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Estuary Special Protection Areas:
Establishing baseline targets
for shorebirds

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Estuary Special Protection Areas:
Establishing baseline targets for shorebirds

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Executive summary

1. The question addressed by this report is how to monitor the food biomass density and levels of disturbance in an SPA in such a way that one can demonstrate that the quality of the habitat is being maintained at a sufficiently high standard to support the bird populations for which the estuary was designated as an SPA.

2. To do this, one needs to show that the feeding conditions in the SPA are sufficient to maintain the present-day rates of overwinter survival and pre-migratory fat storage at the end of the winter at the current population size and in the current climatic conditions. This would mean that the quality of the SPA is being maintained at a level sufficient to achieve the goal for which that SPA was set up.

3. We explore in this Report the idea that the ratio between the biomass density of the main food and the biomass density of the birds in autumn (the 'food/bird biomass ratio') can, in principle, reliably predict whether the current foods stocks are sufficient to maintain the current rates of survival and fat storage in the SPA. It also explores how the ratio needed to do this is affected by disturbance and habitat heterogeneity.

4. The ratio would provide the easiest guide to monitoring if, in response to a decrease in the ratio, there were to be a 'step response' increase in the proportion of birds starving and/or failing to attain their target mass in spring. That is, below this ratio, most birds would fail whereas, above it, most would succeed and the proportion doing so would fluctuate without trend as the ratio increased still further. We therefore explored by modelling (i) whether step responses were likely to occur generally, and (ii) whether a small number of ratios, selected according to a limited range of species characteristics, can be used as a reliable 'rule of thumb' to assess habitat quality.

5. In sight-feeding birds of all body sizes, most simulations showed that, once the food/bird biomass ratio had risen to a certain value, the mortality rate and proportion of birds failing to reach target mass fell to an asymptotic low level. In fact, both quantities dropped very suddenly from 100% to the asymptotic rate, and so followed a 'step response'. This step function is due to the fact that the gradient of the functional response in sight-feeding waders was assumed to be very steep, as all the empirical evidence suggests that it is. This means that most birds starve at the same point as food become depleted, so that individual differences in performance exert only a small effect.

6. The simulations showed that the step change in the proportion of birds starving and failing to reach target mass was often replaced by a more gradual response when the absolute biomass densities of both the food and the birds were low. Therefore, in order to fully evaluate the ratio approach, it will be important to establish first whether food/bird biomass ratios in SPAs are generally high or generally low. But as SPAs are selected because they support high numbers and perhaps densities of birds, and since this can only happen where food abundance is high, we decided to explore the ratio approach further using only high biomass densities of both birds and food.

7.   Features of the natural history of a species that made it more difficult for the birds to acquire their daily energy requirements, such as interference and harsh weather, raised the absolute level of the asymptotes: more starved and fewer reached their target mass when conditions were harsh. However, most of the natural history characteristics that were investigated did not affect whether or not a step function was obtained in sight-feeding birds. These characteristics were: the amount of individual variation in foraging efficiency; whether interference was caused by food depression or kleptoparasitism; the extent to which interference was intensified by the birds aggregating while feeding; food size and the inclusion of three realistic, although in two cases rather harsh, environmental factors either singly or in combination. Step responses were therefore a very robust features of the simulations with sight-feeding birds.

8.   In sight-feeding birds, the food/bird biomass ratios at which the step response occurred was affected by only a limited number of factors. These were: the degree to which birds aggregated while feeding, and thus the intensity of interference; food size; and bird size.

9.   Step functions occurred over a much more limited range of conditions in touch-feeding birds than in sight-feeders. In fact, gradual decreases in the proportion of birds starving or failing to reach their target mass as the food/bird biomass ratio increased were the rule rather than the exception. This difference from sight-feeders arose because of the differences between their functional responses. The higher asymptote of the functional response of touch-feeders allowed more birds to survive and maintain their mass when food was abundant. But as the ratio was reduced, so that food became more rapidly depleted during the winter, the gradual gradient of the functional response of the touch-feeders allowed individual variations in foraging performance to be expressed so that birds no longer starved *en masse*. Contest competition was expressed so that some birds starved well before others, which led to a gradual response rather than to a step response.

10.   Although occurring at higher food/bird biomass ratios than in sight-feeders, step changes did occur in touch-feeders when they were able to supplement their food consumption at low water by feeding upshore as the tide ebbed and flowed. This arose because, even in the harsh conditions modelled, upshore feeding provided time for failing birds to make up for their poor performance over low tide. By allowing the poorer performers to make up their deficit as the tide ebbed and flowed, upshore feeding reduced the variation in performance between individuals and thus prevented the full effects of contest competition from being expressed. This important result suggests that, when evaluating the use of the food/bird biomass ratio approach, the opportunities available to birds for supplementing their food consumption when their main low tide feeding grounds are unavailable will have to be taken into account.

11.   The frequent absence of a step function in touch-feeding birds results from the very gentle gradient of their functional response used in the simulations. While this report was being written, new evidence arose which suggested that the gradient of the functional response in touch-feeders is more similar than previously thought to the steep gradients found in sight-feeders. If this proves to be the case, the food/bird biomass ratio approach should be much easier to apply because the change in the

proportions of birds starving and failing to achieve their target mass as the food/bird biomass ratio increases would follow a step function in most, if not all, species.

12.   Increasing the intensity of disturbance up to the point at which 50% of the feeding grounds were disturbed, and thus unavailable to the birds, during daylight on every day of the winter only affected the proportions of birds dying and failing to achieve their target mass when the environmental conditions were harsh, so that the birds were already hard-pressed. However, the step response was maintained in sight-feeding birds, but not in touch-feeders.

13.   Distributing the food biomass a little unevenly across five patches at first caused the step response to be replaced by a more gradual, concave response. This means that, with a given quantity of food on an estuary, a higher food/bird biomass ratio was required to maintain a given mortality rate when the food supply was distributed rather unevenly across a number of patches than when it all occurred in one patch. However, when the food was very highly aggregated, so that 80% of the food occurred in just one patch, the concave response was replaced by a step function which occurred at a very high food/bird biomass ratios. This happened because putting virtually all the food in one of the five patches caused most birds to feed in that patch. This was equivalent to aggregating the birds by a factor of five, and thus greatly intensifying interference. These simulations showed that, depending on the degree to which the food supply was aggregated, the spatial distribution of the food supply can influence both the shape of the response and the value of the food/bird biomass ratio at which the asymptote was reached. In further evaluating the ratio approach, it will therefore be very important to quantify the spatial heterogeneity with which food supplies are generally distributed in SPAs.

14.   The real world case of oystercatchers on the Exe estuary illustrates that, in one species at least, the real-world values of the factors which prevent functions from being step responses combine to produce a rather gradual concave function such that, even at very high food/bird biomass ratios, an asymptote is only just being reached. It also illustrates the point that a high present-day food/bird biomass ratio does not mean that a decrease in the amount of food per capita would not result in a reduction in population size. We cannot assume that a high present-day food/bird biomass ratio implies that reductions in the food supply, or increases in disturbance, would have no effect on population size. It all depends on the values of the parameters that most influence the form of the response to changes in the food/bird biomass ratio.

15.   We conclude that, depending on the present-day ratios between food and bird biomass in SPAs, and on the degree to which the food supply there is aggregated, there are reasons to believe that the ratio approach could, in principle, be used to monitor the quality of SPAs, even in touch-feeding birds. However, before recommending that this is done in practice, we would stress the importance of (i) first finding out the values of the ratios that apply in SPAs at the present time and establishing the spatial aggregation of the main food supplies, (ii) establishing the present-day values of the proportions of birds that starve or fail to achieve their spring target mass - which are the targets that policy should aim to maintain - and (iii) describing some aspects of the ecology and behaviour of some species, particularly touch-feeding waders and wildfowl.

16.   The next stage of the evaluation of the food/bird biomass ratio approach should (i) undertake a review of the magnitude of certain parameter values in the real world and (ii) apply the approach to more real-world examples. The purpose of the Report has been to test whether step responses are likely to be widespread in coastal birds. If they are, the task of deciding whether the ratio recorded on an SPA is adequate for maintaining the present demographic rates would be made more simple. But if step functions do not prove to be the rule, the models can still be used for determining the target ratio needed in a particular SPA. The ratio would need to be determined on a site-by-site and species-by-species basis. This would be less convenient than using a small number of universally-applicable ratios, but would nonetheless be perfectly feasible.

Contents

List of Figures

1. Introduction

The question addressed by this report is how can one easily determine the targets for (i) food biomass density and (ii) levels of disturbance that are required in order to show whether the quality of the habitat is being maintained at a sufficiently high standard to support the bird populations for which the estuary was designated as an SPA.

Monitoring bird numbers on an estuary alone is not itself a reliable way of assessing whether the quality of the habitat is beginning to fall below the level required to maintain the present-day population size, even if it is the only way in which to measure its conservation importance relative to that of other estuaries. First, there may be a lag between the decline in habitat quality and a detectable fall in numbers because established birds may be reluctant to change site. Second, and more fundamentally, the numbers of birds on any one SPA depends not only on the conditions in that SPA but also on conditions elsewhere in the non-breeding range and on the breeding grounds. If numbers in one SPA decline over a period of years, this might have happened because the quality of the SPA itself has indeed declined, so that fewer birds are attracted to it. However, its quality may equally have remained the same, or even increased, yet numbers there declined for two reasons: (i) the quality of other parts of the non-breeding range has improved, so birds go there instead, or (ii) the reproductive rate on the breeding grounds has decreased, and/or the mortality rate there has increased, so that the size of the greater population to which the birds using the SPA belong has decreased. Much effort and expense may then be spent trying to reverse a local decline in numbers whose causes actually lie elsewhere in the species range.

This report explores another way by which the quality of an SPA might be monitored in an easily-implemented programme. It is based on the fact that population size in migratory shorebirds (waders *Charadrii* and wildfowl *Anatidae*) is a function of the interaction between (i) the mortality and reproductive rates in the breeding range and (ii) the mortality rate in the non-breeding range, including the migratory routes. Since the objective of non-breeding shorebird conservation policy is to maintain present bird abundance, the best measure of habitat quality is one which, either directly or indirectly, determines these demographic rates. For migratory shorebirds during the non-breeding season, this means that habitat quality should be measured in terms of if its effect on two quantities. First, the fat reserve levels needed to fuel migration and, in spring also to breed successfully after the birds have reached the breeding grounds. Second, the starvation rates during the non-breeding season, perhaps especially during severe winter weather. If one can show that the feeding conditions in the SPA are sufficient to maintain the present-day rates of fat storage and survival at the current population size and in the current climatic conditions, then one will know that the quality of the SPA is being maintained at a level sufficient to achieve the goal for which that SPA was set up. If the population nonetheless declines, then the cause needs to be sought elsewhere.

We define 'feeding conditions' in terms of the combined effect of the food supply itself and disturbance on the ease with which the birds can obtain their energy requirements. We explore in this Report the idea that the ratio between the biomass density of the main food and the biomass density of the birds in autumn can, in principle, reliably predict whether the current food stocks are sufficient to maintain the current rates of fat storage and survival in the SPA. It also explores how the ratio needed to do this is affected by disturbance. To state the

idea in its simplest form, a certain minimum amount of food per bird in autumn must be required to maintain the current survival rate and body condition in spring; if there was not enough food per bird in autumn, the food stocks would run out and birds would either die or leave the SPA before spring. We explore here whether it might be possible to use a limited number of values of such a ratio to assess habitat quality across a range of species, estuaries and climatic conditions.

The ratio would provide the clearest guide to monitoring if, in response to a decrease in the ratio, there were to be a 'step response' increase in the proportion of birds starving and/or failing to attain their target mass in spring. That is, below this ratio most birds would fail whereas, above it, most would succeed and the proportion doing so would fluctuate without trend as the ratio increased still further. Such an outcome would suggest that it should be possible to give a clear guide as to the minimum size of the ratio required to maintain the *status quo*, and a 'safety margin' could be included for its use to remain consistent with the precautionary principle. But were this not to be the case, and were responses generally to be rather gradual as the ratio increased, it would be necessary to calculate a separate ratio for each species in each SPA. This can, of course, be done, but this outcome would decrease the speed with which the method could be introduced.

The ideal outcome, perhaps, would be that a food biomass/bird biomass ratio of, for example, a minimum ratio of 50:1 would always maintain current rates of fat storage and survival, in all systems! But as the ratio is likely to be affected by climate, bird species, food species and levels of disturbance, we did not expect the outcome to be as convenient as this. Rather, we expected only to determine whether, in principle, (i) step responses were likely to be the norm rather than the exception, and (ii) a small number of ratios, selected according to species biology, can be used as a reliable 'rule of thumb' to assess habitat quality for the main species involved. If this 'in principle' exercise proved to be successful, we would then propose that further research based on this approach should be conducted to calculate the ratios for particular species and SPAs.

But how can one determine whether the feeding conditions in the SPA are being maintained at the necessary level to keep fat storage and survival rates at their current level? CEH has developed and tested models that predict the effect of changes in the autumn standing crop of the food supply and amounts of disturbance on the (i) body condition and (ii) overwinter survival rate, and thus population size, of a wader (oystercatcher) and wildfowl (brent goose) species. This report explores whether these models can be used to establish the target baseline quality of habitats that are required to put EN's habitat quality monitoring programme on a firm scientific basis for all the main species.

We used the oystercatcher-mussel model, and a simplified version of it, to achieve the following objectives:

- To test whether the ratio between the biomass density of the main food and the biomass density of the birds in autumn can be used reliably to determine the food abundance required to maintain present-day rates of fat storage and winter mortality.

- To explore by how much the required the ratio between the biomass density of the main food and the biomass density of the birds in autumn is changed by different amounts of disturbance on the feeding grounds.

- To test whether the degree to which the food supply is clumped has a significant effect on the ratio between the biomass density of the main food and the biomass density of the birds in autumn that is required to maintain current rates of fat storage and survival.

- To test the approach by applying it to the well-studied case of oystercatchers eating mussels on the Exe estuary.

Having demonstrated that, in many circumstances (which are defined) a simple survey of the main food organisms carried out in autumn would enable baseline habitat quality to be defined and monitored, we conclude by suggesting how a monitoring survey could be conducted in the simplest and most cost-effective way. We also suggest further research that would take this approach closer towards applying it routinely.

2. The model

The model was developed and tested in one system, Exe estuary oystercatchers *Haematopus ostralegus* eating bivalve molluscs (*Mytilus edulis*, *Cerastoderma edule* and *Scrobicularia plana*) in the intertidal zone and earthworms *Lumbricidae* over high tide in fields. A full description of the model is given in Stillman *et al* (2000) and the reasons for its development, and the philosophy underlying the approach upon which it is based, are discussed in Goss-Custard and Stillman (submitted). It has been used to explore the effects of current and putative levels of disturbance on the Exe estuary on the overwinter survival of oystercatchers (West *et al.* submitted) and of current and putative levels of shellfishing on the Exe estuary and Burry Inlet (Stillman *et al* submitted). The model has recently been extended to include all the common species of waders and one wildfowl species (the brent goose *Branta bernicla bernicla*). Under contract to the EU, attempts are now being made to apply the approach to the main common wildfowl species too. It is now being used under contract to explore a wide range of estuary management issues in several species in five European countries.

The oystercatcher model for the Exe estuary is briefly described here to indicate how it works and to describe the principles upon which it is based. The inter-tidal, low water feeding areas in the model consist of 10 food patches of differing quality, this depending on prey size (length), numerical density and ash-free dry mass (AFDM). Individual birds are allocated to age and feeding method and choose in a game-theoretical and ideal-free way where to feed from amongst these patches; thus, the choices made by one competing individual are contingent upon those made by all the others. Each model bird decides on each low water period (day and night) on which patch it would achieve its highest intake rate (*ie* maximise its intake rate) over low water, and moves there. To choose a patch, each bird must know its potential intake on each patch under the prevailing conditions. The potential intake rates of each individual on each bed are calculated in two steps. First, the interference-free intake rates of individuals of differing efficiencies are calculated from the densities, sizes and energy contents of the prey present on each patch using an empirically-parameterised 'Charnov' rate-maximising foraging submodel; night intake rates are calculated as an empirically-determined fraction of day-time rate. Second, the reduction in intake rate arising from interference is calculated for each individual on each patch from its dominance, given the density and fighting abilities of the other birds present on each patch at that time. The potential intake rate is calculated by subtraction and the bird spends the low water period where its intake rate is highest. As the spatial scale is small, the model assumes that no time and energy costs are incurred by birds moving between patches in a site.

In every daily iteration during the non-breeding season (15 September - 15 March), each individual decides where it should feed on each low tide period. Many birds change feeding patch during the winter as the relative qualities of patches alter through prey depletion; at the end of each day, the total biomass eaten by all the birds on each patch is summed and removed, resulting in depletion of the resources on a day to day basis. Empirically-derived reductions in prey biomass from other sources, such as overwinter loss in prey body condition or storms, are also incorporated. Each day, the model calculates the temperature-dependent daily energy requirements of each bird and its daily energy acquisition if it were to feed for the entire time available on its chosen intertidal patches. This depends upon two factors, the amount of time for which each patch is available per day and the instantaneous intake that can be achieved when a patch is available. The availabilities of intertidal patches vary from

day to day according to a springs-neaps tidal exposure cycle. Birds failing to obtain enough energy from the intertidal patches over low water feed, at empirically-determined rates, on alternative inter-tidal food - upshore of the ten patches - as the tide advances and recedes and also, over high water, on earthworms in fields; field availability is determined by day-length as most waders seldom use fields at night. Individuals exceeding their energy maintenance requirements convert the excess into fat reserves with a literature-derived efficiency.

Fat storage is constrained by two literature-derived limits; a maximum rate of daily mass increase and an upper limit to total body mass. If constrained by either of these two limits, a bird roosts. A bird that fails to meet its maintenance requirements despite feeding for all the time available to it – so that it is 'hard-pressed' - draws upon its fat reserves to make up the shortfall. Birds starve when they run out of reserves. The overwinter mortality rates predicted by this model are then used in a simple, year-round demographic population model to predict how any predicted change in overwinter mortality rate affects the overall population size on the site.

The model was tested by comparing its predicted overwinter mortality (starvation) rates with the observed rates for a sample of winters during which the wader population increased (Figure 1). It successfully predicted the observed density-dependent increase in mortality rate, and did so for a range of population sizes above that for which the model had been parameterised. Other tests showed that the predicted mortality rate was based on realistic behaviour of waders within the model. The foraging submodel predicted intake rates with good precision and the ideal-free distribution submodel predicted well the numbers and densities of birds on the different food patches at low water. The model as a whole also predicted (i) the stage of the winter at which the birds starved, (ii) the numbers of minutes birds spent feeding at low water, (iii) the dates at which birds supplemented their intake over low water by feeding on supplementary prey upshore in the intertidal zone and in fields over high water, and (iv) the proportion of the mussel biomass present in autumn that oystercatchers removed by spring (observed 12.1%; predicted 11.4%).

A simplified version of the model is used for most of the simulations in this report. The main difference is that intake rates are not calculated from an optimality submodel but from a simple two-parameter equation that relates the intake rate of the bird to the biomass density of the food; this function is referred to as the 'functional response'. Recent research has obtained the values of these parameters from a survey of published work on shorebird intake rates (J D Goss-Custard, unpublished information). Also, some natural history details, that are specific to the oystercatcher system, are omitted.

3. Specific modelling objectives

3.1 Definition of the food/bird biomass ratio

The food/bird biomass ratio is the ratio between the biomass of food present and the biomass of the birds that eat it. It measures how many grammes of food there are per gramme of bird.

The measure of food biomass was the standing crop biomass density (g/ha) of the food organism that occurred above the threshold biomass density below which it was not possible for the bird in question to obtain its daily energy requirements in the foraging time available to it; see section 4.2. Food biomass that occurred at too low a density for the birds to use it was therefore not considered to be of any use to them. In most simulations, we used the food biomass present in the autumn, when the birds arrived. This was measured as the product of numerical density and the mean mass of the individual food items. However, in the simulations in which the mass of individual food items declined over the winter (see section 4.5), we used the mean mass of the food items at the end of the winter.

3.2 Species characteristics

The aim here was to investigate the relationship between the food/bird biomass ratio and both the (i) spring body mass and (ii) overwinter mortality rate of shorebirds, across a wide range of bird/food species 'systems', in order to explore the idea that a limited number of values of the ratio can, in principle, be chosen that will maintain present-day rates of fat storage and winter survival.

The system characteristics that were varied across simulations were: (i) carnivory and herbivory; (ii) degree of individual variation in competitive ability, defined in terms of both foraging efficiency and susceptibility to interference; (iii) shape of functional response, (iv) the presence of supplementary feeding opportunities upshore of the main low water feeding areas, (v) overwinter decreases in food abundance due to factors other than depletion by the birds themselves, (vi) winter climate, (vii) food (= food item) size, and (viii) preference of the bird for the food organism in question. These are the main factors that determine how food abundance affects the body condition and mortality rates of these birds.

Item (viii) was needed because most shorebirds can switch from their most preferred food species to another one when the preferred one is scarce. Habitat quality therefore needs to be defined in terms of, perhaps, two or three food organisms, of decreasing preference. It was thought likely that the dependence on the food/bird biomass ratio of the proportion of birds starving and failing to achieve their target mass would be different with the least preferred food than with the most preferred. This could be important as EN staff would need to judge whether, in years with low abundance of a preferred food, the alternatives available would be of sufficient abundance to maintain the required fat storage and survival rates of the birds.

3.3 Disturbance

Disturbance prevents birds using some areas and forces them to congregate in the reduced area of undisturbed feeding ground that remains. Since the SPA regulation considers the levels of disturbance as part of the suite of factors that affect habitat quality, simulations were run to

explore its effect on the dependence on the food/bird biomass ratio of the proportion of birds starving and failing to achieve their target mass.

3.4   Habitat patchiness

Monitoring habitat quality would be much easier if it were possible to sample the food supply with a very limited sampling programme, carried out at a very low sampling intensity over much of the estuary. The danger here, though, is that the extent of areas of good and poor food abundance could not be defined with confidence. Thus, one could get the same average food abundance across the whole estuary either by food being spread widely at low densities or concentrated in a few smaller areas of high density. This difference in food dispersion could affect how well the birds can forage.

We therefore tested whether the degree to which the food supply was clumped significantly affected the dependence on the food/bird biomass ratio of the proportion of birds starving and failing to achieve their target mass. These simulations were designed to show whether, even with a clumped food resource, a simple measure of food density across the whole estuary would be sufficient to provide a reliable estimate of the required food/bird biomass ratio.

3.5   Application to a real case

In order to apply the concept of the required food/bird biomass ratio to a real system, and thus to demonstrate that any general across-species conclusions from the simplified model do apply to particular cases, we made a series of simulations with the Exe estuary oystercatcher-mussel model. Had time allowed, we would also have done the same for brent geese eating *Zostera* spp. and grass. But the simulations with the oystercatcher-mussel model were in any case regarded as being sufficient to show how well the required food/bird biomass ratio might work in a real system.

4. Simulation procedure

Some features common to all simulations are described here. Details of the parameter values used in all simulations are given in Appendix 1.

4.1 Varying the food/bird biomass ratio

A given food/bird biomass ratio can arise when a low food biomass supports a low biomass of birds or when a high food biomass supports a high biomass of birds. In each case, the ratio may be changed by varying either the biomass of the birds or the biomass of their food. Changing the initial stock of food biomass affects how quickly a given number of birds depletes the food supply to the point at which intake rate begins to fall below the asymptote. Changing the initial density of birds affects the amount of interference experienced by the birds and also affects the rate at which a given stock of food is depleted. Individuals will also experience higher levels of interference when the densities of both the birds and their food are high, but little or no interference when both are low. Therefore, the precise way by which the ratio is reached and varied is likely to affect important processes that bear upon the probability that birds will starve.

The food/bird biomass ratio could therefore be varied in four ways: (i) low bird and food biomasses, and varying food biomass (**LP**); (ii) low bird and food biomasses, and varying bird biomass (**LB**); (iii) high bird and food biomasses, and varying food biomass (**HP**), and (iv) high bird and food biomasses, and varying bird biomass (**HB**). The first two are referred to as 'low ratio' simulations, while the latter two are called the 'high ratio' simulations. However, since the purpose of the work is to explore whether a given food/bird biomass ratio would maintain current mortality rates and body condition at current population sizes, we often chose only to vary the ratio by varying the food biomass and leaving bird density the same.

4.2 Functional responses

As illustrated in Figure 2(a), sight feeding waders reach the asymptote of their functional response very rapidly as food biomass density increases; the gradient is thus very steep (J D Goss-Custard, unpublished information). Quite remarkably, these birds are able to feed at their maximum rate even when food is very scarce. This, in turn, means that, as food is depleted over the winter, a point is reached when most birds starve together, even if the birds vary greatly in how efficiently they forage and how effectively they compete with others. In effect, scramble competition is introduced into a system in which one might think contest competition would be paramount (Goss-Custard and West in press). Once the food supply has been depleted to very low levels, all birds 'fall over the cliff' together, and starve *en masse*.

In contrast, the present very limited evidence suggests that, although the asymptote is higher than in sight-feeding birds eating food of the same size, the gradient of the functional response in touch-feeding waders is much less steep, as indicated in Figure 2(b). This means that, as food density falls through depletion, individual variations in competitiveness have a much greater opportunity to be expressed, allowing contest competition to exert its well-known effects. We therefore ran simulations with both the kinds of functional responses illustrated in Figure 2.

Figure 2 also illustrates that, in order to acquire its food requirements in the time available for it to feed, a wader needs a certain minimum intake rate, which is referred to as its 'threshold intake rate'. The minimum food biomass that enables a bird of average foraging efficiency to achieve its threshold intake rate, the 'threshold food biomass', is also shown.

It is important to note again that, when calculating the food/bird biomass ratios, we used the biomass of food that occurred above the threshold food biomass. This was done on the grounds that the food biomass that occurred at a lower food biomass density was, in effect, useless to most birds, except for the most efficient. By the time the food supply had fallen to that level, most birds would have starved.

4.3   Foraging efficiency

Individual birds vary in the efficiency with which they exploit the food in the absence of interference; *ie.* they differ in 'foraging efficiency' (FE). The magnitude of this variation is measured from the variation between individuals in their 'interference-free' intake rate at all points along the functional response. Here, a value of 5%, for example, means that the standard deviation in FE is 5% of the mean interference-free intake. This means that 99% of the individuals vary in intake rate within *circa* 85% - 115% of the mean rate, the frequency distribution within these limits following a normal distribution. In these simulations, we used values of the variation in FE of 5%, 15% (equivalent to the value found in oystercatchers) and 25% - which is probably unrealistically high.

4.4   Interference

Interference in foraging shorebirds arises in two ways. In interference through 'food depression', the presence of a bird on the surface of the substrate causes the food to take anti-predator action, such as retreating down a burrow. This makes the food less accessible to the birds, whose intake rate therefore falls. In this case, all individual birds are affected equally by the decline in food availability as bird density increases. In interference through 'kleptoparasitism', the intake rate of subdominant birds is reduced because their feeding sites and food items are stolen from them by more dominant individuals. In this case, subdominant birds are most affected by interference while the intake rate of the dominants may not be affected at all as bird density rises. Interference can be an important process in waders; for example, it is kleptoparasitic interference which alone causes the density-dependent overwinter starvation in oystercatchers feeding mainly on mussels on the Exe, with food depletion playing no part at all (Goss-Custard *et al* submitted).

The model can simulate either kind of interference. The amount of interference experienced by the birds was, on average, the same in both cases but, with kleptoparasitism, its effects varied between individual birds, falling most heavily on subdominants. Interference was assumed to begin above a threshold bird density of 50/ha, a typical value in waders (Stillman, Goss-Custard and Caldow 1997).

At the densities used in these simulations, interference would only have affected intake rates in the high ratio simulations when bird densities varied between 50 and 100 birds/ha. We only explored the effect of interference using HP simulations, in which bird density remained constant at 100 birds/ha across all the range of food/bird biomass ratio by varying only food biomass. The alternative procedure (HB) of varying bird density while keeping food density

constant would have meant that both the intensity of interference and the ratio changed in parallel, making interpretation difficult. We therefore only ran high ratio simulations, and only by varying food biomass density (ie HP). In these simulations, we used variations in individual FE of 15%, as this is a mid-range value and approximates the only field estimate yet available.

In the first simulations with interference, the birds were assumed to spread out over the whole of the patch of food. In the real world, however, birds often aggregate into parts of a patch. This increases the density of birds, of course, and thus intensifies any interference that occurs.

We simulated the effect of this aggregation in the model by using an 'aggregation factor' that, in effect, squeezes birds together into just part of the patch. An aggregation factor of 2 means that the birds use only half the patch, so that density is double what it would be were they all to spread out over the whole patch. An aggregation factor of 10 means that the birds use only one tenth of the patch, and that densities are 10 times higher than would otherwise be the case.

In the simulations, we used the range of aggregation factors of 1 to 10, this covering the values we have recorded in waders of many species in many estuaries.

4.5   Environmental factors

In the initial simulations, the birds were only able to feed over the 6 hrs per tidal cycle for which the single food patch was exposed over low tide whereas, in the real world, birds are able to feed for an extra hour or so either side of this period on the upshore flats, which are usually of poorer quality. In addition, in the initial simulations, the flesh-content of individual food items was assumed to remain constant from autumn to spring, whereas in nature it may decline over that period by as much as 50%, although it is usually less. Finally, the climate was assumed in the initial simulations to be the same as that on the Exe, whereas in many estuaries, the weather is much colder. As all these real-world environmental factors are known to affect the survival chances and body condition of waders, we explored the effect of including these three factors individually and together, using the parameter values shown in Appendix 1.

To explore the effect that these environmental factors had, singly and in combination, simulations were first run with FE=15% and without interference. To include the effect of interference, the simulations were repeated with food depression interference included but, for the reasons given earlier, only for the HP case.

4.6   Target body and fat sass in Spring

Target body masses used were the body masses of birds on the Wash, taken from Johnson (1985). In the first series of simulations, we chose the criterion that birds should achieve a body mass within 5% of their target mass at the end of the winter, just prior to migration. The target mass itself was the observed population mean at that time of year. This stringent criterion was chosen in order to put the whole methodology under as severe test a possible.

However, in some simulations, very few birds were able to keep their body mass at or above 95% of the target they had been given. In order to see whether less stringent conditions might be applied, we looked at the distribution of body masses in oystercatchers on the Exe (for

which we had the necessary data) at about the time that they leave for the breeding grounds. The results showed clearly that many birds left with body masses well below 95% of the population mean, yet returned the next autumn. We therefore relaxed the criterion so that a bird was only required to achieve a target mass in spring of 75% or more of the population mean at the end of winter. Furthermore, we also changed to a threshold of 75% of the target weight of *fat* rather than 75% of the target mass of the whole body. This was done to allow easier comparison between species of different sizes, since the lean mass of large waders comprises a smaller percentage of total weight than that of small waders.

This decision was discussed with Simon Bates at our progress meeting in February. It was agreed that this procedure would suffice as an interim measure with which to evaluate the whole approach. But were the methodology to be applied to real birds in real SPAs, it was agreed that further review of the mass distribution of birds just prior to departure would be advisable. In this report, however, a minority of the simulations used the 95% criterion because we did not have time to re-run them using the less stringent criterion. While this certainly affects the absolute proportions of birds that failed to meet their target mass, it did not affect the way in which the proportion changed as the food/bird biomass ratio was increased. The question as to whether or not a step response would generated was therefore unaffected by the precise value used.

In this Report, we have used as the target mass the spring values appropriate for overwintering birds departing for the breeding grounds. The model can, however, be set up to distinguish between autumn passage migrants, winter visitors, spring migrants and cold-weather immigrants *etc.*, with each category of bird being given its own target mass and date at which the target should be reached. This is being done at present, for example, in a model of the oystercatchers in the baie de Somme, France, where large numbers arrive in winters when the Wadden Sea freezes over. For simplicity, this has not been done in the present report, but could be done in any future contract. It would certainly need to be done in real-world cases that involve categories of birds other than winter visitors.

4.7   Disturbance

Disturbance was incorporated by preventing the birds from feeding on between 5% and 50% of the feeding area - but only during daylight which is when most disturbance usually occurs on estuaries. We considered it important to explore the effect of disturbance under natural conditions. We therefore included, both singly and in combination, depression-based interference and the real environmental conditions of upshore supplementary feeding and the rather extreme cases of a 50% overwinter decline in food mass and an ambient temperature 5°C below those actually occurring on the Exe.

4.8   Bird species

The main ways in which wader and wildfowl species vary in the context of their foraging ecology is in their body mass, whether they are carnivorous or herbivorous and whether they detect their food by sight or by touch. Body mass affects the balance between rates of energy consumption and rates of energy acquisition.

Large waders consume food at a relatively slow rate compared to small birds; *ie* they have a rather low intake rate per gramme of bird. However, the energy requirement per gramme of a

small wader is greater than that of a large wader, partly because the lower critical temperature (LCT) in small birds is much higher; eg. 21°C in dunlin but 9°C in curlew. The balance between the rates of energy expenditure and energy acquisition in waders is such that, generally, it is easier for large birds to obtain their requirements in the time available.

The essential difference between herbivores and carnivores is that interference levels tend to be low in herbivores and all their food is often easily accessible and available all the time (Goss-Custard and Charman 1976). Herbivores can gather in large flocks in the best places and 'hoover' up the food supply there before spreading out onto the next most profitable place, and so on. It is not uncommon for herbivores to quickly graze down their initial food stocks to very low levels everywhere (eg *Zostera* spp.), whereupon they move on to another supply altogether (eg saltmarsh plants). In contrast, high levels of interference are common in carnivores and a high proportion of their food may be inaccessible at any one time. The birds must spread out much more widely than do most herbivores, and are therefore do not have the 'consumption' power to deplete their food supplies in any one place at a high rate. Instead, they gradually reduce the food supplies over the winter, depleting the stocks in a repeated series of low-consumption passes over each spot.

This diversity of systems is represented in our simulations by three 'species' of notional birds that, between them, cover the main categories of wintering wading birds and wildfowl. First, a large number of simulations across the whole range of conditions were run with a medium-sized bird, such as a redshank, grey plover or godwit; for reasons of nostalgia, we refer to these as 'redshank'. In the simulations, the birds either detected their food by sight or by touch, the difference expressing itself in the gradient and asymptote of the functional response. Then, in order to explore any effect of bird size, a smaller number of simulations were run for a narrower range of conditions with a small bird, which we call a 'dunlin' (it might equally well be a ringed plover), and a large bird, which we call 'curlew' (although it could be a duck or goose). In both cases, the birds detected their food by sight. This suite of notional species covers the main dimensions of variation in waders and wildfowl as a whole.

4.9   Habitat heterogeneity

The effects of sub-dividing the main low tide food supply into a number of patches with differing densities of food were explored by having five patches of equal area, in all of which the initial food biomass density in autumn exceeded the threshold biomass density. The simulations were run on sight-feeding redshank whose foraging efficiency variation was 15%. The birds were subjected to interference through food depression.

The way in which the food biomass was distributed across the five patches in the five simulations was as follows:

Scenario	Amount of food in each patch (% of total)				
1	20	20	20	20	20
2	40	30	15	10	5
3	60	20	10	5	5
4	80	5	5	5	5

5. Results - species characteristics

Our overall approach was to gradually build up the realism of the models by adding components that are either known, or suspected, of affecting the ease with which waders obtain their food requirements in winter. We also explored a range of values which we are sure would encompass the range that might occur in nature. In some cases, however, this approach results in our using conditions which are really quite extreme and are unlikely ever to apply in the real world. But our view was that, if the ratio approach looks promising even in these circumstances, its potential usefulness would have been better explored than would otherwise have been the case.

5.1   Sight-feeding redshank

The first simulations were run with a typical medium-sized wader that detects its food by sight, such as a redshank *Tringa totanus*. The food was a polychaete worm, such as the widely-taken *Hediste (Nereis) diversicolor*, each one having the typical mass of 20 mgAFDM. The following values were used, chosen as being typical of the densities of this species and of its food in nature. In the low ratio simulations, bird density was held at 5/ha (equal to 750 g/ha) in the LP simulations while food biomass was held at 5 g/m^2 (50,000 g/ha) in the LB simulations. Both these quantities were multiplied by 10 in the high ratio simulations. The remaining parameter values used in these simulations are given in Appendix 1. Note that, in these first simulations, the food was restricted to one homogeneous patch.

5.1.1 Variation in foraging efficiency alone

Figures 3-5 shows the winter mortality rate and percentage of birds failing to reach the spring target mass according to the variation in FE and whether high or low food-bird biomass ratios were used. With both kinds of high ratio, the mortality rate and the proportion of birds failing to reach target mass were level across most of the range of ratios; we refer to these from now on as the 'asymptotic' rate. Once the food/bird biomass ratio had risen to a certain value, the mortality rate and proportion of birds failing to reach target mass did not change any more. In fact, both quantities dropped very suddenly from 100% over a sharp 'threshold' food/bird biomass ratio range of 30-40. This 'step function' reflects the fact that, with a sight-feeding functional response, most birds starve at the same point as food becomes depleted to a very low level.

Above the threshold ratio, the asymptotic rates increase as the variation in FE rises from 5% to 25%; a greater proportion of birds 'fail' in both ways as the variation in FE amongst them increases. This arises because, even with plentiful food, the very inefficient individuals are unable to feed fast enough to store maximum fat or to avoid starvation and the larger the variation between birds in their FE, the greater the proportion that are too inefficient to survive or to reach the target mass.

Whether high or low ratios are used has some influence on mortality rate but it has more effect on the proportion of birds failing to reach target mass. But although rather fewer birds starved and failed to achieve target body masses in the high ratio simulations than in the low ratio ones, the response to the increasing food/bird biomass ratio in both high and low ratio simulations followed a step function.

5.1.2 Variation in interference alone

Figures 6 and 7 shows that whether the interference arises through food depression or kleptoparasitism makes little difference to the outcome, the two pairs of graphs being essentially the same. However, comparison with Figure 4 shows that, at even the low levels of interference used, and without aggregation, adding interference greatly increased the mortality rate and the proportion of birds failing to achieve their target masses in spring. Nonetheless, the response remained a step-function, with the food/bird biomass ratio at which the step change occurred remaining in the region of 30-40.

Figure 8 shows that aggregating the birds closer and closer together increased the asymptotic mortality rate and proportion failing to achieve the target mass because of the intensifying interference amongst them. The magnitude of the effect was initially very high as the aggregation first doubled, from 1 to 2, and then doubled again from 2 to 4. But as the increases in density with further increases in aggregation were proportionately smaller (eg by 50% from 4 to 6), the magnitude of the effect also became smaller.

Nonetheless, a step-function response was essentially retained across the whole range of aggregation factors. However, the food/bird biomass ratio at which the step response occurred decreased as aggregation, and thus the interference, intensified. At the highest levels of aggregation, the step response fell at a food/bird biomass ratio of 20-25 rather than 30-40. This happened because, at the higher levels of interference caused by high levels of bird aggregation, many individuals starved early in the winter. The subsequent rate of depletion of the food was therefore reduced, which allowed the smaller number of very efficient birds that could survive the intensified interference to do so on lower initial stocks of food.

This example shows that, when selecting food/bird biomass ratios for real birds in real SPAs, it will be important to be able to assess the level of interference experienced by the birds in question.

5.1.3 Environmental factors

5.1.3.1 Upshore feeding

Comparison of Figure 9 with Figure 4 shows that allowing birds to feed for extra time (3 hours per tidal cycle) on the upshore flats reduced the asymptotic rates of mortality and failure to achieve the target mass very considerably, even though the food biomass density and mass of the individual food items were only 25% of those in the low tide feeding areas (Appendix 1). This occurred without interference and with depression-based interference and an aggregation factor of one.

Additional feeding was effective because it enabled the poor performers to acquire the extra food they needed. There was again a step response, this falling at a food/bird biomass ratio within the range of 30-40. Above this ratio, no birds died and most gained the target mass. Furthermore, the patterns were similar in the high and low ratio simulations, and however the food/bird biomass ratio was varied.

5.1.3.2 Decline in food mass

Note that the scale of the x-axis is much reduced in the simulations in which the food lost mass over the winter. This happens because we used the food biomass based on food item size at the end of winter to calculate the food/bird biomass ratio instead of the food biomass based on food item size in autumn as we have done in all the other simulations.

Reducing the flesh-content of food over the winter caused the high ratio and low ratio simulations to diverge considerably (Figure 10). In the high ratio simulations, the response to increasing food/bird biomass ratio remained a step function, this being especially marked when interference occurred. Furthermore, the threshold food/bird biomass ratio at which the step change occurred remained in the region of 30-50. But in contrast, the response was more gradual in the low ratio simulations for both mortality and the proportion failing to achieve their target mass. There was also a considerable difference according to whether the ratio was changed by varying the density of the birds or that of the food.

5.1.3.3 Cold weather

Reducing the ambient temperature by 5°C each day throughout the winter increased mortality, especially at low ratios, and raised the proportion of birds that were unable to reach the spring mass target (Figure 11). It is again noticeable that, in the high ratio simulations, the threshold food/bird biomass ratio at which the very clear step change occurred in both the mortality rate and the proportion of birds failing to reach target mass was again in the region of 30-40. Adding interference to the high ratio simulation increased both the mortality rate and the proportion of birds failing to achieve their target mass, but the response was again a step function which occurred at a slightly lower food/bird biomass ratio than in the absence of interference. But with the low ratio simulations, there was again no step-function in the mass target curves; rather, the change was more gradual and differed somewhat between the two ways in which the food/bird biomass ratio was varied.

5.1.3.4 Upshore feeding, decline in food mass and cold weather together

In the final simulations in Figure 12, we included all three environmental features. In the high ratio simulations, the extra feeding provided by the upshore flats counteracted the difficulties posed by the low ambient temperature and overwinter decline in flesh-content. In fact, the response against the food/bird biomass ratio was similar to those shown in Figure 4, without interference, and in Figure 6, with interference. The 'provision' of supplementary feeding at the higher shore-levels seems completely to have compensated for the difficulties imposed by low temperatures and large declines in food mass. With low ratios, however, the functions remained much more gradual and differed between the two ways in which the food/bird biomass ratio was varied, especially in the graphs showing the proportion of birds that failed to achieve their target masses.

No significance should be read into the fact that the step change in Figure 12 occurs in the region of 20-30, rather than 30-40 as was the case in most of the preceding simulations. This happened because the food biomass calculations were made using the end-of-winter food item mass rather than the autumn mass as was used in the other simulations.

5.1.4 The use of high and low ratios

By now, it had become clear that the food/bird biomass ratio at which base levels were reached was most stable in the high ratio simulations. When high densities of birds coincided with high densities of food, the marked step function consistently fell in the range of 20-50. Furthermore, it made little difference how the food/bird biomass ratio was varied. With the low ratio simulations, however, the step-function was often replaced by a more gradual response, with the asymptotic rates being reached at food/bird biomass ratios that were higher than 20-50. To provide a full evaluation of the ratio concept, it will be important to establish first whether ratios in SPAs are generally high or generally low.

It seemed likely to us that SPAs would be characterised by high rather than low ratios. Sites are selected for SPA status largely because they support high numbers, and perhaps densities, of birds, and this can only happen where food abundance is relatively high. On this assumption, we decided to explore the ratio concept further using only high ratios.

5.1.5 Food size

Intake rates in shorebirds depend a great deal on the size of the food they eat. For a given bird species, intake rate increases sharply as the mean mass, measured as ash-free dry mass (AFDM), of their food increases. We therefore ran simulations covering a wide range of food sizes with environmental conditions most likely to cover the range experienced by real birds. The first simulations included only depression-based interference, and represented relatively benign conditions - although supplementary feeding upshore was not allowed. The second simulations included both interference and the three environmental factors of upshore feeding, a food mass decline of 50% and the ambient temperature reduced on every day by 5°C. Although the birds were able through upshore feeding to compensate for the decline in food mass and low ambient temperature, these conditions were probably more harsh than those experienced by most waders in most estuaries in Britain.

At the smallest size of food considered (5 mg AFDM), few sight-feeding birds achieved their spring target masses or survived the winter in either pair of simulations (Figures 13 and 14). As food size was increased, the asymptotic values of the mortality rate and the proportion of birds that failed to reach the target spring mass decreased, as had been expected. But most importantly in the present context, the response was always a step function and the food/bird biomass ratio at which the step occurred remained in the region of 30-50. Interestingly, however, the food/bird biomass ratio at which the step response occurred decreased as the size of the food consumed decreased; this was quite contrary to what had been expected. But this happened because, with a small food size, many birds starved early in the winter, thus reducing the rate at which the food was depleted thereafter. This left more food for the highly efficient survivors, which meant that smaller stocks were required in autumn to support the small numbers of birds that were destined to survive the whole winter. With larger food, more birds survived the autumn so the food was depleted more, and a higher ratio was therefore required at the start, in autumn, to support them through the entire winter.

5.1.6 Food preference

The birds were provided with two patches. In one, food items were large (20 mg) and therefore more profitable and so preferred. In the other, the food items were small (5 mg). The effect was

to introduce a double step-function (Figure 15). At high values of the food/bird biomass ratio, the birds fed for the whole simulation in the patch with the larger food items, and most survived. But as the food/bird biomass ratio fell, there came a point when the birds depleted the more profitable patch to the point at which it was more profitable for the birds to use the patch with the small food items. Since intake rates thereby fell, many of the least efficient birds starved, which caused the first step response. At even lower food/bird biomass ratios, the patch with the small food items also became so depleted by late winter that no birds were able to survive, which generated the second step response.

In sight-feeding birds, therefore, the presence of a less preferred and less profitable food can introduce a change in the shape of the functions that relate the proportion of birds that either starve or fail to achieve target mass to the food/bird biomass ratio. However, even though we used quite extreme differences in food preference, the effect was not to remove the step function but only to displace it to the rather higher food/bird biomass ratio of 45-55 rather than 30-40.

5.2   Touch-feeding redshank

Present evidence suggests that the gradient of the functional response in touch-feeding birds is much more gradual than it is in sight-feeding birds, whereas the asymptote is higher. The higher asymptote means, of course, that touch-feeding birds feed at a faster rate when food is abundant than do sight-feeding birds, and thus a greater proportion were able in these conditions to survive and achieve their body mass target. But the more gradual gradient of the functional response means that individual variations in foraging efficiency and competitive ability are able to exert a strong influence on intake rates as the food become depleted towards the threshold biomass food density, which in turn allows contest competition to be expressed (Goss-Custard and West in press). This difference was expected to introduce a more gradual change in the rates of starvation and failure to reach target mass as the food/bird biomass ratio was varied. The main issue, however, was whether the step response, that had been so generally present in the simulations for sight-feeding redshank, would be completely removed, or just made slightly less steep.

