaining in March again reached a peak, rather than a plateau (Figure 4ii). The dome-shaped pattern was even more pronounced with no interference (Figure 4iii). In many of the simulations with reduced or no interference, no oystercatchers remained at the end of the winter after very large numbers had been recruited the previous September.

The reason for the change from a plateau to a dome-shaped curve, of course, is that, with reduced or no interference, large numbers of recruits quickly reduced food abundance to such low levels that only the most efficient foragers – if any – could feed by the end of the winter at the rate required to survive. In these circumstances, if carrying capacity were to be defined as the numbers remaining at the end of the winter, capacity would usually be zero! With little or no interference occurring, carrying capacity can only be measured in terms of the total
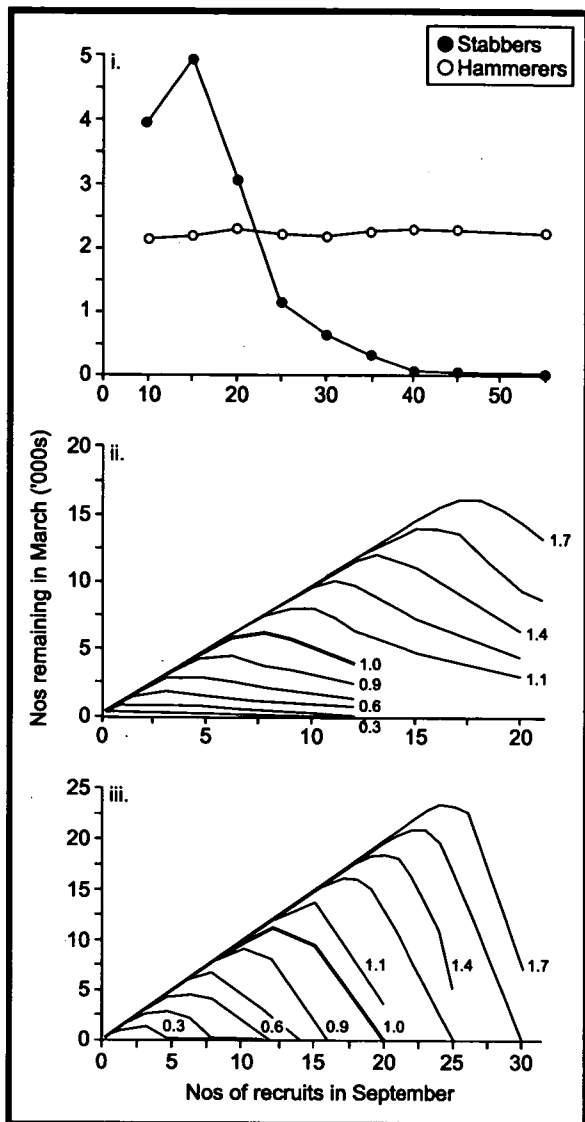
Figure 4. Model predictions for the numbers of oystercatchers remaining on the Exe estuary mussel beds at the end of winter (March), as a function of the numbers settling there during the previous September, according to the intensity of the interference between foraging birds

i. The recruits in September consist entirely of birds that open mussels either (i) by stabbing, and so experience low levels of interference, or (ii) by hammering, and experience high levels of interference

ii. Using the procedure detailed in Goss-Custard *et al.* (1995), the interference levels are set at half those observed on the Exe, with birds of both feeding methods occurring in the simulated population in the proportions observed in nature

iii. As (ii), but with no interference allowed

In both (ii) and (iii), the numbers of oystercatchers of both feeding methods remaining on the mussel beds at the end of winter (March) are shown in relation to the abundance of mussels present on the 12 beds in the previous September, with mussel biomass expressed as in Figure 3

bird-days over the winter, and not as the numbers remaining at the end of winter.

To explore the effect of measuring capacity in terms of bird-days per winter, the relationships between the numbers of recruits, initial food abundance and bird-days per winter for selected simulations are

shown in Figure 5. With present-day levels of interference at three representative levels of food abundance, the total number of bird-days per winter tended to plateau as the numbers of September recruits increased (Figure 5i). Bird-days were calculated only from 1 October onwards; otherwise, the calculation was inflated by the sometimes large numbers of birds that, despite having a zero intake rate because of the intense interference, lived for several days into September on the fat reserves they were assumed – probably unrealistically – to carry when they arrived. However, the curves in Figure 5i show two important differences from those shown in Figure 1, in which capacity was measured in terms of the numbers of survivors in March. With capacity measured in bird-days per winter, the plateaux are less clearly defined. It also takes approximately ten times more September recruits for capacity to be reached. Although in systems with strong interference one therefore has the option of measuring carrying capacity either in terms of the numbers of birds remaining at the end of the winter or as the numbers of bird-days per winter, the two definitions differ in the clarity with which plateaux can be identified and give very
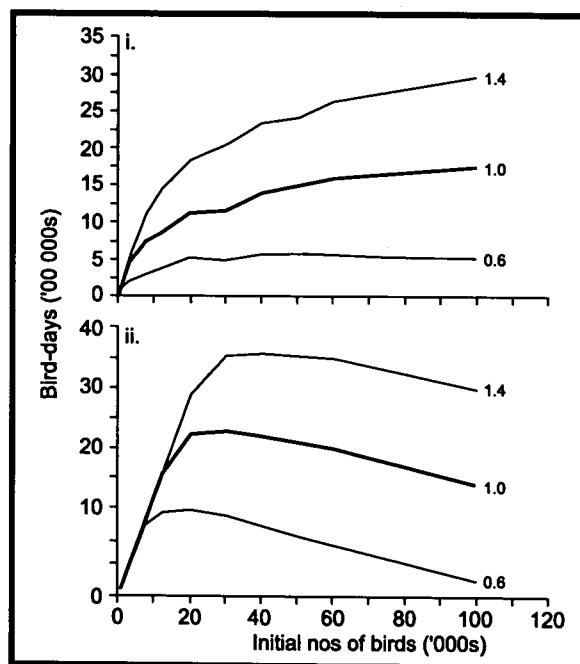

Figure 5. Model predictions for the total number of oystercatcher bird-days from October to March, as a function of the numbers settling there during the previous September, at three levels of mussel abundance on the 12 beds in September, with mussel biomass expressed as in Figure 3
i. With present-day levels of interference
ii. With no interference

different predictions as to the number of September recruits that are required for them to be reached.

When no interference between foraging birds was assumed to occur, no plateaux were reached (Figure 5ii); rather, the relationships were dome-shaped as before, although substantially flatter (compare Figures 5ii and 4iii). This means that, without interference, the predicted carrying capacity measured in bird-days per winter depends critically on the numbers of birds that arrive in September. The reason again is that, when large numbers arrive in September, the food supply is rapidly reduced and, because of the non-linear shape of the functional response that relates intake rate to food abundance and because of individual variations in foraging efficiency, the consequences for intake rate and thus bird survival later in the winter are not simple. We conclude that defining carrying capacity in terms of bird-days per winter rather than in terms of the numbers remaining in March does not solve the difficulties of defining and measuring capacity in systems without significant interference. In such systems, simply measuring capacity in bird-days per winter – as is so often done –

may provide only a poor prediction because the total number of bird-days per winter depends on the numbers that arrive in autumn.

Capacity and annual variability in food supply
A striking feature of the simulations with present-day levels of interference was that it required over 8000 recruits in September for the carrying capacity of 3200 to be reached (Figure 1). Far more recruits than can be supported at capacity are needed if the full capacity is to be realised. As a result, the carrying capacity of an area may not be reached on many occasions simply because the supply of recruits available falls below the number needed to exploit the area fully (Goss-Custard *et al.* 1996).

One of several mechanisms preventing enough recruits arriving in an area is annual variation in the feeding conditions (Goss-Custard *et al.* 1996). Figure 6 shows the effect of varying the combined biomass of mussels on the 12 mussel beds around the long-term observed average by using multiples of the observed standard deviation in the annual biomass recorded over eight Septembers to calculate the annual fluctuations in the food supply. Each year, the adults that survived the winter returned the following September with 0.5 juveniles per adults. The potential capacity of the mussel beds in each winter, given the mussel biomass present at the start, was obtained from the plateaux shown in Figure 3.