5.2.1 Variation in foraging efficiency alone

A comparison of the high ratio simulations in Figures 3-5 with those in Figures 16-18 reveal that, in the absence of interference, increasing the individual variation in foraging efficiency had a quantitatively different effect in touch-feeding birds than in sight-feeding birds. First, as the magnitude of the individual variation increased from 5% to 25%, the response became more gradual and smoothly concave and so less of a step function. This reflects the increasing, and expected, role played by contest competition in touch-feeders as the degree of individual variation increased. Second, the asymptotes were lower in the touch-feeders than in the sight-feeders; *ie* at high food/bird biomass ratios, more touch-feeders than sight-feeders survived. This arose because the asymptote of the functional response in touch-feeding birds is higher than in sight-feeding birds eating food of the same size. Third, in contrast to the results of the sight-feeding simulations, the asymptotes in the proportion of birds starving or failing to reach target mass both differed between the HP and HB simulations, especially with 25% variation in foraging efficiency. This arose because the proportion of the food biomass that was below the threshold was constant across the range of food/bird biomass ratios in the HB simulations. In contrast, in the HP simulations, the proportion below the threshold became smaller as the

food/bird biomass ratio increased. Therefore, in the HB simulations, depletion more rapidly reduced the food biomass to the threshold density across the whole range of food/bird biomass ratios explored, and thus more birds starved.

Despite these differences, the responses in the proportion of birds starving and failing to achieve their target masses remained essentially a step response, although it now occurred more in the range of food/bird biomass ratios of 40 - 60.

5.2.2 Variation in interference alone

A comparison of Figures 19 and 20 shows that, as in sight-feeding redshank, whether interference arose from food depression or kleptoparasitism made little difference to the outcome in touch-feeding birds. However, a comparison of Figures 6 and 7 with Figures 19 and 20 reveals that interference in touch-feeding birds generated a much more gradual response than it did in sight-feeding birds, although the asymptotic rates were still lower. That is, at a given food/bird biomass ratio, the proportion of birds either starving or failing to achieve their body mass targets were lower in touch-feeding birds than in sight-feeders.

These differences between touch-feeders and sight-feeders arose because of the differences in the functional responses of these two groups of birds. The higher asymptote of the functional response of touch-feeders allowed more birds to survive and maintain their mass when food was abundant. But as the food/bird biomass ratio was lowered, so that food became more rapidly depleted during the winter, the more gradual slope in the functional response of the touch-feeders allowed contest competition to be expressed. The least efficient birds starved first, thus reducing the rate of depletion of the food, allowing the more efficient birds to survive even longer, which in turn made the response to changes in the food/bird biomass ratio more gradual.

As would be expected, these trends were made even more pronounced when interference was intensified by forcing birds to aggregate in an ever smaller proportion of their feeding grounds (Figure 21). Compared with sight-feeders (Figure 8), the response to changes in the food/bird biomass ratio were very much more gradual, with the step function being replaced by a curve. In touch-feeders, the predicted proportion of birds that starve or fail to reach their target mass changes gradually over a wide range of food/bird biomass ratios, especially when the intensity of interference is high. The curves do reach an asymptote but generally do so at very much higher food/bird biomass ratios than occurred in the equivalent simulations with sight-feeding redshank.

5.2.3 Environmental factors

The same difference between touch-feeding and sight-feeding redshank that had been found when simulating the effect of variations in foraging efficiency and an increasing intensity of interference were found in the simulations in which additional environmental factors were introduced (Figures 22-25). The change in the proportion of birds starving or failing to achieve their target mass as the food/bird biomass ratio changed was more gradual, and the proportions lower, in the touch-feeding birds. Also, there was a large difference between the results of the HP and HB simulations.

The main conclusion is that the more gradual slope of the functional response of touch-feeders can have a substantial effect on the way in which changes in the food/bird biomass ratio affect the proportion of birds starving or failing to achieve their target mass. Importantly in the present context, the step-response found in sight-feeders was again often replaced by a much more gradual response. However, the effect on the shape of the response was most pronounced in the simulations in which the environment was made much more difficult by reducing the mass of individual food over the winter and by lowering the ambient temperature. When upshore feeding was also introduced, the response returned to more closely approximating a step function (Figure 25). This was especially noticeable in the starvation functions, in which the step change again occurred in the food/bird biomass ratio range of 30-50.

As noted earlier, the presence of upshore feeding had this effect because it minimised the effect of individual variations in foraging performance that are particularly expressed when the slope of the functional response is gradual. By allowing the poorer performers to make up their deficit as the tide ebbed and flowed, upshore feeding reduced the variation in performance between individuals and thus prevented the full effects of contest competition from being expressed.

This result is important because upshore feeding is a widespread occurrence in wintering wading birds. It suggests that, when evaluating the use of the food/bird biomass ratio, it will be important to take into account the opportunities available to the birds for supplementing their food consumption when their main low tide feeding grounds are unavailable to them.

5.2.4 Food size

Figures 26 and 27 show that, as expected, the asymptotic rates in the proportion of birds starving and failing to achieve their target mass increased sharply as food size decreased. Once again, and in contrast to the results obtained in sight-feeding redshank (Figures 13 and 14), the responses with small food were very gradual as the food/bird biomass ratio increased and only approached a step function with the larger food sizes. But even then, the step occurred at high food/bird biomass ratios, in the region of 50 - 100.

These results point to the importance of knowing the sizes of food taken by touch-feeding waders in any site where the ratio approach to monitoring the condition of the SPA is adopted.

5.2.5 Food preference

As in sight-feeding redshank, the presence of alternative and less profitable food displaced the function to the right, to a higher food/bird biomass ratio (Figure 28). Although there was a suspicion of a double step, it was barely discernible. This was because there was a greater opportunity for individual variation in foraging performance to moderate the response.

5.3   Sight-feeding dunlin

Sight-feeding dunlin in the model ate food weighing 10 mg AFDM, a typical value for these birds when eating *Nereis diversicolor*, one of their staple food species.

A comparison of Figures 3-12 with Figures 29-38 shows that, qualitatively, the results for sight-feeding dunlin were essentially the same in all simulations as in sight-feeding redshank. The main quantitative difference was that the step function in dunlin occurred at the higher food/bird biomass ratios of 60-70 instead of 30-40 where it occurred in sight-feeding redshank. The proportion of birds starving was also generally higher in dunlin than in redshank while the proportion failing to achieve their target spring mass was generally lower. Both these differences were due to the smaller-sized dunlin storing a lower amount of fat relative to their body size than do the larger redshank.

The simulations with environmental factors were run a second time in sight-feeding dunlin to explore the effects of increasing amounts of aggregation. A comparison of Figures 35-38 with Figures 39-42 shows that the asymptotes in the proportion of birds starving and failing to achieve their target mass increased as the birds experienced increasing amounts of interference because of being aggregated more closely together. The step response was generally maintained, but it occurred at lower and lower food/bird biomass ratios as aggregation was increased, falling from 60-70 as low as 30. This was a similar outcome to those found without aggregation in sight-feeding and touch-feeding redshank.

5.4   Sight-feeding curlew

Figures 43 - 51 show that the same patterns found in sight-feeding redshank and dunlin were largely repeated in sight-feeding curlew. The responses in both the mortality rate and in the proportion of birds failing to achieve their target masses were again step functions, even in the case of the simulations with environmental factors (Figures 48-51) and, once again, whether the interference was due to food depression or kleptoparasitism made little difference (Figures 46 and 47).

There were, however, two striking differences from the results with the other two smaller species. First, the step response occurred at much lower food/bird biomass ratios by falling in the range 15-20. As discussed below, this is simply a consequence of body size. Second, the asymptotic values in the proportion of birds failing to achieve their target mass were much higher than in redshank and dunlin, whether we used the very stringent 95% criterion (Figures 43-45) or the less stringent 75% criterion (Figures 46-51). This finding is less easy to understand and may suggest that, in the real world, curlew are able to consume more food than our model at present assumes, probably by feeding extensively over high water in fields around the estuary.

5.5   Effect of body size

The food/bird biomass ratio is equivalent to the total grams of consumable food per gram of bird per season. If the step had occurred at the same ratio in all three species investigated, it would have meant that a gram of dunlin required the same amount of energy as a gram of curlew. This in turn would have implied that energy requirements scale on a one-to-one basis with body size, eg a curlew needs 800/50 = 16 times as much energy as a dunlin. Whereas the Nagy, Girard and Brown (1999) equation used to calculate energy requirements in the model states that:

Energy requirement = 10.5 * body mass$^{0.681}$

so the increase in energy requirements with body mass is not linear. A large bird, like a curlew, therefore requires less energy *per unit mass* than a small one, such as a dunlin. This difference is increased even more by the lower critical temperature of the dunlin being so much higher than that of the curlew. Thus there is a genuine difference in the ratio required for birds of different sizes.

6. Results - disturbance

Disturbance simulations were carried out in a manner most likely to cover the range of conditions experienced by real birds. First, depression-based interference always occurred. Second, the environmental factors ranged from the most benign (upshore feeding allowed but with no decline in food AFDM over the winter) to the most demanding, in which either food mass declined by 50% or the ambient temperature was reduced on every day by 5°C. The final simulation included the simultaneous effect of all three environmental factors, so that upshore feeding was able to compensate for the decline in food mass and low ambient temperature. Not only are these conditions probably quite extreme compared with those experienced by most waders in most estuaries, but we used very high levels of disturbance compared with the real world. In the most extreme case, we assumed that the birds were prevented from using 50% of their main feeding grounds on low tides during daylight, on both neaps and spring tides. By way of comparison, on the Exe estuary, oystercatchers are prevented from using *circa* 10% and then only on spring tides (West *et al* submitted). On the other hand, the model does not yet not include the time and energy costs borne by birds when they are disturbed. It would be advisable in future modelling studies to include these, since they could increase the impact of disturbance on the birds.

6.1   Sight feeding redshank

Disturbance at all intensities had no effect on the proportion of birds starving or failing to achieve their target masses when the birds were allowed to feed upshore as the tide ebbed and flowed (Figure 52). Furthermore, there was a step responses at all levels of disturbance at a food/bird biomass ratio of 30-40. The birds were therefore able to compensate for the effects of disturbance in daylight by feeding for longer in the upshore areas as the tide ebbed and flowed and by feeding at night.

In contrast, increasing the intensity of disturbance did have an effect when the mass of individual food declined by 50% over the winter (Figure 53) and when the ambient temperature was decreased by 5°C (Figure 54). But again, in both cases, the response remained a clear step function.

When all three environmental factors were included together, the asymptotes in the mortality rate and in the proportion of birds failing to achieve their spring target masses increased as the intensity of disturbance increased (Figure 55). In these circumstances, the birds were not able completely to compensate for the disturbance by feeding upshore, as had been the case in the absence of disturbance (Figure 12). The clear step response to the changing food/bird biomass ratio was also replaced by a more gradual response but remained sufficiently clear-cut to be able to say that the asymptotes were reached in the range of food/bird biomass ratios of 25-50.

6.2   Touch-feeding redshank

Introducing increasing amounts of disturbance on daylight tides to simulations with the three environmental factors, separately and in combination, had the same effect in touch-feeders (Figures 56-59) as it had in sight-feeders (Figures 52-55). With only upshore feeding included, disturbance had no effect on the proportions of birds either starving or failing to achieve their target mass; birds were able to compensate for the disturbance by feeding for longer and by

feeding undisturbed at night. When the environmental conditions were made substantially worse by either reducing the food mass over the winter by 50% or by lowering the ambient temperature by 5°C on every day, interference increased the proportion of birds starving or failing to achieve their target mass across most of the range of the food/bird biomass ratio. However, once again, allowing the birds to feed upshore both reduced the impact of disturbance and also introduced more of a step function (Figure 59). However, the step change occurred over the high range of food/bird biomass ratios of 25-75.

6.3   Sight-feeding dunlin

With sight-feeding dunlin only able to feed over the six hours of the low tide period, increasing intensities of disturbance increased the asymptotic rates in both the proportion of birds starving and the proportion failing to achieve their target weights (Figure 60). But, as with sight-feeding redshank, disturbance at all intensities had no effect on the proportion of birds starving or failing to achieve their target masses when the birds were allowed to feed upshore as the tide ebbed ands flowed (Figure 61). With or without upshore feeding, there was a step responses at all levels of disturbance at a food/bird biomass ratio of 50-60. The birds were able to compensate for the effects of disturbance in daylight by feeding for longer in the upshore areas as the tide ebbed and flowed and by feeding at night.

In contrast, and again as in sight-feeding redshank, increasing the intensity of disturbance did have an effect when the mass of individual food declined by 50% over the winter (Figure 62) and when the ambient temperature was decreased by 5°C (Figure 63). But again, in both cases, the response remained a clear step function.

When all three environmental factors were included together, the asymptotes in the mortality rate and in the proportion of birds failing to achieve their spring target masses increased as the intensity of disturbance increased (Figure 64). In these circumstances, the birds were not able completely to compensate for the disturbance by feeding upshore, as had been the case in the absence of disturbance (Figure 60). In contrast to sight-feeding redshank, a clear step response to the changing food/bird biomass ratio was retained except at the very highest intensity of disturbance (50% of area disturbed) when a rather more gradual response occurred. Nonetheless, the phase of rapid change was sufficiently clear-cut to be able to say that the asymptotes were reached in the range of food/bird biomass ratios of 30-50.

Overall, the results for sight-feeding dunlin confirmed those for sight-feeding redshank, the main difference being in the values of the food/bird biomass ratios over which the asymptote was reached.

7. Results - habitat heterogeneity

7.1 Sight-feeding redshank

In the first scenario, the food supply was distributed equally amongst the five patches. As had been expected, this produced results that were identical to those obtained with a single patch (Figures 65-67). Gradually increasing the degree to which the food was aggregated at first caused the responses to changes in the food/bird biomass ratios to become more gradual or concave in shape (Figures 65-67). However, the response turned convex in the most extreme case in which much of the food was aggregated into a single patch. Indeed, the convex shape was so marked that, in effect, a step response had returned, although occurring at the much higher food/bird biomass ratio of 120-140. Furthermore, the curve now had two step responses at low food/bird biomass ratios.

These patterns remained the same with no environmental factors included (Figure 65) or with either a 50% decline in food AFDM (Figure 66) or the ambient temperature reduced by 5°C (Figure 67).

Increasing the aggregation of the food supply had these effects for the following reason. When the prey distribution was homogeneous (Figure 65, line **1**), birds depleted all the patches equally and fed on all of them throughout the winter. With the opposite, very heterogeneous, distribution (Figure 65, line **4**), prey biomass in the low-density patches at high food/bird biomass ratios was still large enough for these patches to be used all through the winter. However, as the food/bird biomass ratio dropped, there came a point at which all four low-density patches were depleted below the threshold before the end of winter and all the birds were forced to feed on the remaining high-density patch. This was equivalent to aggregating the birds by a factor of five and resulted in a similarly high mortality rate (*cf* Figure 8). With degrees of heterogeneity between these two extremes, lower-density patches were not all depleted below the threshold at once so that, as food/bird biomass ratio decreased, they were aggregated more gradually onto fewer patches. This led to the more gradual changes in mortality with intermediate degrees of heterogeneity. Indeed a number of small 'steps' can be seen in these lines as birds were forced to feed on progressively fewer patches, thus becoming more aggregated, as the food/bird biomass ratio declined.

7.2 Touch-feeding redshank

The same trends were found in touch-feeding redshank with the response changing from concave to convex as the degree to which the food was aggregated increased (Figures 68-70).

8. Results - oystercatchers and mussels on the Exe Estuary

Two simulations were run. In one, the food supply, including alternative food and spatial heterogeneity, and the general environmental conditions of exposure time, ambient temperature, the presence of supplementary feeding on upshore mudflats and in fields over high tide were included using real world parameter values (Stillman *et al* 2000). This is the 'real world' model whose predictions were tested in Figure 1. In the second simulation, 50% of the feeding areas were denied to the birds by disturbance on the intertidal feeding areas, but only during daylight.

The results reveal a concave function which reaches its asymptote in the region of a food/bird biomass ratio of 125-150 (Figure 71). Although the mean food/bird biomass over the 13 years in which it has been estimated on the Exe since 1976 was 180, the ratio did fall within the range of 125-150 on several occasions (Figure 72). All along the function, disturbance increased the proportion of birds starving but by only a small amount until the ratio fell well below 100 (Figure 71(a)). Disturbance had a much greater affect on the proportion of birds failing to achieve their spring target mass, even at the high ratios typical of the Exe at present (Figure 71(b)).

The small increase in mortality due either to a reduction in the food/bird biomass ratio or to disturbance should not be assumed to necessarily to have only a small impact on population size. The equilibrium population size of birds with low annual mortality rates is very sensitive to increases in mortality (Figure 73). Whether the density dependence in the summer is strong or weak, an increase in annual adult mortality rate from, for example, 4% to 6% causes the equilibrium population size to be substantially reduced. The reason is that, although an absolute percentage increase in mortality of 2% is small, it actually causes the annual mortality rate to increase by 50%, thus greatly reducing the equilibrium population size at which birth and death rates are, on average, equal.

The real world 'concave' case of the oystercatcher illustrates that, in one species at least, the real-world values of the factors which prevent functions from being step responses combine to produce a rather gradual concave function such that, even at very high food/bird biomass ratios, an asymptote is only just being reached. This means that, even though the present-day food/bird biomass ratio is high, a decrease in the amount of food per bird would lead in some years to a slight increase in winter mortality. We cannot therefore assume that a high present-day food/bird biomass ratio implies that reductions in the food supply, or increases in disturbance, would have no effect on population size. This situation arises because the present-day mortality is density-dependent, as is shown in Figure 1. As always in matters of coastal wintering bird population management, the key issue is whether the present-day starvation and rates of mass gain are density-dependent or would become so in the circumstances being explored. As both rates in oystercatchers are already density-dependent, reducing the quantity of food *per capita* causes both rates to increase.

In order to devise an SPA monitoring scheme, we first need to find out in a greater number of species the values of the parameters which determine (i) whether step functions are likely to occur and (ii) whether the population is currently subject to density dependence in the non-breeding season. We believe that this can be done, mainly by review of existing information and some further modelling of some particular systems.

9. Results - summary of main conclusions

The question addressed by this report is how to monitor the food biomass density and levels of disturbance in an SPA in such a way that one can demonstrate that the quality of the habitat is being maintained at a sufficiently high standard to support the bird populations for which the estuary was designated as an SPA.

The objective of non-breeding shorebird conservation policy is to maintain present bird abundance. Therefore the best measure of habitat quality is one which, either directly or indirectly, determines these demographic rates. For migratory shorebirds during the non-breeding season, this means that habitat quality should be measured in terms of its effect on two quantities. First, the fat reserve levels needed to fuel spring migration and, in spring also to breed successfully after the birds have reached the breeding grounds. Second, the starvation rates during the non-breeding season, perhaps especially during severe winter weather. If one can show that the feeding conditions in the SPA are sufficient to maintain the present-day rates of fat storage and survival at the current population size and in the current climatic conditions, then one will know that the quality of the SPA is being maintained at a level sufficient to achieve the goal for which that SPA was set up.

In this Report we explore the idea that the ratio between the biomass density of the main food and the biomass density of the birds in autumn can, in principle, reliably predict whether the current foods stocks are sufficient to maintain the current rates of survival and fat storage in the SPA. It also explores how the ratio needed to do this is affected by disturbance and habitat heterogeneity. To state the idea in its simplest form, a certain minimum amount of food per bird in autumn must be required to maintain the current survival rate and body condition in spring; if there was not enough food per bird in autumn, the food stocks would run out and birds would either die or leave the SPA before spring. We explore here whether it might be possible, in principle, to use a limited number of values of such a ratio to assess habitat quality across a range of species, estuaries and climatic conditions.

The ratio would provide the easiest guide to monitoring if, in response to a decrease in the ratio, there were to be a 'step response' increase in the proportion of birds starving and/or failing to attain their target mass in spring. That is, below this ratio, many birds would fail whereas, above it, most would succeed and the proportion doing so would fluctuate without trend as the ratio increased still further. We therefore explored by modelling (i) whether step responses were likely to occur generally in waders and wildfowl wintering and on passage on British estuaries, and (ii) whether a small number of ratios, selected according to a limited range of natural history characteristics of the birds, can be used as a reliable 'rule of thumb' to assess habitat quality.

The system characteristics that were varied across simulations were: (i) carnivory and herbivory; (ii) degree of individual variation in competitive ability, defined in terms of both foraging efficiency and susceptibility to interference; (iii) shape of functional response, (iv) the presence of supplementary feeding opportunities upshore of the main low water feeding areas, (v) overwinter decreases in food abundance due to factors other than depletion by the birds themselves, (vi) winter climate, (vii) food size, and (viii) preference of the bird for the food organism in question. These are the main factors that determine how food abundance affects the body condition and mortality rates of these birds.

The most extensive range of simulations were carried out using a typical, medium-sized wader that detected its food either by sight or by touch; we had the redshank in mind. But in order to explore the effect of bird body size, simulations were also run for comparison on a small and a large sight-feeding wader; we had dunlin and curlew in mind.

In sight-feeding birds of all body sizes, most simulations showed that, once the food/bird biomass ratio had risen to a certain value, the mortality rate and proportion of birds failing to reach target mass fell to an asymptotic low level. In fact, both quantities dropped very suddenly from 100% to the asymptotic rate, and so followed a 'step response'. This step function is due to the fact that the gradient of the functional response in sight-feeding waders was assumed to be very steep, as all the empirical evidence suggests that it is. This means that most birds starve more-or-less at the same point as food becomes depleted during the course of the winter, so that individual differences in performance exert only a small effect. Thus, even though individuals in the model - as in the real world - vary greatly in foraging performance, the system has all the characteristics of scramble competition, and thus the step response to changes in the feeding conditions that is the characteristic of such systems.

The simulations showed that the step change in the proportion of birds starving and failing to reach target mass was often replaced by a more gradual response when the absolute biomass densities of both the food and the birds were low. The reasons for this are discussed. This important result means, however, that in order to fully evaluate the ratio approach, it will be important to establish first whether food biomass to bird biomass ratios in real SPAs are generally high or generally low. In the absence of this information, we assumed for the remainder of this report that SPAs have generally high biomasses of both birds and food. Our reasoning was that, as SPAs are selected because they support high numbers and perhaps densities of birds, and since this can only happen where food abundance is high, these sites are likely to have high biomass densities of both birds and food.

Features of the natural history of a species that made it more difficult for the birds to acquire their daily energy requirements, such as interference and harsh weather, raised the absolute level of the asymptotes, of course: more starved and fewer reached their target mass when conditions were harsh. However, most of the natural history characteristics that were investigated did not affect whether or not a step function was obtained in sight-feeding birds. These characteristics were: the amount of individual variation in foraging efficiency; whether interference was caused by food depression or kleptoparasitism; the extent to which interference was intensified by the birds aggregating while feeding; food size and the inclusion of three realistic, although in two cases rather harsh, environmental factors either singly or in combination. Step responses were therefore a very robust features of the simulations with sight-feeding birds. For such birds, therefore, the ratio approach does seem to provide, in principle, a very promising approach to monitoring the quality of an SPA.

In sight-feeding birds, the ratio of food biomass to bird biomass at which the step response occurred was affected by only a limited number of factors. These were: the degree to which birds aggregated while feeding, and thus the intensity of interference; food size; and bird size. The lowest ratios occurred with small food, high levels of interference and in large-sized birds. The reasons for these trends are discussed. For example, the ratio decreases with bird body size because the energy required per gram of bird decreases as body size increases.

Simulations with touch-feeding redshank suggested that step functions occurred over a much more limited range of conditions in these birds than in sight-feeders. In fact, gradual decreases in the proportion of birds starving or failing to reach their target mass as the food/bird biomass ratio increased were the rule rather than the exception in this case. This difference from sight-feeders arose because of the differences between their functional responses. The higher asymptote of the functional response of touch-feeders allowed more birds to survive and maintain their mass when food was abundant. But as the amount of food per bird in autumn was decreased, so that food became more rapidly depleted during the winter, the gradual gradient of the functional response of the touch-feeders allowed individual variations in foraging performance to be expressed so that birds no longer starved *en masse*. Contest competition was expressed with the result that some birds starved well before others, which led to a gradual response rather than to a step response.

Nonetheless, a very interesting and promising case of a step function occurring in a touch-feeder was discovered. Although occurring at higher food/bird biomass ratios than in sight-feeders, step changes did occur in touch-feeding redshank when they were able to supplement their food consumption at low water by feeding upshore as the tide ebbed and flowed. This arose because, even in the harsh environmental conditions that were modelled, upshore feeding provided time for failing birds to make up for their poor performance over low tide. By allowing the poorer performers to make up their deficit as the tide ebbed and flowed, upshore feeding reduced the variation in performance between individuals over the tidal cycle as a whole and thus prevented the full effects of contest competition from being expressed. This important result suggests that, when evaluating the use of the ratio approach, the opportunities available to birds for supplementing their food consumption when their main low tide feeding grounds are unavailable will have to be taken into account. Since the opportunities do seem to be widespread in British estuaries, it seems likely that the ratio approach will also be applicable to birds, such as touch-feeders, whose functional response has a shallow gradient.

The results of the simulations in the report confirm that the presence of upshore feeding areas can be very important for maintaining shorebird survival rates and body condition, as indeed can supplementary feeding over high tide in brackish and terrestrial habitats. In long estuaries, such as the Humber, the difference in the timing of high tide at different points along the estuary means that birds that at low tide feed in the areas that are covered first by the advancing tide can continue foraging upstream in areas that are covered much later. This greatly extends the time available for foraging and probably plays an important role in their survival. In shorter estuaries, this opportunity can only be provided by high level flats, which have sometimes been removed by land-claim *etc*, and by brackish and terrestrial habitats above the high water mark. It would be worthwhile to conduct a desk survey of SPAs to identify those in which upshore and terrestrial feeding opportunities do not appear to occur. Some back-up field visits might also prove to be desirable.

One word of caution is necessary here, however. Often the shorebirds that are most vulnerable to attack by land-based raptors are the poor performers foraging near the marsh edge as the tide ebbs and flows. In estuaries where the predation risk is high, the difference in survival chances between good and poor competitors would again be re-stored. This, in effect, might allow contest competition to be re-introduced. The result of this would be that the effect of changes in the food/bird biomass ratio on the proportion of birds dying (rather than starving) might revert to being more gradual and less of a step-function. To test this idea, we recommend that simulations be run using a version of the model that includes raptor predation.

While this report was being written, new evidence arose which suggested that the gradient, B, of the functional response in touch-feeders is more similar than previously thought to the steep gradients found in sight-feeders. In our simulations in this Report, we used for the gradient a value of 8.8346 for touch-feeding redshank, which is considerably larger than the value of 0.2512 used for sight-feeding redshank. This value was based on an unpublished survey of the limited number of estimates of B that were available. Most of these estimates were for sight-feeders, and only three were available from touch-feeders. Of these three, one was based on a very small sample size and the other on data that may have been biased. In February 2001, we obtained three further estimates of B for touch-feeding birds; two for black-tailed godwits eating bivalve molluscs (J Gill, personal communication) and one for knot eating cockles (M G Yates, personal communication). These three estimates were based on very good data sets, and all fall in the range of 2-3. If such low values prove on subsequent research to be more typical of touch-feeding waders than the very high value we used for touch-feeding redshank in our simulations, the ratio approach may be much easier to apply. It would mean that the change in the proportions of birds starving and failing to achieve their target mass as the bird/food biomass ratio increases might more frequently approach a step function.

The effect of disturbance was explored in simulations with both sight-feeding and touch-feeding redshank. Increasing the intensity of disturbance up to the point at which 50% of the feeding grounds were disturbed, and thus unavailable to the birds, during daylight on every day of the winter only affected the proportions of birds dying and failing to achieve their target mass when the environmental conditions were harsh, so that the birds were already hard-pressed. However, the step response was maintained in sight-feeding birds, but not in touch-feeders.

Distributing the food biomass across several patches, with increasing heterogeneity in its allocation amongst patches, at first caused the step response to be replaced by a more gradual, concave response, which occurred at higher food/bird biomass ratios. At a given quantity of food on an estuary, a higher food/bird biomass ratio is required the more unequally the food supply is aggregated into patches. At very high levels of aggregation, however, the concave response was replaced by a step function, but this occurred at very high food/bird biomass ratios indeed. These simulations showed that the degree to which the food supply is aggregated has a great influence on both the shape of the response and on the value of the food/bird biomass ratio at which the asymptote is reached. In further evaluating the ratio approach, it will therefore be very important to establish the degree to which food supplies are generally aggregated in SPAs.

The real world 'concave' case of the oystercatcher illustrates that, in one species at least, the real-world values of the factors which prevent functions from being step responses combine to produce a rather gradual concave function such that, even at very high food/bird biomass ratios, an asymptote is only just being reached. This means that, even though the present-day food/bird biomass ratio is high, a decrease would lead to a slight increase in winter mortality. We cannot therefore assume that a high present-day food/bird biomass ratio implies that reductions in the food supply, or increases in disturbance, would have no effect on population size. This situation arises because the present-day mortality is density-dependent, as is shown in Figure 1. As always in matters of coastal wintering bird population management, the key issue is whether the present-day starvation and rates of mass gain are density-dependent or would become so in the circumstances being explored. As both rates in oystercatchers are

already density-dependent, reducing the quantity of food *per capita* causes both rates to increase.

In order to devise an SPA monitoring scheme, we first need to find out in a greater number of species the values of the parameters which determine (i) whether step functions are likely to occur and (ii) whether the population is currently subject to density dependence in the non-breeding season. We believe that this can be done, mainly by review of existing information and some limited further modelling of some particular systems.

10. Evaluation of the ratio concept as a monitoring device

10.1 Step function responses

The results suggest that, as the biomass of food available per bird in autumn increases, there is a step function change in the proportion of sight-feeding birds that either starve or fail to achieve their spring target mass. The step responses remained even in the presence of disturbance but not when the habitat was assumed to be very heterogeneous. For these birds, therefore, whether the ratio approach would provide a very promising method for evaluating the quality of an SPA depends in part on the extent to which the food supplies in estuaries are aggregated. With this *proviso*, the results suggest that it should be possible to define a ratio above which the survival and need to store a certain amount of body reserves by spring would be ensured.

A step response was generally not found in touch-feeding birds, however, even when the food supply was not unequally distributed amongst several patches. The notable exception was when the birds were able to supplement their consumption over low water by feeding upshore as the tide ebbed and flowed. The step response occurred, and at quite a low ratio, even though the birds were only allowed an extra 1.5 hours of feeding either side of the low water period. In nature, many waders also supplement their consumption by feeding in fields over high water. Therefore, the opportunity to minimise the difference in performance between individuals, and thus to introduce step change, is even greater in nature than was assumed in the models. Furthermore, very recent evidence suggests that the gradients of the functional responses used in the simulations for touch-feeding birds were probably too shallow. As this was the cause of the infrequent occurrence of step responses in touch-feeding birds, it seems likely that our simulation procedure was too pessimistic. This does strongly suggest that the ratio approach may well be easier to apply to touch-feeding birds than some of the results in this report might suggest.

These conclusions do depend critically, however, on the scaling in the ratios that were used in the simulations. We used as our maximum a ratio of 200. That is, we assumed that in autumn, there was up to 200 g of food biomass for every 1g of bird biomass. This value was derived from our work on oystercatchers and mussels on the Exe estuary. The responses were step functions only because this high ratio was used as the extreme. Had we used a much narrower range of ratios, ones that fell in the region of the step response, the curves would have looked much more gradual because of the reduced scale along the x-axis.

The oystercatcher-mussel system is a very rich system, and may not be typical of all species in all SPAs. We must therefore caution that, before a final evaluation of the ratio approach can be made, research should be carried out on the values of the real ratios that apply to a range of species in British SPAs.

10.2 Level of the Asymptote

To apply the ratio approach in the real world, it will be important to ensure that the predicted rates of mortality and fat storage failure match those occurring under current conditions in the SPA in question. This means that, in order to apply the ratio approach, one would need to know the present-day values for the proportions of birds that starve in winter or fail to achieve

their target mass by spring, because these are the targets that SPA policy should aim to maintain.

The simulations showed that a variety of factors affect the level of the asymptotes. In general, and as would be expected, the asymptotes rose higher as (i) the rates of energy intake of the birds were decreased through disturbance, intensifying interference and reducing food energy content, or (ii) the demands of the birds for energy increased, through reduced ambient temperature.

These findings mean that some details of the species ecology in the SPA will need to be known were the method to be applied to managing SPAs. One not mentioned so far is the overwinter decrease, and spring increase, in the biomass of food organisms due to factors other than the birds themselves. In waders, for example, this includes losses in food due to gales and other predators, such as fish and the growth of food in spring. These requirements for additional data are not a major constraint, however, since so much is known about the ecology of waders already. A literature review, supplemented by direct approaches to scientists throughout Europe, would be able to fill many of the present gaps. It is the ready availability of so much information on waders, after all, that is the reason that the models discussed here are able to be applied so widely at the present time to many species and systems across Europe.

10.3 Wildfowl

Although the simulations conducted here include the main natural history characteristics of wildfowl ecology, we do not know whether, in general, wildfowl have functional responses with steep or shallow gradients. Our 'from the literature' impression is that they are often steep, as in sight-feeding waders and - in the light of recent findings - perhaps in touch-feeding waders too. In order to investigate the applicability of the ratio method to wildfowl, we suggest that a review be conducted of the critical functions in wildfowl ecology that are required for the model.

10.4 Designing a monitoring programme

10.4.1 Birds

The purpose of the approach is to test whether a given ratio of food/bird biomass will maintain the current levels of the demographic rates for overwinter starvation and fat storage in spring. It would therefore be advisable to review the evidence on both these topics so that the targets for SPAs can be firmly established. In addition, the models often need calibrating and the easiest way in which to do this is by comparing the model's predictions for the average numbers of hours spent feeding by birds on daylight tidal cycles. Since there is a substantial amount of data on this, it would be useful to review the information available to check that the models produce realistic predictions on how long birds in SPAs take to obtain their daylight food requirements.

10.4.2 Food supplies

We had hoped that the degree of aggregation would have rather little effect on both the shape of the response and the value of the food/bird biomass ratio at which the asymptote in the

proportion of birds starving and failing to achieve their target masses occurred. But this proved not to be the case. Rather, an increasing degree of food aggregation changed the shape of the response from a step-function, through a more gradual concave function and then back to a step function, with the step occurring at a much higher food/bird biomass ratio. This means that the sampling scheme of the food supplies will have to take the spatial variation in the initial stocks into account. Should the ratio approach be adopted, this finding suggests that the samples should be placed on a grid so that the spatial arrangement of the food can be established.

In applying the ratio approach, it would be necessary to establish the main food species of the birds in question. But then any approach that monitored the food supply rather than some aspect of the birds themselves, such as their stress levels, would require some knowledge of the foods that the birds consume. In practice, this is very easy information to obtain. The food species that are present in the SPA would be known from the survey of the food supplies. So much is known about the diet of estuarine birds that one could normally predict from that survey information the identity of the main food species of each bird species. In cases of doubt, direct observation or faecal analysis can often establish very quickly whether a particular food species is being eaten in that particular site. But this would seldom be necessary. The model would only need to identify as food the species that are known to be eaten by the bird in question, even if a particular food species was not being eaten in that particular SPA at the particular time it was being monitored. For example, given a choice between *Corophium* and *Nereis*, redshank take *Corophium*. So one might find that only this species is currently being consumed by redshank in an SPA. But a proper evaluation of the state of the SPA would also include *Nereis* as the prey to which redshank would turn in the event of *Corophium* being eaten out or washed away by a gale. And so on through *Hydrobia*, *Macoma etc*. So much is known about the diets of these birds that it should be possible easily in any one SPA to identify the main species of known food and to include them as food supplies in the model. Although the simulations in the present report deal only with rather simple two-prey choices, 'real world' models have already been set up with as many prey species included as are necessary for the estuary in question. Furthermore, the effect that competitor bird species have on each other's food supply is also included. For example, many species of waders eat *Nereis* and the size ranged consumed overlaps between bird species. So the *Nereis* eaten by an oystercatcher cannot later be eaten by a curlew. The real-world model include this inter-species depletion effect.

10.4.3 What would need to be monitored

If a 'rule of thumb' ratio can be identified, one would only need to monitor food/bird biomass ratio in the years that monitoring is required. The main requirement then would be to measure the food supply in the autumn, probably using a grid scheme and sampling techniques of the kinds that are widely used already. This would give the necessary information on the food supplies at all shore levels, prey size and the food/bird biomass ratio itself. Some determination of the frequency and intensity of disturbance would also be necessary, although this could be restricted to certain critical times of the non-breeding season when birds are under most stress; *eg* late winter. Information on the presence or absence of raptors, if it proves to be necessary, and on the extent to which birds use terrestrial habitats should be available from local ornithologists.

If, instead of a rule of thumb, a model of the particular estuary has to be built, the same information would be required. Most of the parameters in the models are already available, or should be available, in the literature. For example, quite apart from the several oystercatcher-shellfish systems that we are modelling in France, Wales and Ireland, we are currently building estuary-specific models for all the common wader species that overwinter on the Humber and Seine estuaries, and further estuaries are under discussion. We can do this because so many of the parameters are already known from the three decades of research that has now been conducted on these animals and their food organisms.

The main requirement would therefore be for a survey of the food supplies carried out at the frequency determined by legislation (every 6 years). Depending on the size of the estuary, a full survey might require up to 12 person-months. However, after the first 'baseline' survey had been completed, it should be possible to design a monitoring programme that only samples representative parts of the estuary, and so save expenditure.

In some cases, recent work may already provide the baseline survey required. For example, CEH will sample all the macro-invertebrates of the whole Exe estuary in autumn 2001 as part of a contract for the European Community and has very recently surveyed the Wash. Once the baseline survey has been made, suitable more limited surveys might already be being conducted by other authorities, such as the Environment Agency. If so, these might provide much or all of the data required to monitor the estuary at a reduced intensity until it was felt that another more extensive survey might be desirable.

10.5 Conclusion

We conclude that, depending on the present-day ratios between food and bird biomasses in SPAs, and on the degree to which the food supply there is aggregated, there are reasons to believe that the ratio approach could, in principle, be used to monitor the quality of SPAs, even in touch-feeding birds. However, before recommending that this is done in practice, we would stress the importance of (i) first finding out the values of the ratios that apply in SPAs at the present time and establishing the spatial aggregation of the main food supplies, (ii) establishing the present-day values of the proportions of birds that starve or fail to achieve their spring target mass - which are the targets that policy should aim to maintain - and (iii) describing some aspects of the ecology and behaviour of some species, particularly touch-feeding waders and wildfowl.

The next step of the evaluation of the ratio approach should be (a) to undertake a review of the magnitude of certain parameter values in the real world, and (b) to apply the approach to more real-world examples, as has been done in this Report with the oystercatchers of the Exe estuary. In order to devise an SPA monitoring scheme, we first need to find out in a greater number of species the values of the parameters which determine (i) whether step functions are likely to occur and (ii) whether the population is currently subject to density dependence in the non-breeding season. We believe that this can be done, mainly by review of existing information and some limited further modelling of some particular systems.

The simulations in this Report have identified the conditions that will determine whether step responses to changes in the food/bird biomass ratio are likely to occur and whether the population is currently subject to density dependence in the non-breeding season. Step-functions are likely to occur when (i) the gradient of the functional response is steep; (ii) when

there is a high biomass of both food organisms and birds, and (iii) when the food supply is spread rather homogeneously over the estuary or concentrated mainly in one part of it. In these circumstances, step functions occur irrespective (a) of the magnitude of the individual variation in foraging efficiency; (b) of the means by which interference is produced and the extent to which its effects are exacerbated by birds aggregating in parts of their feeding area; (c) of the size of food items, and (d) of the presence of upshore-feeding, severe decreases in the value of individual food items or severe weather. Conversely, concave responses are likely to occur (i) when the gradient of the functional response is shallow; (ii) when the biomass densities of both the food organisms and of the bird are low; (iii) when the food supply is unevenly distributed over the estuary, and (iv) when birds have opportunities to supplement their consumption in upshore areas in the intertidal zones or in terrestrial habitats over high tide. As much of the information needed to establish whether these conditions apply generally is already available in the literature and in unpublished reports, one could go a long way to establishing the real-world values of these crucial parameters without further immediate fieldwork. However, given the crucial importance of the gradient of the functional response and the relative scarcity of information of its value in a range of species, further fieldwork on this would be desirable immediately - although much is in progress already.

Reviews on these topics would also help to inform us as to whether present-day wintering populations lie within the range of food/bird biomass ratios in which density dependence occurs; *ie*. within the region of the 'response', whether it is a step response or a concave response. Whether this is the case will depend simply on the values of the parameters detailed above and so should become more apparent after the proposed reviews have been carried out.

A key issue is to what extent we can rely on general values for model parameters applicable to most sites. This will influence how much fieldwork will be required at the individual site level in order to set parameters. For example - can we establish a general 'rule of thumb' ratio of prey biomass to bird biomass applicable to most SPAs, or will the ratio be so variable that we will need to carry out field work to establish ratios on each SPA?

In view of this, we should perhaps reiterate that the purpose of the present research is to see whether step responses are likely to be widespread in coastal waders and wildfowl. If they are, the task of deciding whether the ratio recorded on an SPA is adequate for maintaining the present demographic rates would be made more simple. But if step functions do not prove to be the rule, the models described in this report can still be used for determining the target ratio needed in a particular SPA. In these circumstances, the ratio would need to be determined on a site-by-site and species-by-species basis. This would be less convenient than using a small number of universally applicable ratios, but would nonetheless be perfectly feasible.

11. Recommendations for further research

In conclusion, we recommend that the next steps in evaluating the ratio approach should be literature research and some new field work to better estimate the parameters that have been identified by this study as having an important influence on whether a step response occurs. The specific research topics to address are listed below. The source of much of the information would be a review of the literature and of unpublished reports of which we think there might be many. It will also often be necessary to contact the authors concerned to elucidate methods and parameters and to acquire unpublished data. Although it is very difficult to anticipate, an approximate guide is also given to the likely maximum amount of time that would be required to conduct the work by one person:

- Review of the ratio of food biomass to bird biomass in major British estuaries [Desk work: 3 months].

- Review of the degree to which the main food supplies are aggregated in the major British estuaries [Desk work: 3 months].

- Literature search and fieldwork on the gradient of the functional response in touch-feeding waders. [Desk work and fieldwork: 9 months].

- Review of functional responses in wildfowl. [Desk work: one month].

- Review of extent to which interference is likely to occur in waders and wildfowl. [Desk work: one month].

- Review of the size of food taken by touch-feeding waders. [Desk work: 1 month].

- Review of the intake rates of waders in upshore and terrestrial supplementary habitats. [Desk work: one month].

- Review of the occurrence of upshore and terrestrial feeding opportunities in SPAs. [Desk work and site visits: 3 months].

- Review of the numbers of hours spent feeding by waders on daylight tides in a sample of estuaries. [Desk work: 3 months].

- Review the reduction in overwinter supplies due to causes (eg gales) and species (eg fish, gulls, crabs) other than waders and wildfowl, and of losses due to human activities, such as bait-digging and commercial shellfishing. [Desk work: 3 months].

- Include in the model the time and energy costs of moving when birds are disturbed. [Modelling work: one month].

- Add raptor predation to the model and explore its effect on the ratios approach. [Modelling work: one month].

- Review of mortality rates and spring body masses in waders and wildfowl. [Desk work: 3 months. Ideally, the BTO would be contracted to estimate winter mortality rates from their ringing data. Perhaps JNCC would be prepared to fund such work].

- Apply the ratio approach to further real bird populations, as was done here with oystercatchers on the Exe. [Modelling work: 6 months].

The total amount of time is thought unlikely to exceed 39 person-months. However, some of the work may be conducted under other contracts and any work shared with EN would also be shared-cost.

12. Acknowledgements

13. References

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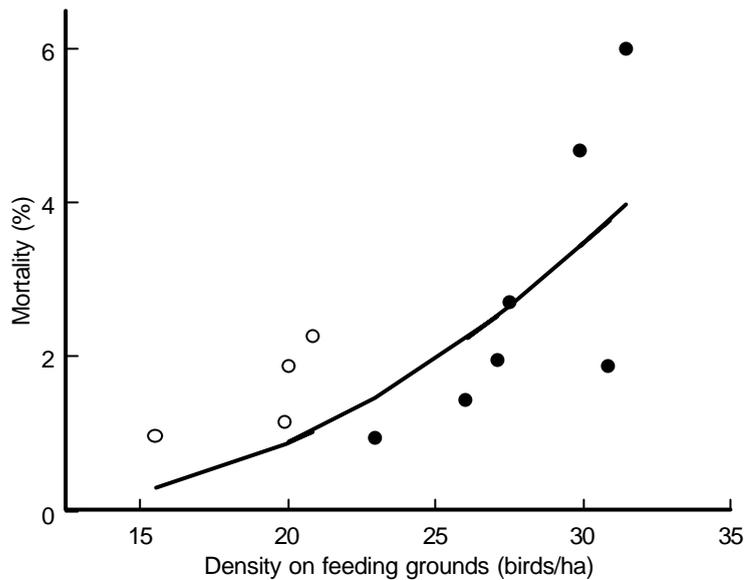
Figure 1 Predicted and observed rates of overwinter mortality from starvation in oystercatchers that eat mussels on the Exe estuary. Symbols show the observed rates for each of the 11 winters for which data are available. The model predicted rates are shown as a curve through the predicted values for the same 11 years.

Rates are plotted against the density of the birds on the feeding grounds over the winter. Open symbols refer to the four years for which the model was calibrated. Closed symbols refer to the seven subsequent years when mortality rates were predicted from the abundance of the birds and their food supply present in each year. Two-thirds of the discrepancy between the model predicted rates and the observed rates in those seven years is accounted for by annual variations in the winter climate that were not included in the model (Durell *et al* in press). Observed rates exclude deaths caused by accidents. No birds were killed by predators.