With no annual variation in mussel biomass, the numbers of oystercatchers surviving each winter – although declining – remained close to carrying capacity (Figure 6i). But as the annual variation in mussel biomass increased from one to three times the observed level, the numbers remaining in March fell increasingly far below the potential capacity of the mussel beds in each winter because, after numbers had fallen sharply in the first winter of food scarcity, too few juveniles arrived in subsequent Septembers for the carrying capacities of later winters to be reached (Figures 6ii–iv). Figure 7 summarises the widening discrepancy as the annual variability in food abundance increased between the mean numbers remaining in March and the average capacity of the mussel beds. With large annual variations in the
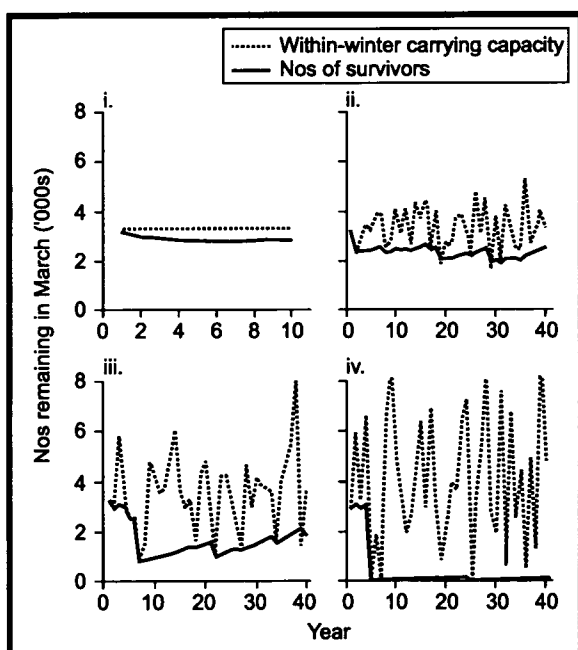

Figure 6. Model predictions for the numbers of oystercatchers remaining (solid line) on the mussel beds at the end of a series of successive winters in which the food supply present in September (i) does not vary between years, or varies at random within the range of (ii) one, (iii) two, and (iv) three standard deviations of the annual variation that was actually observed on the estuary over eight years. The dashed line shows the potential carrying capacity of each winter
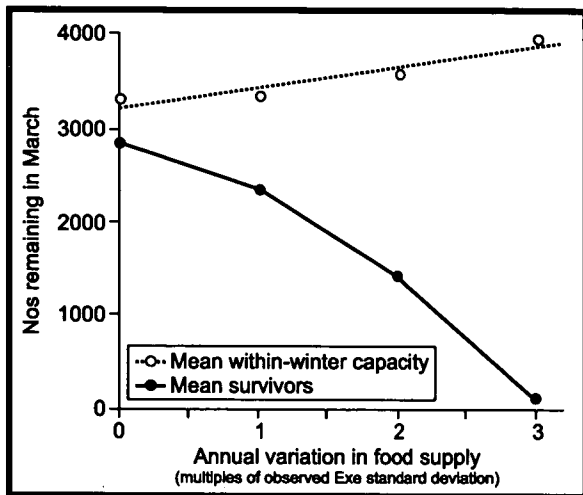
Figure 7. Model predictions for the numbers of oystercatchers remaining in March (solid line) as a function of the annual variation in the mussel food abundance, measured as described in Figure 6. The dotted line shows the numbers that could have remained on the estuary had the supply of recruits in September been sufficient for the potential carrying capacity of the mussel beds to have been realised

feeding conditions, capacity may only be reached in sites which, each year, attract large numbers of oystercatchers from other potential wintering sites (Goss-Custard *et al.* 1996).

CARRYING CAPACITY AND DENSITY DEPENDENCE

These results do suggest that, in many species and localities, carrying capacity often may not be reached in nature, even in systems where interference is strong. The model predicts that the carrying capacity of the Exe estuary mussel beds exceeds the *ca* 2500 oystercatchers that winter on them at present, a conclusion that is consistent with trends in mussel and oystercatcher abundances on the estuary since 1976 (Goss-Custard *et al.* 1997). This finding should not be taken to mean, however, that reducing the quantity or quality of the food supply in a locality, through habitat loss and change, would not affect the numbers of birds remaining in that locality. If competition for food is already sufficiently intense for the rates of emigration or mortality to be density-dependent, reducing the food supply – and thus intensifying competition between birds – through habitat loss and change will reduce local numbers (Goss-Custard 1977; Goss-Custard *et al.* 1995). If birds already emigrate or die because they cannot compete successfully for food, increasing the intensity of competition still further by reducing the

food supply is bound to increase the numbers of birds that have to emigrate or die, and this may happen at levels of competition that are well below the very high levels that occur when capacity has been reached.

Indeed, simulations with the oystercatcher–mussel model show that a locality may be very far below capacity yet numbers would still be reduced by habitat loss and change. Figure 8i shows the density-dependent emigration and/or mortality functions at different biomasses of mussels derived from the model: these graphs show the numbers of birds that disappeared before March rather than the numbers that remained, which are shown in Figure 3. At the present-day levels of mussel biomass, the rates become density-dependent when *ca* 1000 recruits arrive in September. As the biomass of food on the 12 mussel beds is changed from being very high (the lowest
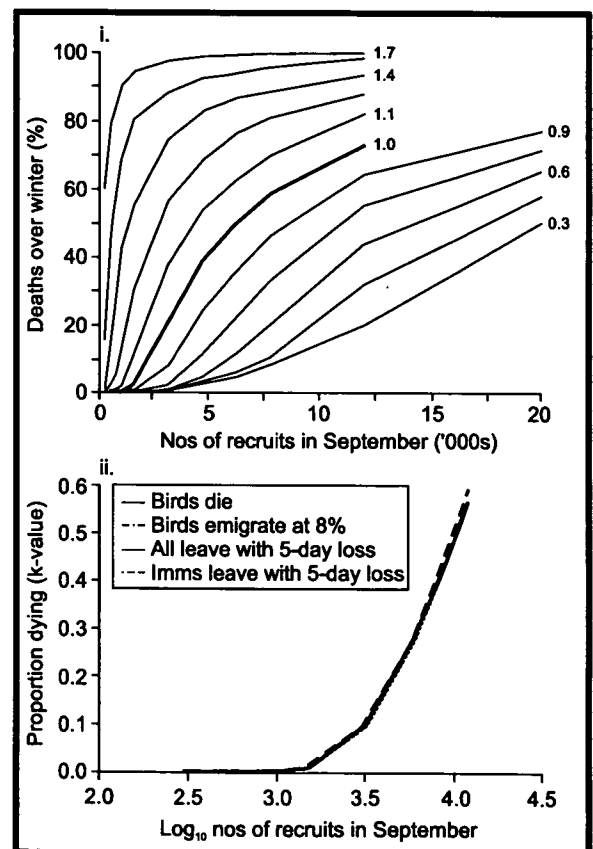

Figure 8. Model predictions for the proportion of oystercatchers starving between September and March, as a function of the numbers settling there during the previous September
  i. Mortality rate in relation to the abundance of mussels present on the 12 beds in September, with mussel biomass expressed as in Figure 3
  ii. Mortality rate expressed as a k-value, and plotted against the logarithm of the September numbers

line) to very low (the topmost line), density dependence starts at an ever lower number of recruits and becomes steeper. In Figure 8ii, the overwinter mortality and emigration rates at the present-day mussel biomass are expressed as k-values (Varley & Gradwell 1960). As discussed in Goss-Custard (1980, 1993), with this formulation, carrying capacity is reached when the slope of k-value against the logarithm of the number of September recruits is 1; this is when one bird dies or leaves for every additional recruit. With the present-day mussel biomass, this occurs at *ca* 8000 recruits (3.9 on the $\log_{10}$ scale). At less than *ca* 1000 recruits, emigration and mortality are broadly independent of density. Therefore, mortality and/or emigration are density-dependent over the range 1000–8000 September recruits before the mussel beds reach capacity. Were the food supplies to be reduced at a time when the numbers of recruits fell within this range, more birds than at present would leave or die because of increased competition for food. Local oystercatcher numbers would therefore be lower than they would have been had the food supplies not been reduced.