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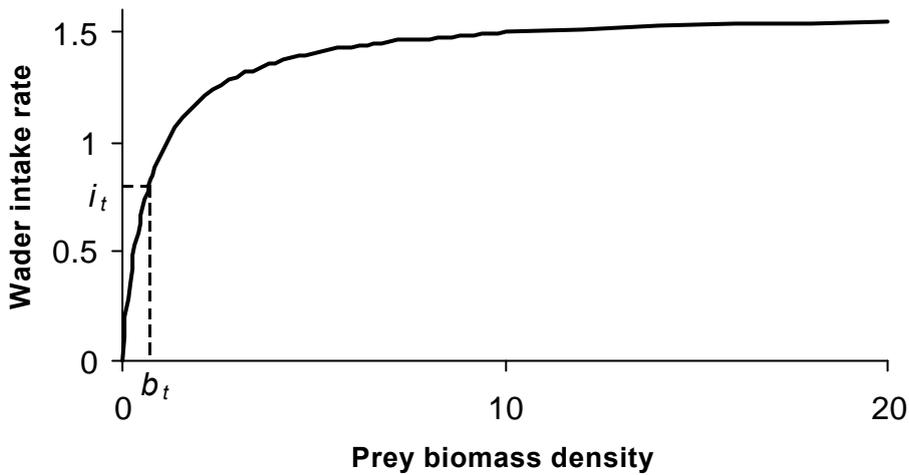
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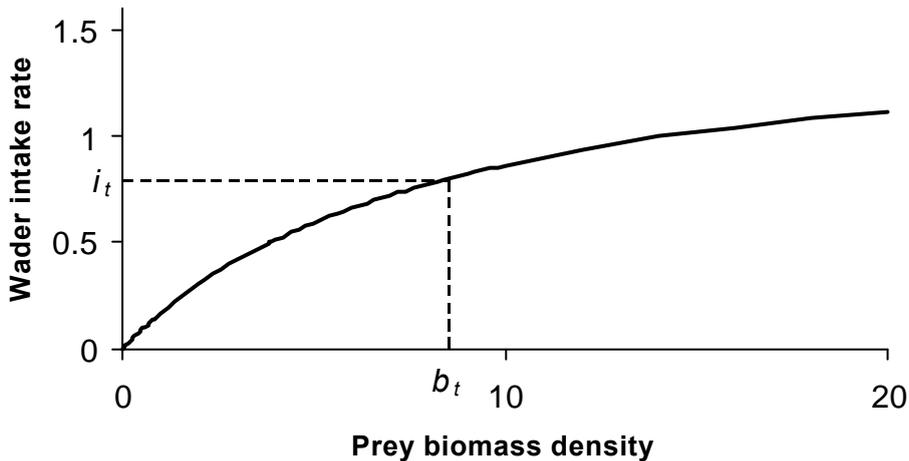
Figure 2 The two kinds of functional responses used in the model. (a) The response typical of visually-hunting waders, with a gradient (*B*) of 0.02 (dunlin), 0.25 (redshank) and 1.63 (curlew). (b) The response of a touch-hunting wader, with a gradient of 8.84 used for redshank. The 'threshold intake rate' (i_t), and the associated 'threshold prey biomass' (b_t), required by an individual of average efficiency to obtain its daily energy requirements in the time available for foraging is also shown. The threshold will vary according to factors that affect the energy requirements, such as the ambient temperature, and the time available for feeding, such as the neaps-springs cycle.

These values of the gradient *B* mean that, in the case of visually-hunting birds, the intake rate increases half way to its asymptotic value, *A*, as the prey biomass increases from 0 to 1 gAFDM/m^2 whereas, in touch-feeders, this does not happen until the prey biomass reaches 8.5 gAFDM/m^2.
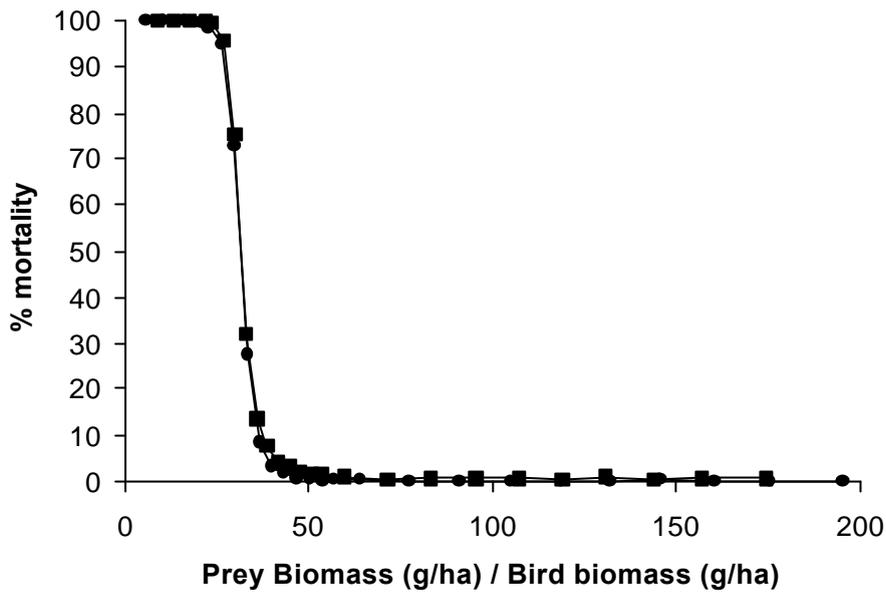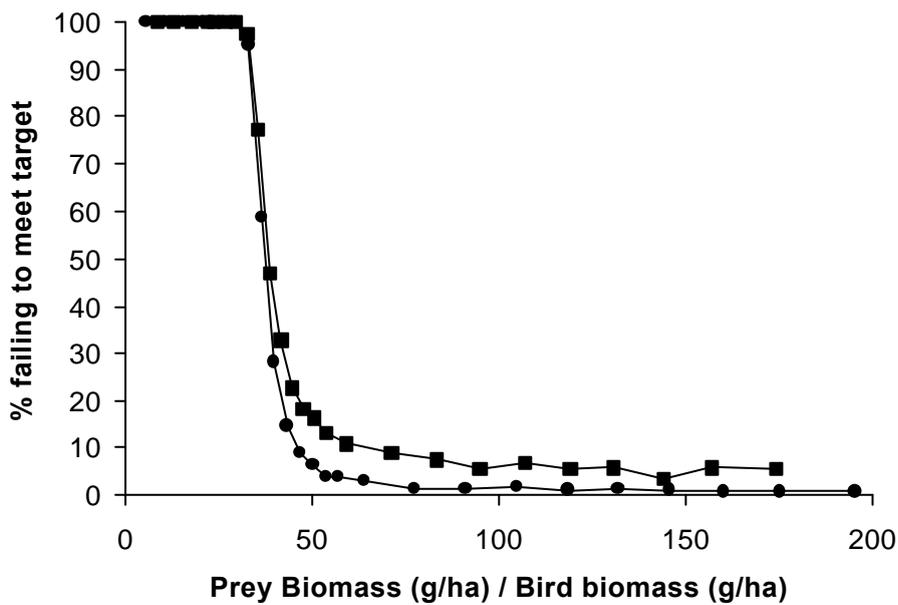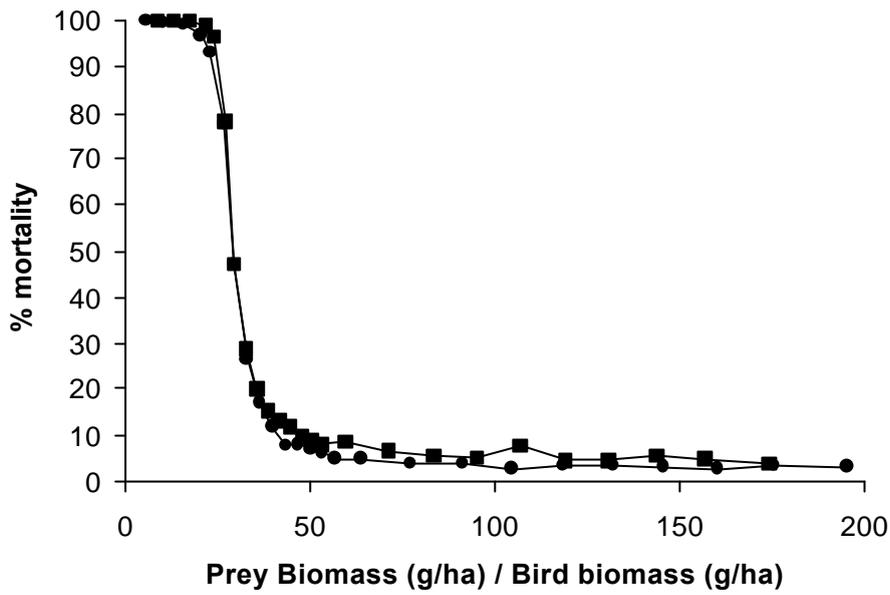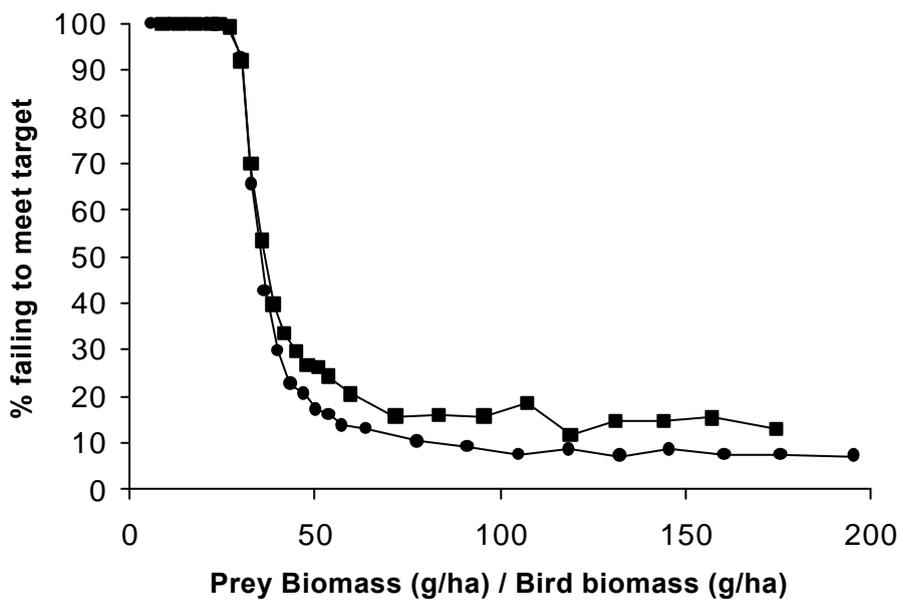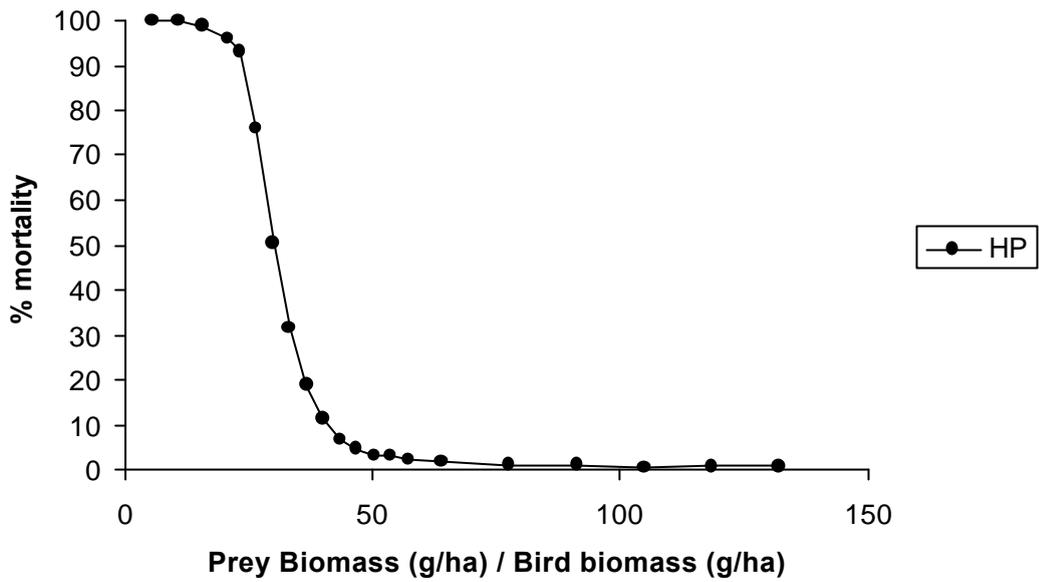
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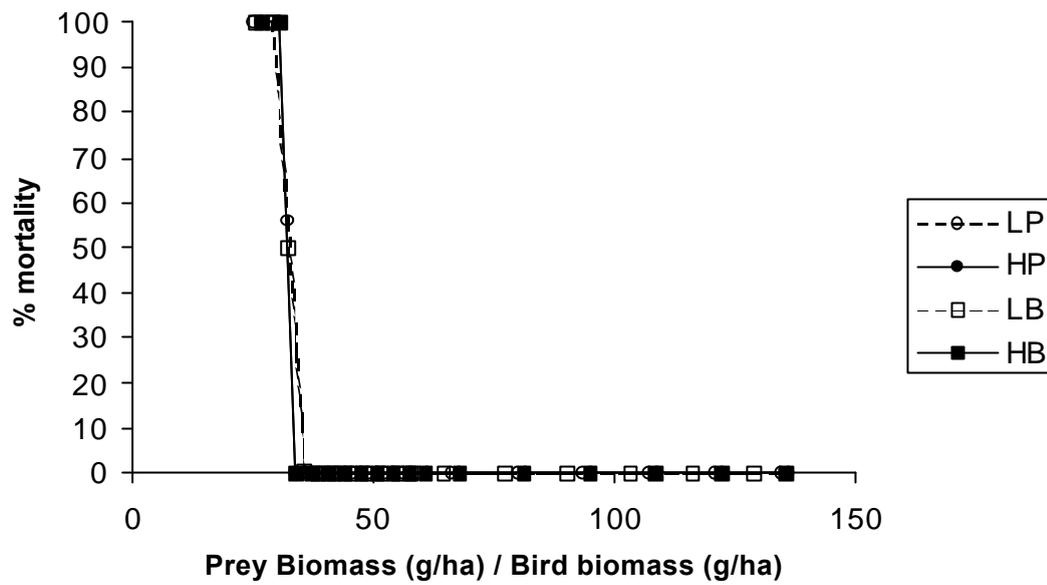
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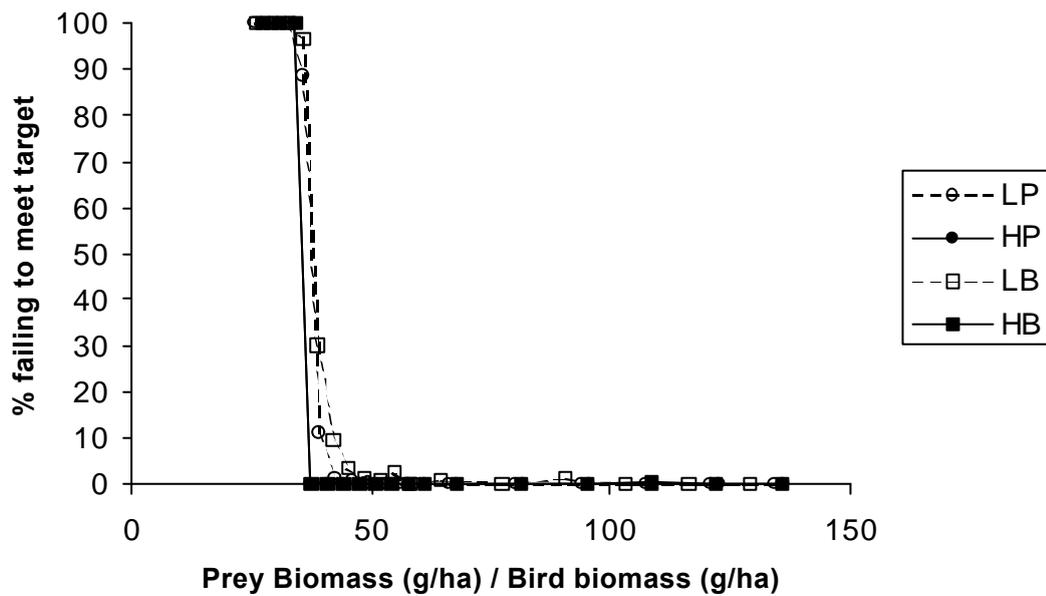
Figure 3 Percent mortality (a) and percent failing to reach 95% of target weight (b) for sight-feeding redshank, with 5% variation in feeding efficiency and no interference.

LP = both bird and prey biomass low, with prey biomass varied; **LB** = both bird and prey biomass low, with bird biomass varied; **HP** = both bird and prey biomass high, with prey biomass varied; **HB** = both bird and prey biomass high, with bird biomass varied.
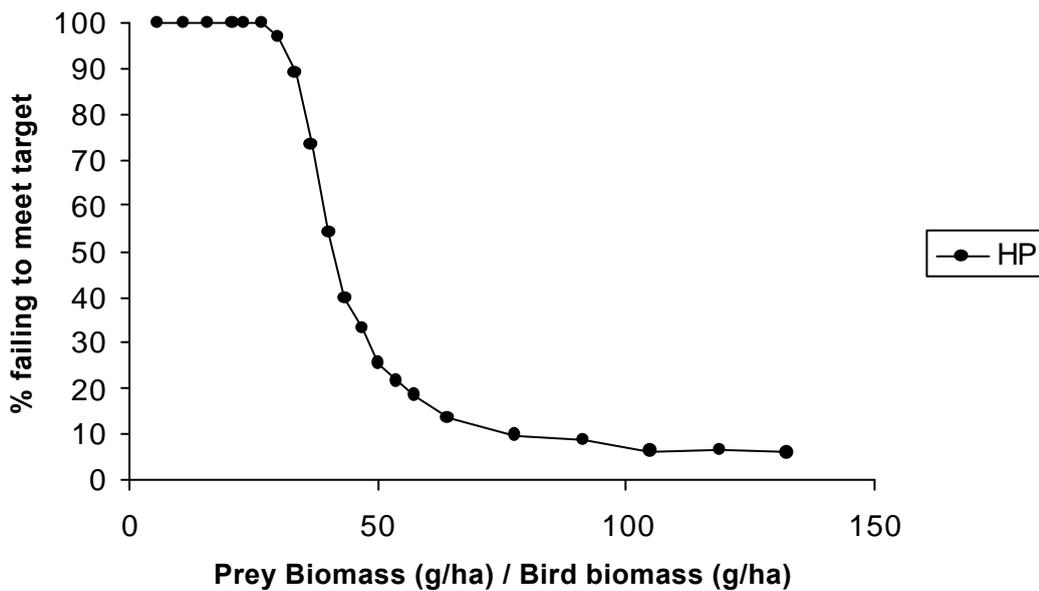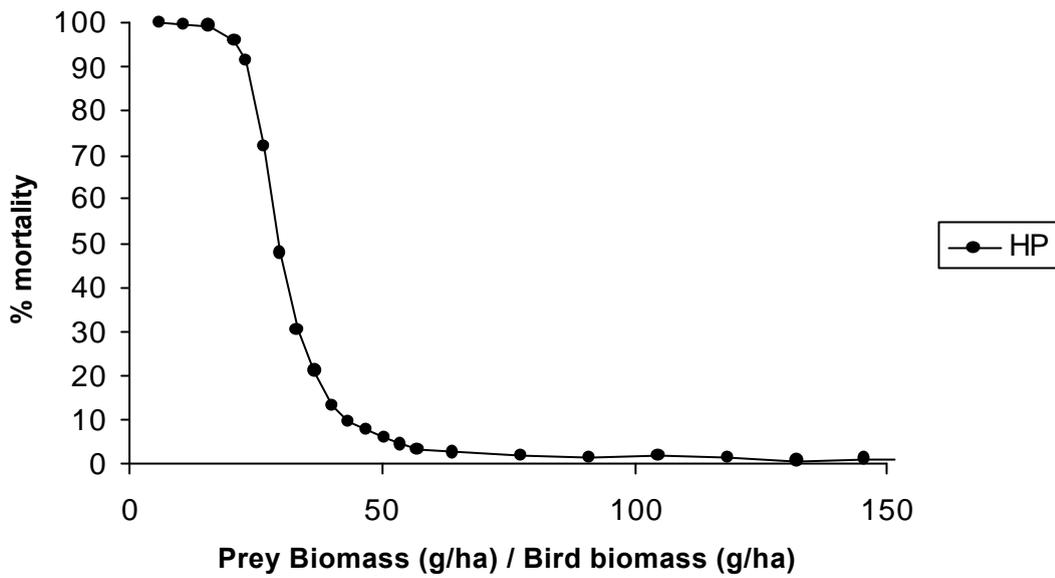
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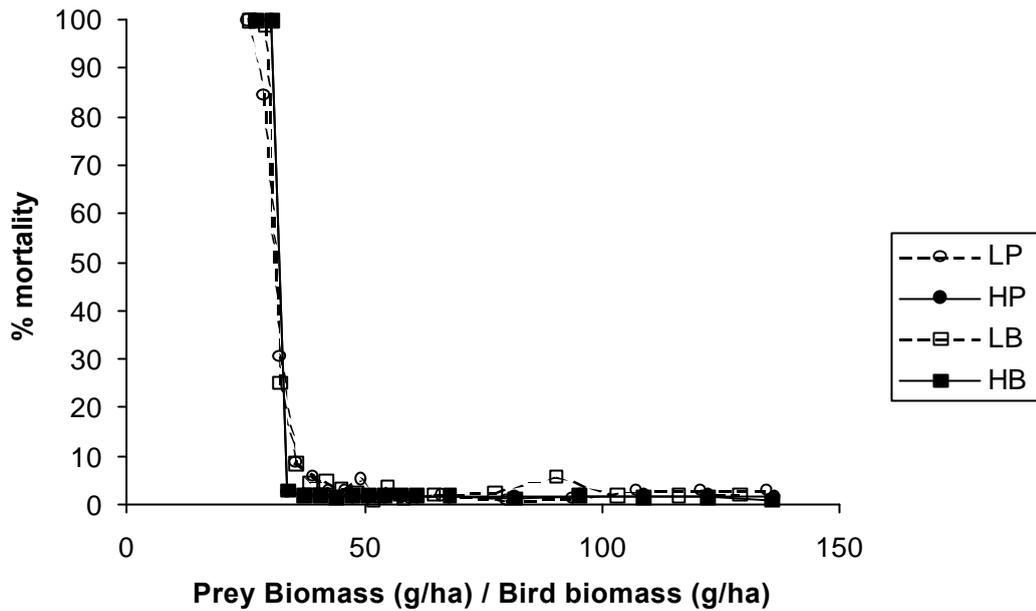
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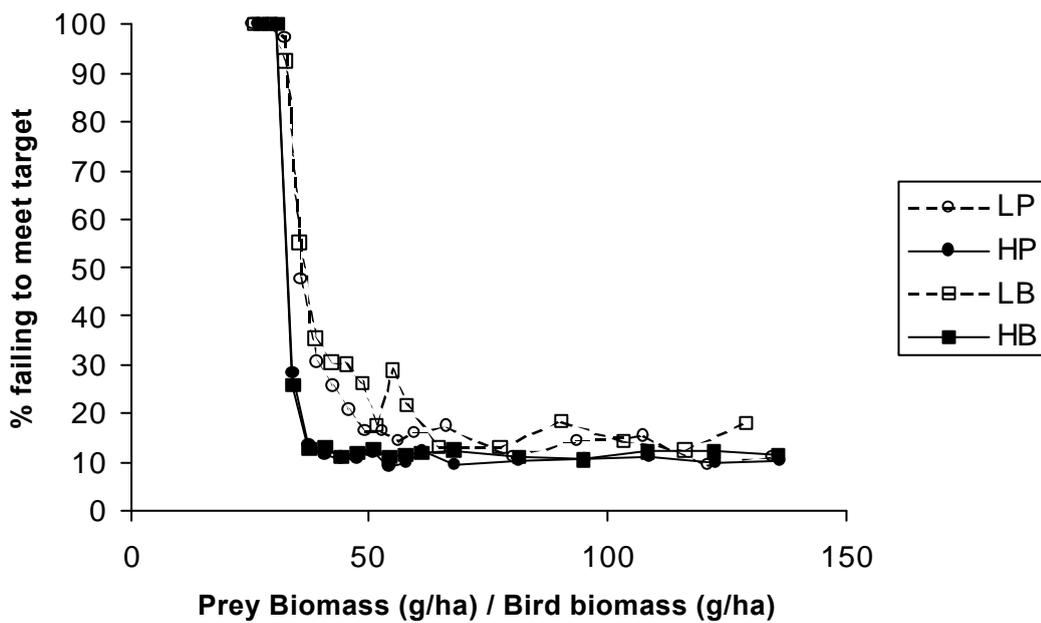
Figure 4 Percent mortality (a) and percent failing to reach 95% of target weight (b) for sight-feeding redshank, with 15% variation in feeding efficiency and no interference.

LP = both bird and prey biomass low, with prey biomass varied; **LB** = both bird and prey biomass low, with bird biomass varied; **HP** = both bird and prey biomass high, with prey biomass varied; **HB** = both bird and prey biomass high, with bird biomass varied.

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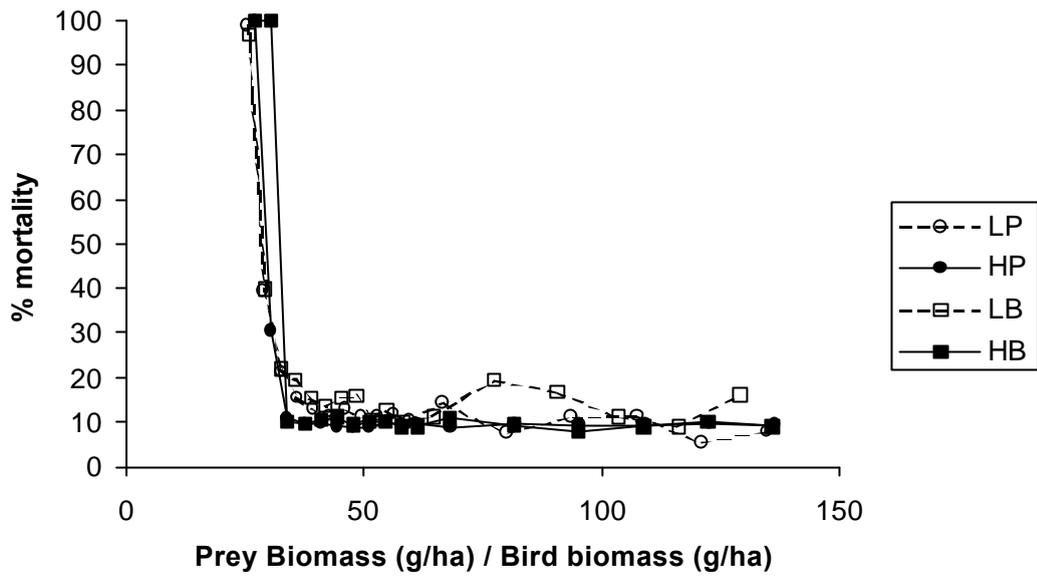
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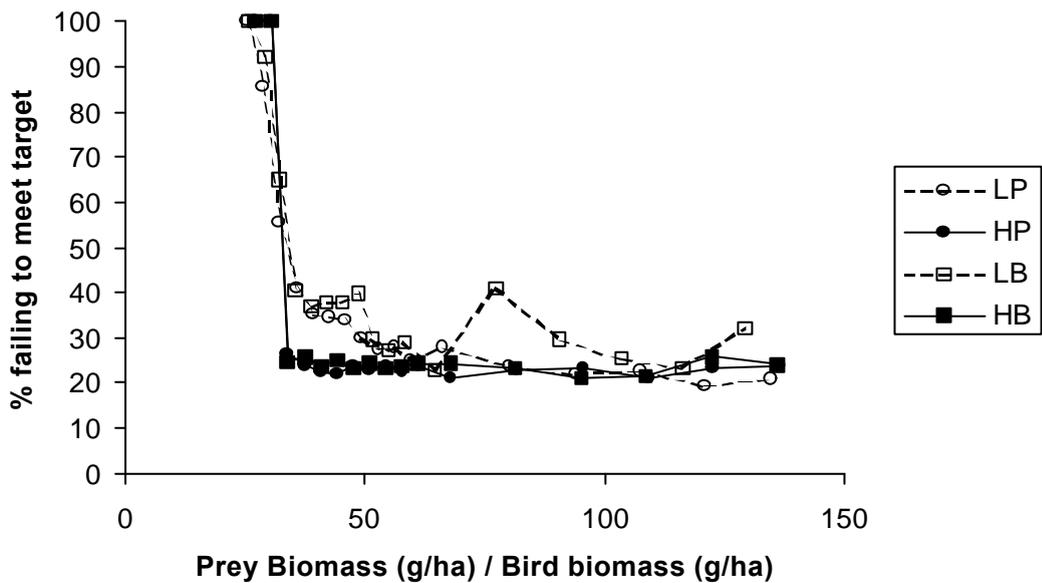
Figure 5 Percent mortality (a) and percent failing to reach 95% of target weight (b) for sight-feeding redshank, with 25% variation in feeding efficiency and no interference.

LP = both bird and prey biomass low, with prey biomass varied; **LB** = both bird and prey biomass low, with bird biomass varied; **HP** = both bird and prey biomass high, with prey biomass varied; **HB** = both bird and prey biomass high, with bird biomass varied.

(a)
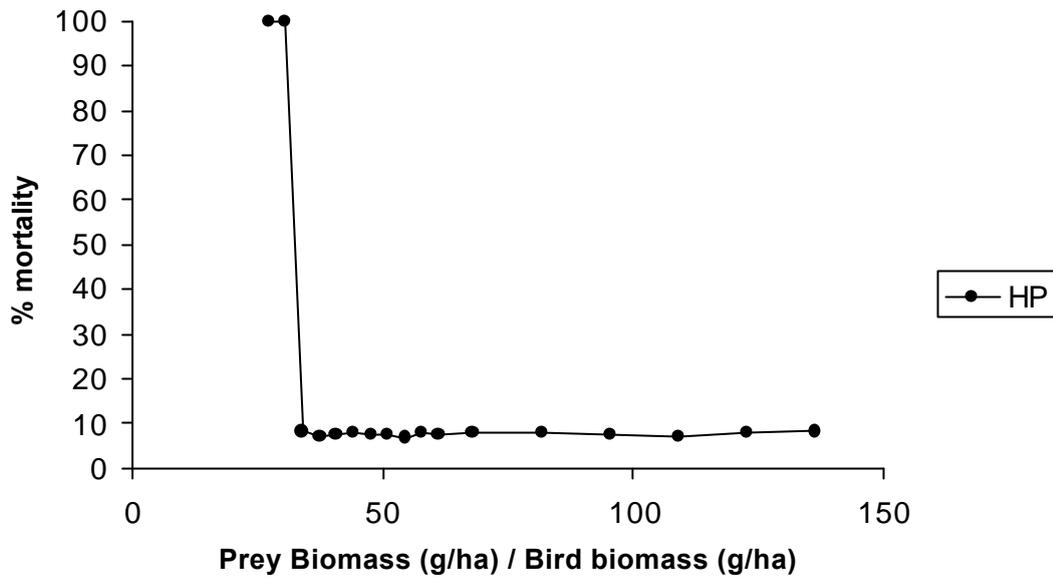
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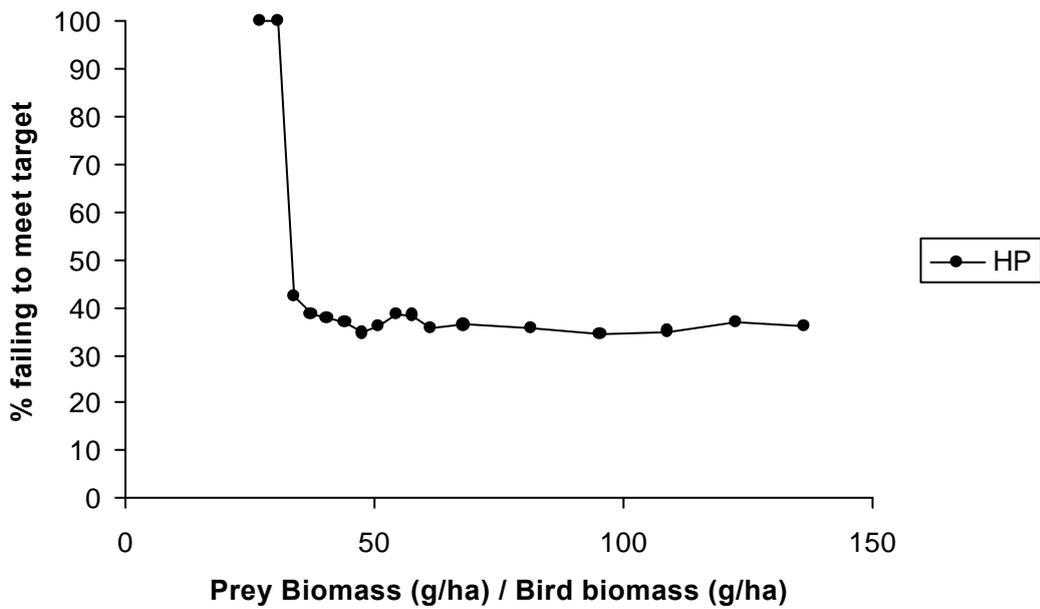
Figure 6 Percent mortality (a) and percent failing to reach 95% of target weight (b) for sight-feeding redshank, with 15% variation in feeding efficiency and interference based on prey depression. No aggregation was allowed.

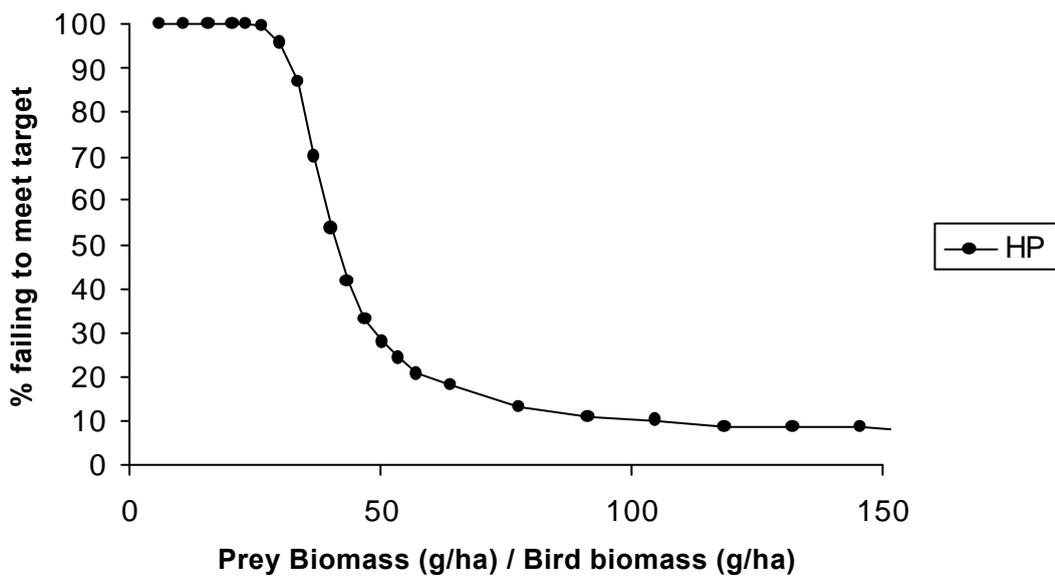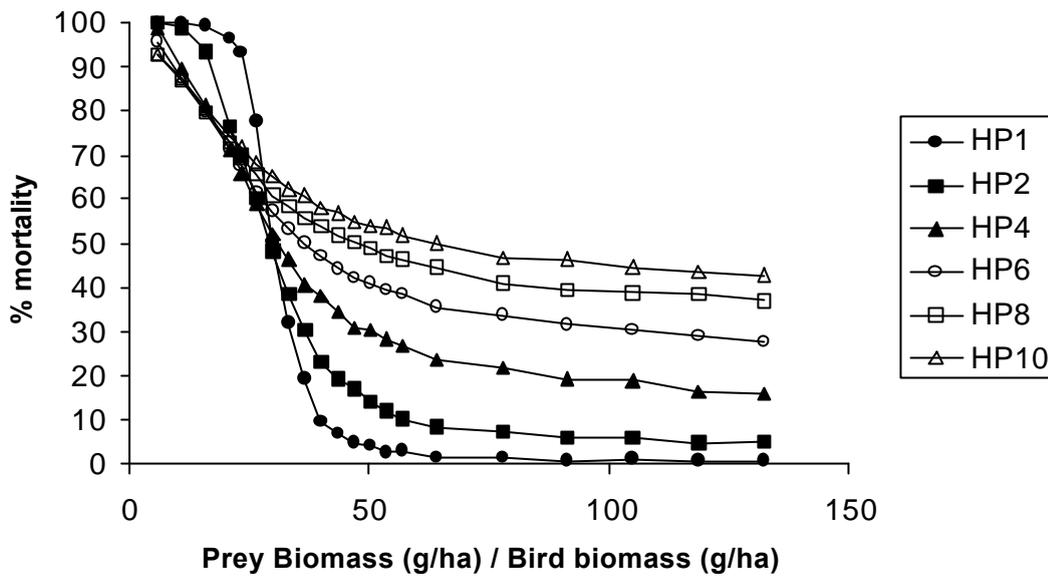**HP** = both bird and prey biomass high, with prey biomass varied

(a)
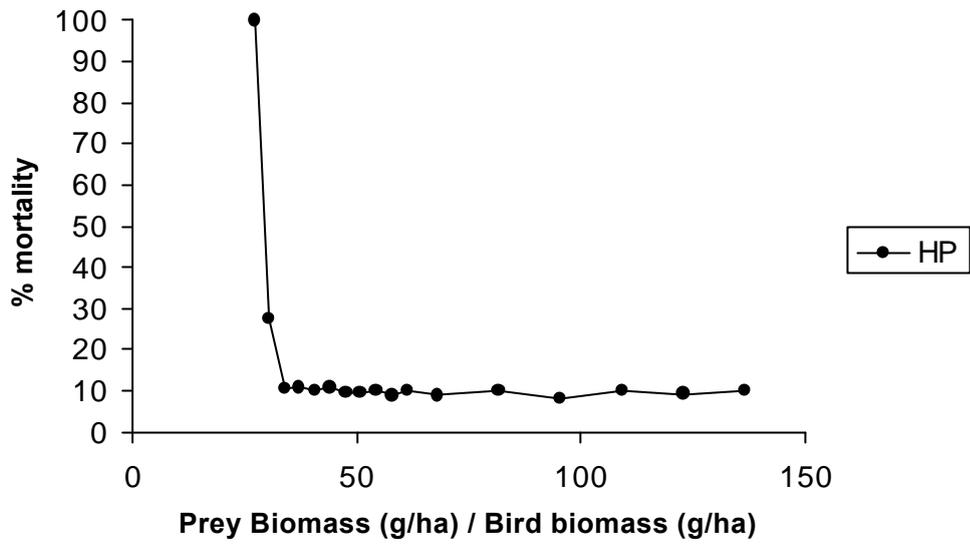
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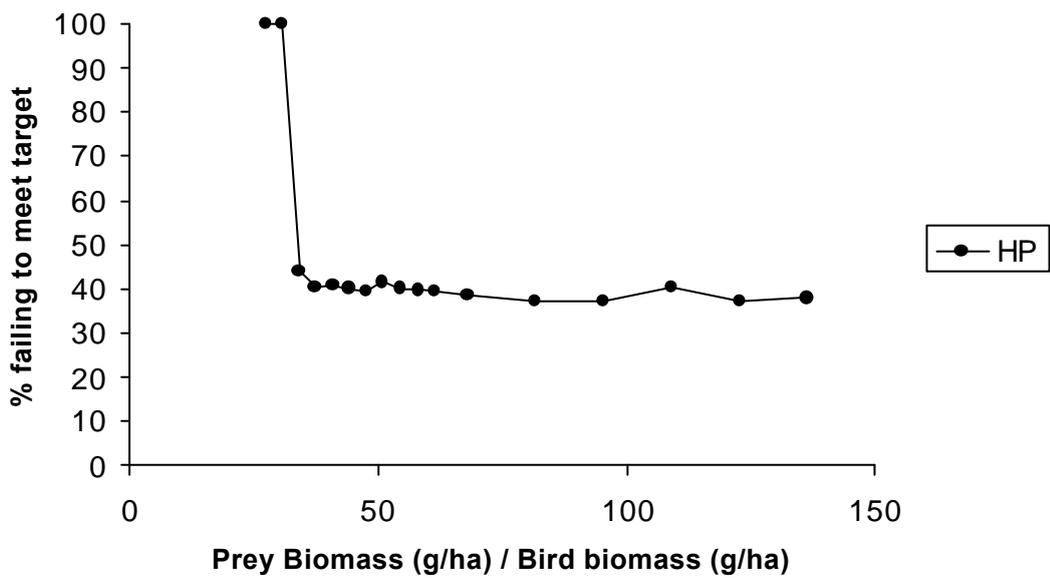
Figure 7 Percent mortality (a) and percent failing to reach 95% of target weight (b) for sight-feeding redshank, with 15% variation in feeding efficiency and interference based on kleptoparasitism. No aggregation was allowed.

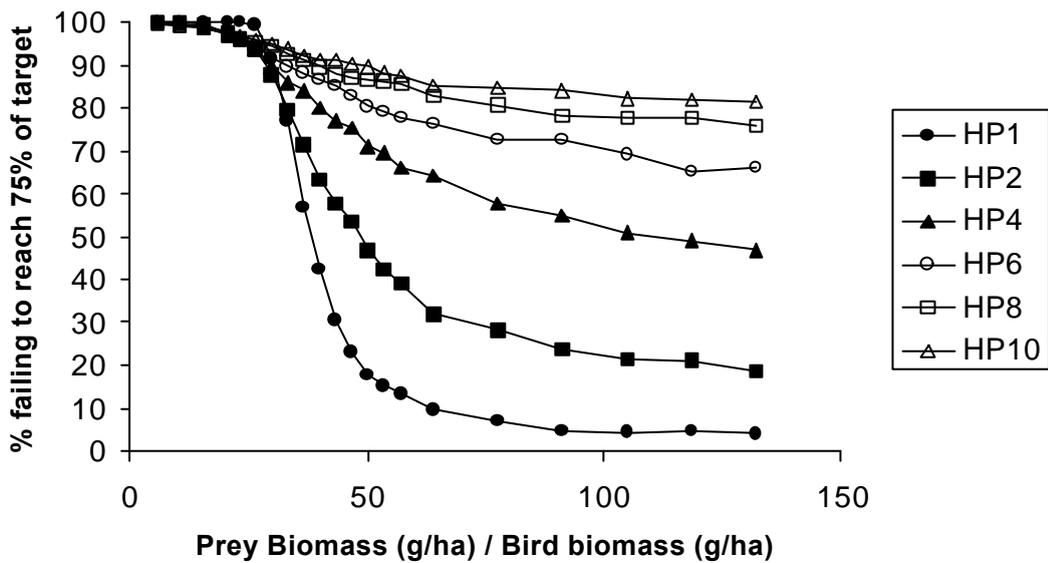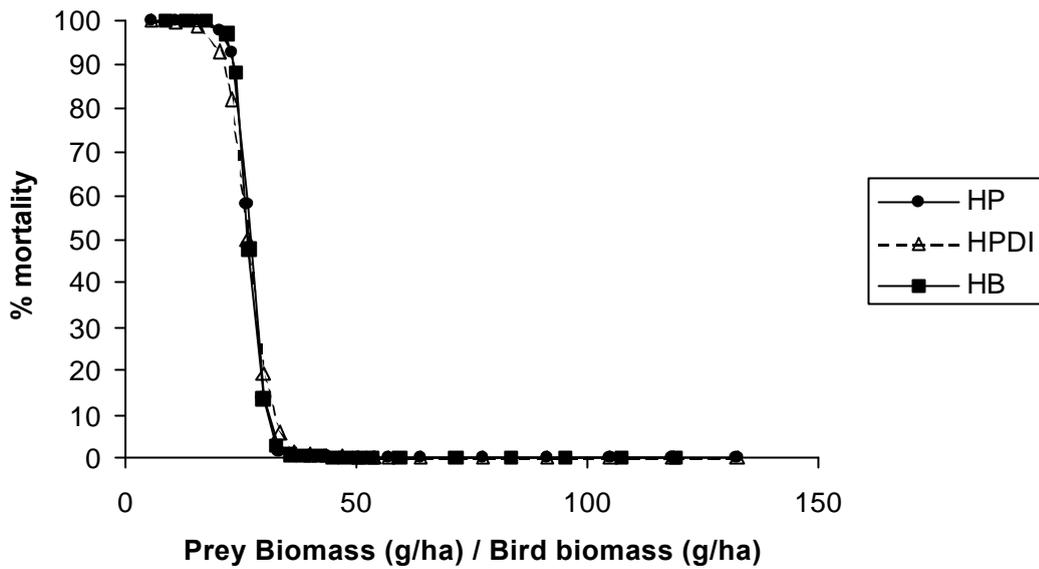**HP** = both bird and prey biomass high, with prey biomass varied.

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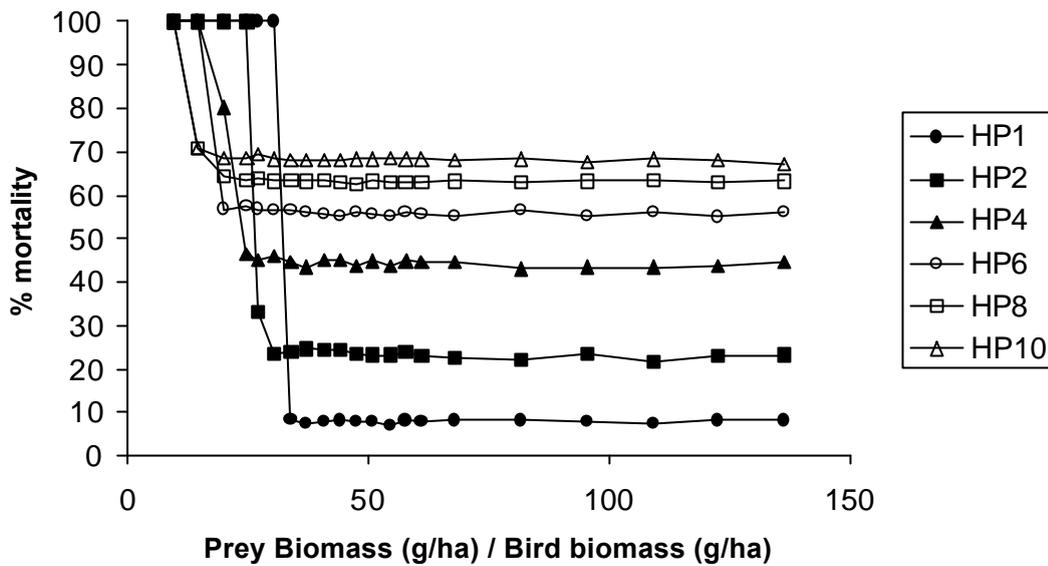
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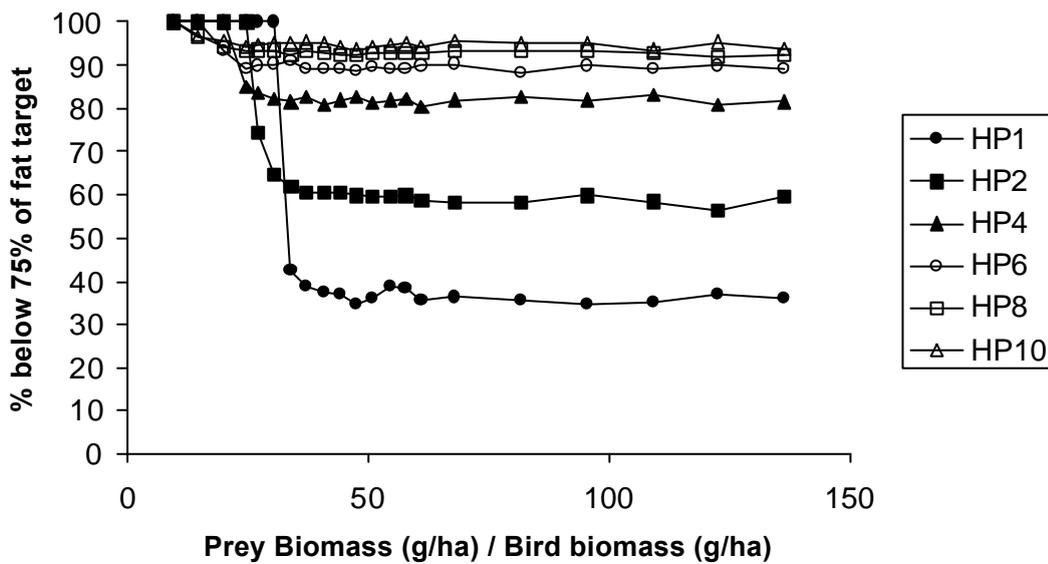
Figure 8 Percent mortality (a) and percent failing to reach 75% of target fat (b) for sight-feeding redshank, with 15% variation in feeding efficiency, interference based on prey depression and varying degrees of aggregation.