The effect of food abundance on the range over which mortality and/or emigration are density-dependent before capacity is reached is explored in Figure 9, in which oystercatcher numbers are expressed as densities. The range over which rates are density-dependent, but the mussel beds are below carrying capacity, expands as the food supply increases, and can be very wide. It would therefore be incorrect to argue that a reduction in food supply through habitat loss or change will not reduce local bird numbers, unless the area is at capacity; a reduction will happen well before the numbers of recruits are high enough for capacity to have been reached.

DISCUSSION

As oystercatcher densities reach densities of 25 birds ha⁻¹ very widely in Europe, Figure 9 might be used to argue that the removal of any mussel bed is likely to increase the rates of emigration or mortality. However, this would be a premature conclusion. Version 2 of the model contains some functions that are now being revised and this is expected to have the effect of increasing the densities
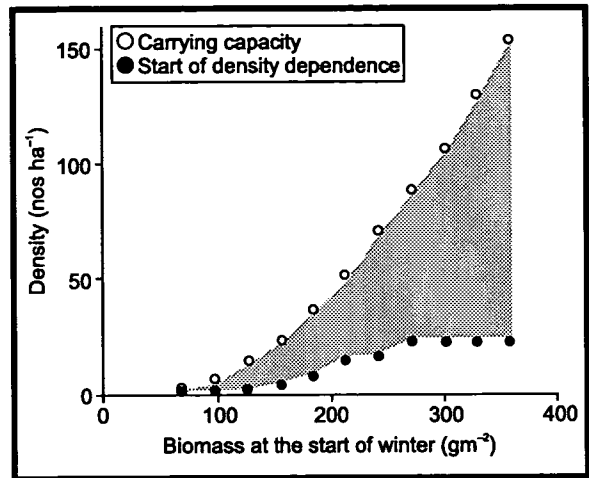

Figure 9. The density of oystercatchers in September in relation to the biomass density of mussels on the 12 mussel beds in September:
i. at which the subsequent overwinter mortality rate becomes density-dependent (●)
ii. at which the carrying capacity is reached (o)

at which competition begins seriously to affect oystercatcher emigration and survival rates. For example, interference is now known to reduce intake rates only at higher oystercatcher densities than was assumed in Version 2 (Stillman *et al.* 1997). Similarly, the opportunity for oystercatchers to compensate for low consumption rates on mussels at low tide by feeding at high tide on alternative food supplies upshore of the mussel beds and in fields around the estuary was represented in Version 2 by a single value for all population sizes, which is certainly unrealistic. We suspect that recent improvements in the parameterisation of the model will increase the predicted carrying capacity of the mussel beds and the densities at which mortality and emigration become density-dependent.

On the other hand, this preliminary version of the model has enabled us to explore the concept of carrying capacity and to take further the earlier attempts to investigate the effect that the presence of interference has on the way in which it might be thought about and measured (Goss-Custard & Charman 1976). When interference amongst birds is strong, capacity can be defined in terms of the number remaining at winter's end because, as the numbers of September recruits increased, the numbers remaining by spring reached a plateau. When the birds were assumed not to experience interference, however, the simulations showed that the numbers of autumn recruits

could be increased to the point at which no birds remained by spring because food density had been reduced to below the levels required for all the birds – however efficient they were – to survive. In systems with little or no interference, therefore, carrying capacity can only be defined in terms of the total number of bird-days per winter. However, the simulations showed that the relationship between bird-days per winter and the number of September recruits is still dome-shaped; the predicted carrying capacity therefore still depends critically on the numbers of birds that arrive in September. Defining carrying capacity in terms of bird-days per winter rather than in terms of the numbers remaining in March does not solve the difficulties of defining and measuring capacity in systems without interference. In such systems, measuring capacity in bird-days per winter – as is so often done – may provide only a poor prediction because the total number of bird-days per winter depends on the numbers that arrive in autumn, and this is not normally taken into account. Such predictions may therefore best be regarded only as approximations of the actual ability of an area to support birds.

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