HP = both bird and prey biomass high, with prey biomass varied; **1** = birds spread out over the whole feeding area, **2** = birds aggregate so their density is doubled (although bird numbers and patch area remain the same), **4** = birds aggregate so their density is quadrupled, etc.
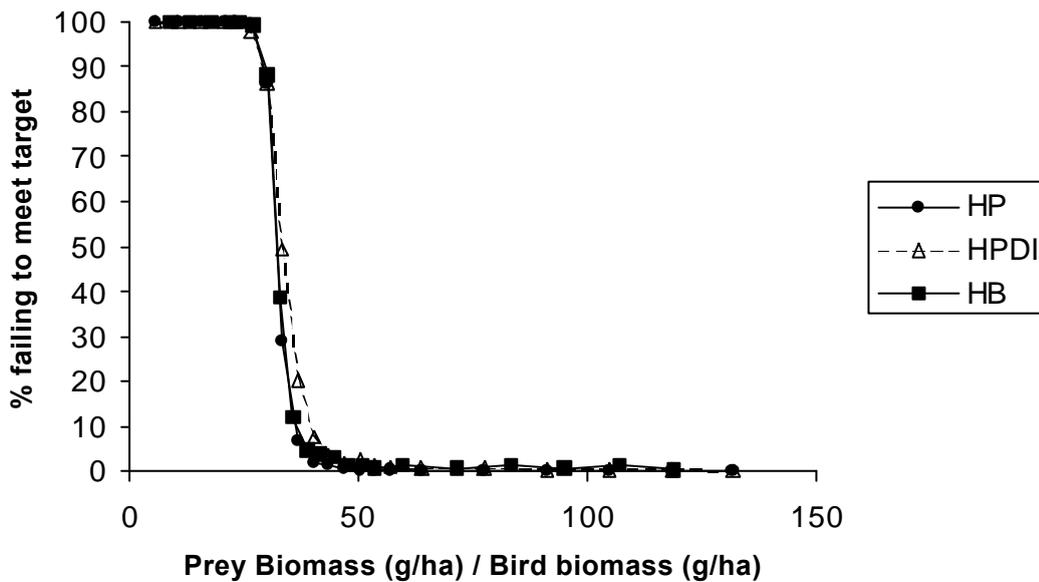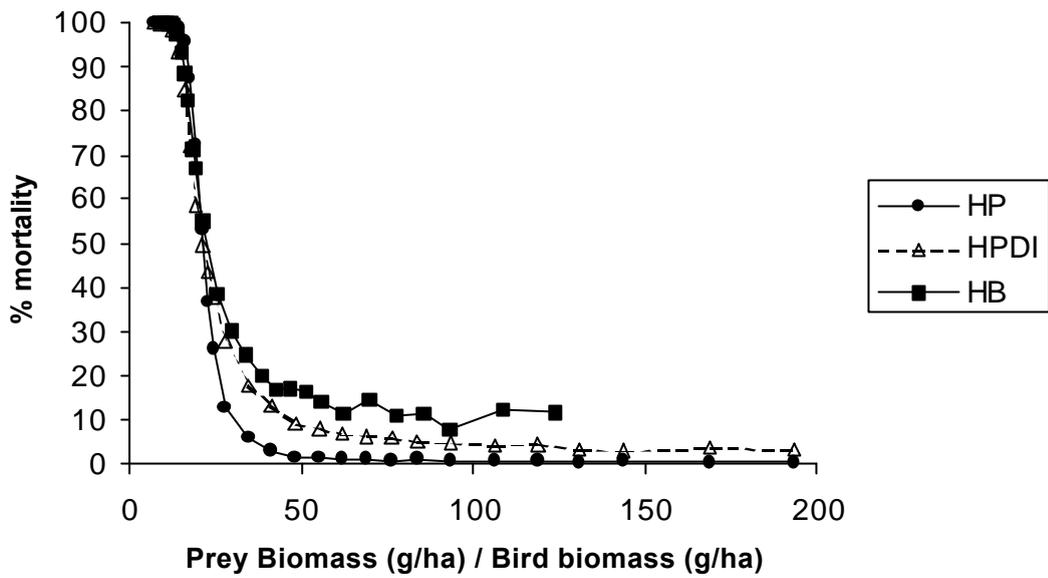
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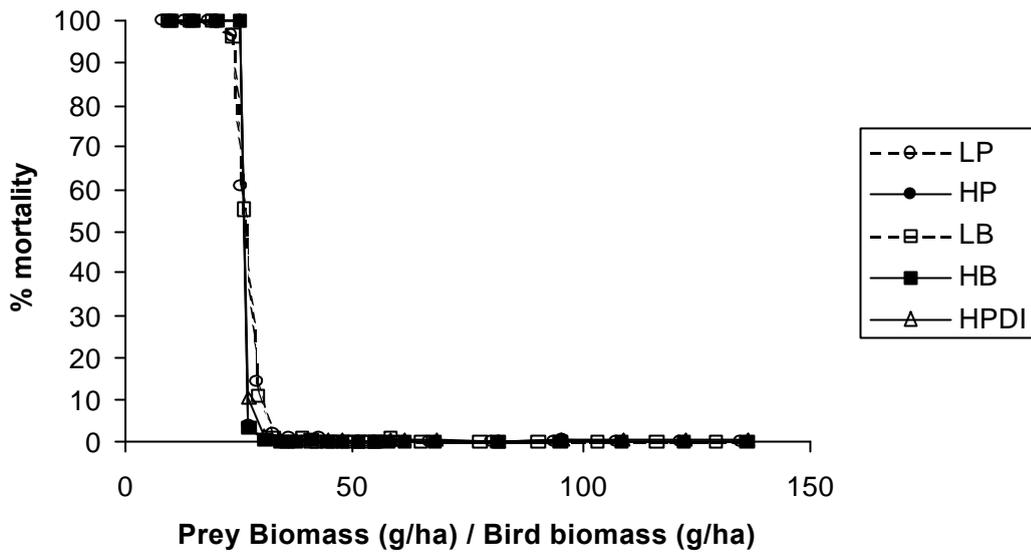
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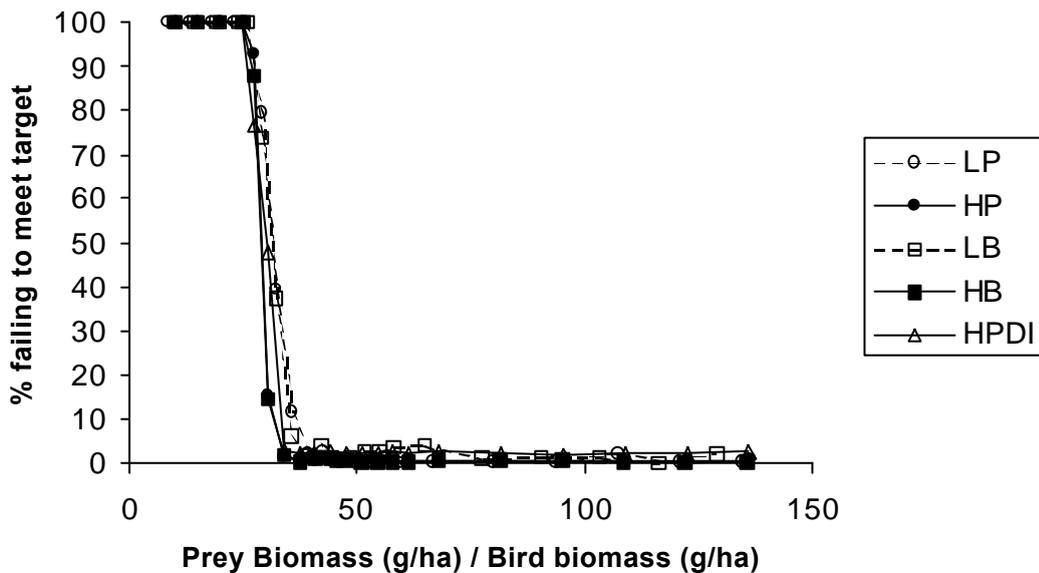
Figure 9 Percent mortality (a) and percent failing to reach 95% of target weight (b) for sight-feeding redshank, with 15% variation in feeding efficiency and either with or without interference. An upshore feeding area of the same size and prey density as the downshore, but with smaller prey is present.

LP = both bird and prey biomass low, with prey biomass varied; **LB** = both bird and prey biomass low, with bird biomass varied; **HP** = both bird and prey biomass high, with prey biomass varied; **HB** = both bird and prey biomass high, with bird biomass varied; **HPDI** = both bird and prey biomass high, with prey biomass varied and with depression-based interference.
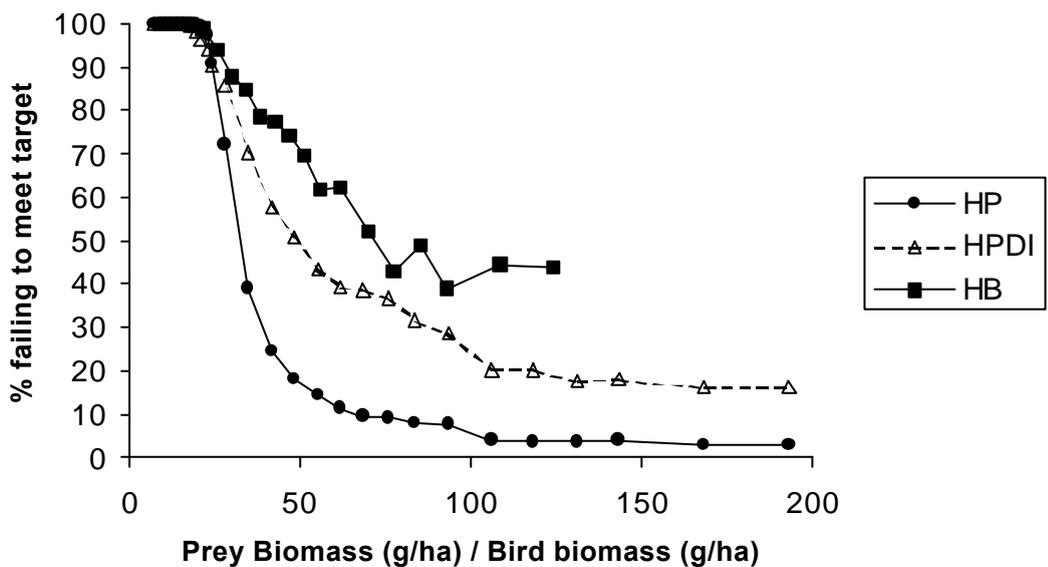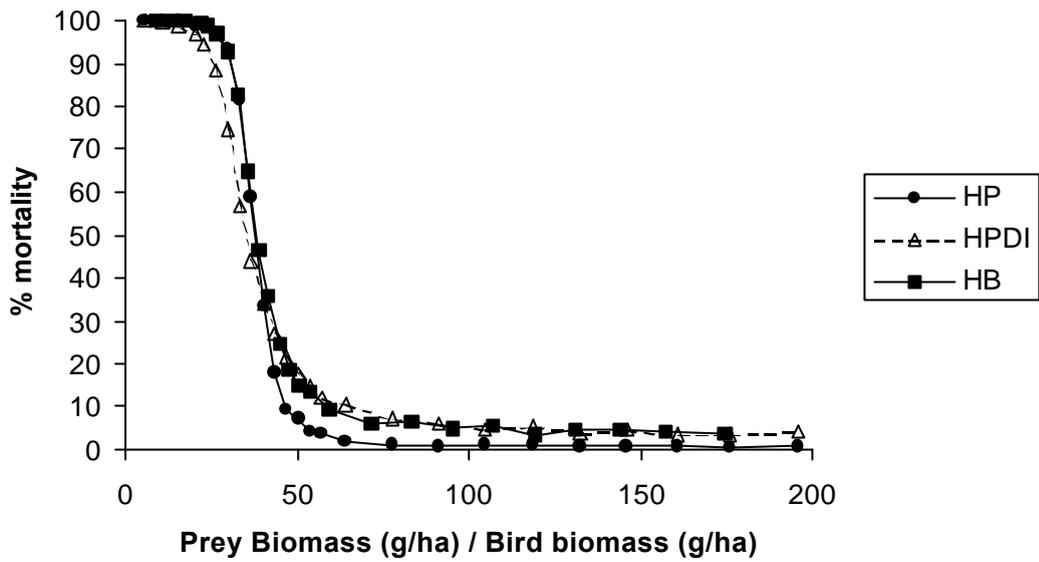
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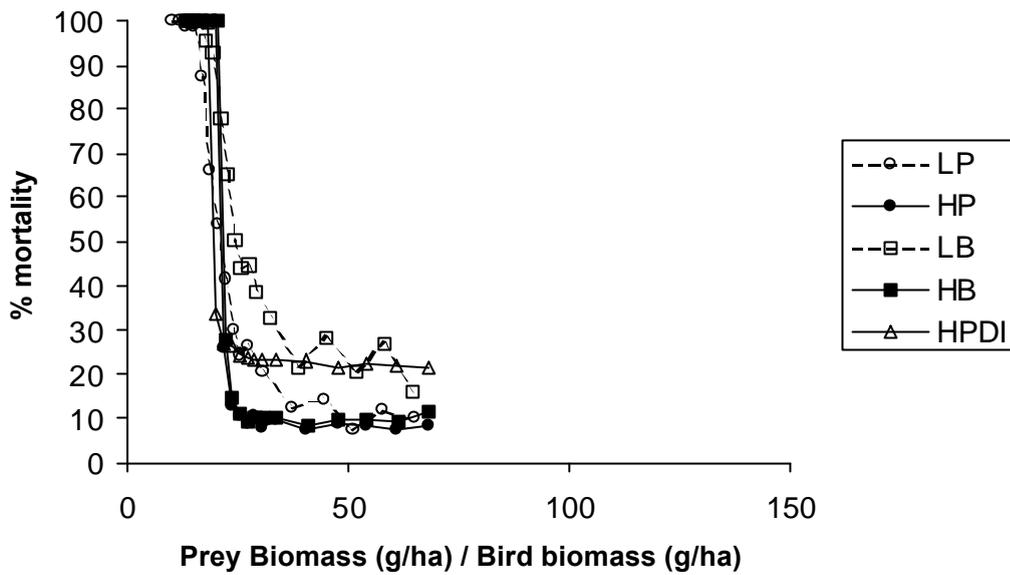
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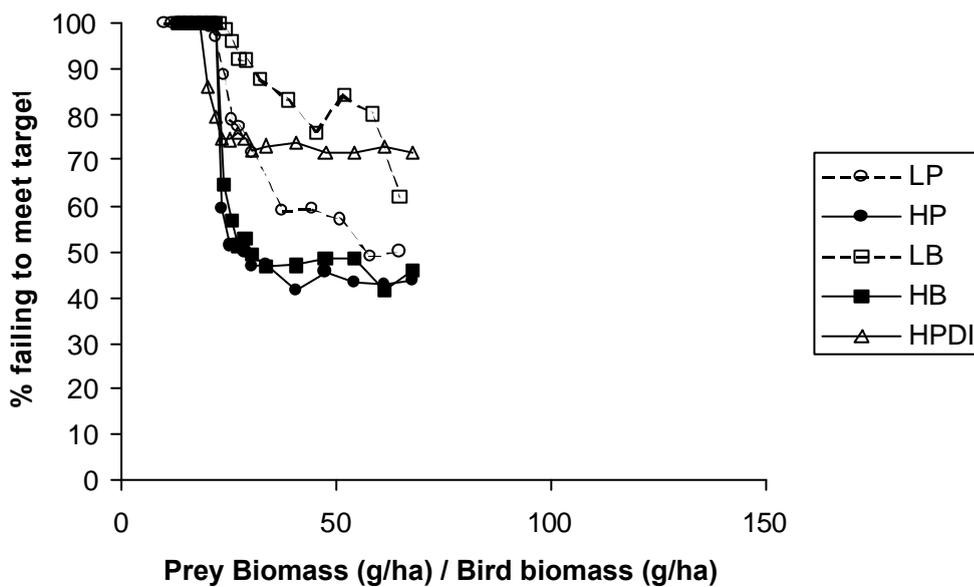
Figure 10 Percent mortality (a) and percent failing to reach 95% of target weight (b) for sight-feeding redshank, with 15% variation in feeding efficiency and either with or without interference. Prey ash-free dry mass declines by 50% over the winter.

LP = both bird and prey biomass low, with prey biomass varied; **LB** = both bird and prey biomass low, with bird biomass varied; **HP** = both bird and prey biomass high, with prey biomass varied; **HB** = both bird and prey biomass high, with bird biomass varied; **HPDI** = both bird and prey biomass high, with prey biomass varied and with depression-based interference.
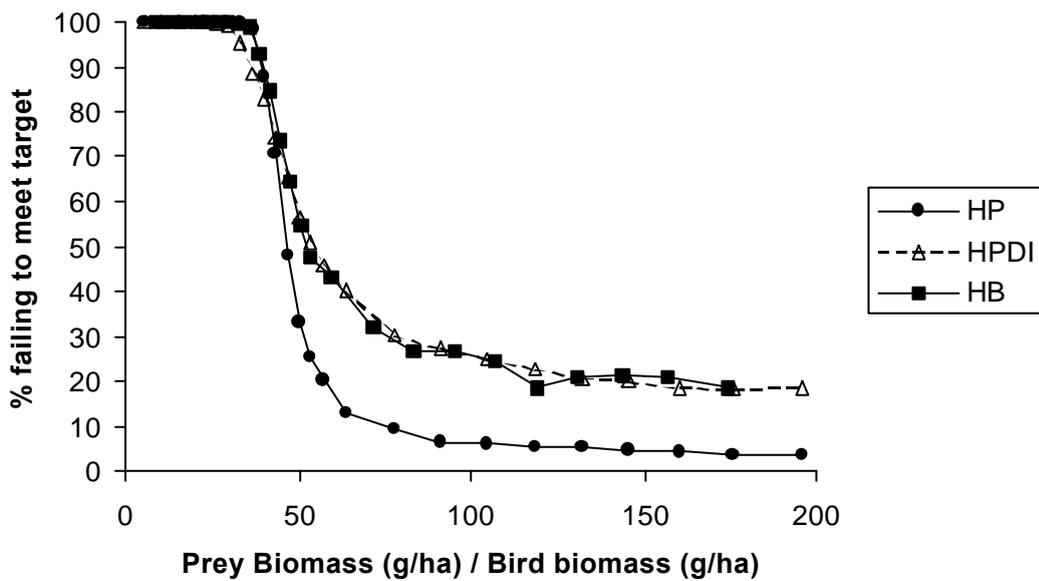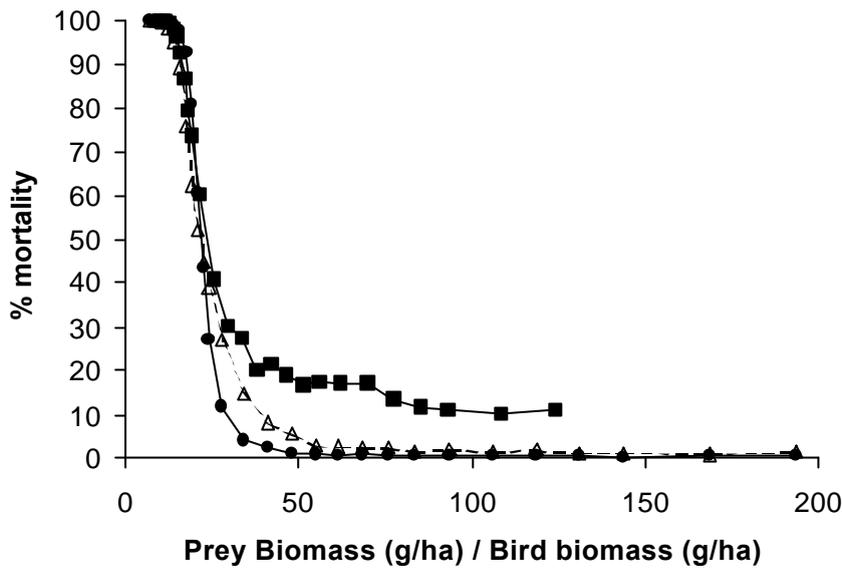
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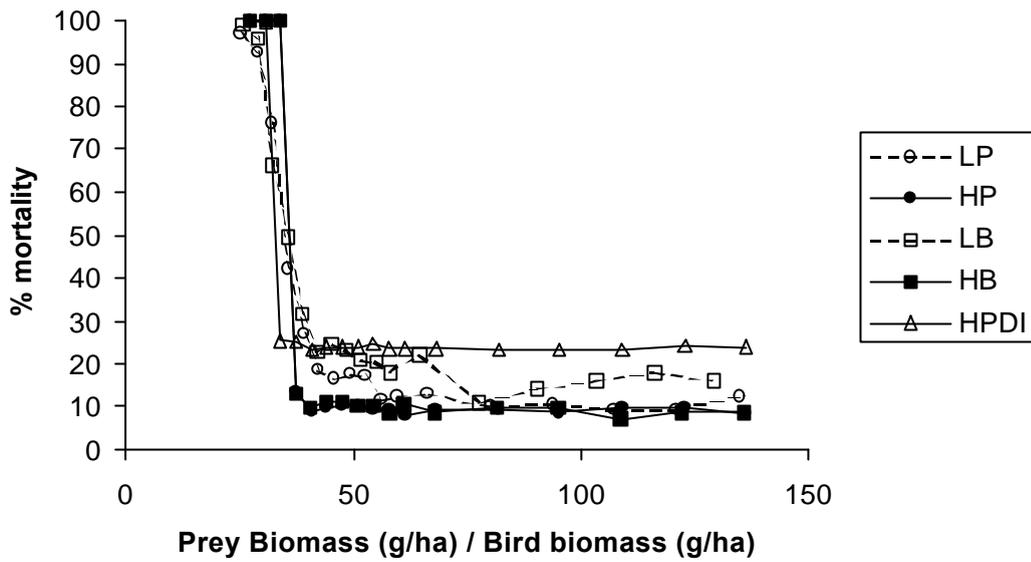
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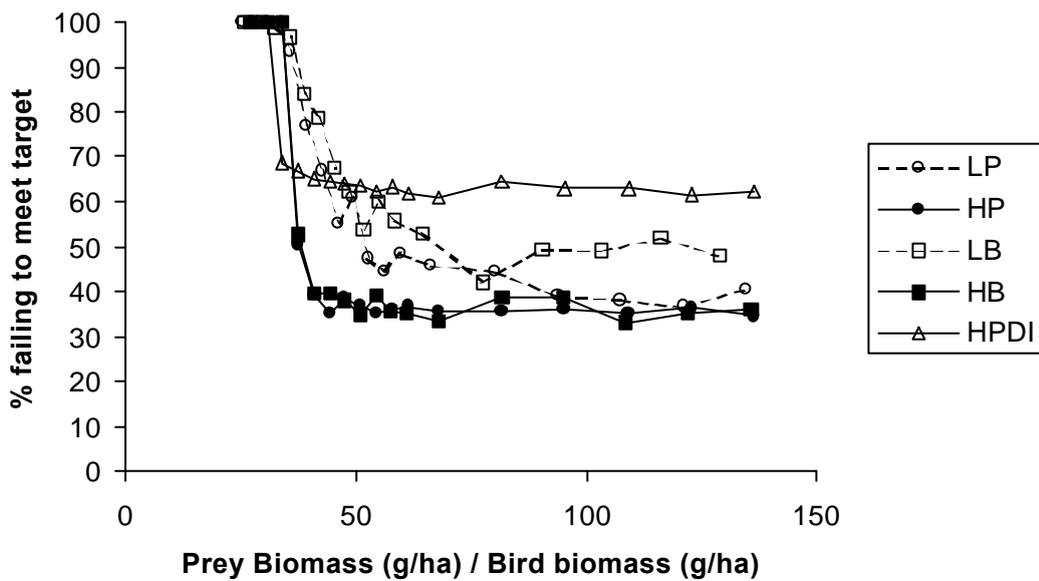
Figure 11 Percent mortality (a) and percent failing to reach 95% of target weight (b) for sight-feeding redshank, with 15% variation in feeding efficiency and either with or without interference. Temperature is consistently 5°C lower than normal.

LP = both bird and prey biomass low, with prey biomass varied; **LB** = both bird and prey biomass low, with bird biomass varied; **HP** = both bird and prey biomass high, with prey biomass varied; **HB** = both bird and prey biomass high, with bird biomass varied; **HPDI** = both bird and prey biomass high, with prey biomass varied and with depression-based interference.
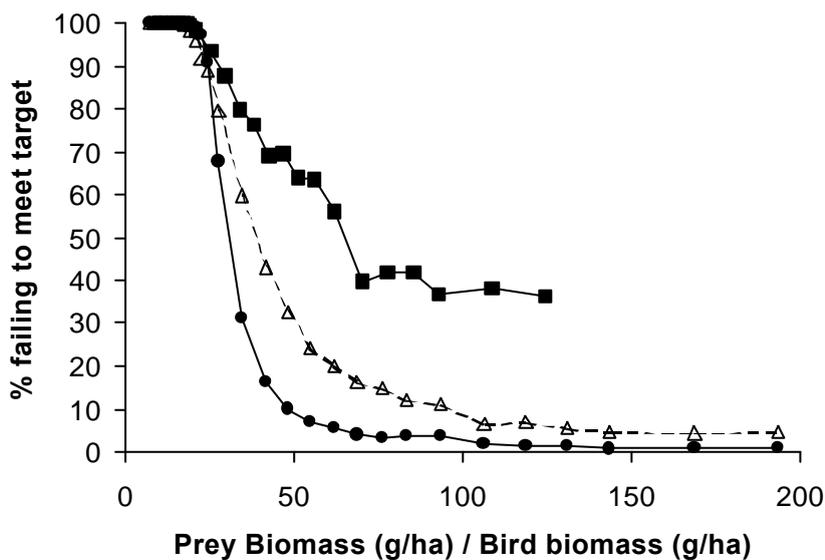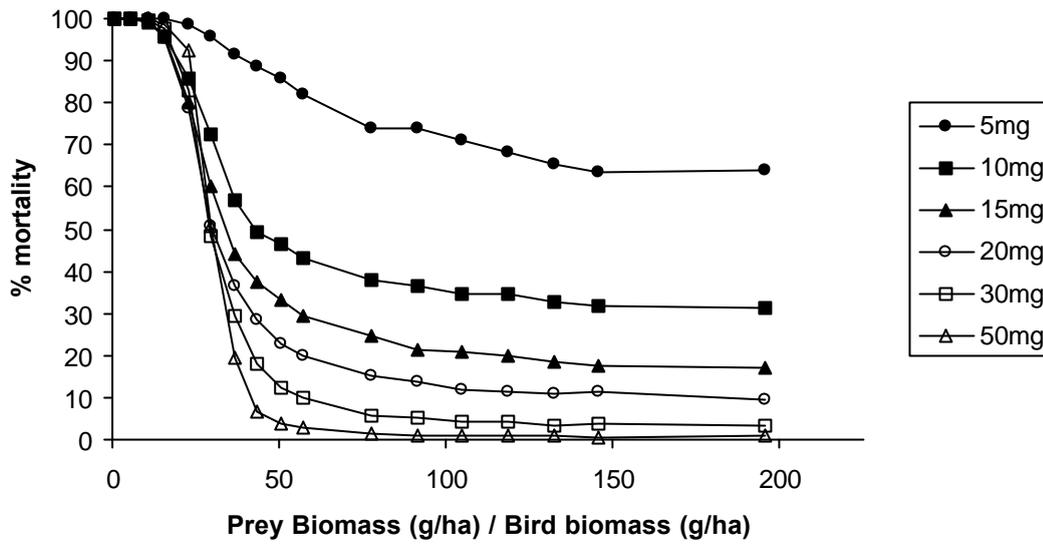
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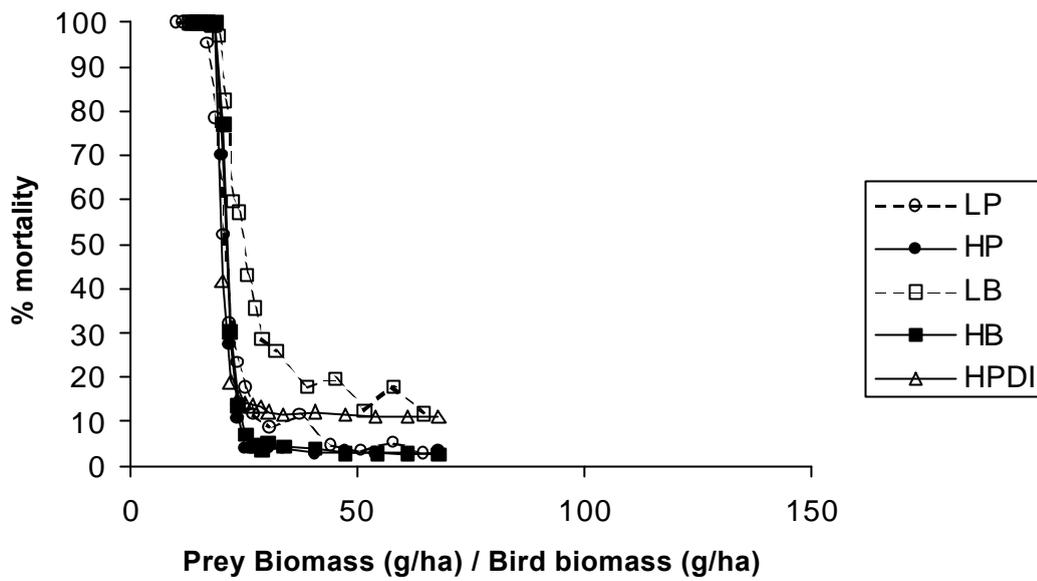
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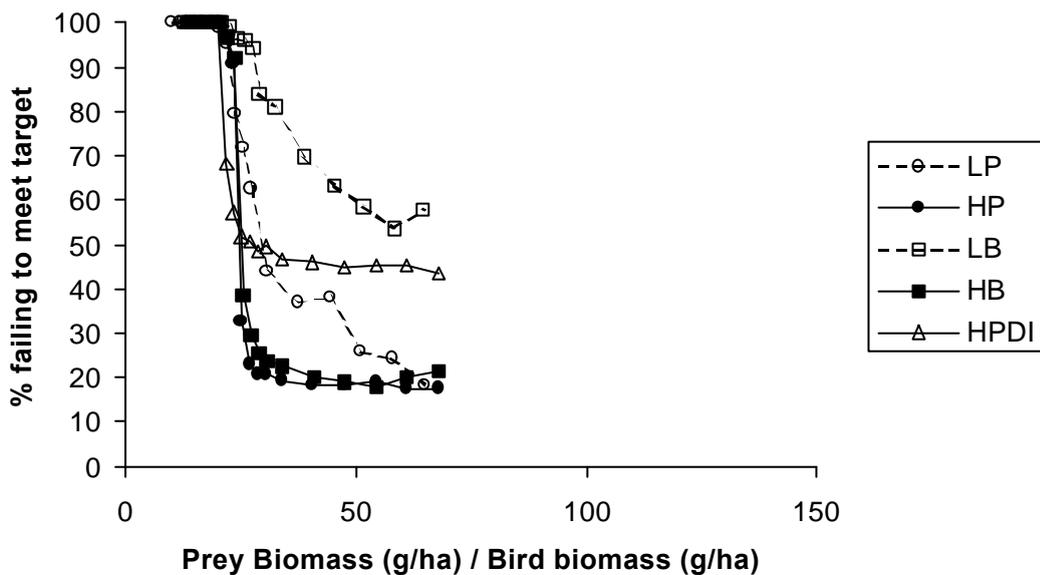
Figure 12 Percent mortality (a) and percent failing to reach 95% of target weight (b) for sight-feeding redshank, with 15% variation in feeding efficiency and either with or without interference. Upshore area, prey decline and cold weather included.

LP = both bird and prey biomass low, with prey biomass varied; **LB** = both bird and prey biomass low, with bird biomass varied; **HP** = both bird and prey biomass high, with prey biomass varied; **HB** = both bird and prey biomass high, with bird biomass varied; **HPDI** = both bird and prey biomass high, with prey biomass varied and with depression-based interference.
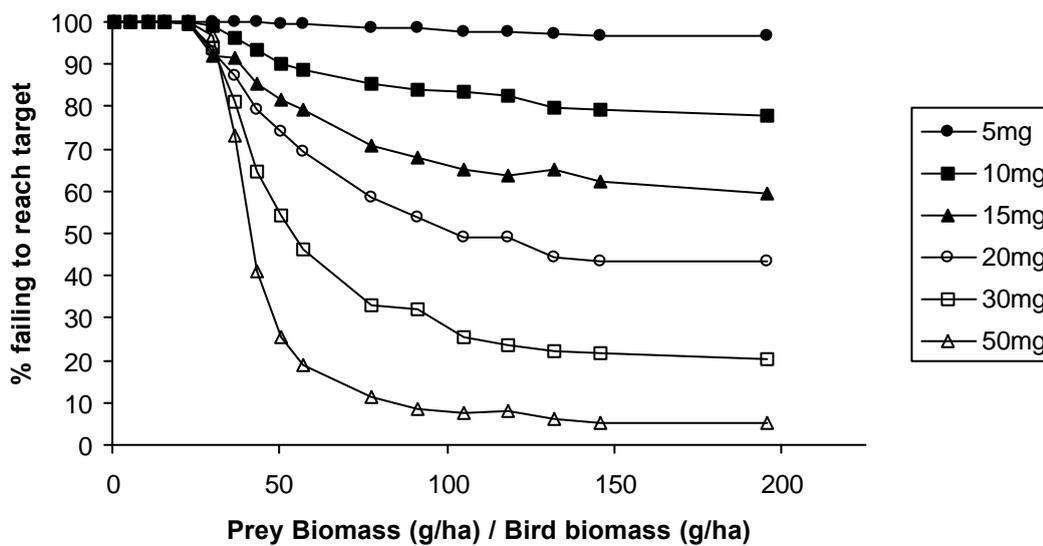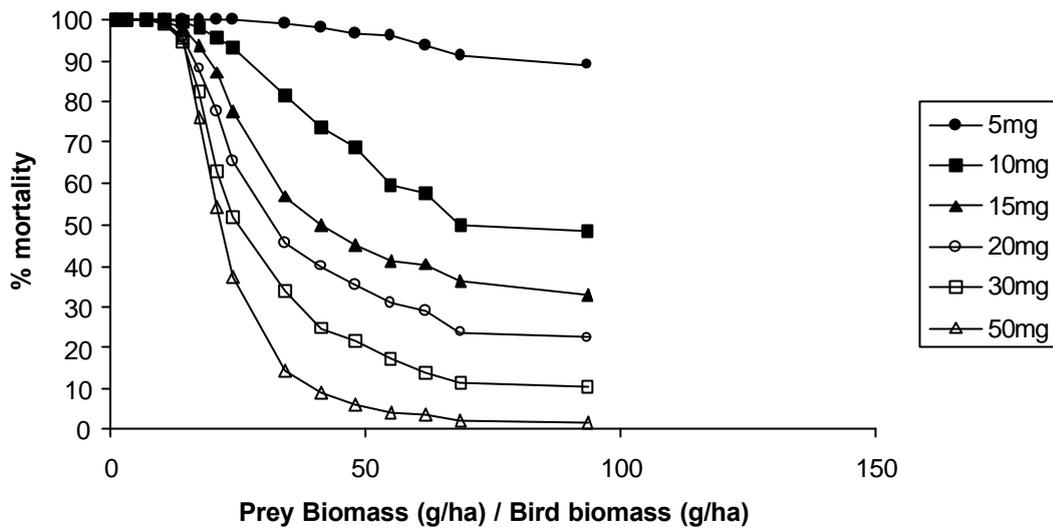
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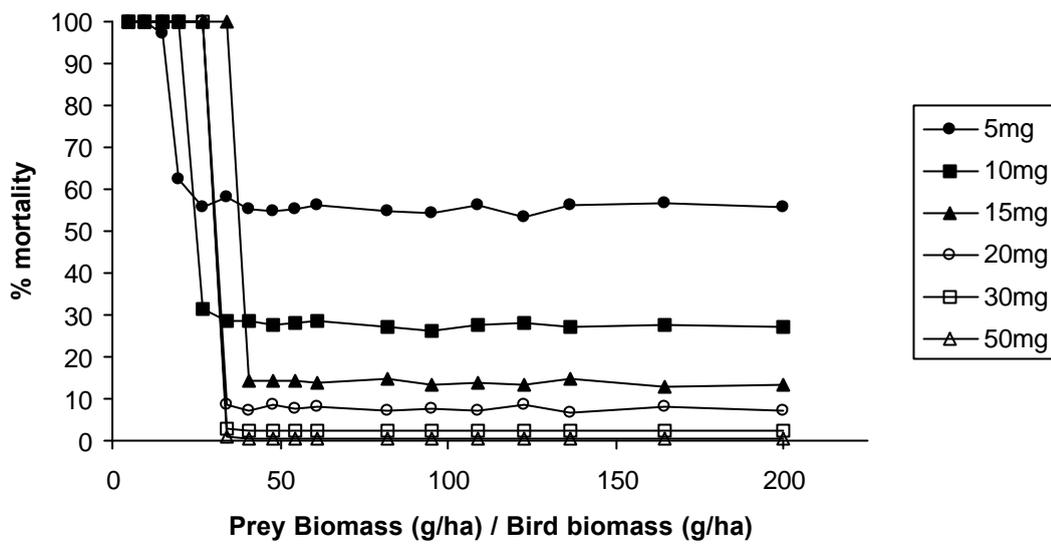
(b)
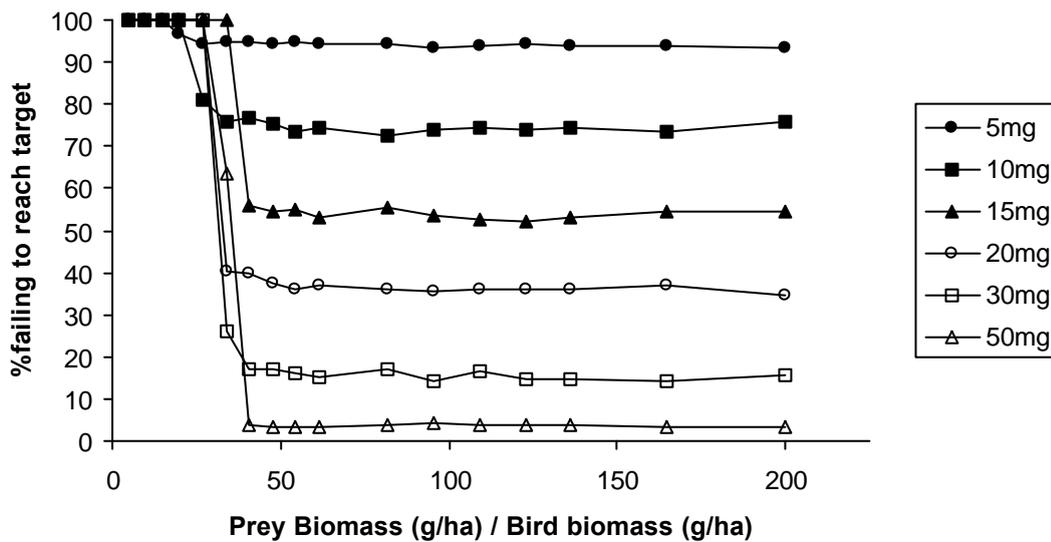
Figure 13 Percent mortality (a) and percent failing to reach 95% of target weight (b) for sight-feeding redshank, with 15% variation in feeding efficiency, interference based on prey depression and varying prey size.

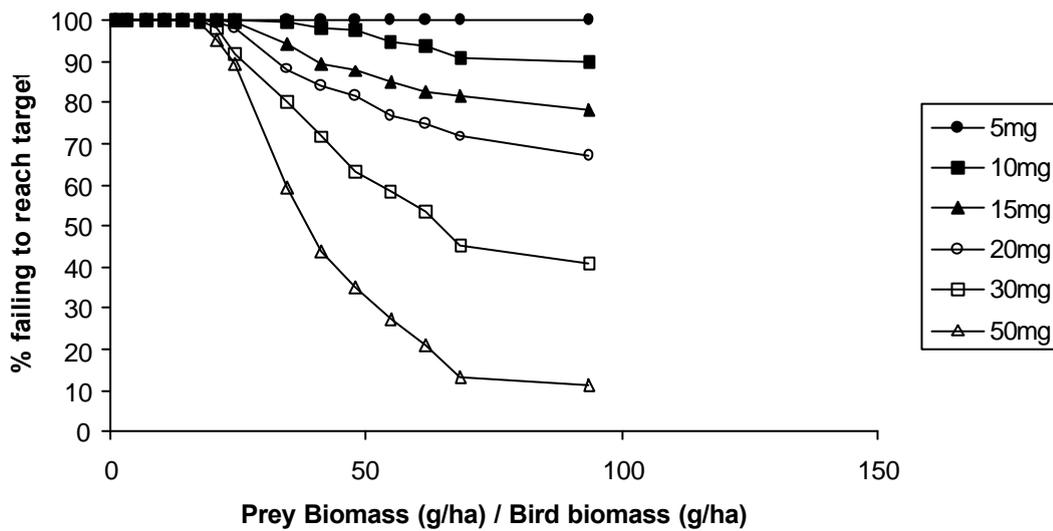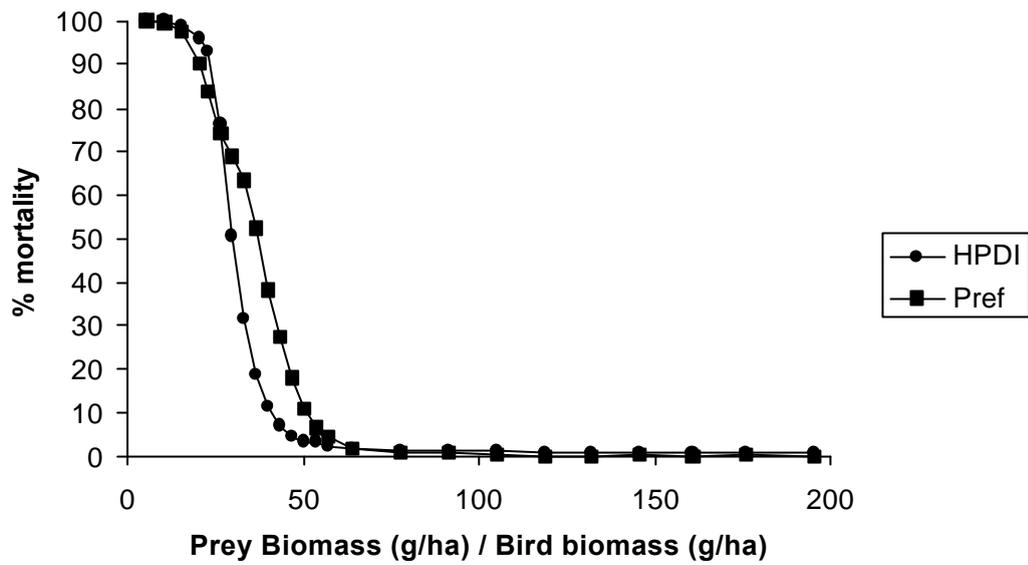**HP** = both bird and prey biomass high, with prey biomass varied

66

(a)
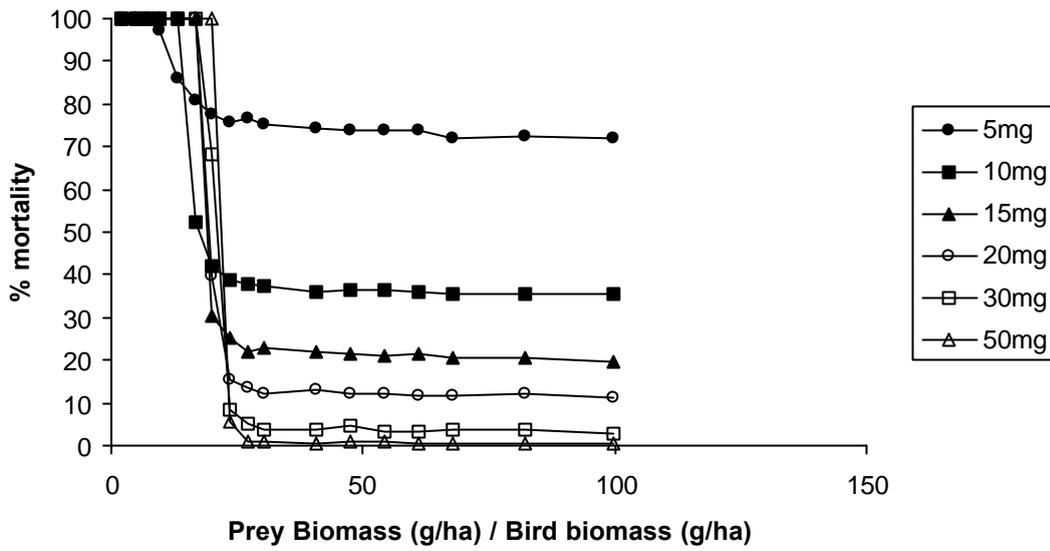
(b)
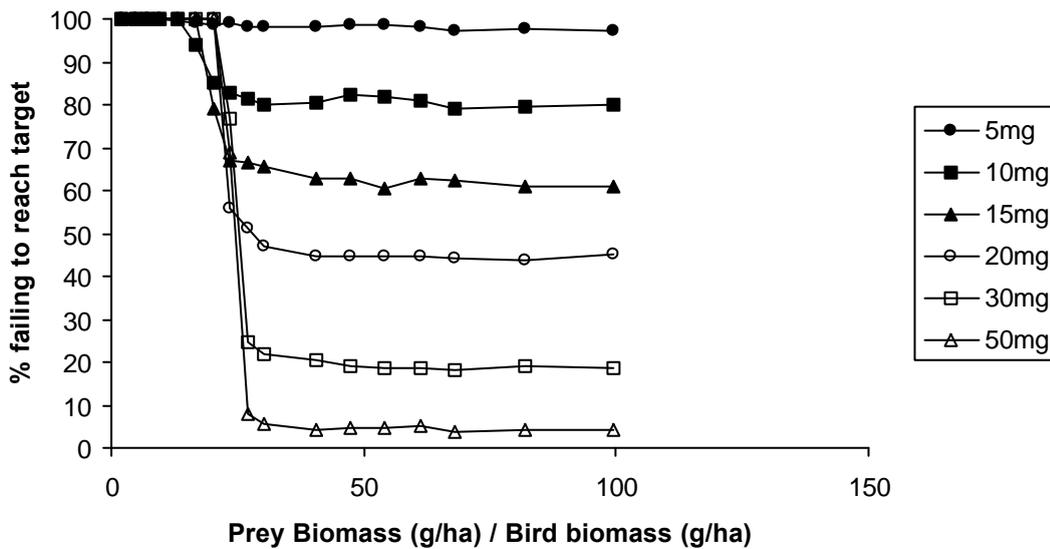
Figure 14 Percent mortality (a) and percent failing to reach 95% of target weight (b) for sight-feeding redshank, with 15% variation in feeding efficiency, interference based on prey depression and varying prey size. Upshore area, prey decline and cold weather included.

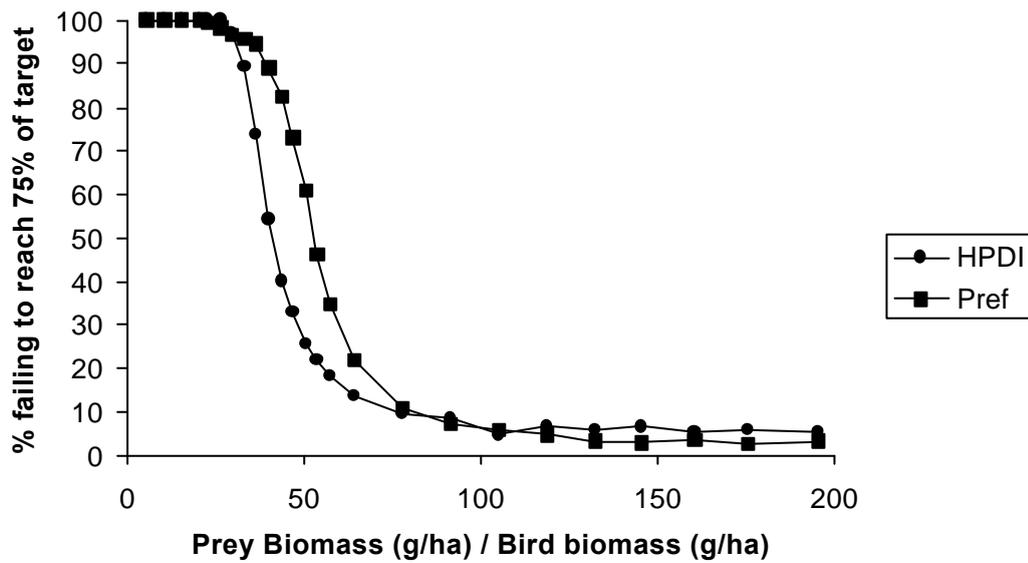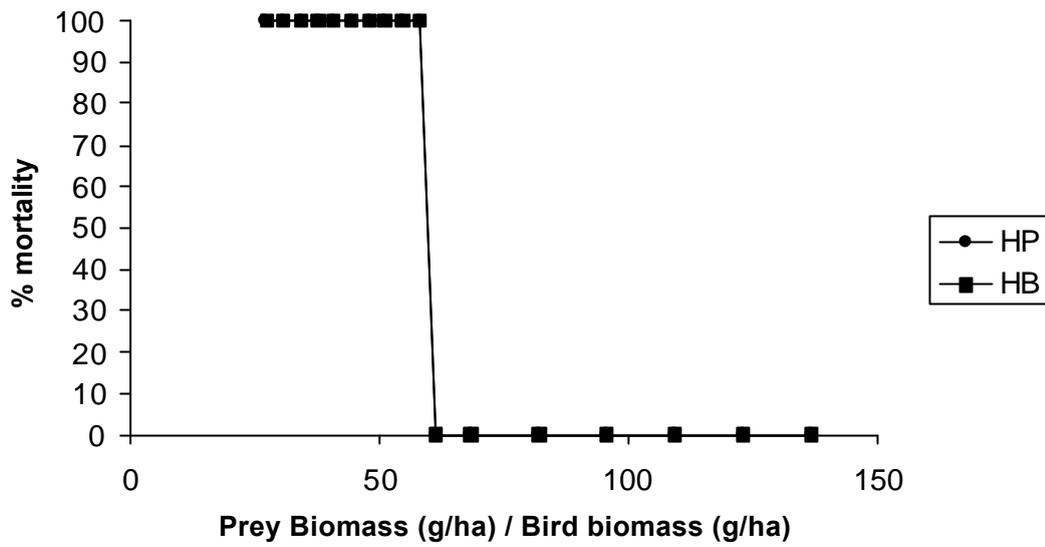**HP** = both bird and prey biomass high, with prey biomass varied

(a)
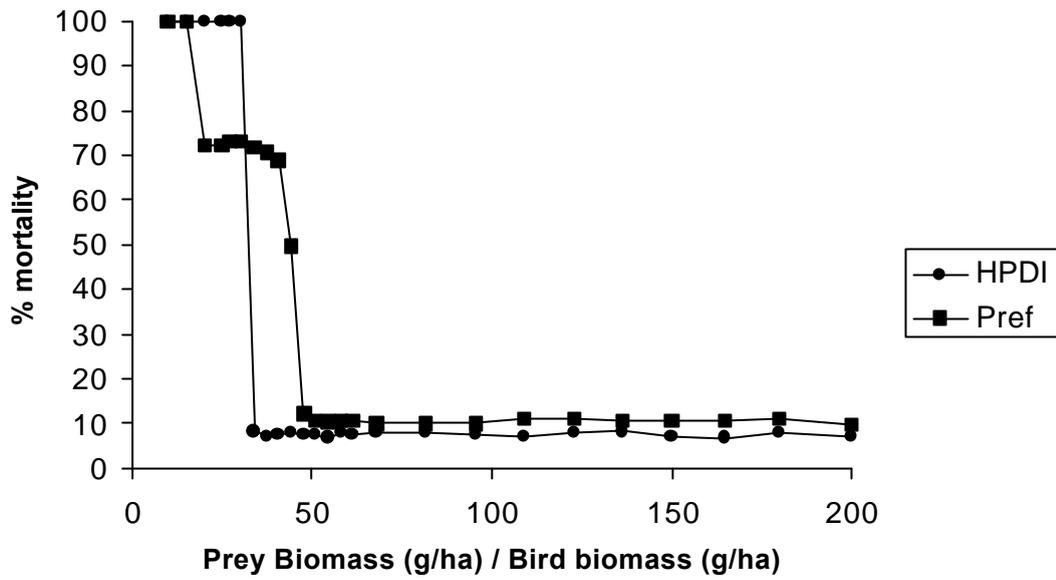
(b)
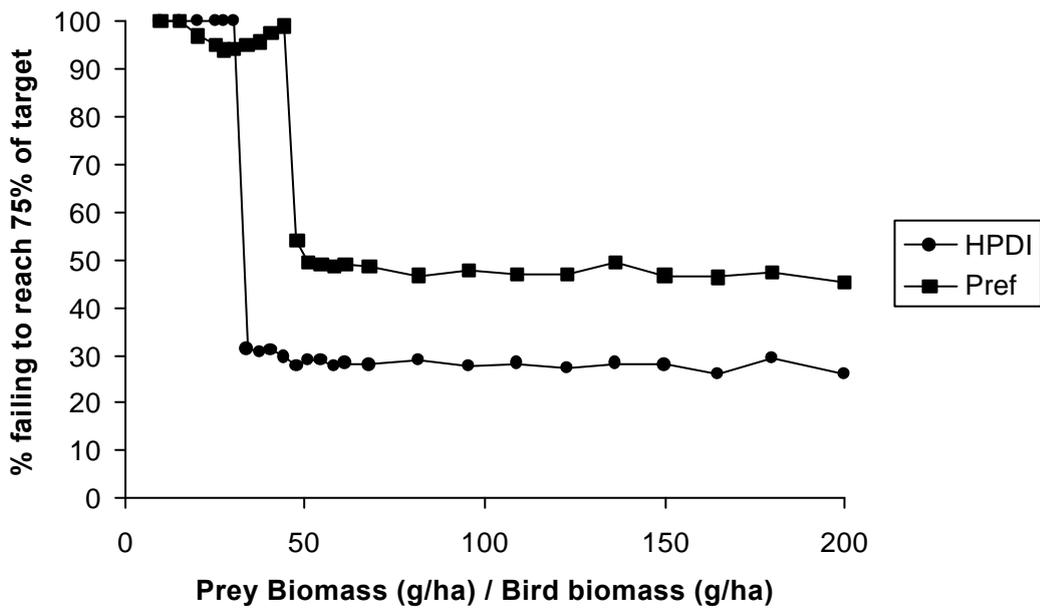
Figure 15 Percent mortality (a) and percent failing to reach 75% of target fat (b) for sight-feeding redshank, with 15% variation in feeding efficiency and depression-based interference.

HPDI = prey are in a single patch; **Pref** = Prey are distributed over 2 patches with differing prey sizes (20mg and 5mg). The biomass is the same in each patch.
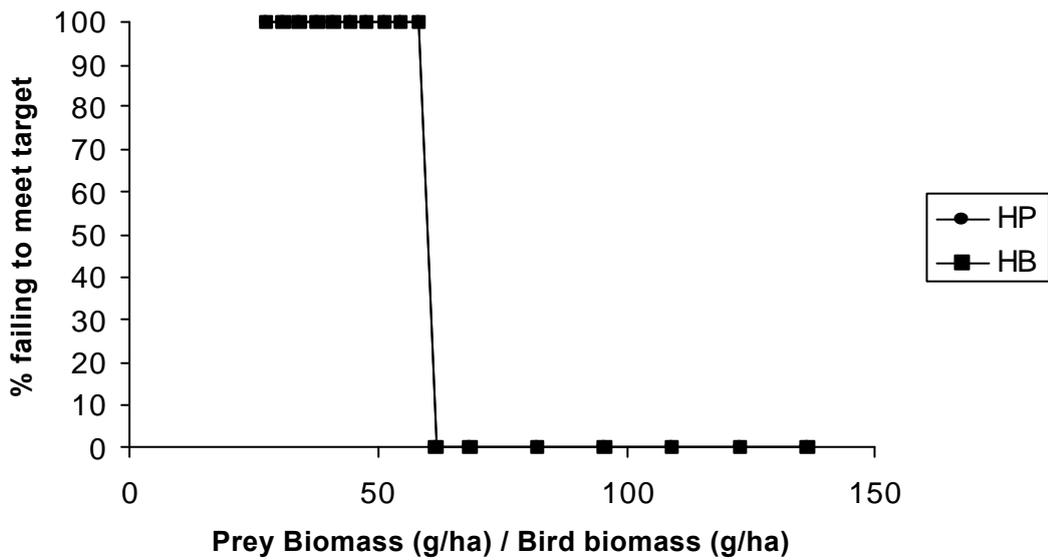
(a)
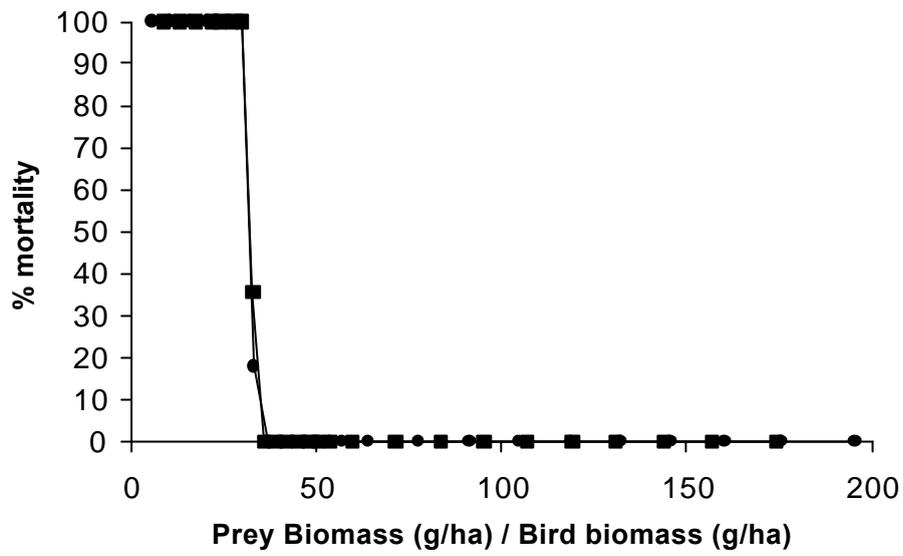
(b)
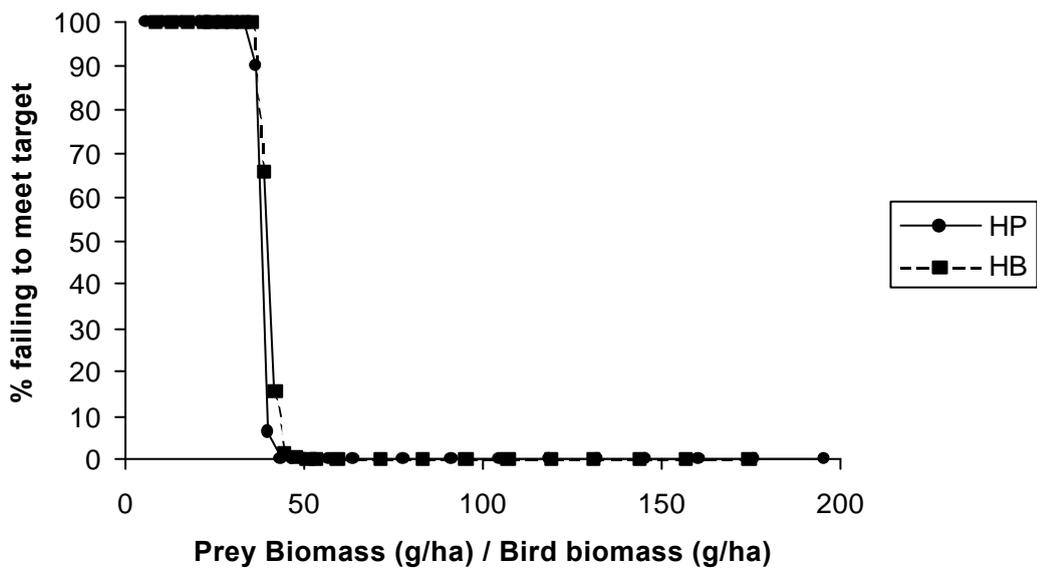
Figure 16 Percent mortality (a) and percent failing to reach 95% of target weight (b) for touch-feeding redshank, with 5% variation in feeding efficiency and no interference.

HP = both bird and prey biomass high, with prey biomass varied; **HB** = both bird and prey biomass high, with bird biomass varied.
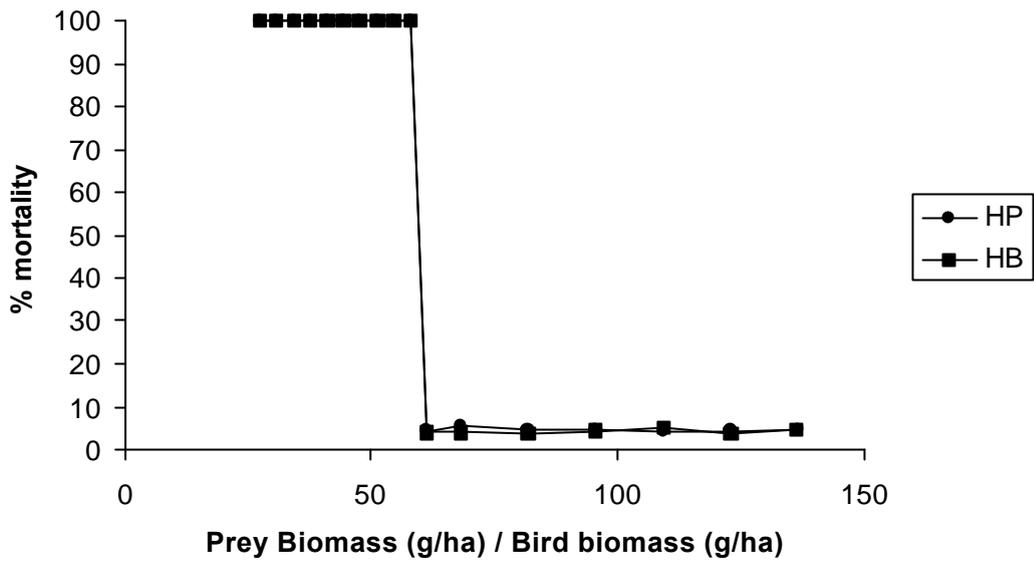
(a)

(b)

Figure 17 Percent mortality (a) and percent failing to reach 95% of target weight (b) for touch-feeding redshank, with 15% variation in feeding efficiency and no interference.

HP = both bird and prey biomass high, with prey biomass varied; **HB** = both bird and prey biomass high, with bird biomass varied.

(a)

(b)

Figure 18 Percent mortality (a) and percent failing to reach 95% of target weight (b) for touch-feeding redshank, with 25% variation in feeding efficiency and no interference.

HP = both bird and prey biomass high, with prey biomass varied; **HB** = both bird and prey biomass high, with bird biomass varied.
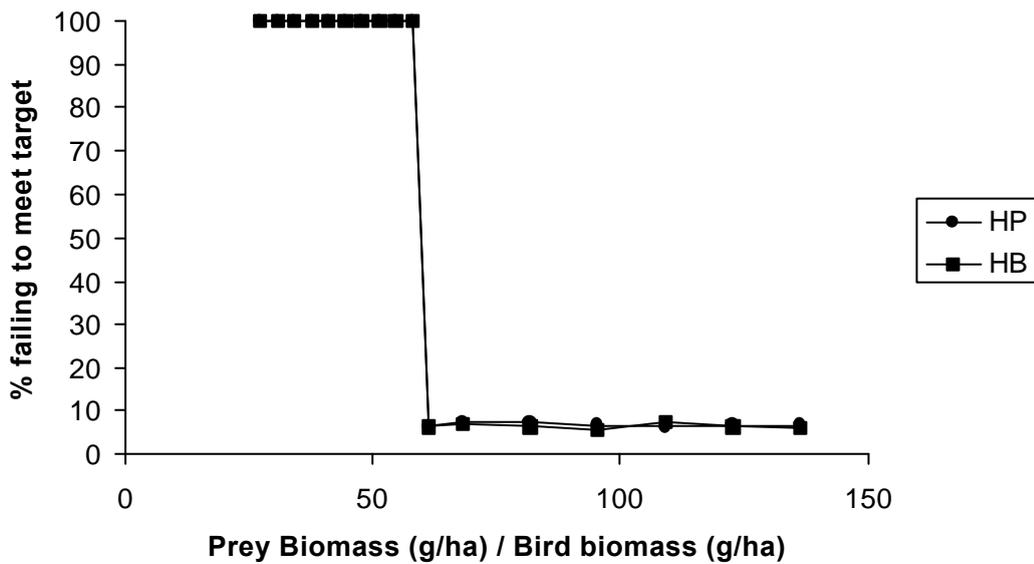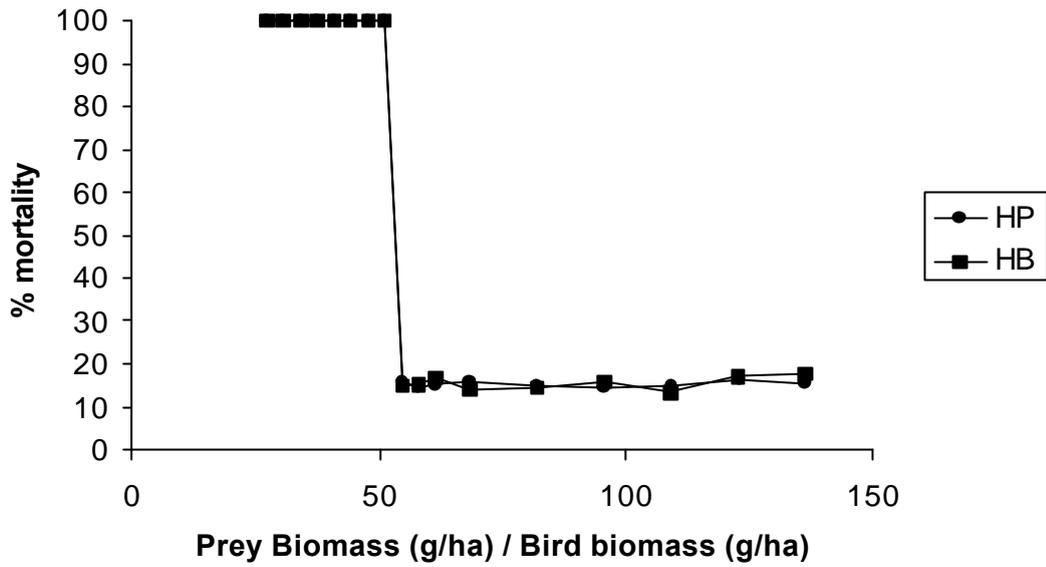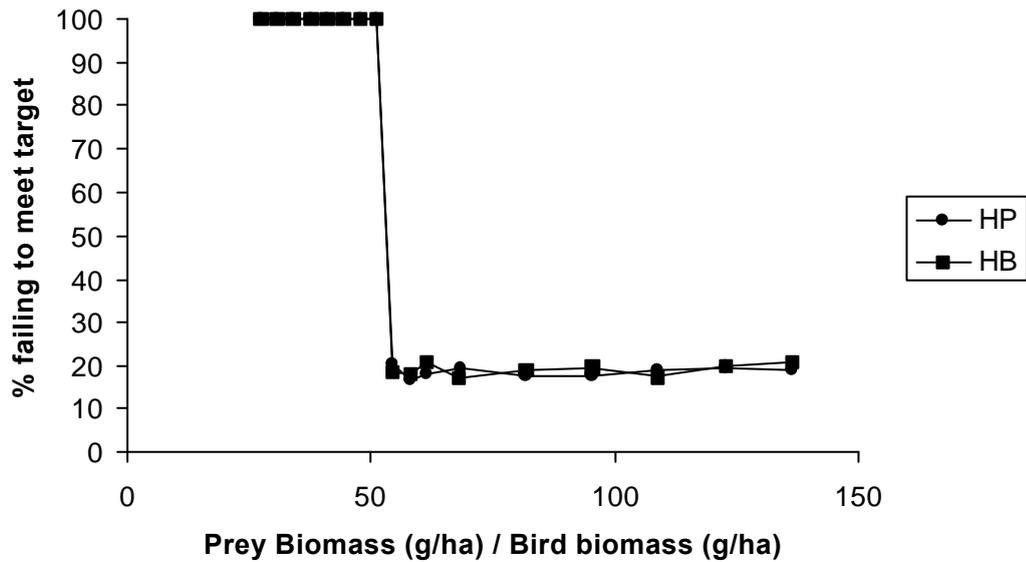
(a)

(b)

Figure 19 Percent mortality (a) and percent failing to reach 95% of target weight (b) for touch-feeding redshank, with 15% variation in feeding efficiency and interference based on prey depression. No aggregation was allowed.

HP = both bird and prey biomass high, with prey biomass varied
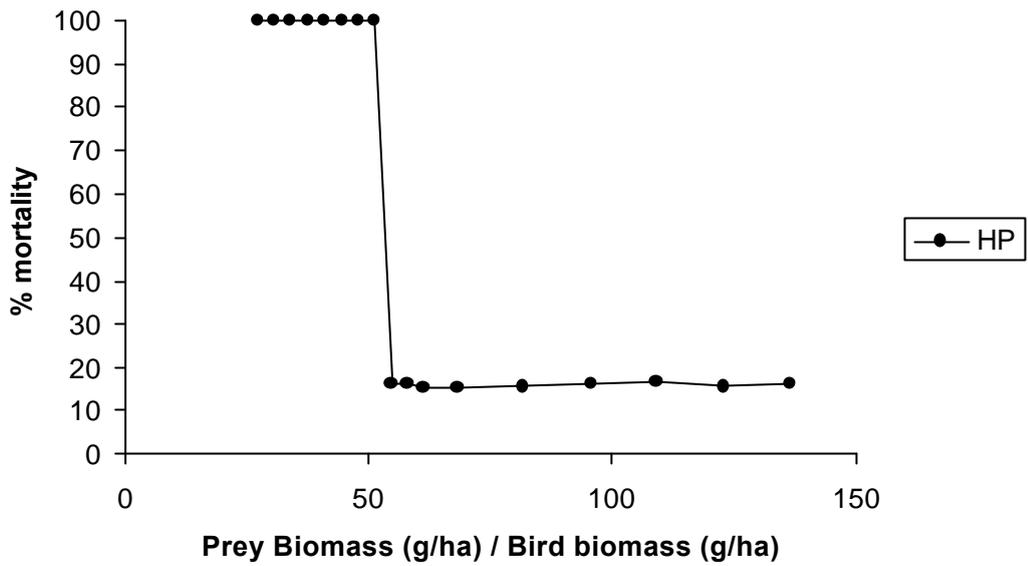
72

(a)

(b)

Figure 20 Percent mortality (a) and percent failing to reach 95% of target weight (b) for touch-feeding redshank, with 15% variation in feeding efficiency and interference based on kleptoparasitism. No aggregation was allowed.

HP = both bird and prey biomass high, with prey biomass varied.

(a)

(b)

Figure 21 Percent mortality (a) and percent failing to reach 75% of target fat (b) for touch-feeding redshank, with 15% variation in feeding efficiency, interference based on prey depression and varying degrees of aggregation.

HP = both bird and prey biomass high, with prey biomass varied; **1** = birds spread out over the whole feeding area, **2** = birds aggregate so their density is doubled (although bird numbers and patch area remain the same), **4** = birds aggregate so their density is quadrupled, etc.

(a)

(b)

Figure 22 Percent mortality (a) and percent failing to reach 95% of target weight (b) for touch-feeding redshank, with 15% variation in feeding efficiency and either with or without interference. An upshore feeding area of the same size and prey density as the downshore, but with smaller prey present.

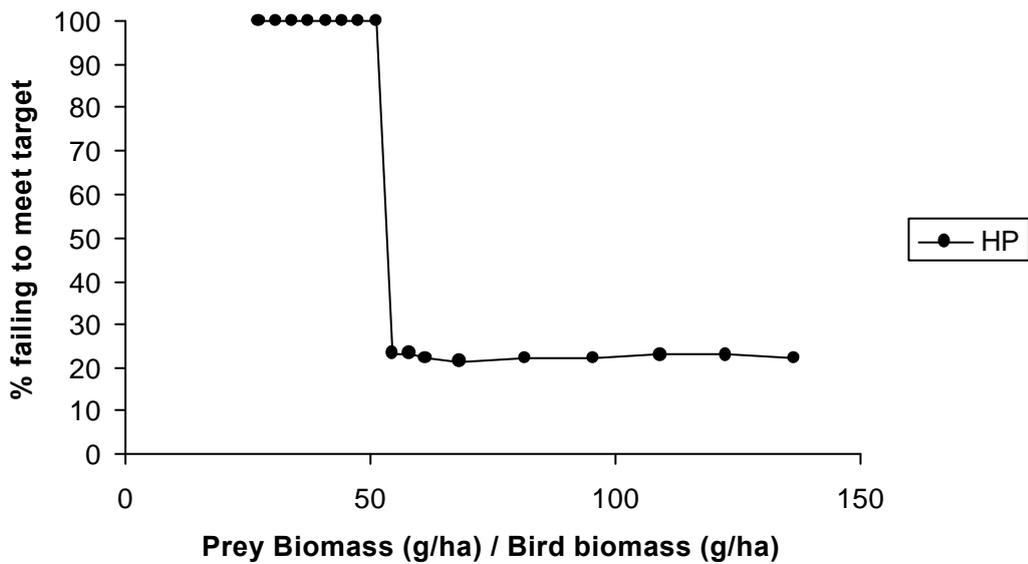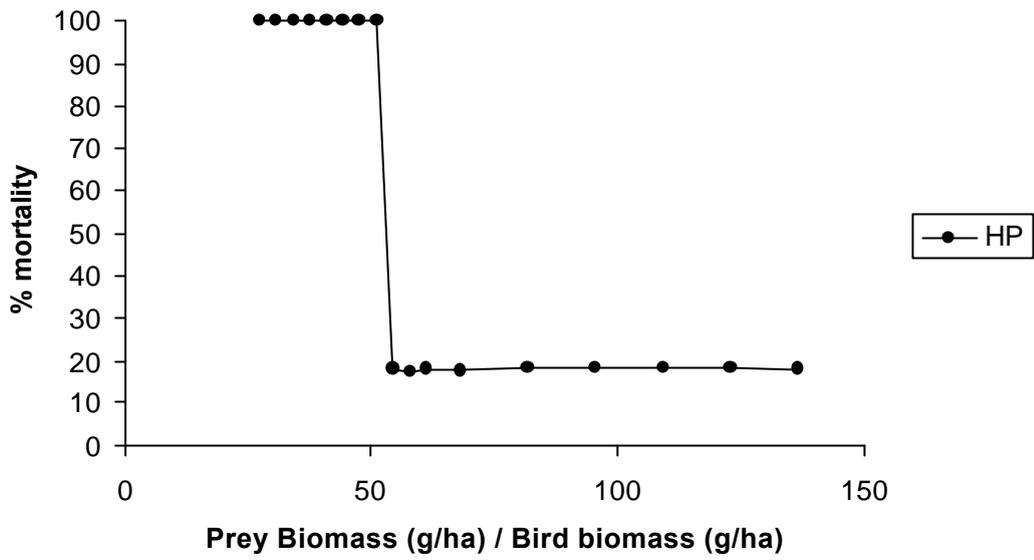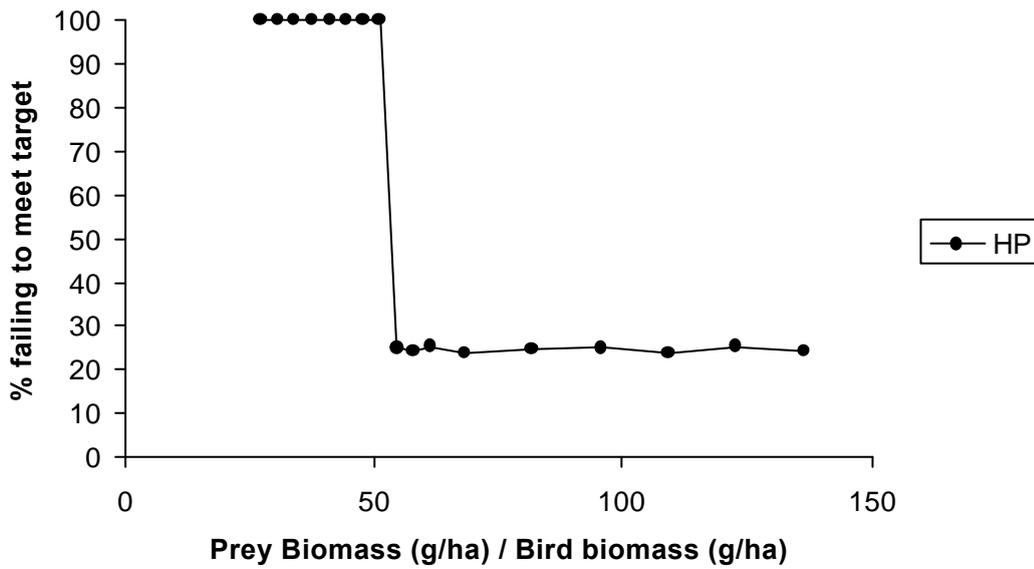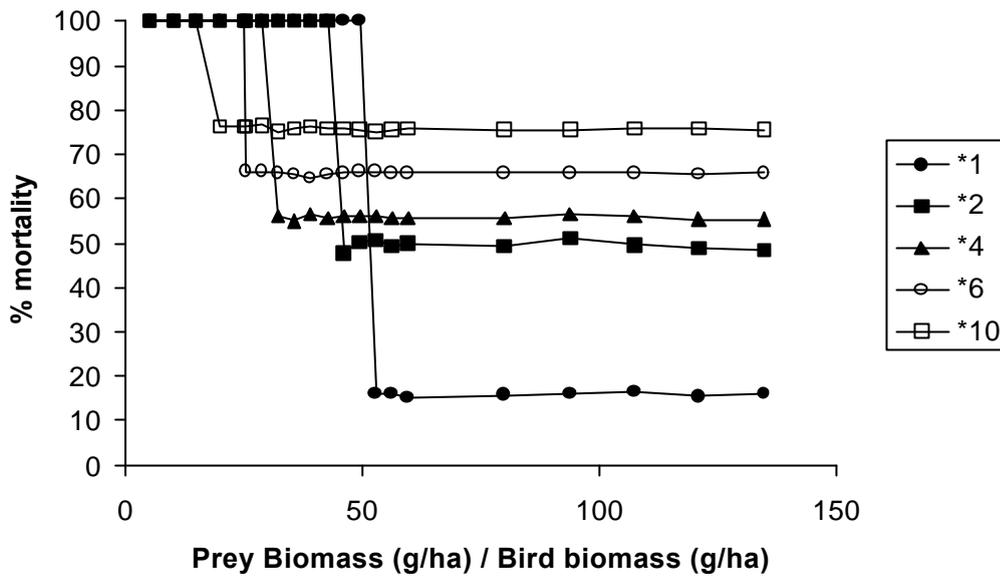**HP** = both bird and prey biomass high, with prey biomass varied; **HB** = both bird and prey biomass high, with bird biomass varied; **HPDI** = both bird and prey biomass high, with prey biomass varied and with depression-based interference.
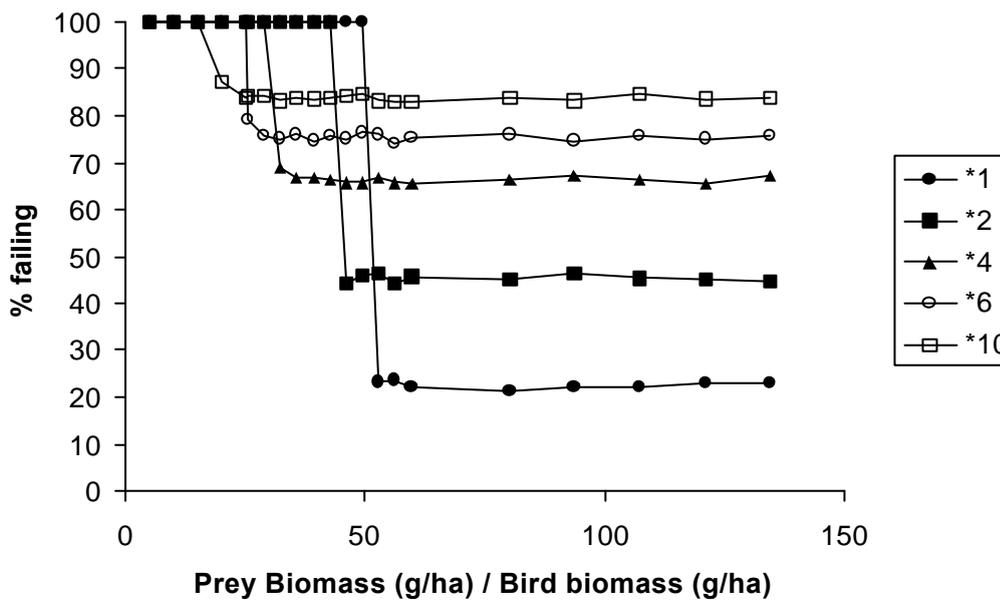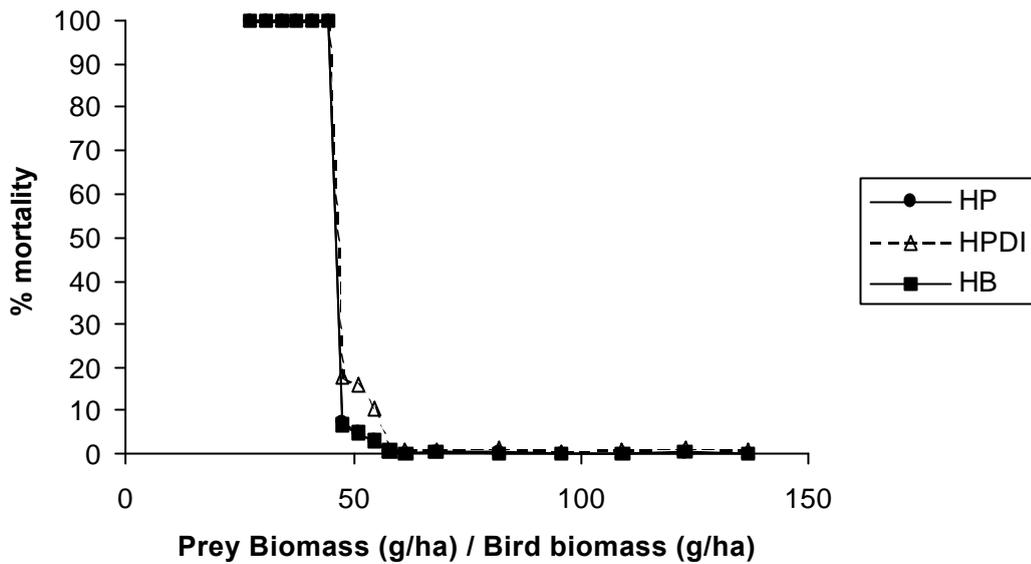
(a)

(b)

Figure 23 Percent mortality (a) and percent failing to reach 95% of target weight (b) for touch-feeding redshank, with 15% variation in feeding efficiency and either with or without interference. Prey ash-free dry mass declines by 50% over the winter.

HP = both bird and prey biomass high, with prey biomass varied; **HB** = both bird and prey biomass high, with bird biomass varied; **HPDI** = both bird and prey biomass high, with prey biomass varied and with depression-based interference.
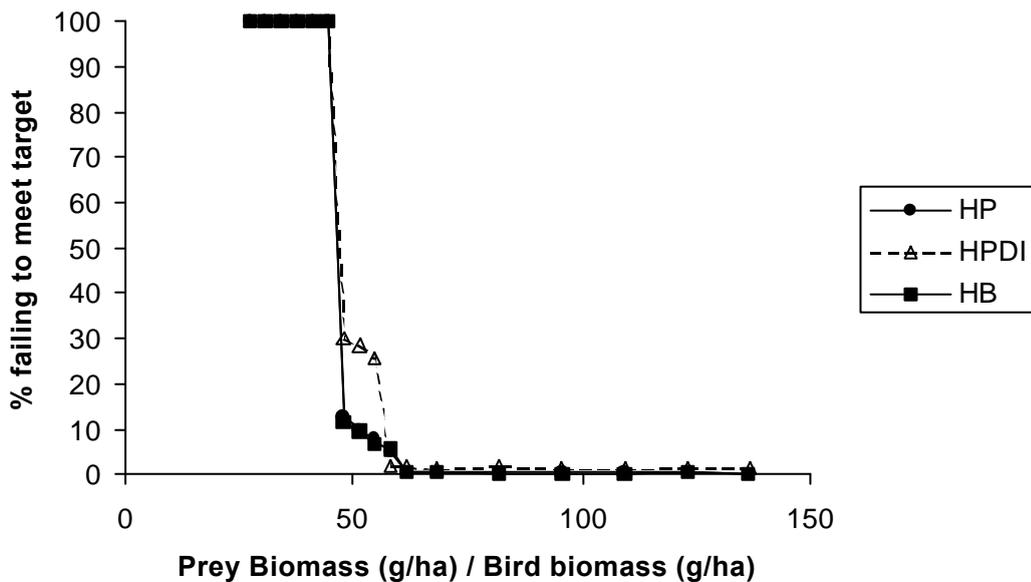
(a)

(b)

Figure 24 Percent mortality (a) and percent failing to reach 95% of target weight (b) for touch-feeding redshank, with 15% variation in feeding efficiency and either with or without interference. Temperature is consistently 5°C lower than normal.

HP = both bird and prey biomass high, with prey biomass varied; **HB** = both bird and prey biomass high, with bird biomass varied; **HPDI** = both bird and prey biomass high, with prey biomass varied and with depression-based interference.
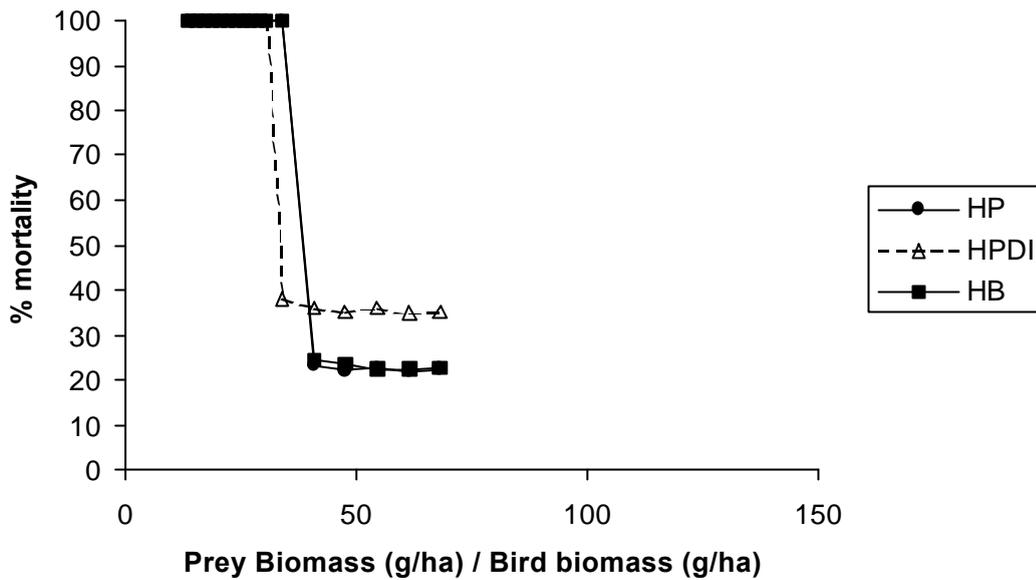
(a)

(b)

Figure 25 Percent mortality (a) and percent failing to reach 95% of target weight (b) for touch-feeding redshank, with 15% variation in feeding efficiency and either with or without interference. Upshore area, prey decline and cold weather included.

HP = both bird and prey biomass high, with prey biomass varied; **HB** = both bird and prey biomass high, with bird biomass varied; **HPDI** = both bird and prey biomass high, with prey biomass varied and with depression-based interference.
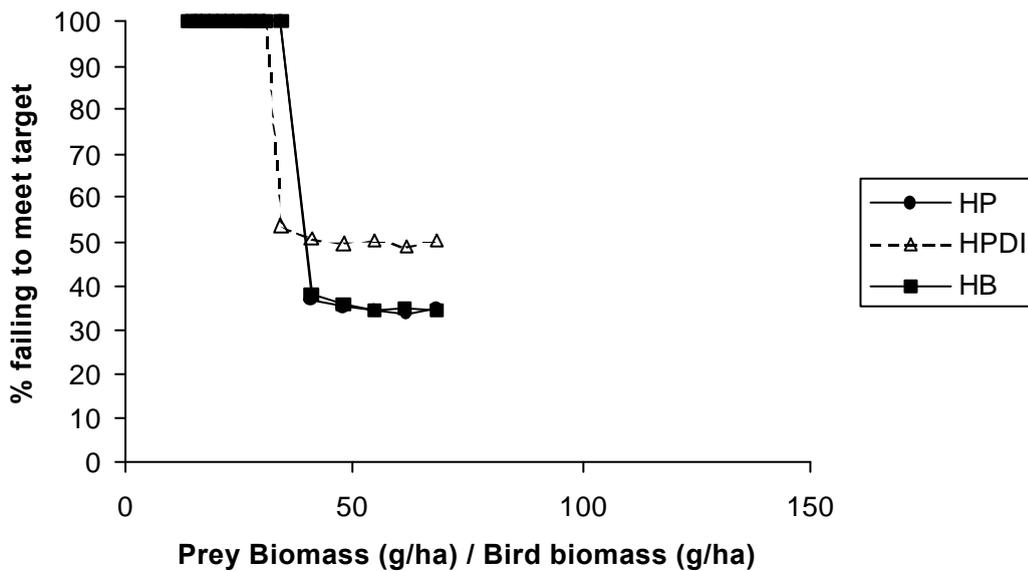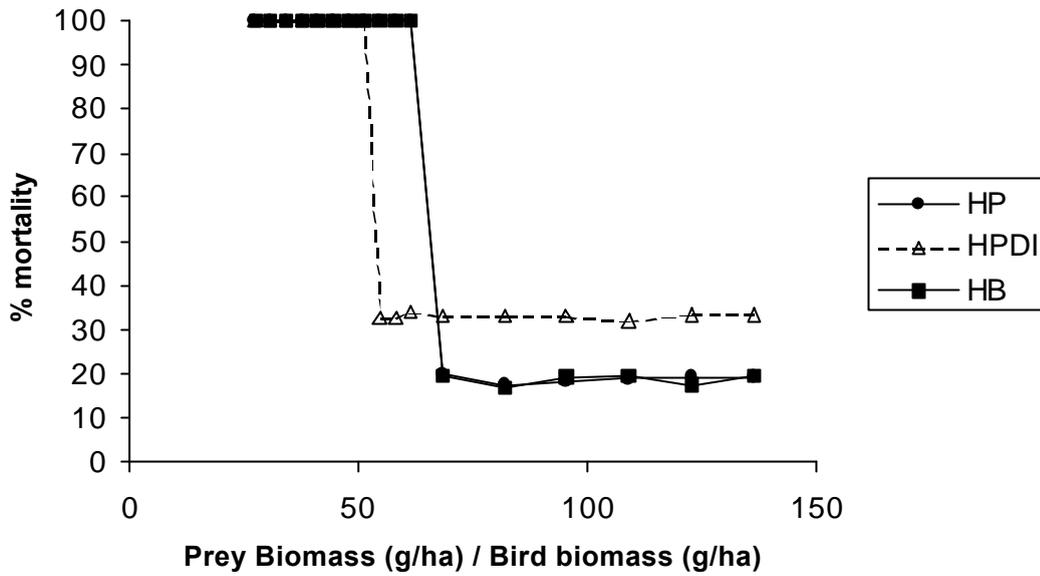
(a)

(b)

Figure 26 Percent mortality (a) and percent failing to reach 95% of target weight (b) for touch-feeding redshank, with 15% variation in feeding efficiency, interference based on prey depression and varying prey size.

HP = both bird and prey biomass high, with prey biomass varied.

(a)

(b)

Figure 27 Percent mortality (a) and percent failing to reach 95% of target weight (b) for touch-feeding redshank, with 15% variation in feeding efficiency, interference based on prey depression and varying prey size. Upshore area, prey decline and cold weather included.

HP = both bird and prey biomass high, with prey biomass varied
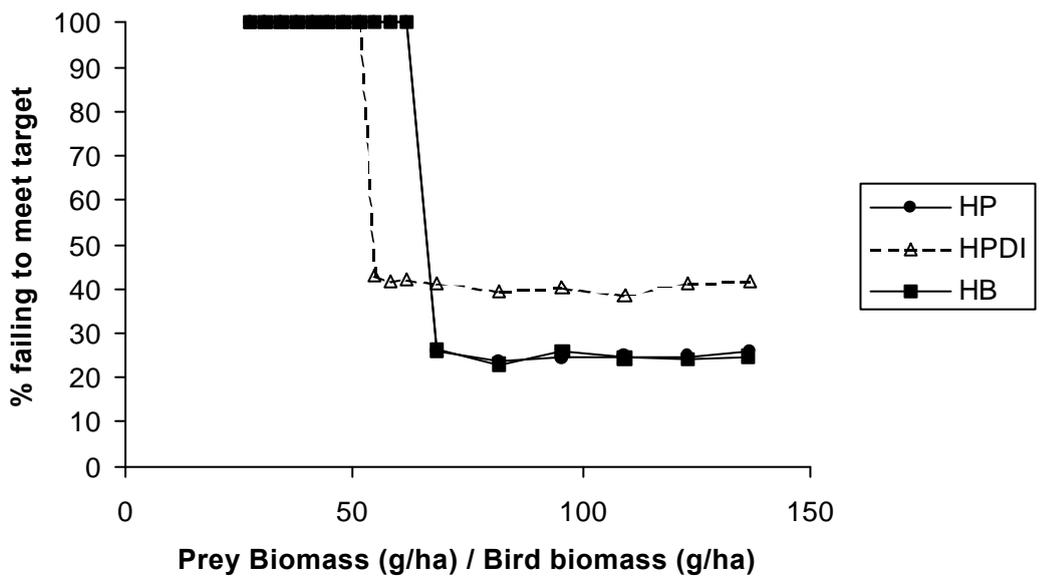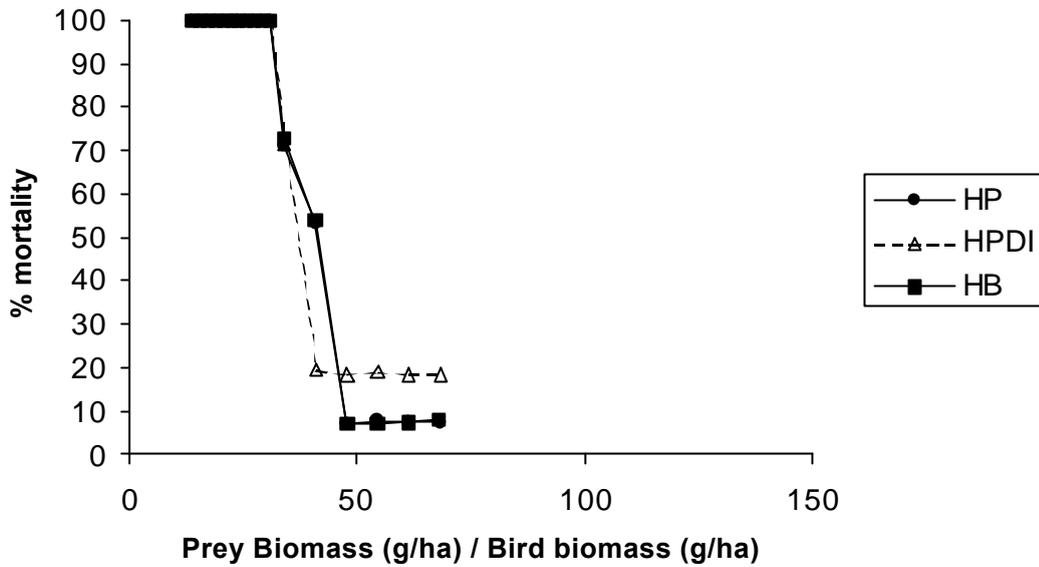
(a)

(b)

Figure 28 Percent mortality (a) and percent failing to reach 75% of target fat (b) for touch-feeding redshank, with 15% variation in feeding efficiency and depression-based interference.

HPDI = prey are in a single patch; **Pref** = Prey are distributed over 2 patches with differing prey sizes (20mg and 5mg). The biomass is the same in each patch.
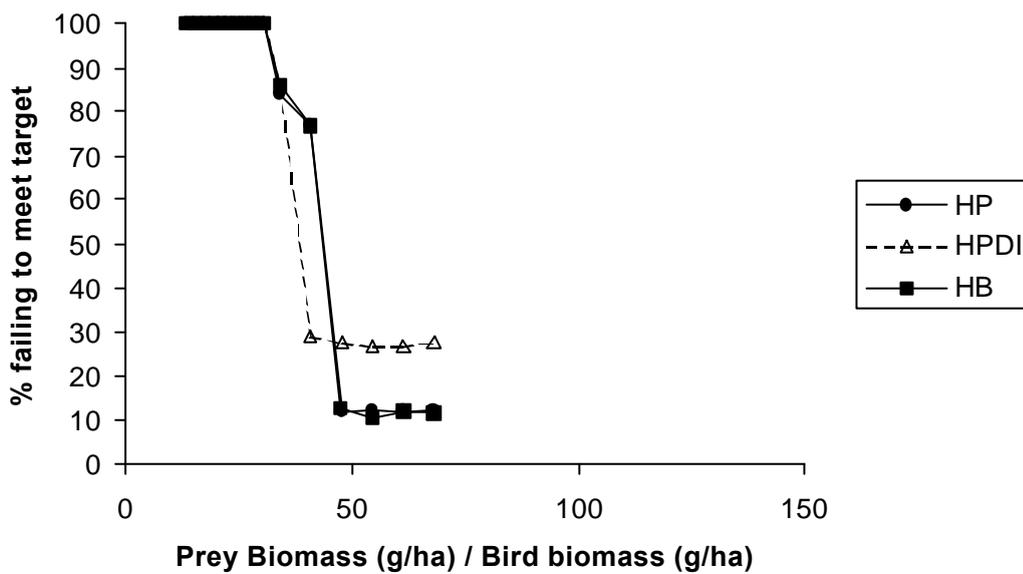
(a)

(b)

Figure 29 Percent mortality (a) and percent failing to reach 95% of target weight (b) for sight-feeding dunlin, with 5% variation in feeding efficiency and no interference.

HP = both bird and prey biomass high, with prey biomass varied; **HB** = both bird and prey biomass high, with bird biomass varied.
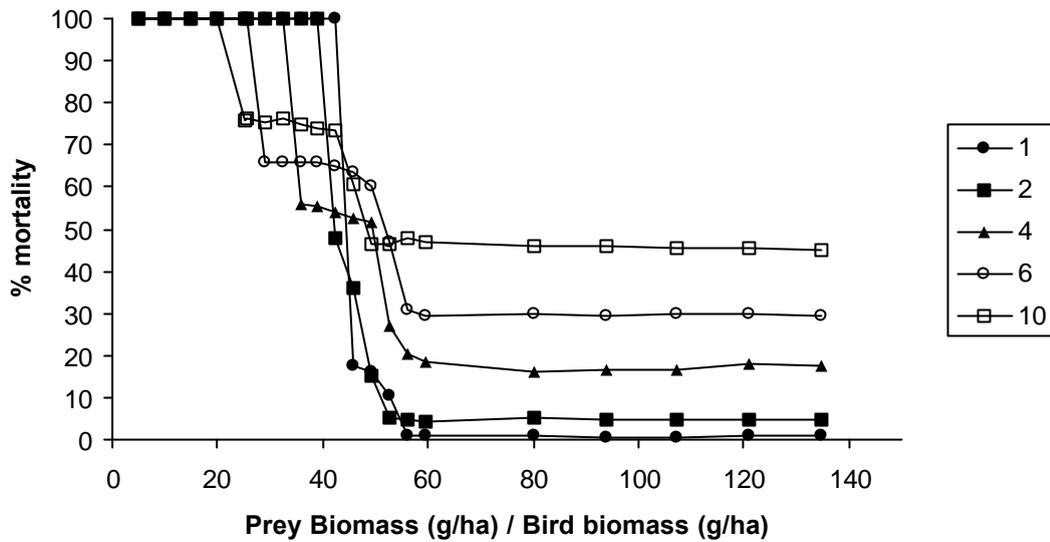
(a)

(b)

Figure 30 Percent mortality (a) and percent failing to reach 95% of target weight (b) for sight-feeding dunlin, with 15% variation in feeding efficiency and no interference.

HP = both bird and prey biomass high, with prey biomass varied; **HB** = both bird and prey biomass high, with bird biomass varied.
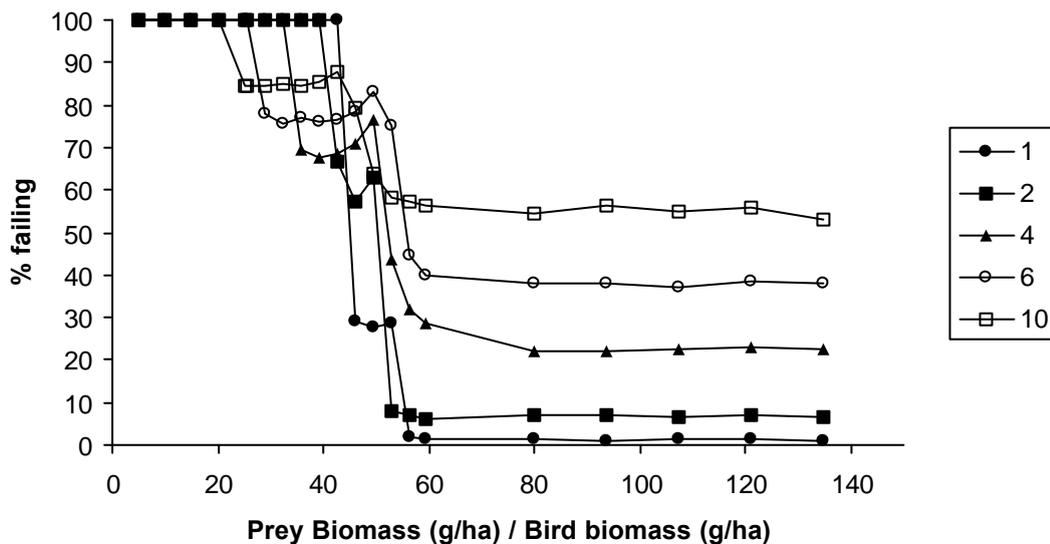
(a)

(b)

Figure 31 Percent mortality (a) and percent failing to reach 95% of target weight (b) for sight-feeding dunlin, with 25% variation in feeding efficiency and no interference.

HP = both bird and prey biomass high, with prey biomass varied; **HB** = both bird and prey biomass high, with bird biomass varied.
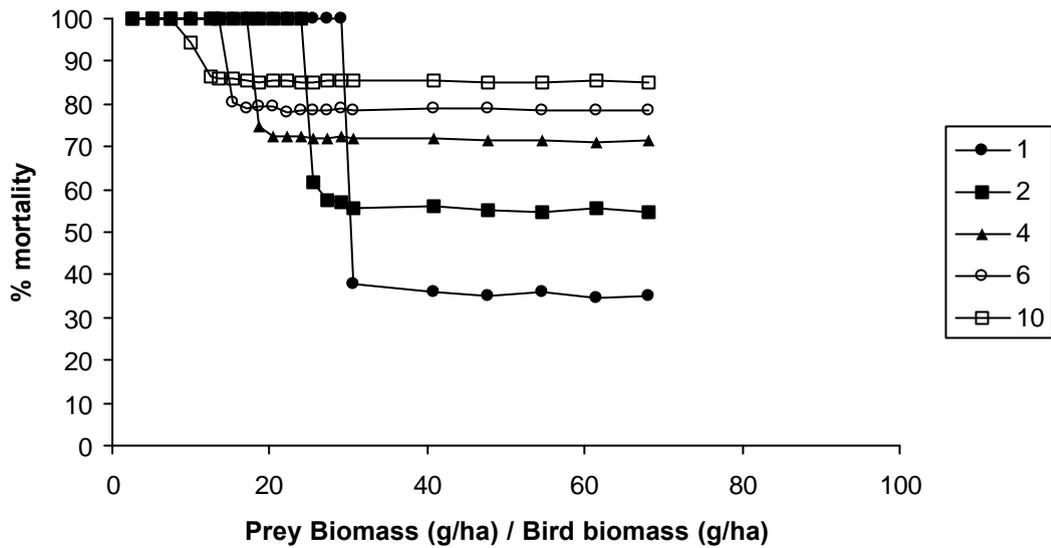
(a)

(b)

Figure 32 Percent mortality (a) and percent failing to reach 95% of target weight (b) for sight-feeding dunlin, with 15% variation in feeding efficiency and interference based on prey depression.

HP = both bird and prey biomass high, with prey biomass varied.

(a)

(b)

Figure 33 Percent mortality (a) and percent failing to reach 95% of target weight (b) for sight-feeding dunlin, with 15% variation in feeding efficiency and interference based on kleptoparasitism.

HP = both bird and prey biomass high, with prey biomass varied.
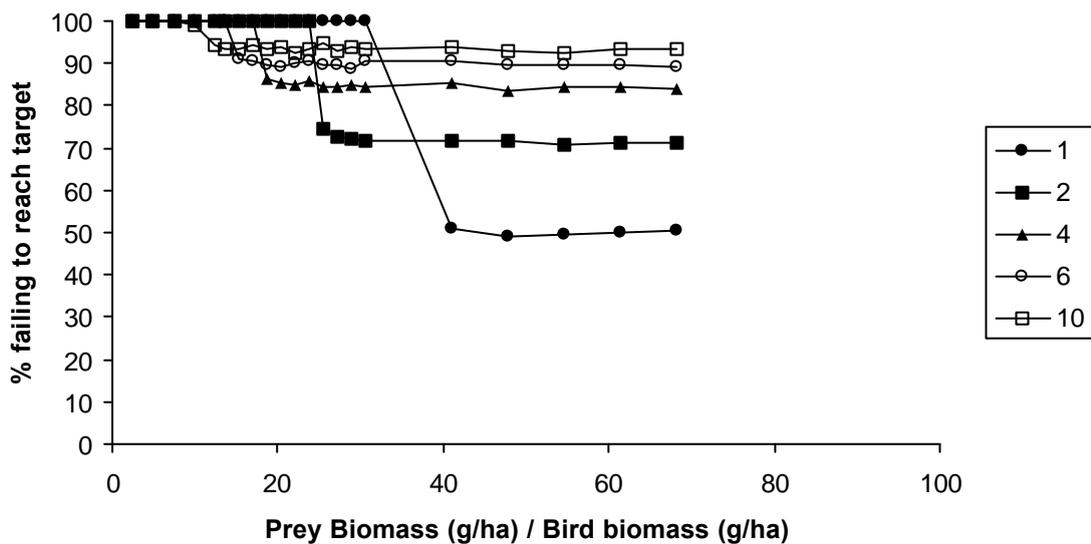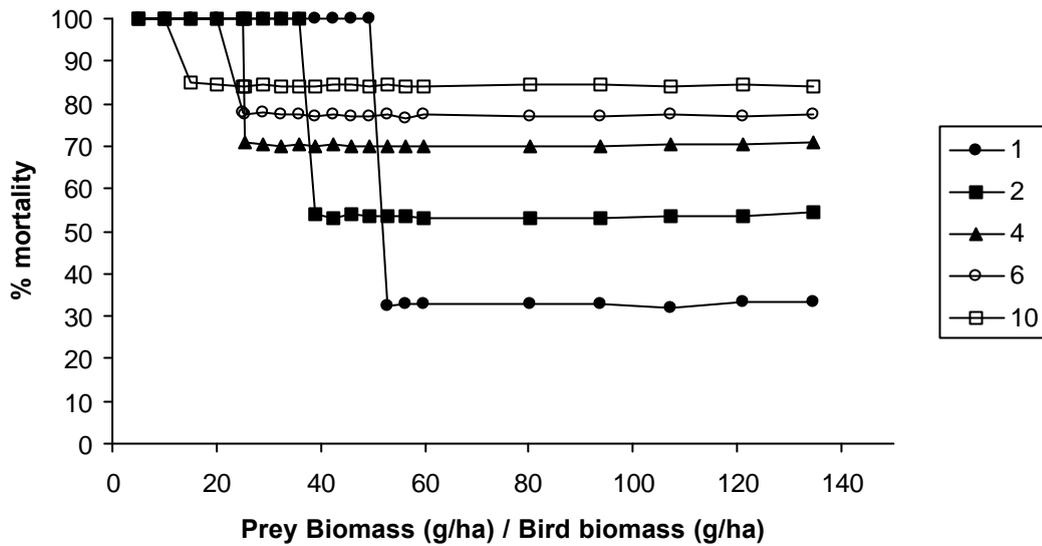
(a)

(b)

Figure 34 Percent mortality (a) and percent failing to reach 75% of target fat (b) for sight-feeding dunlin, with 15% variation in feeding efficiency, interference based on prey depression and varying degrees of aggregation.

HP = both bird and prey biomass high, with prey biomass varied; **1** = birds spread out over the whole feeding area, **2** = birds aggregate so their density is doubled (although bird numbers and patch area remain the same), **4** = birds aggregate so their density is quadrupled, etc.
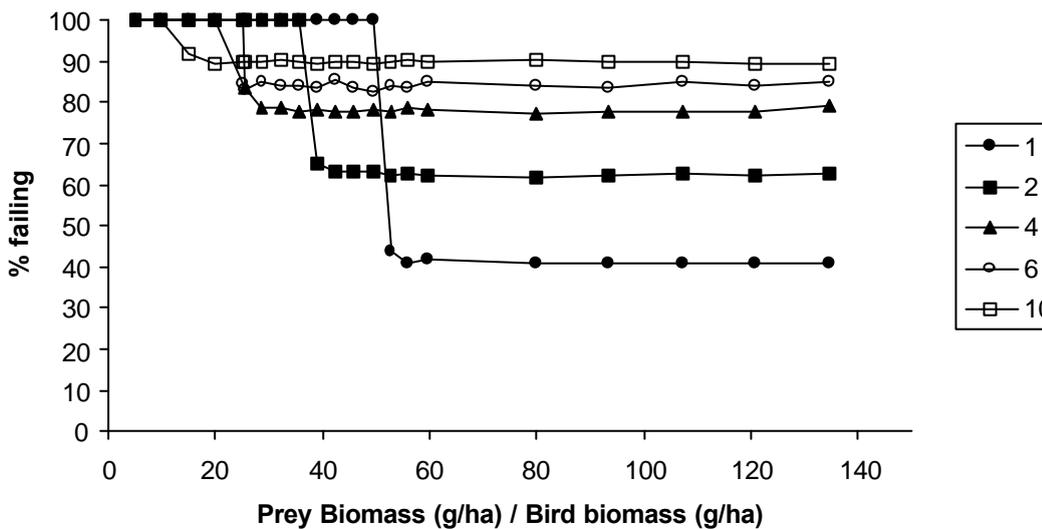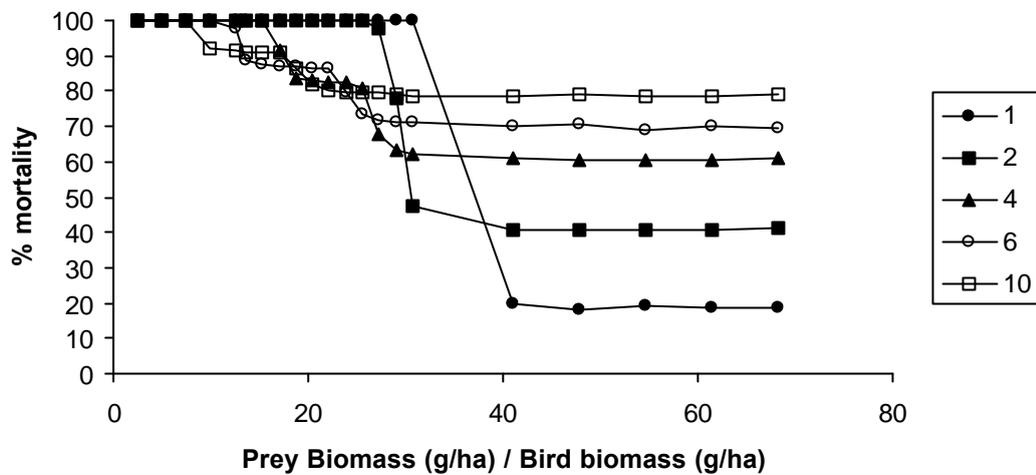
(a)

(b)

Figure 35 Percent mortality (a) and percent failing to reach 95% of target weight (b) for sight-feeding dunlin, with 15% variation in feeding efficiency and with and without interference. An upshore feeding area of the same size and prey density as the downshore, but with smaller prey is present.

HP = both bird and prey biomass high, with prey biomass varied; **HB** = both bird and prey biomass high, with bird biomass varied; **HPDI** = both bird and prey biomass high, with prey biomass varied and with depression-based interference.

(a)

(b)

Figure 36 Percent mortality (a) and percent failing to reach 95% of target weight (b) for sight-feeding dunlin, with 15% variation in feeding efficiency and with and without interference. Prey ash-free dry mass declines by 50% over the winter.

HP = both bird and prey biomass high, with prey biomass varied; **HB** = both bird and prey biomass high, with bird biomass varied; **HPDI** = both bird and prey biomass high, with prey biomass varied and with depression-based interference.
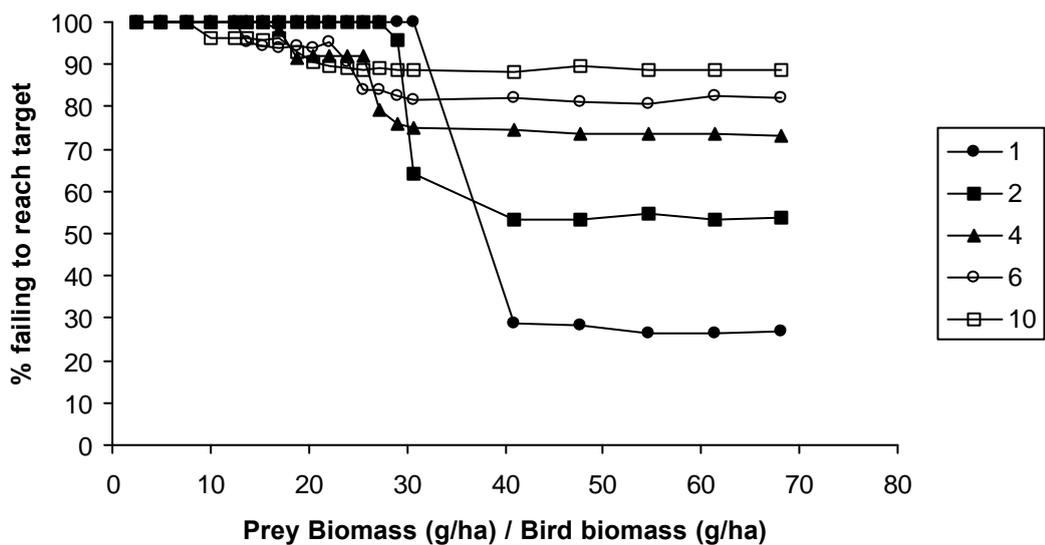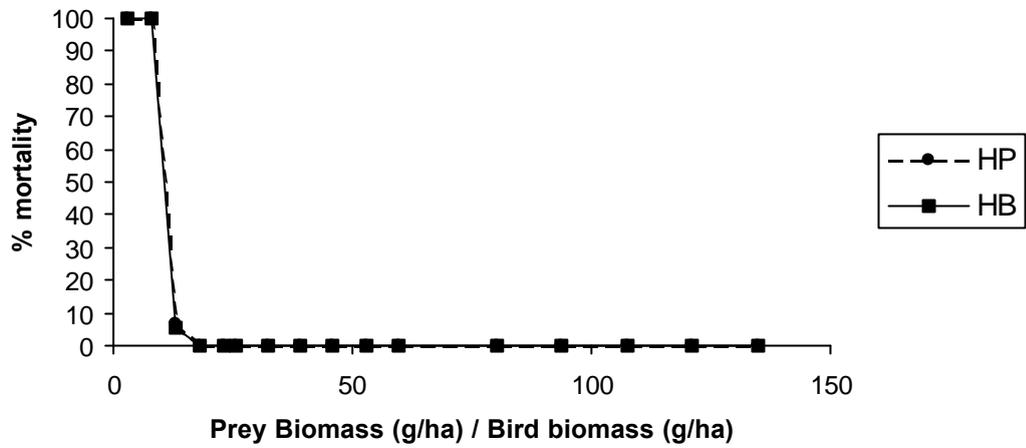
(a)

(b)

Figure 37 Percent mortality (a) and percent failing to reach 95% of target weight (b) for sight-feeding dunlin, with 15% variation in feeding efficiency and with and without interference. Temperature is consistently 5°C lower than normal.

HP = both bird and prey biomass high, with prey biomass varied; **HB** = both bird and prey biomass high, with bird biomass varied; **HPDI** = both bird and prey biomass high, with prey biomass varied and with depression-based interference.
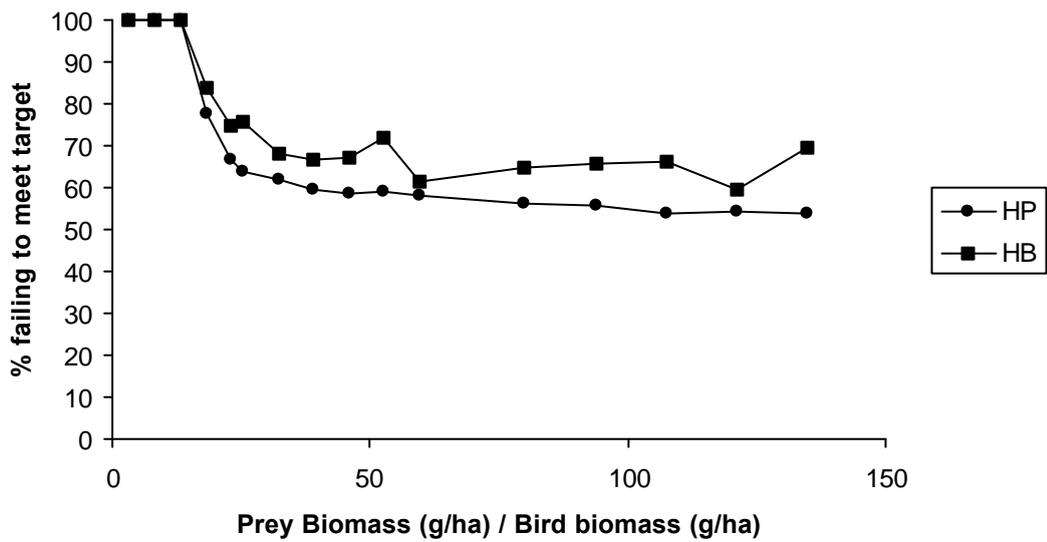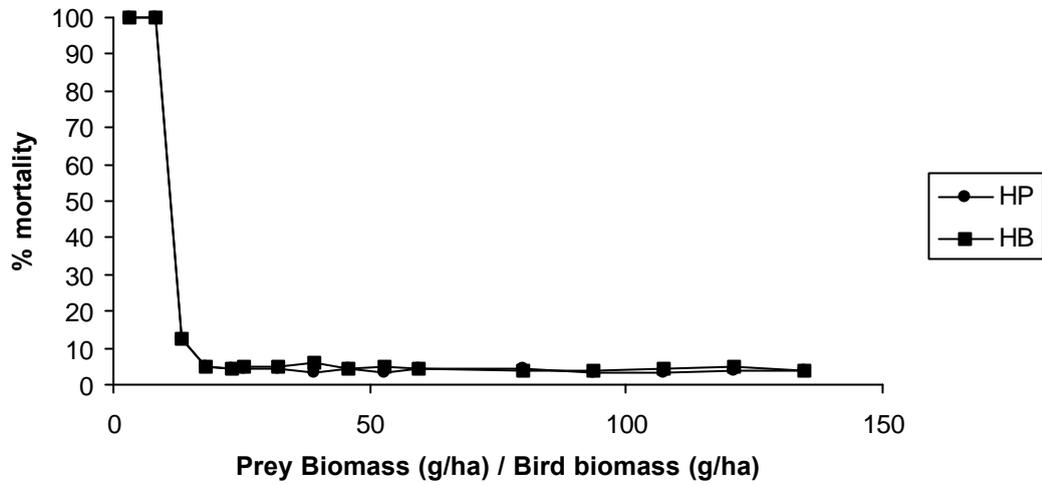
(a)

(b)

Figure 38 Percent mortality (a) and percent failing to reach 95% of target weight (b) for sight-feeding dunlin, with 15% variation in feeding efficiency and with and without interference. Upshore area, prey decline and cold weather included.

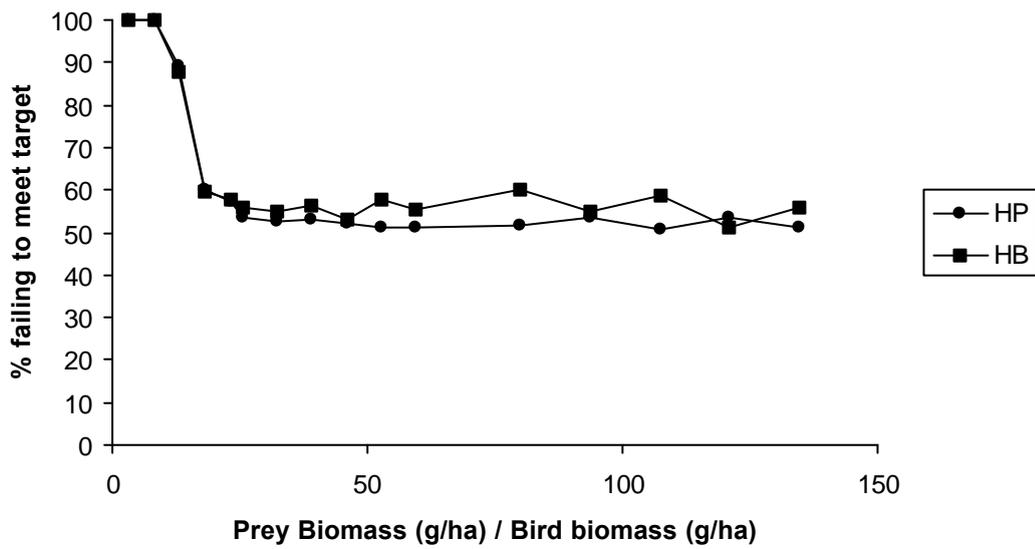**HP** = both bird and prey biomass high, with prey biomass varied; **HB** = both bird and prey biomass high, with bird biomass varied; **HPDI** = both bird and prey biomass high, with prey biomass varied and with depression-based interference.
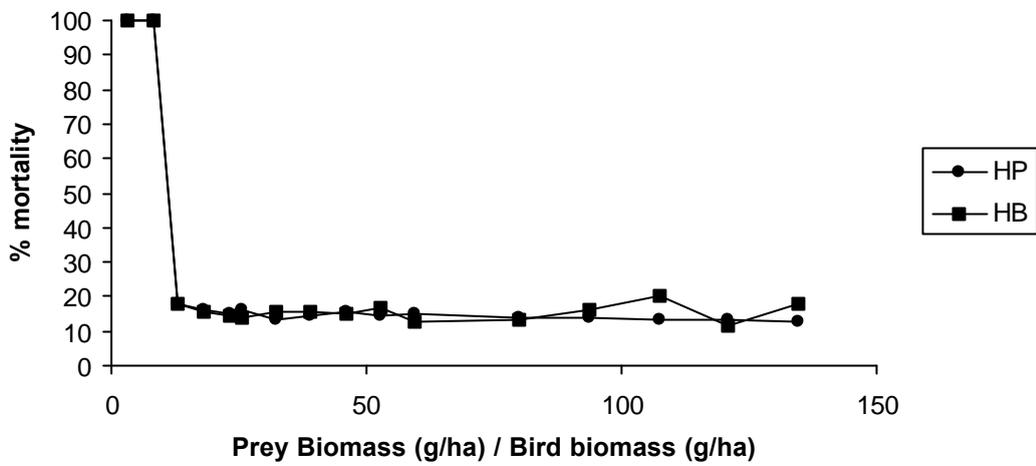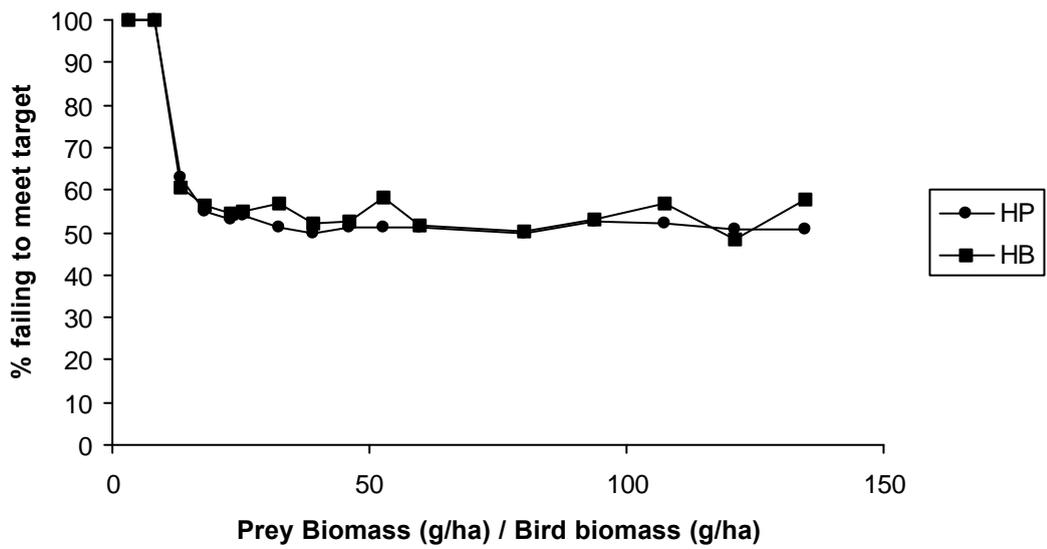
(a)

(b)

Figure 39 Percent mortality (a) and percent failing to reach 75% of target fat (b) for sight-feeding dunlin, with 15% variation in feeding efficiency, depression-based interference and varying degrees of aggregation. An upshore feeding area of the same size and prey density as the downshore, but with smaller prey is present.

HP = both bird and prey biomass high, with prey biomass varied; **1** = birds spread out over the whole feeding area, **2** = birds aggregate so their density is doubled (although bird numbers and patch area remain the same), **4** = birds aggregate so their density is quadrupled, etc.
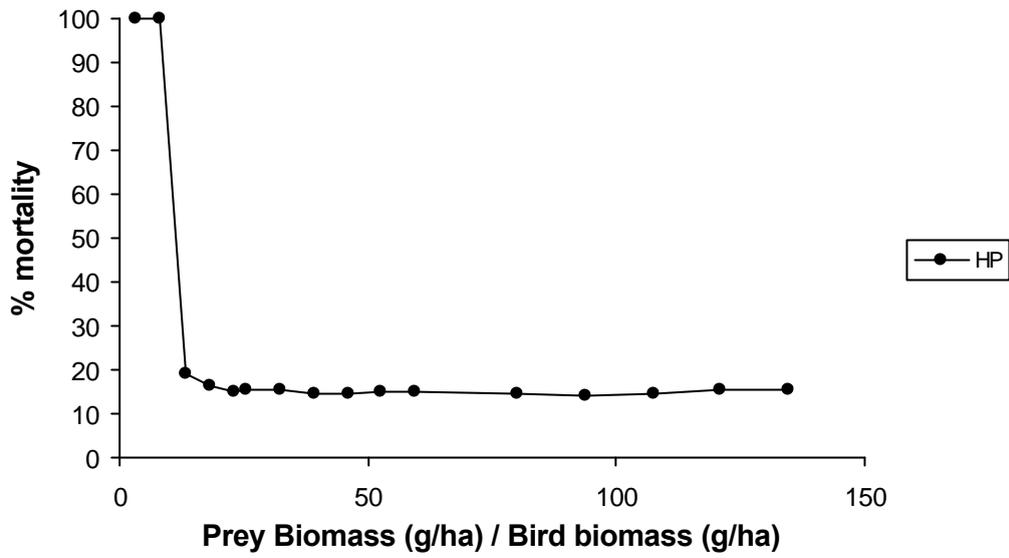
(a)

(b)

Figure 40 Percent mortality (a) and percent failing to reach 75% of target fat (b) for sight-feeding dunlin, with 15% variation in feeding efficiency, depression-based interference and varying degrees of aggregation. Prey ash-free dry mass declines by 50% over the winter.

HP = both bird and prey biomass high, with prey biomass varied; **1** = birds spread out over the whole feeding area, **2** = birds aggregate so their density is doubled (although bird numbers and patch area remain the same), **4** = birds aggregate so their density is quadrupled, etc.
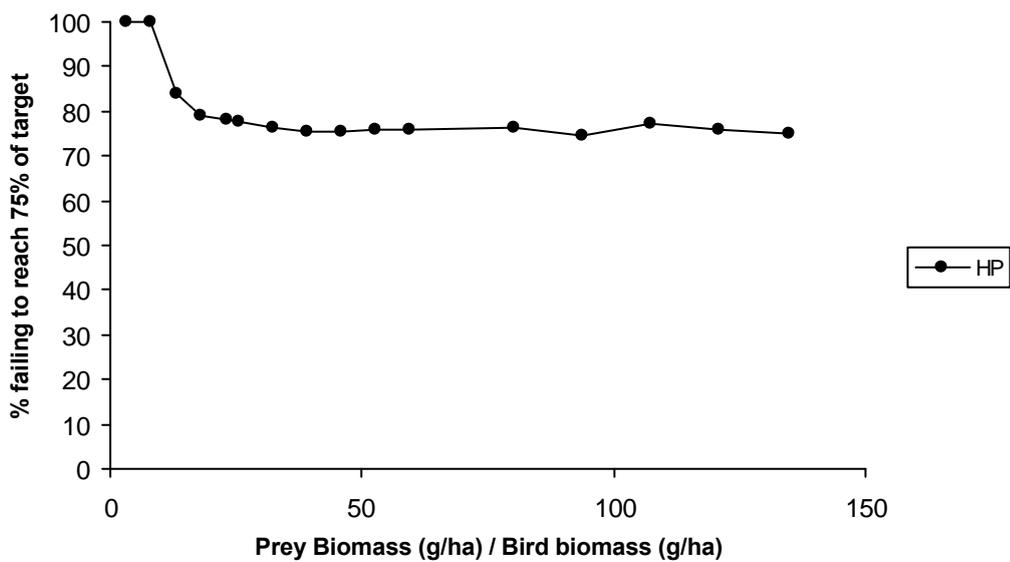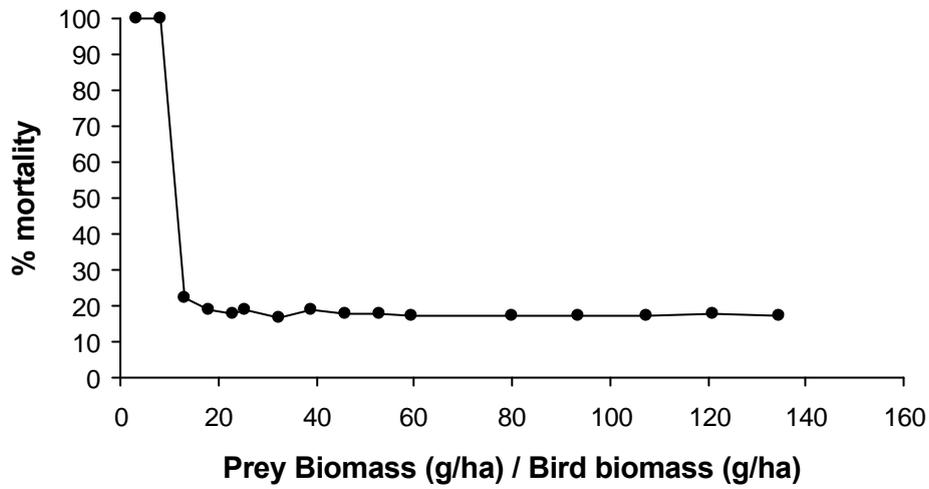
(a)

(b)

Figure 41 Percent mortality (a) and percent failing to reach 75% of target fat (b) for sight-feeding dunlin, with 15% variation in feeding efficiency, depression-based interference and varying degrees of aggregation. Temperature is consistently 5°C lower than normal.

HP = both bird and prey biomass high, with prey biomass varied; **1** = birds spread out over the whole feeding area, **2** = birds aggregate so their density is doubled (although bird numbers and patch area remain the same), **4** = birds aggregate so their density is quadrupled, etc.
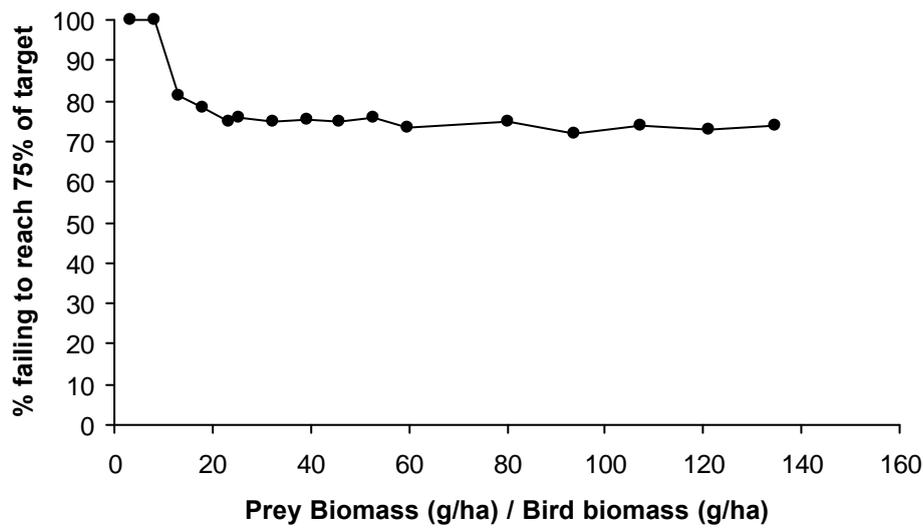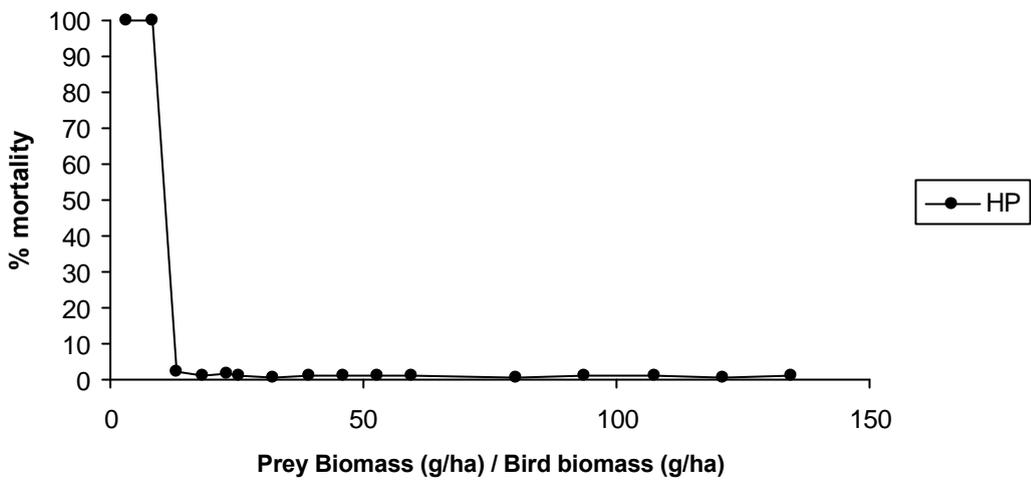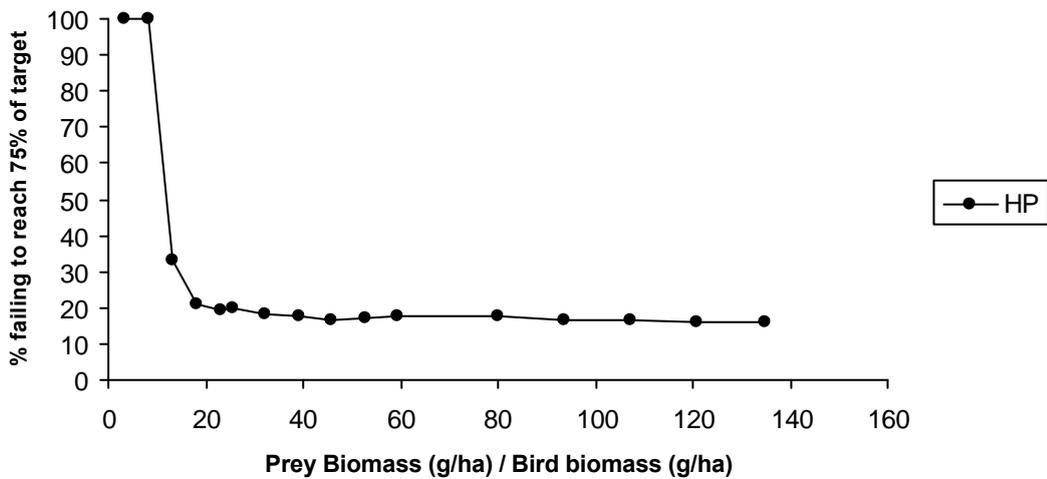
(a)

(b)

Figure 42 Percent mortality (a) and percent failing to reach 75% of target fat (b) for sight-feeding dunlin, with 15% variation in feeding efficiency, depression-based interference and varying degrees of aggregation. Upshore area, prey decline and cold weather included.

HP = both bird and prey biomass high, with prey biomass varied; **1** = birds spread out over the whole feeding area, **2** = birds aggregate so their density is doubled (although bird numbers and patch area remain the same), **4** = birds aggregate so their density is quadrupled, etc.
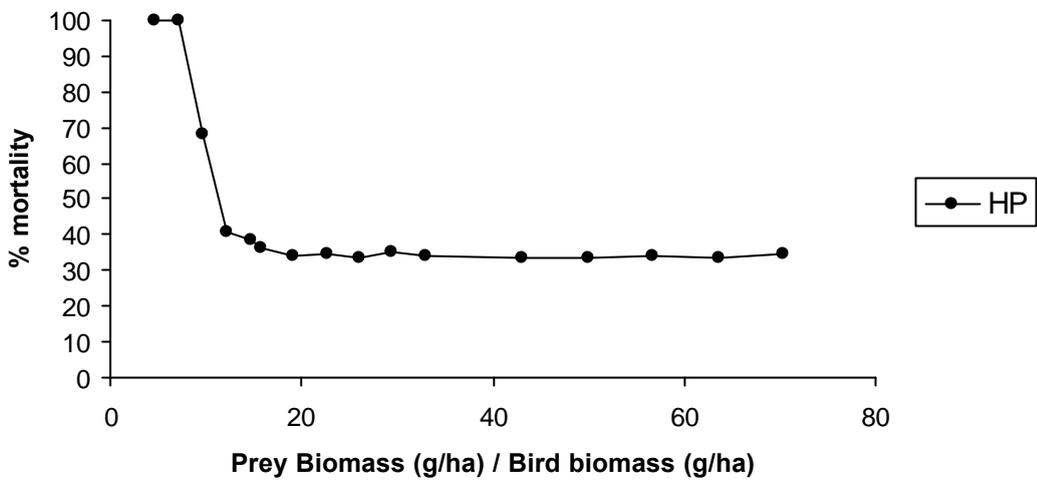
(a)

(b)

Figure 43 Percent mortality (a) and percent failing to reach 95% of target weight (b) for sight-feeding curlew, with 5% variation in feeding efficiency and no interference.

HP = both bird and prey biomass high, with prey biomass varied; **HB** = both bird and prey biomass high, with bird biomass varied.
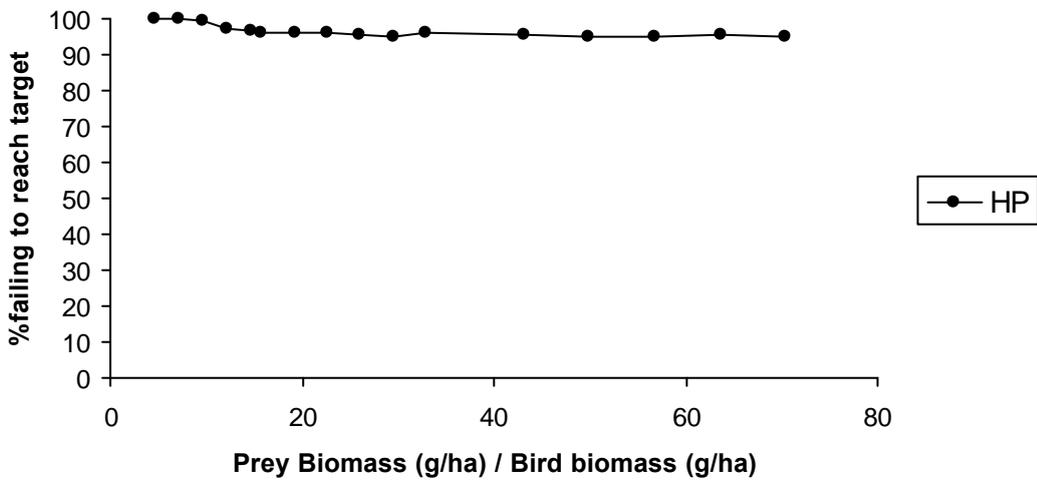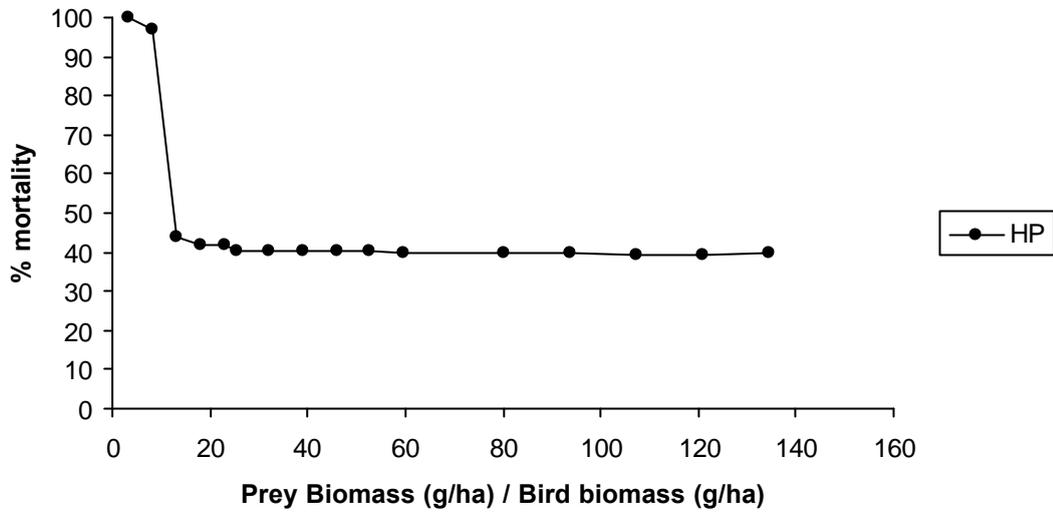
(a)

(b)

Figure 44 Percent mortality (a) and percent failing to reach 95% of target weight (b) for sight-feeding curlew, with 15% variation in feeding efficiency and no interference.

HP = both bird and prey biomass high, with prey biomass varied; **HB** = both bird and prey biomass high, with bird biomass varied.

(a)

(b)

Figure 45 Percent mortality (a) and percent failing to reach 95% of target weight (b) for sight-feeding curlew, with 25% variation in feeding efficiency and no interference.

HP = both bird and prey biomass high, with prey biomass varied; **HB** = both bird and prey biomass high, with bird biomass varied.
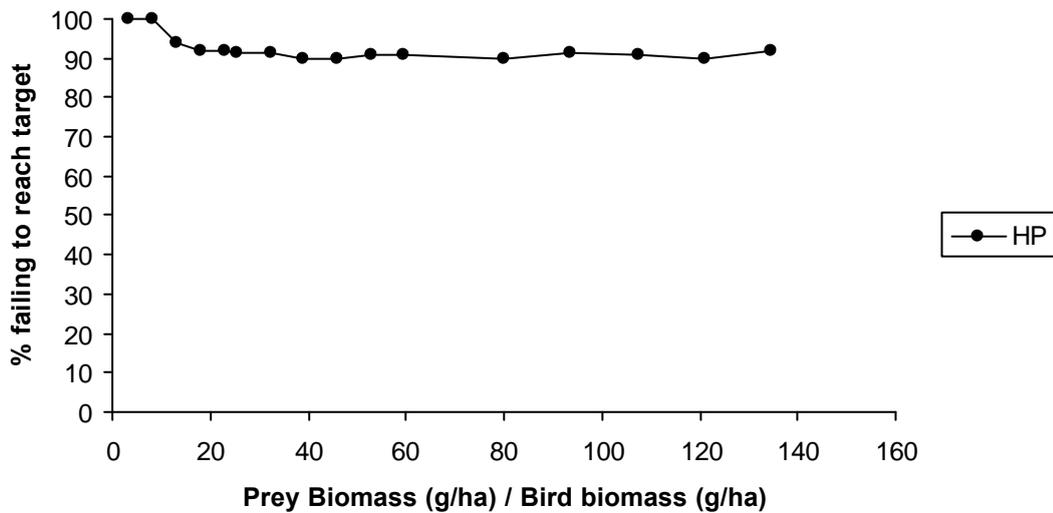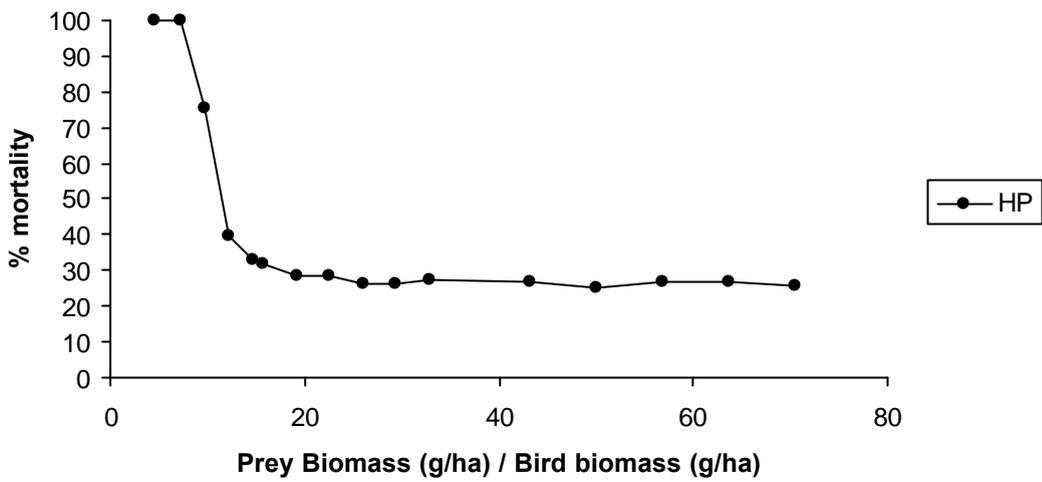
(a)

(b)

Figure 46 Percent mortality (a) and percent failing to reach 75% of target fat (b) for sight-feeding curlew, with 15% variation in feeding efficiency and interference based on prey depression.

HP = both bird and prey biomass high, with prey biomass varied.
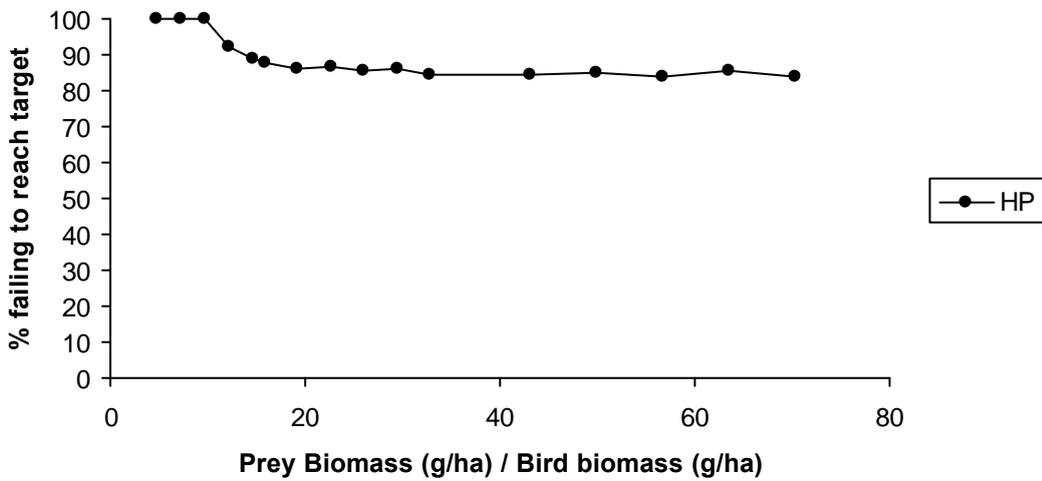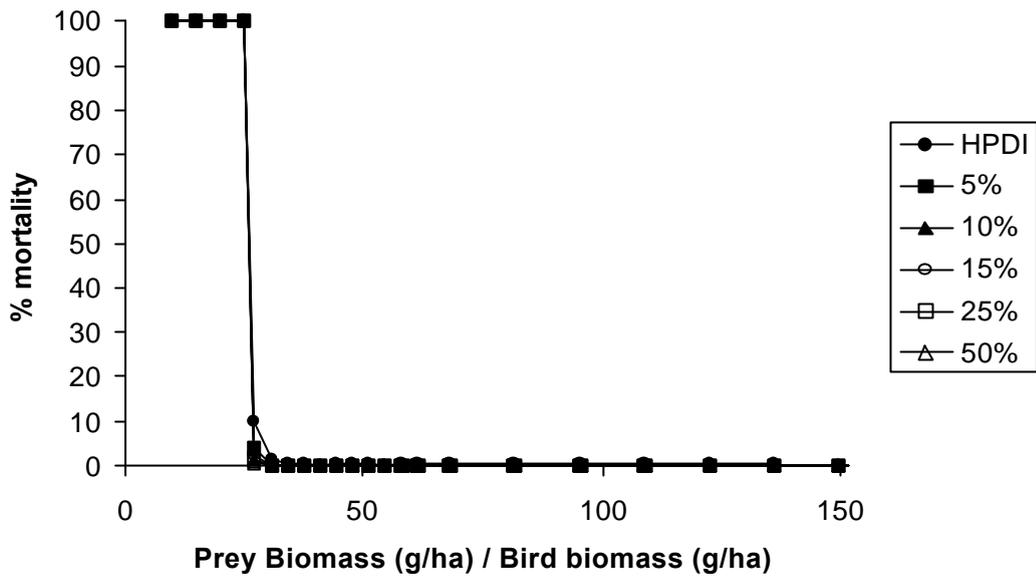
(a)

(b)

Figure 47 Percent mortality (a) and percent failing to reach 75% of target fat (b) for sight-feeding curlew, with 15% variation in feeding efficiency and interference based on kleptoparasitism.

HP = both bird and prey biomass high, with prey biomass varied.
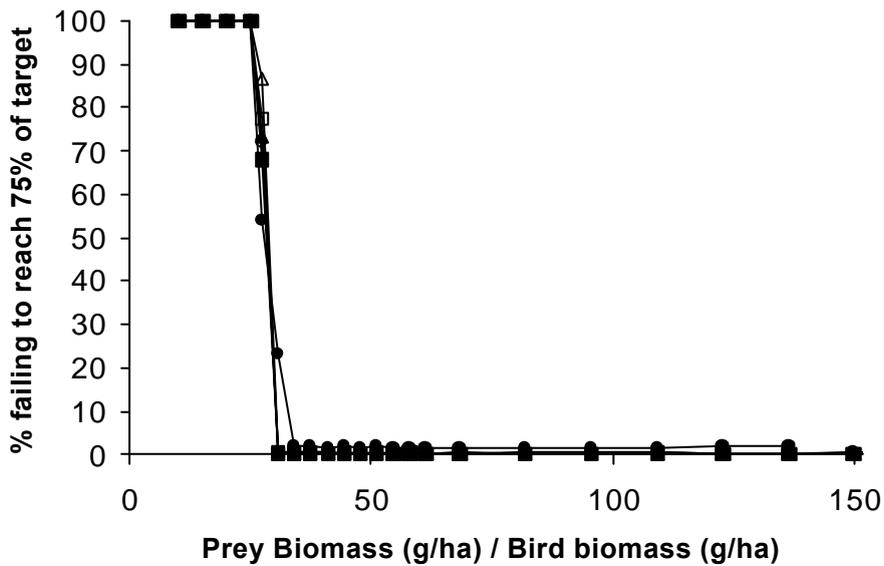
(a)

(b)

Figure 48 Percent mortality (a) and percent failing to reach 75% of target fat (b) for sight-feeding curlew, with 15% variation in feeding efficiency and interference based on prey depression. An upshore feeding area of the same size and prey density as the downshore, but with smaller prey is present.

HP = both bird and prey biomass high, with prey biomass varied.
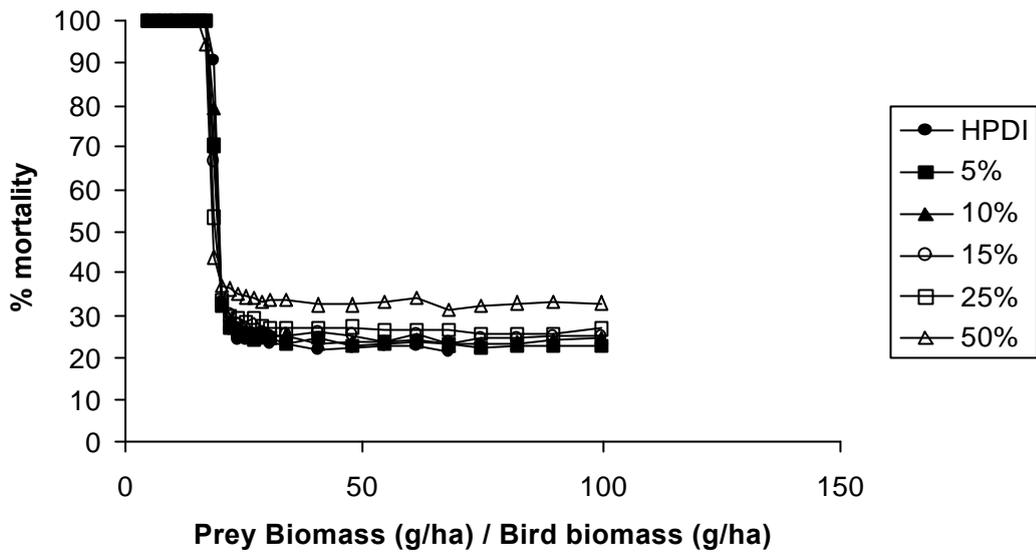
(a)

(b)

Figure 49 Percent mortality (a) and percent failing to reach 75% of target fat (b) for sight-feeding curlew, with 15% variation in feeding efficiency and interference based on prey depression. Prey ash-free dry mass declines by 50% over the winter.

HP = both bird and prey biomass high, with prey biomass varied.
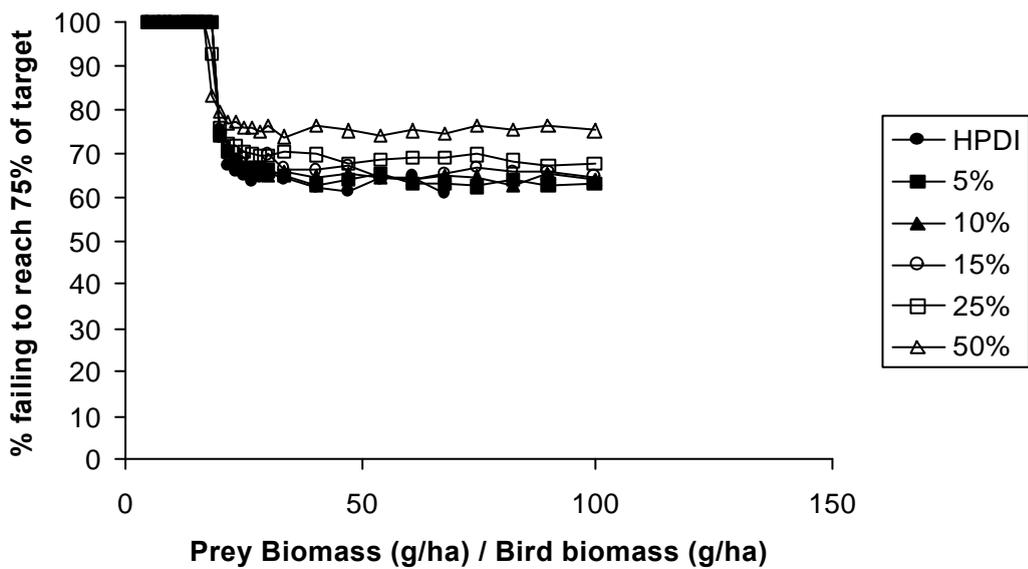
(a)

(b)

Figure 50 Percent mortality (a) and percent failing to reach 75% of target fat (b) for sight-feeding curlew, with 15% variation in feeding efficiency and interference based on prey depression. Temperature is consistently 5°C lower than normal.

HP = both bird and prey biomass high, with prey biomass varied.
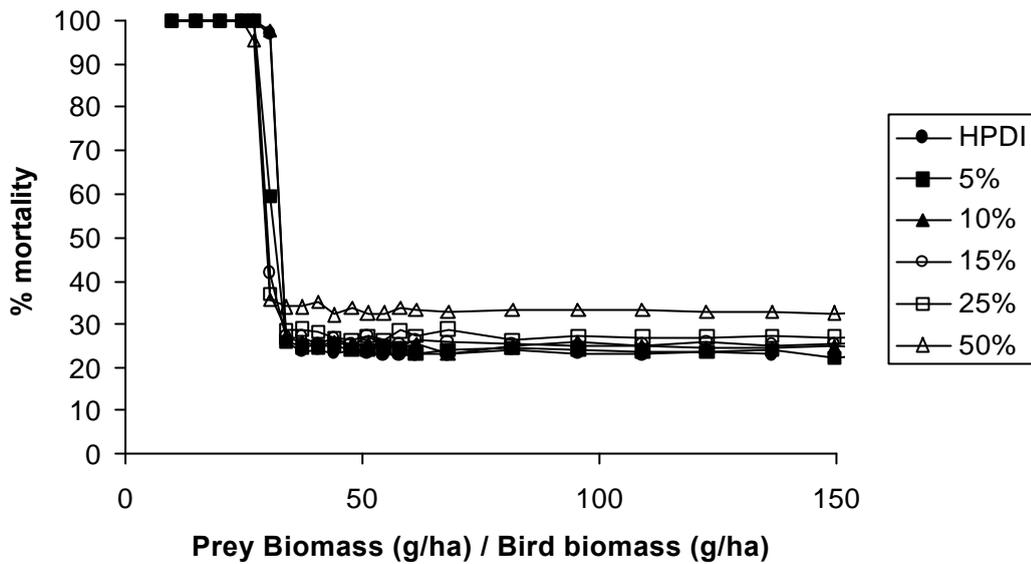
(a)

(b)

Figure 51 Percent mortality (a) and percent failing to reach 75% of target fat (b) for sight-feeding curlew, with 15% variation in feeding efficiency and interference based on prey depression. Upshore area, prey decline and cold weather included.

HP = both bird and prey biomass high, with prey biomass varied.
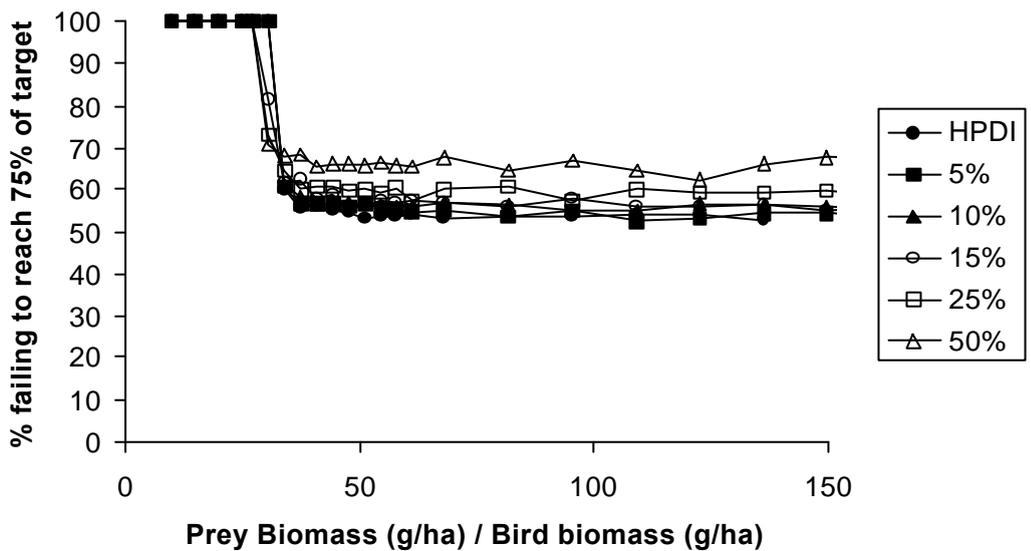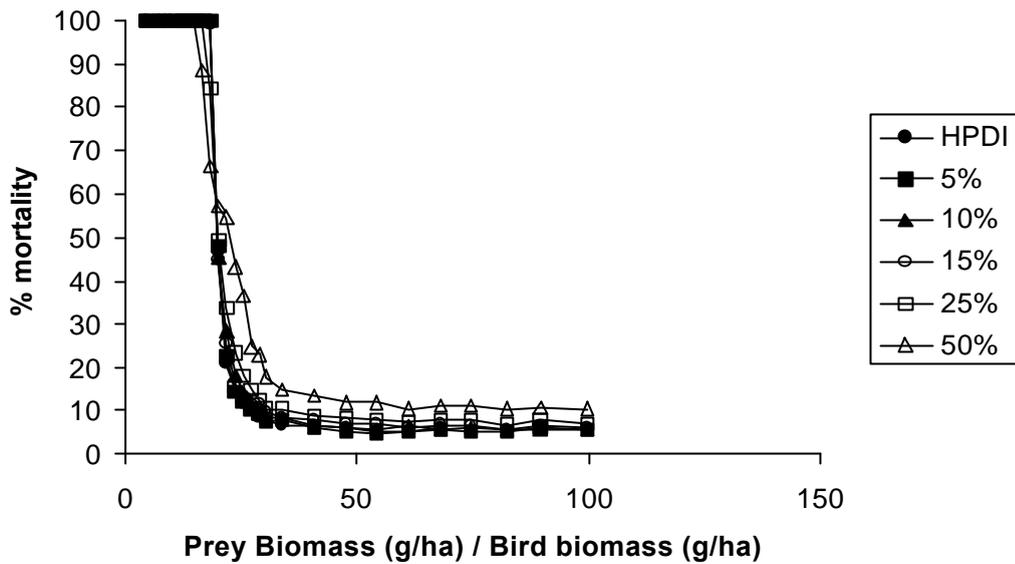
(a)

(b)

Figure 52 Percent mortality (a) and percent failing to reach 75% of target fat (b) for sight-feeding redshank, with 15% variation in feeding efficiency and depression-based interference. Upshore area included. Disturbance takes place.

HPDI = both bird and prey biomass high, with prey biomass varied and with no disturbance. The other lines are as HPDI but with the indicated percentage of area disturbed on downshore and upshore areas during the day.
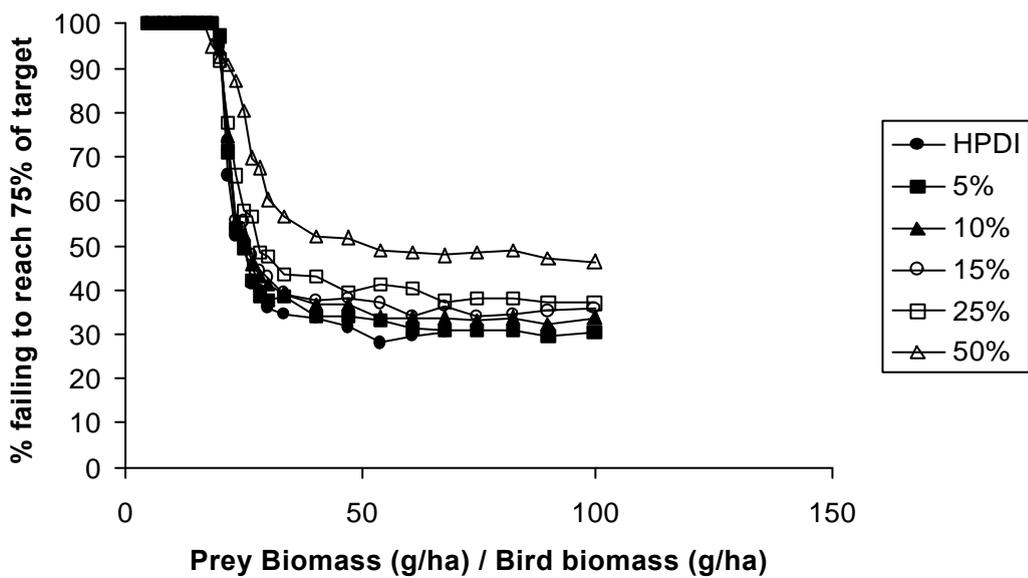
105

(a)

(b)

Figure 53 Percent mortality (a) and percent failing to reach 75% of target fat (b) for sight-feeding redshank, with 15% variation in feeding efficiency and with depression-based interference. Prey ash-free dry mass declines by 50% over winter. Disturbance takes place.

HPDI = both bird and prey biomass high, with prey biomass varied and with no disturbance. The other lines are as HPDI but with the indicated percentage of the patch disturbed during the day.
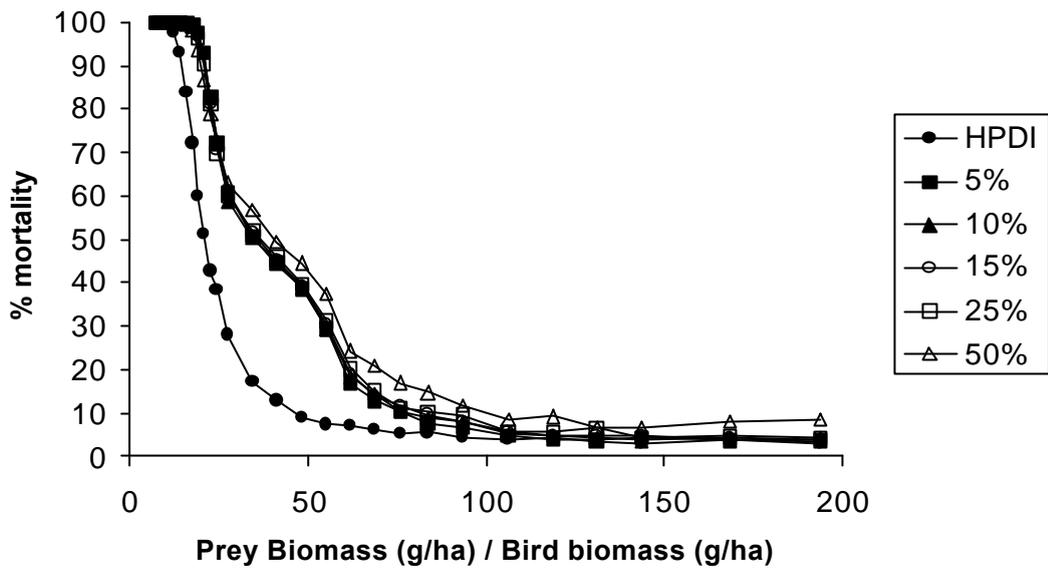
106

(a)

(b)

Figure 54 Percent mortality (a) and percent failing to reach 75% of target fat (b) for sight-feeding redshank, with 15% variation in feeding efficiency and with depression-based interference. Temperature is consistently 5oC lower than normal. Disturbance takes place.

HPDI = both bird and prey biomass high, with prey biomass varied and with no disturbance. The other lines are as HPDI but with the indicated percentage of the patch disturbed during the day.
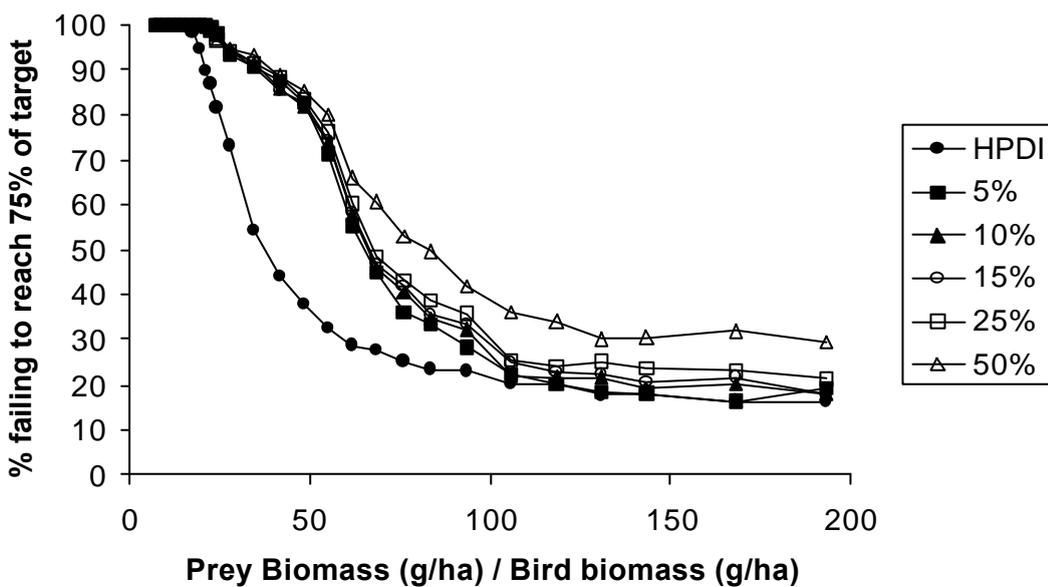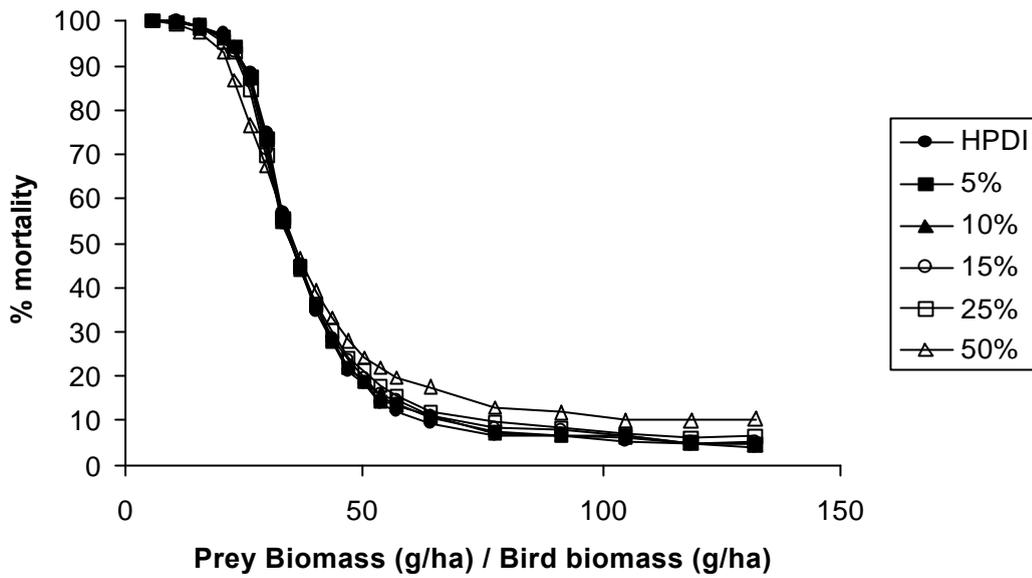
(a)

(b)

Figure 55 Percent mortality (a) and percent failing to reach 75% of target fat (b) for sight-feeding redshank, with 15% variation in feeding efficiency and with depression-based interference. Upshore area, prey decline and cold weather included. Disturbance takes place.

HPDI = both bird and prey biomass high, with prey biomass varied and with no disturbance. The other lines are as HPDI but with the indicated percentage of the patch disturbed during the day.
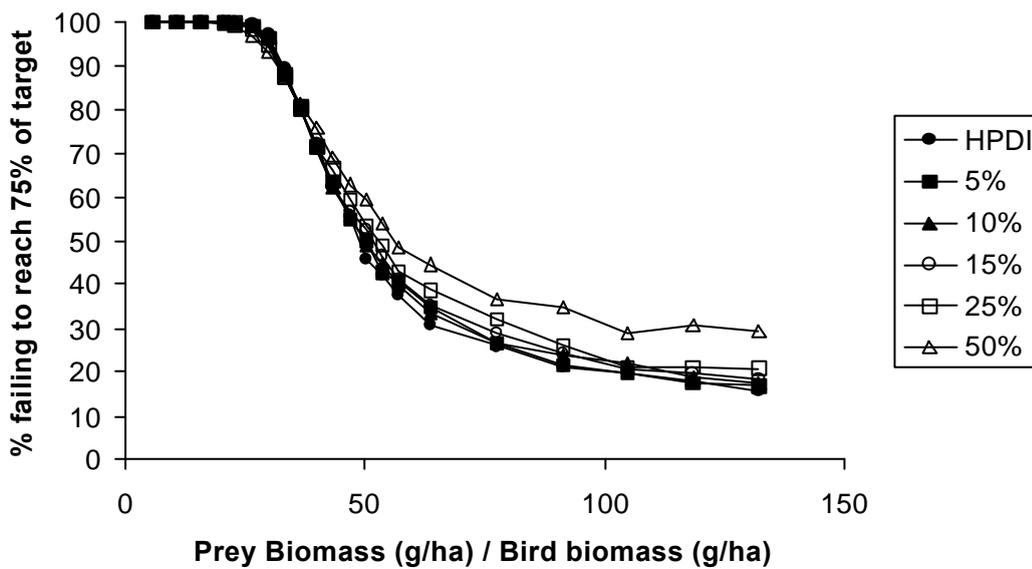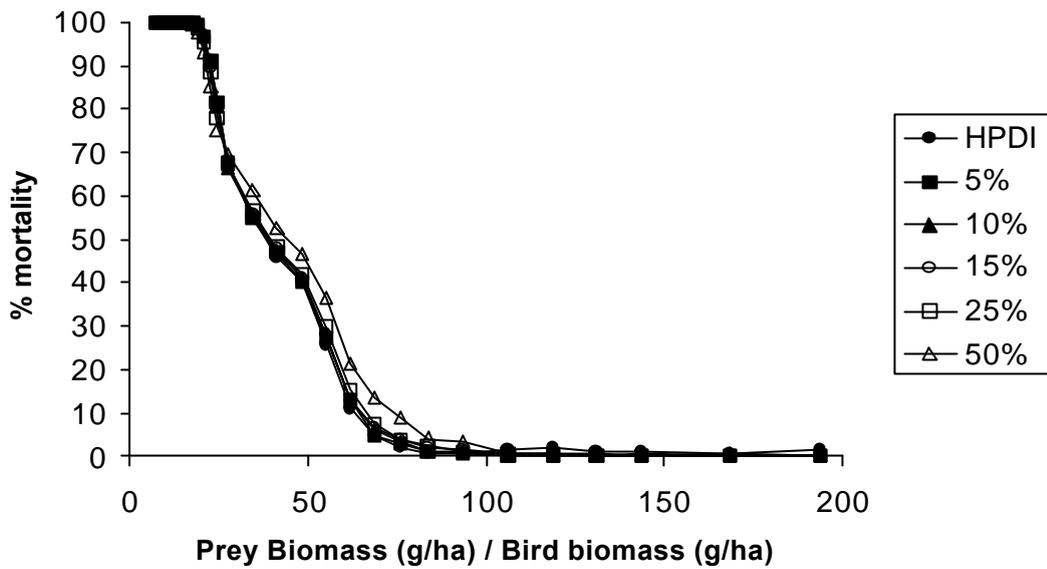
(a)

(b)

Figure 56 Percent mortality (a) and percent failing to reach 75% of target fat (b) for touch-feeding redshank, with 15% variation in feeding efficiency and depression-based interference. Upshore area included. Disturbance takes place.

HPDI = both bird and prey biomass high, with prey biomass varied and with no disturbance. The other lines are as HPDI but with the indicated percentage of area disturbed on downshore and upshore areas during the day.
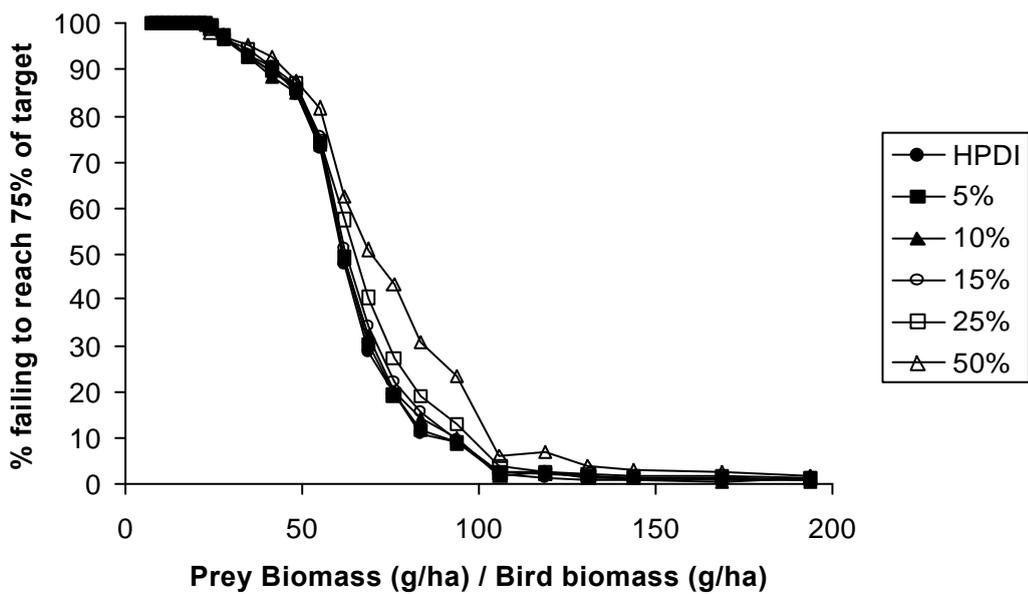
(a)

(b)

Figure 57 Percent mortality (a) and percent failing to reach 75% of target fat (b) for touch-feeding redshank, with 15% variation in feeding efficiency and with depression-based interference. Prey ash-free dry mass declines by 50% over winter. Disturbance takes place.

HPDI = both bird and prey biomass high, with prey biomass varied and with no disturbance. The other lines are as HPDI but with the indicated percentage of the patch disturbed during the day.
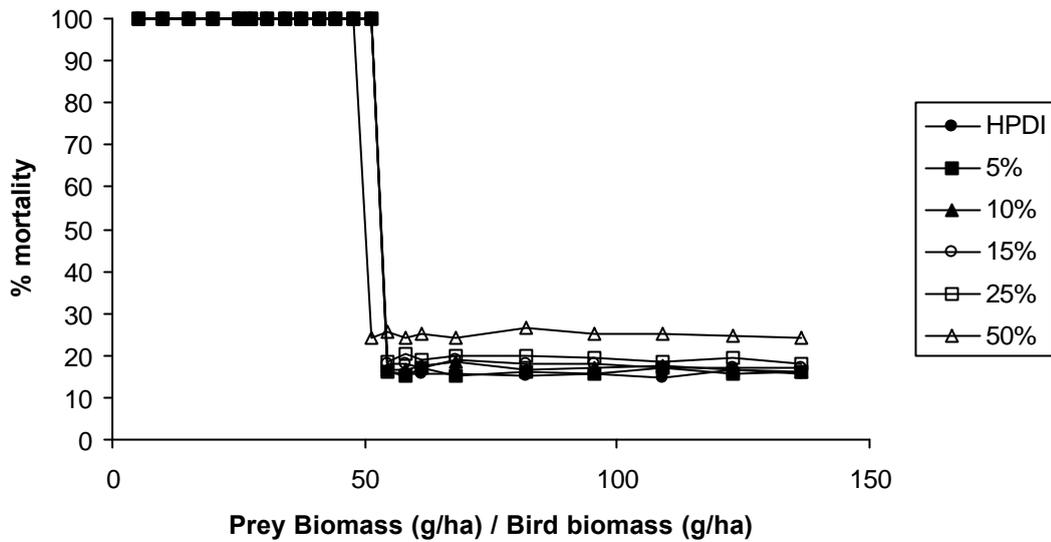
(a)

(b)

Figure 58 Percent mortality (a) and percent failing to reach 75% of target fat (b) for touch-feeding redshank, with 15% variation in feeding efficiency and with depression-based interference. Temperature is consistently 5°C lower than normal. Disturbance takes place.

HPDI = both bird and prey biomass high, with prey biomass varied and with no disturbance. The other lines are as HPDI but with the indicated percentage of the patch disturbed during the day.
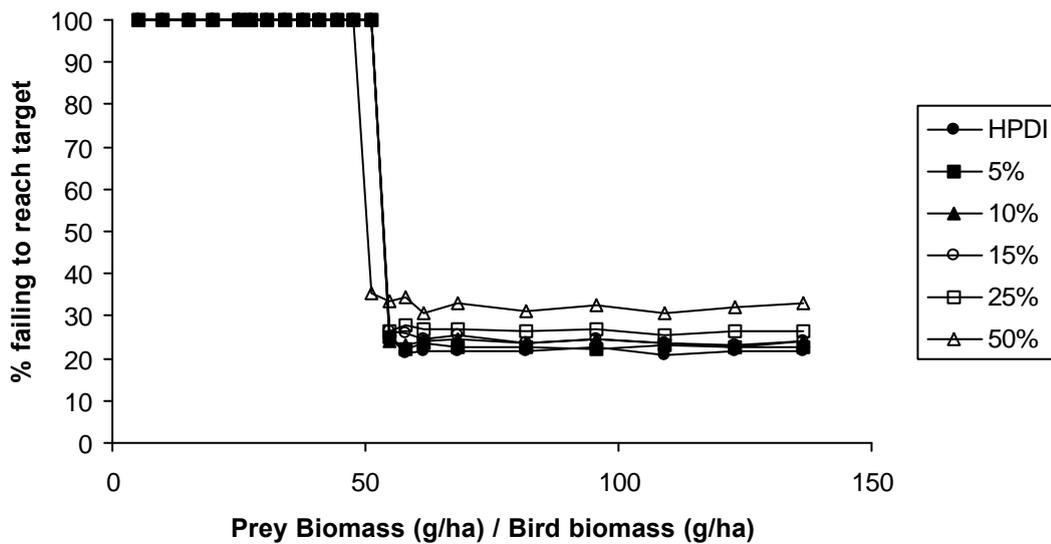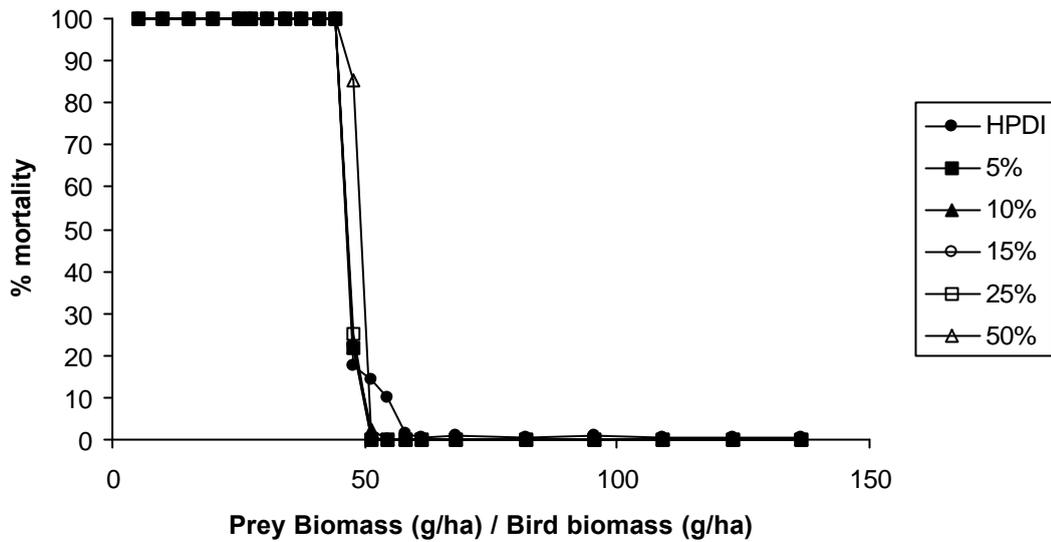
(a)

(b)

Figure 59 Percent mortality (a) and percent failing to reach 75% of target fat (b) for touch-feeding redshank, with 15% variation in feeding efficiency and with depression-based interference. Upshore area, prey decline and cold weather included. Disturbance takes place.

HPDI = both bird and prey biomass high, with prey biomass varied and with no disturbance. The other lines are as HPDI but with the indicated percentage of the patch disturbed during the day.
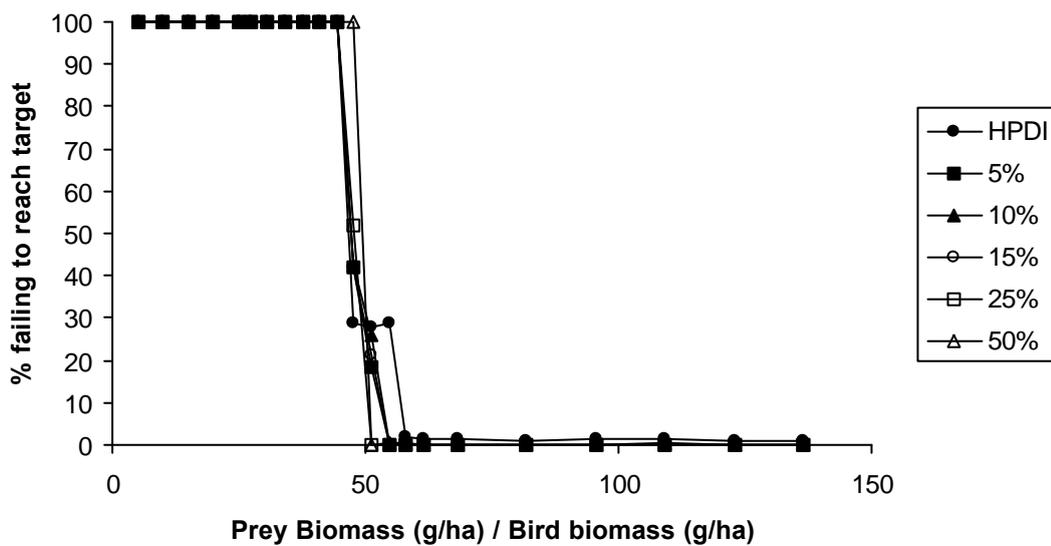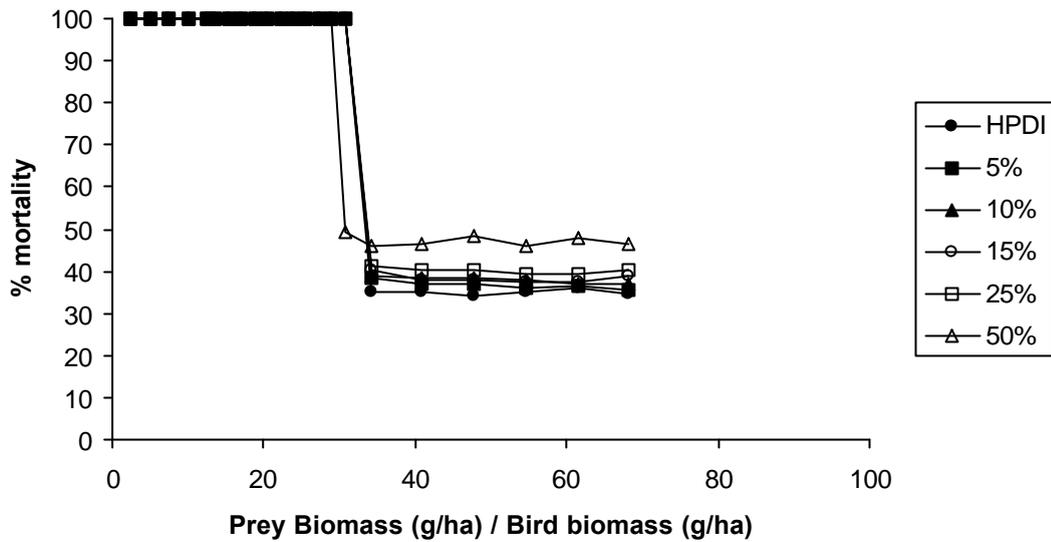
(a)

(b)

Figure 60 Percent mortality (a) and percent failing to reach 75% of target fat (b) for sight-feeding dunlin, with 15% variation in feeding efficiency, depression-based interference and varying degrees of disturbance.

HPDI = both bird and prey biomass high, with prey biomass varied and with no disturbance. The other lines are as HPDI but with the indicated percentage of area disturbed on downshore and upshore areas during the day.
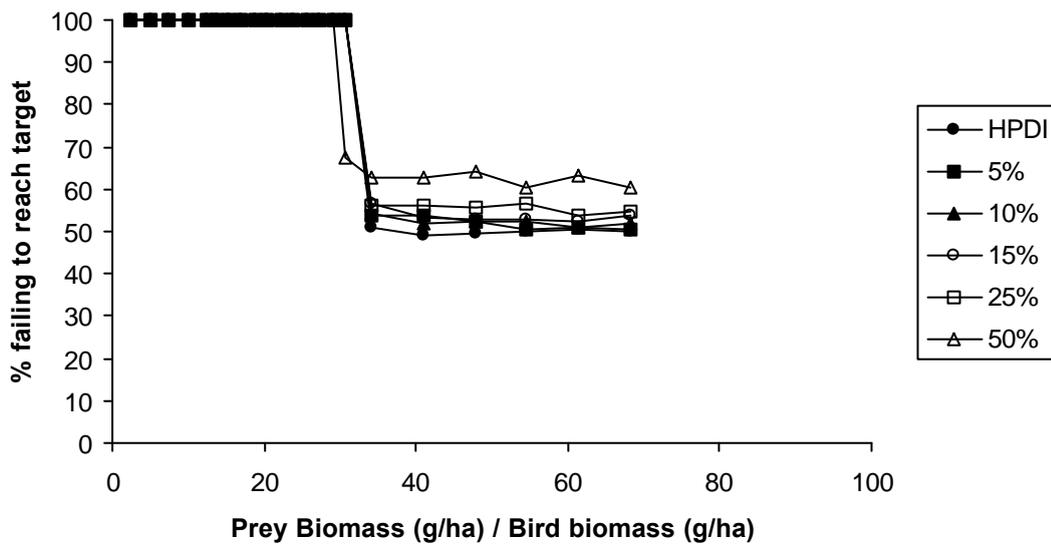
(a)

(b)

Figure 61 Percent mortality (a) and percent failing to reach 75% of target fat (b) for sight-feeding dunlin, with 15% variation in feeding efficiency, depression-based interference and varying degrees of disturbance. An upshore feeding area of the same size and prey density as the downshore, but with smaller prey is present.

HPDI = both bird and prey biomass high, with prey biomass varied and with no disturbance. The other lines are as HPDI but with the indicated percentage of area disturbed on downshore and upshore areas during the day.
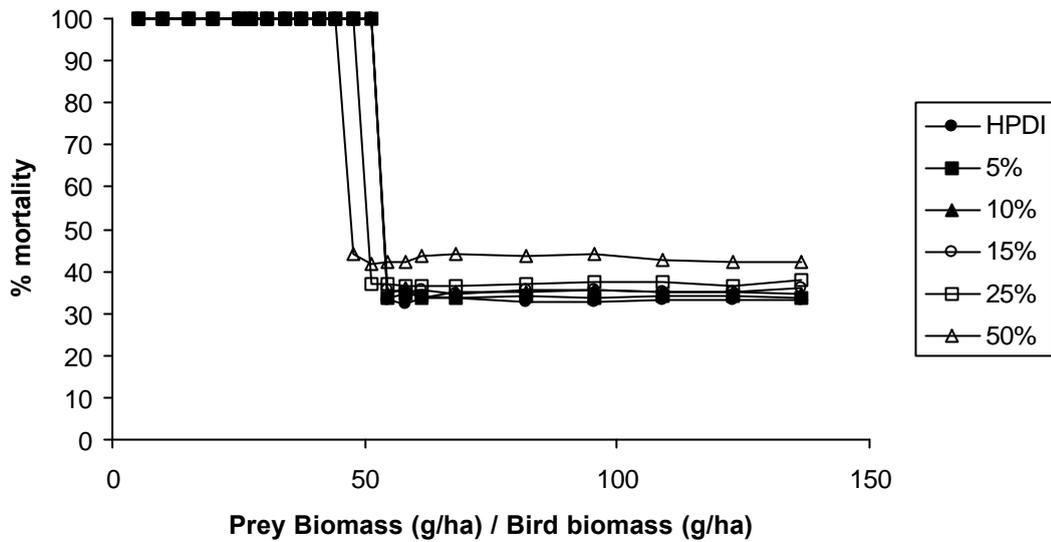
(a)

(b)

Figure 62 Percent mortality (a) and percent failing to reach 75% of target fat (b) for sight-feeding dunlin, with 15% variation in feeding efficiency, depression-based interference and varying degrees of disturbance. Prey ash-free dry mass declines by 50% over the winter.

HPDI = both bird and prey biomass high, with prey biomass varied and with no disturbance. The other lines are as HPDI but with the indicated percentage of area disturbed on downshore and upshore areas during the day.
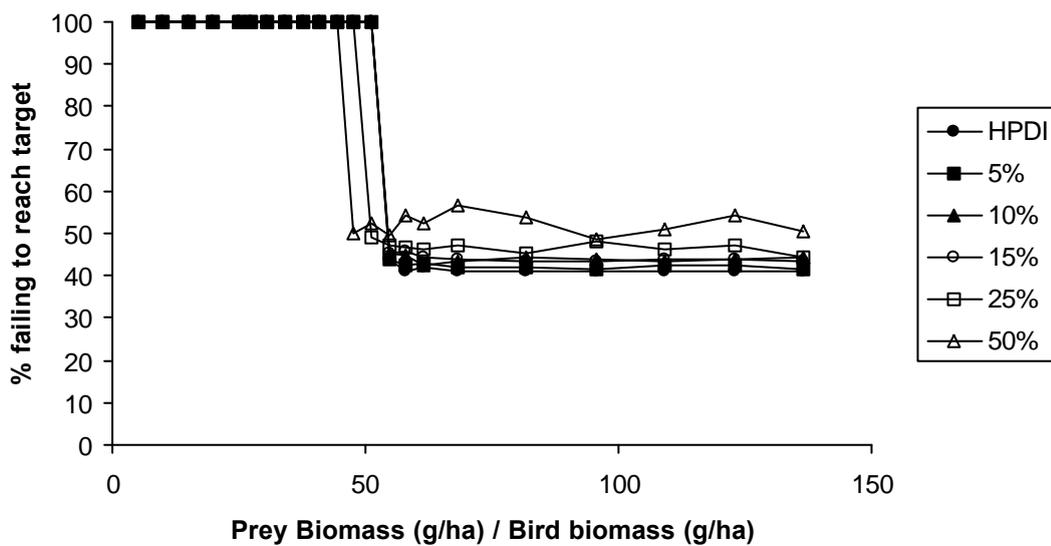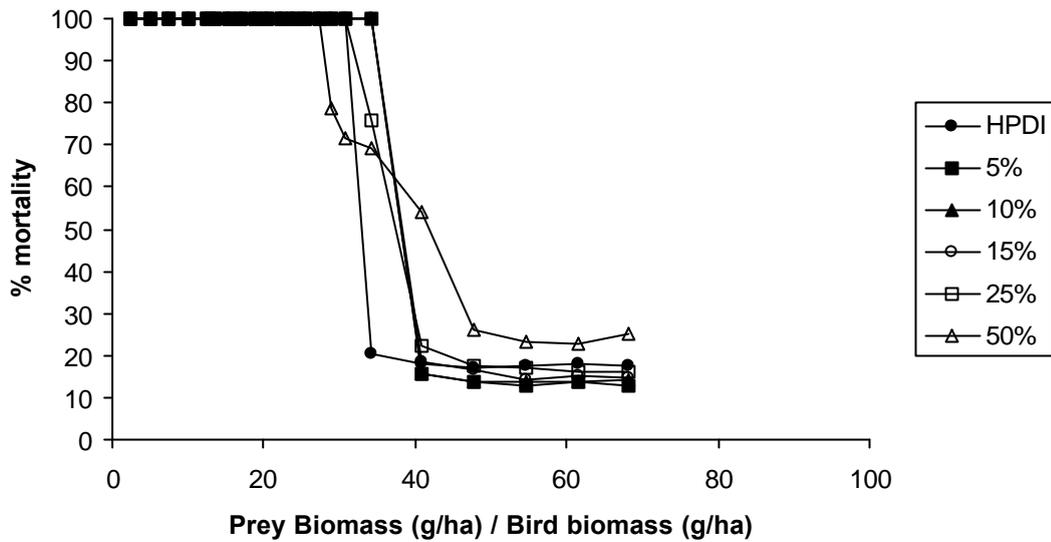
(a)

(b)

Figure 63 Percent mortality (a) and percent failing to reach 75% of target fat (b) for sight-feeding dunlin, with 15% variation in feeding efficiency, depression-based interference and varying degrees of disturbance. Temperature is consistently 5°C lower than normal.

HPDI = both bird and prey biomass high, with prey biomass varied and with no disturbance. The other lines are as HPDI but with the indicated percentage of area disturbed on downshore and upshore areas during the day.
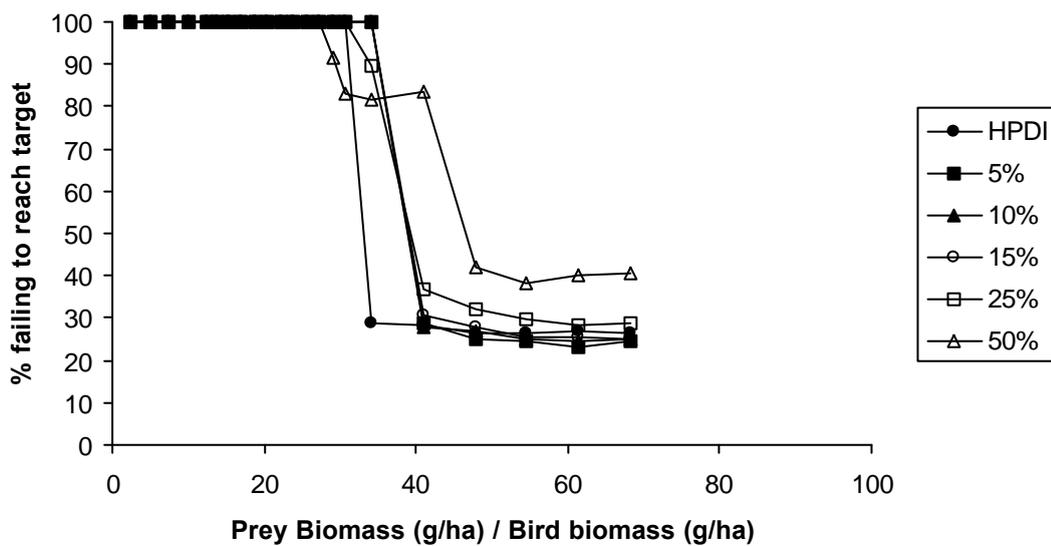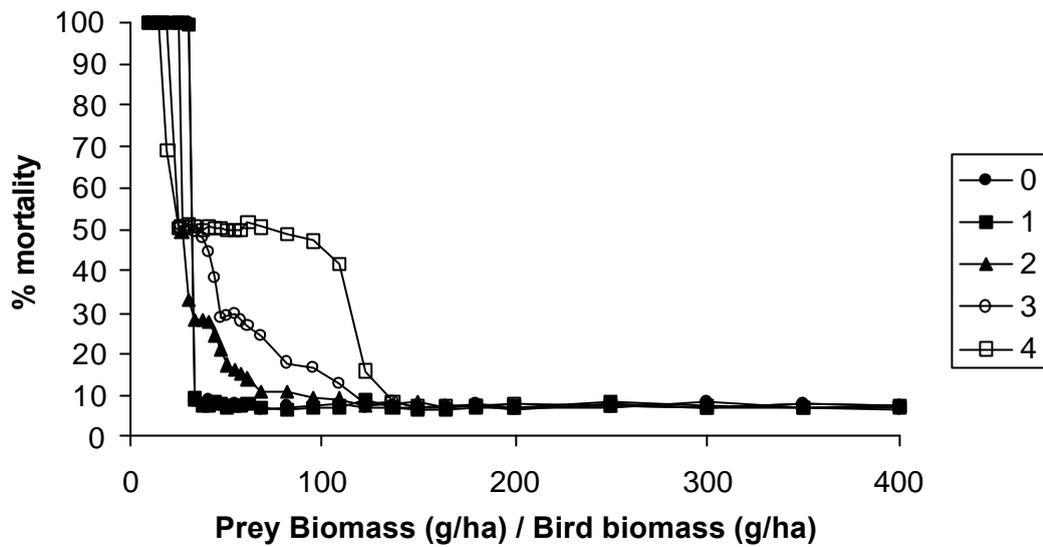
(a)

(b)

Figure 64 Percent mortality (a) and percent failing to reach 75% of target fat (b) for sight-feeding dunlin, with 15% variation in feeding efficiency, depression-based interference and varying degrees of disturbance. Upshore area, prey decline and cold weather included.

HPDI = both bird and prey biomass high, with prey biomass varied and with no disturbance. The other lines are as HPDI but with the indicated percentage of area disturbed on downshore and upshore areas during the day.
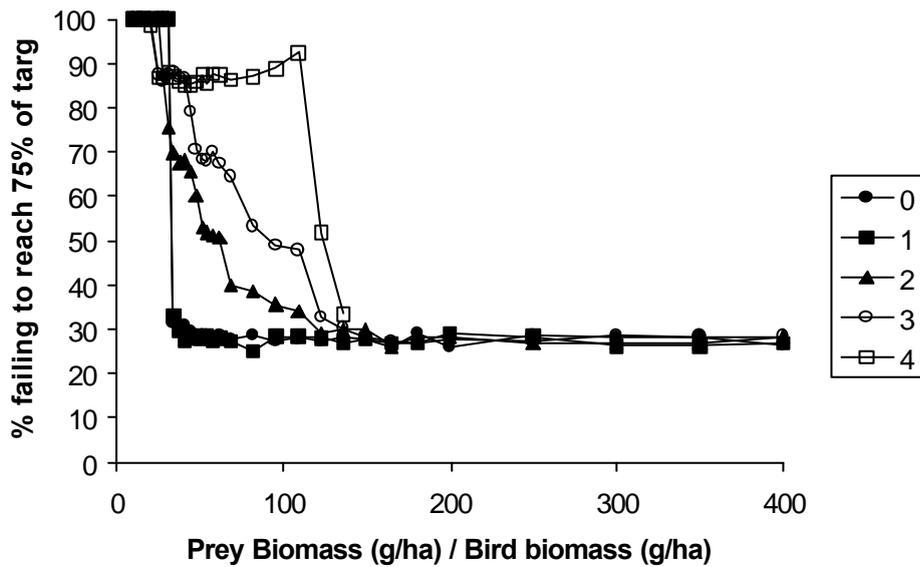
(a)

(b)

Figure 65 Percent mortality (a) and percent failing to reach 75% of target fat (b) for sight-feeding redshank, with 15% variation in feeding efficiency and depression-based interference. Prey are distributed over 5 patches with differing degrees of heterogeneity.

0 = single patch; **1** = 5 patches, homogeneous prey distribution; **4** = 5 patches, very heterogeneous prey distribution.
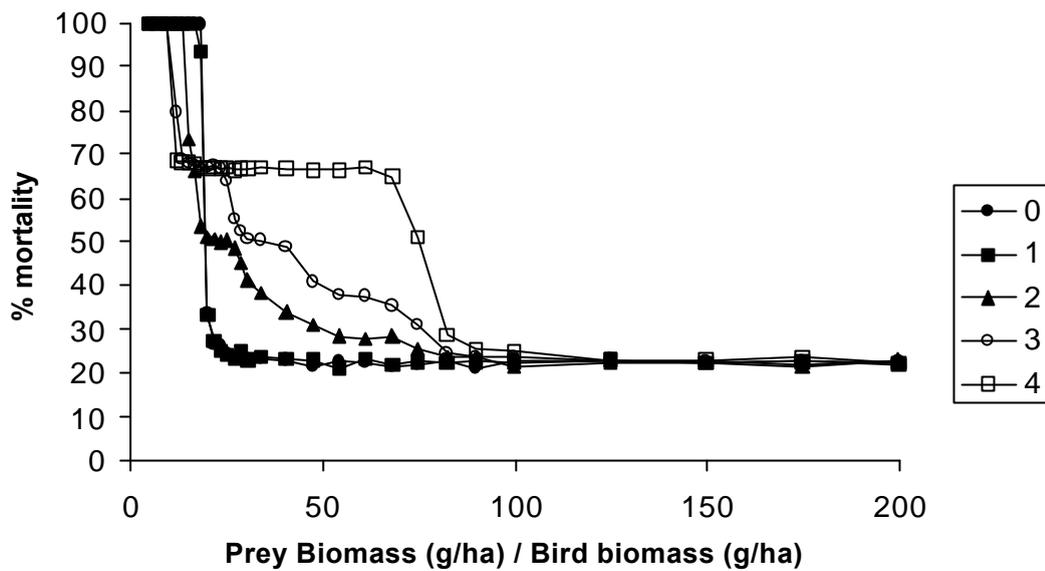
(a)

(b)

Figure 66 Percent mortality (a) and percent failing to reach 75% of target fat (b) for sight-feeding redshank, with 15% variation in feeding efficiency and depression-based interference. Prey are distributed over 5 patches with differing degrees of heterogeneity. Prey ash-free dry mass declines by 50% over winter.

0 = single patch; 1 = 5 patches, homogeneous prey distribution; 4 = 5 patches, very heterogeneous prey distribution.
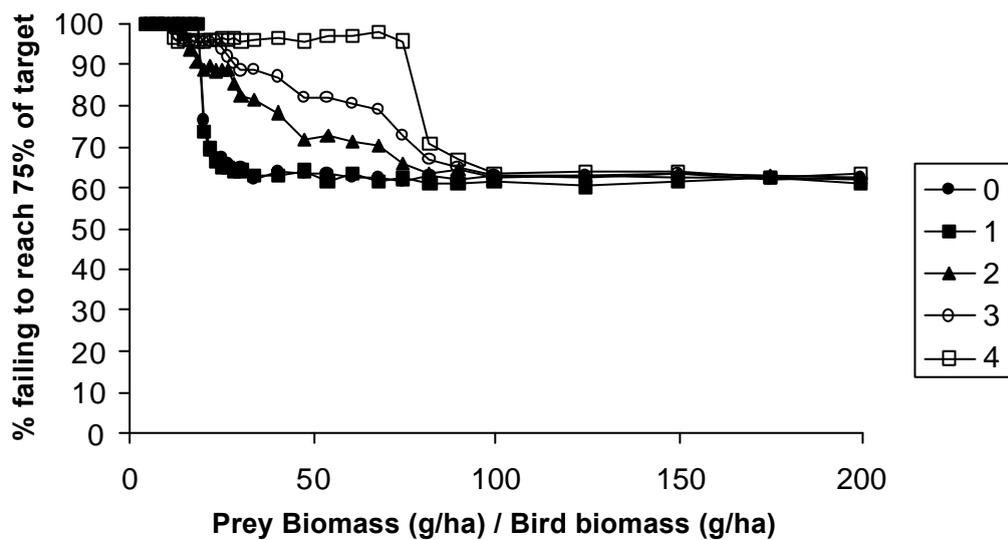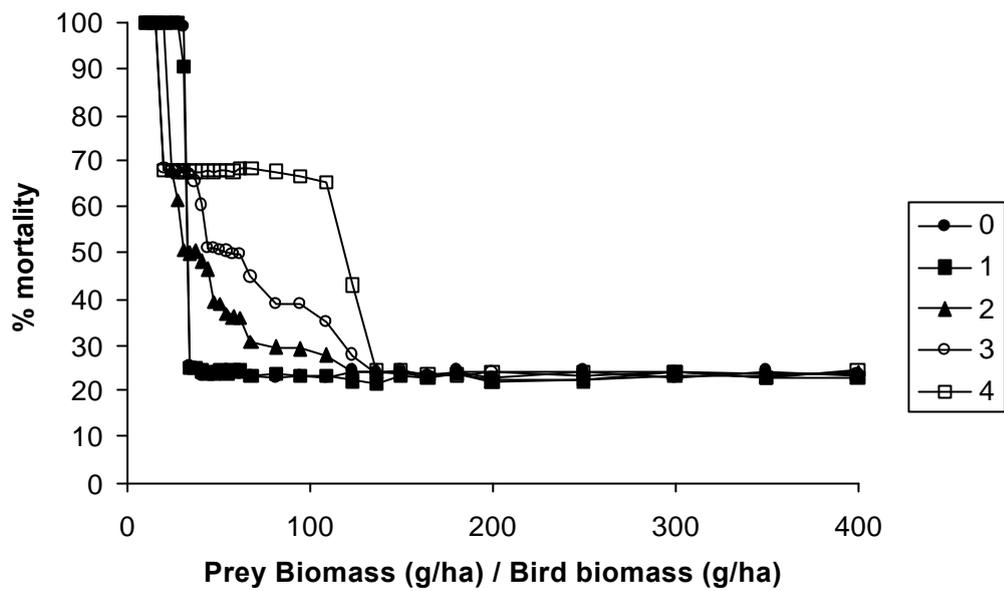
(a)

(b)

Figure 67 Percent mortality (a) and percent failing to reach 75% of target fat (b) for sight-feeding redshank, with 15% variation in feeding efficiency and depression-based interference. Prey are distributed over 5 patches with differing degrees of heterogeneity. Cold weather included.

0 = single patch; 1 = 5 patches, homogeneous prey distribution; 4 = 5 patches, very heterogeneous prey distribution.
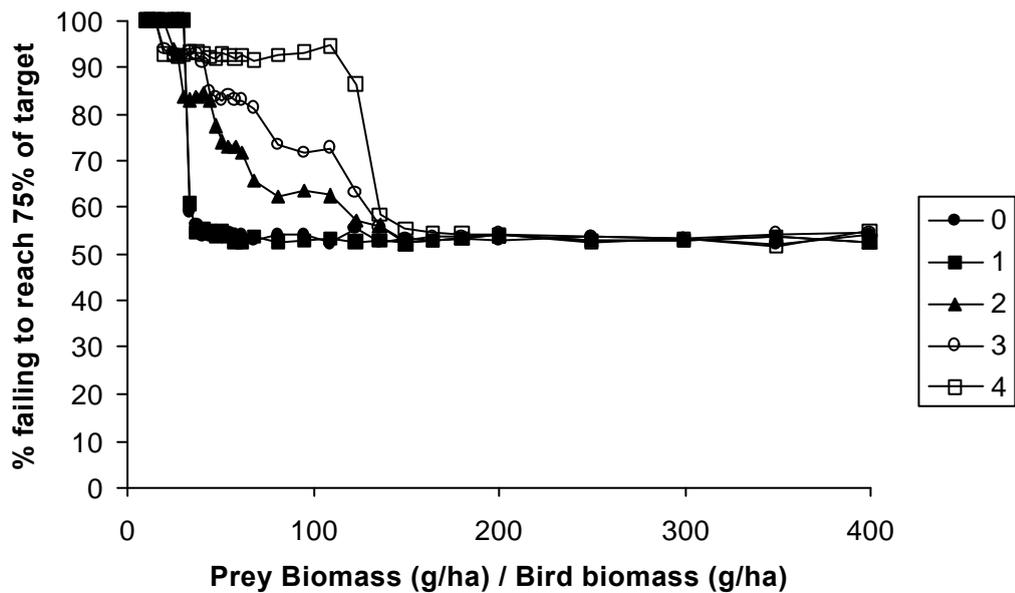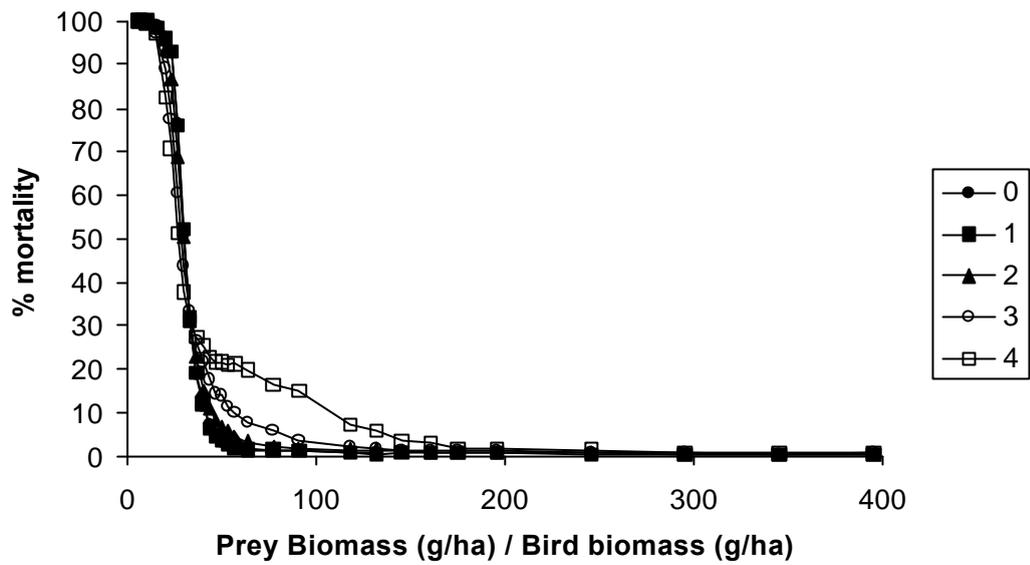
(a)

(b)

Figure 68 Percent mortality (a) and percent failing to reach 75% of target fat (b) for touch-feeding redshank, with 15% variation in feeding efficiency and depression-based interference. Prey are distributed over 5 patches with differing degrees of heterogeneity.

0 = single patch; **1** = 5 patches, homogeneous prey distribution; **4** = 5 patches, very heterogeneous prey distribution.
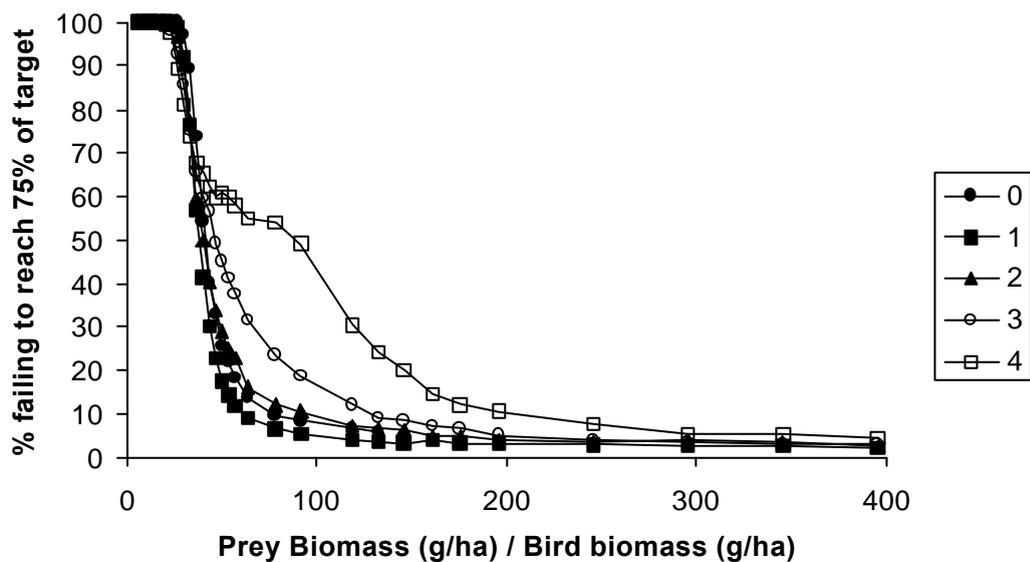
(a)

(b)

Figure 69 Percent mortality (a) and percent failing to reach 75% of target fat (b) for touch-feeding redshank, with 15% variation in feeding efficiency and depression-based interference. Prey are distributed over 5 patches with differing degrees of heterogeneity. Prey ash-free dry mass declines by 50% over winter.

0 = single patch; 1 = 5 patches, homogeneous prey distribution; 4 = 5 patches, very heterogeneous prey distribution.
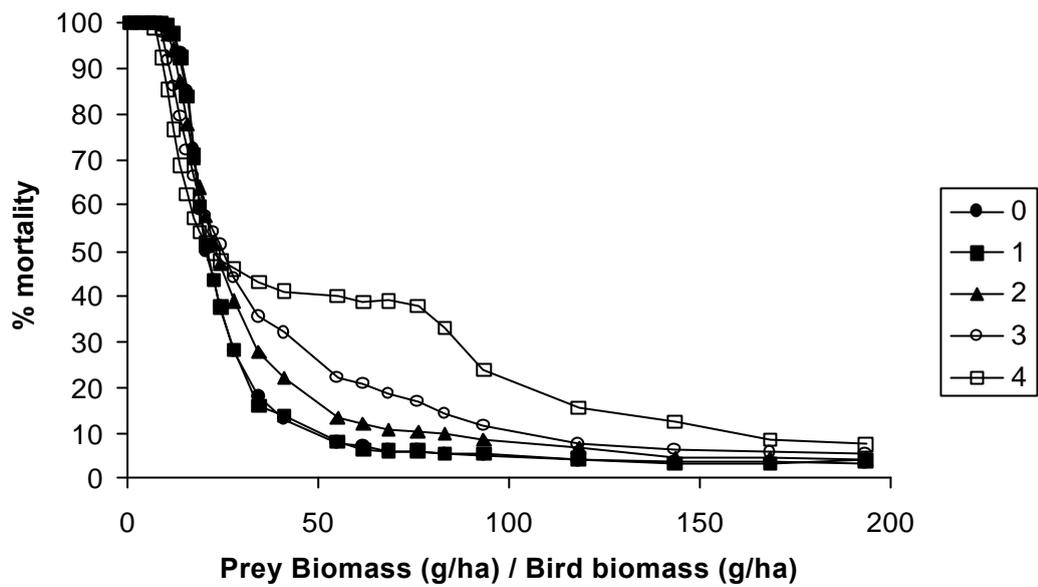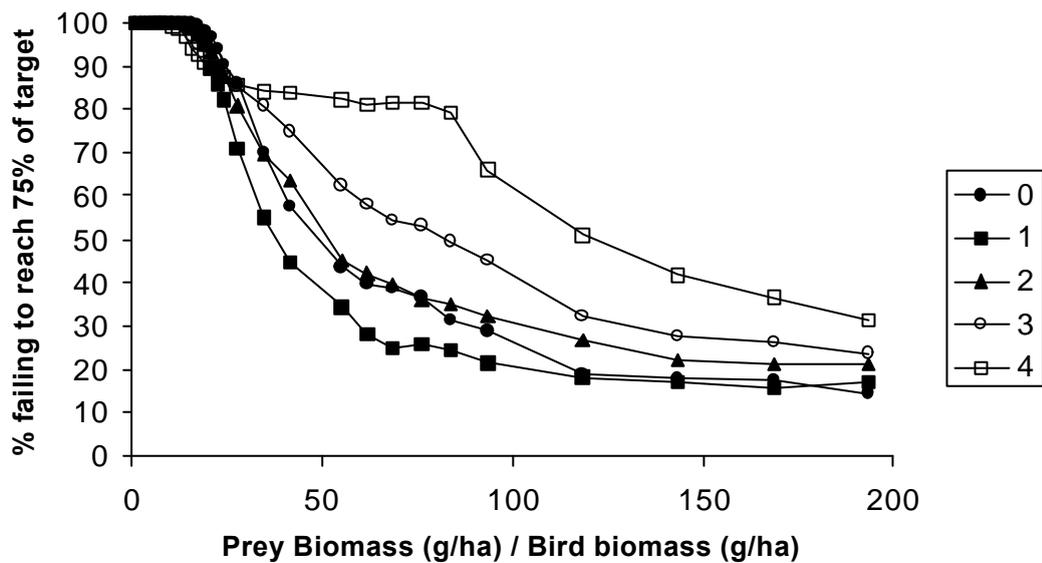
(a)

(b)

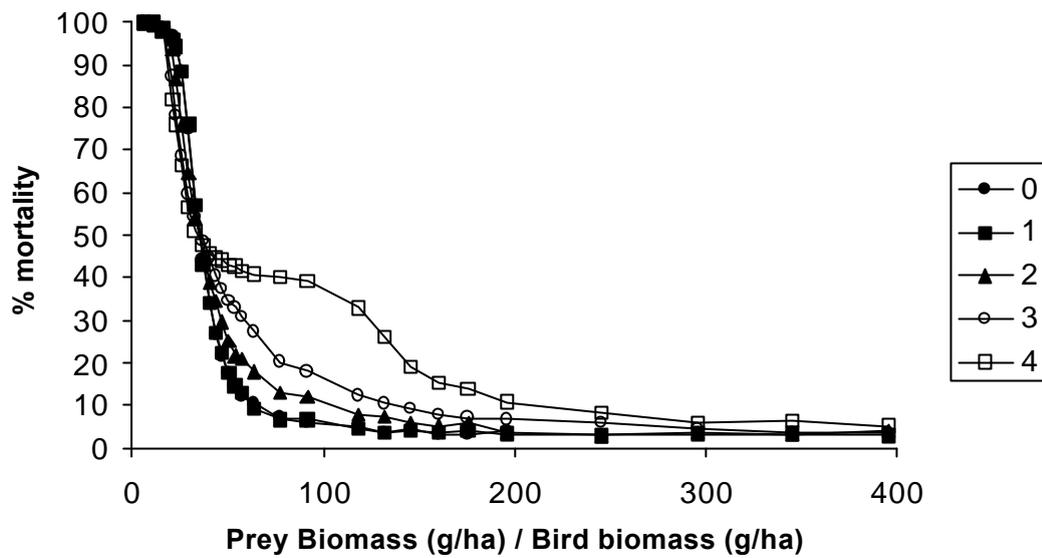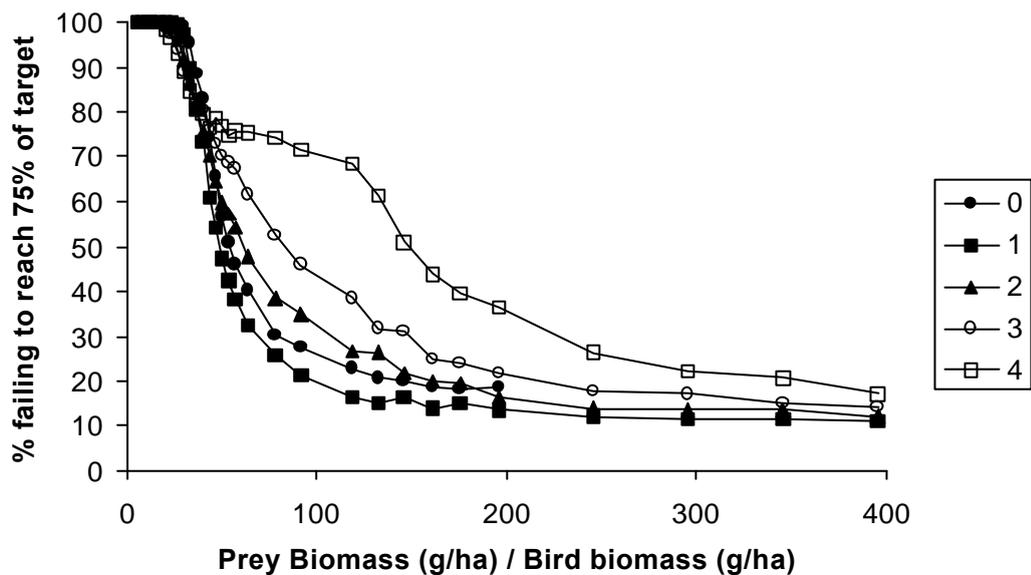**Figure 70** Percent mortality (a) and percent failing to reach 75% of target fat (b) for touch-feeding redshank, with 15% variation in feeding efficiency and depression-based interference. Prey are distributed over 5 patches with differing degrees of heterogeneity. Cold weather included.

0 = single patch; **1** = 5 patches, homogeneous prey distribution; **4** = 5 patches, very heterogeneous prey distribution.

(a)
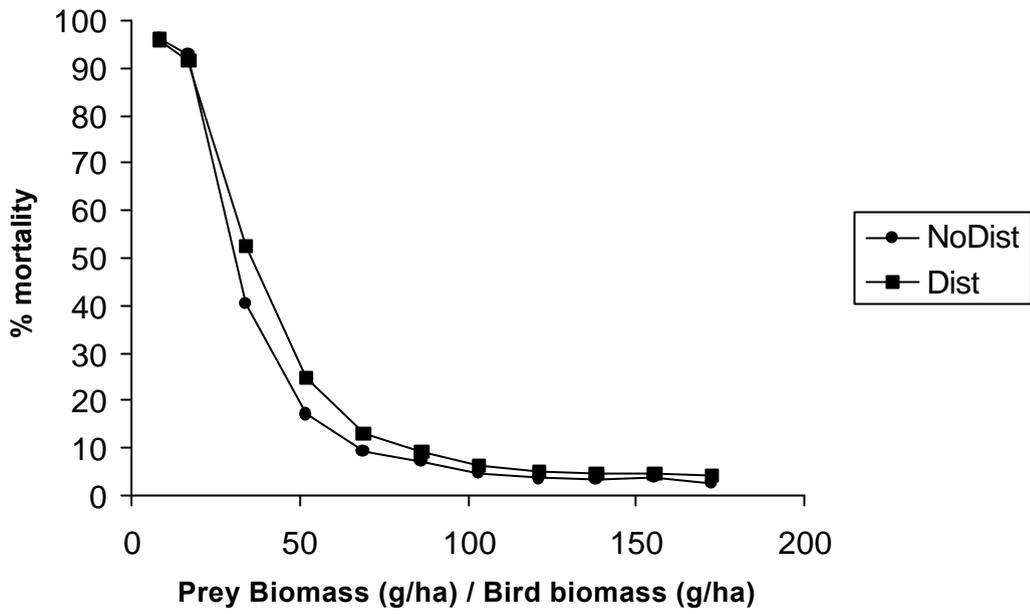
(b)
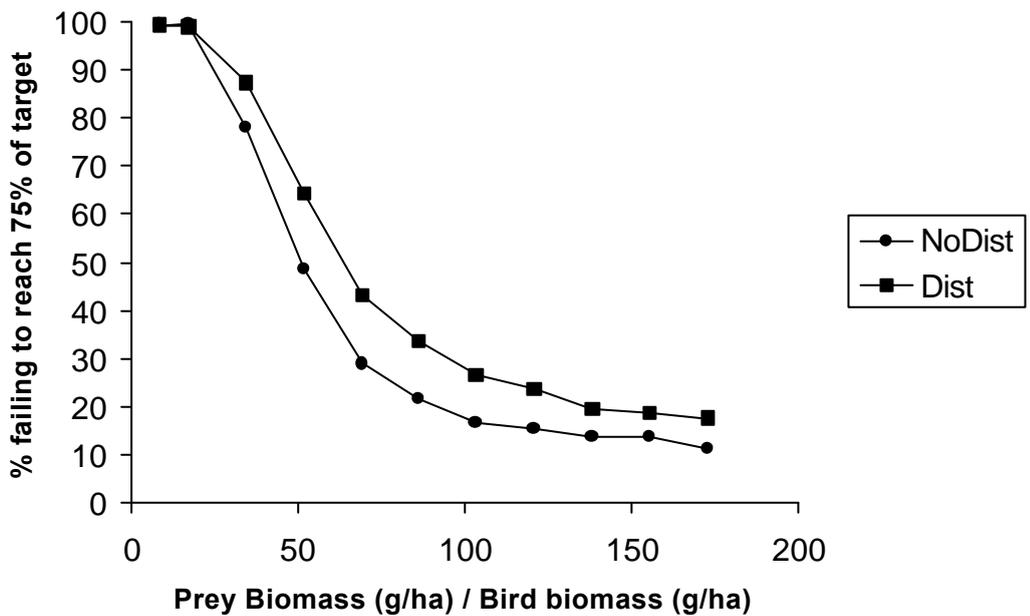
Figure 71 Percent mortality (a) and percent failing to reach 75% of target fat (b) for oystercatchers on the Exe estuary.

NoDist = No disturbance; **Dist =** 50% of the estuary is disturbed at low tide during the day.
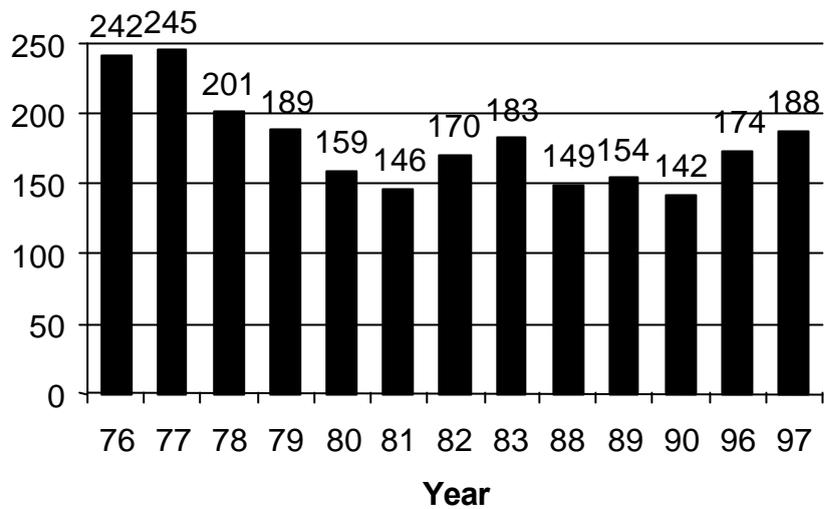
Figure 72 Thirteen estimates of the prey biomass/bird biomass ratios for oystercatchers on mussel beds on the Exe estuary in September. The values are given above each bar of the histogram, and vary between 142 and 242, with a mean of 180.2 and standard deviation of 33.5.
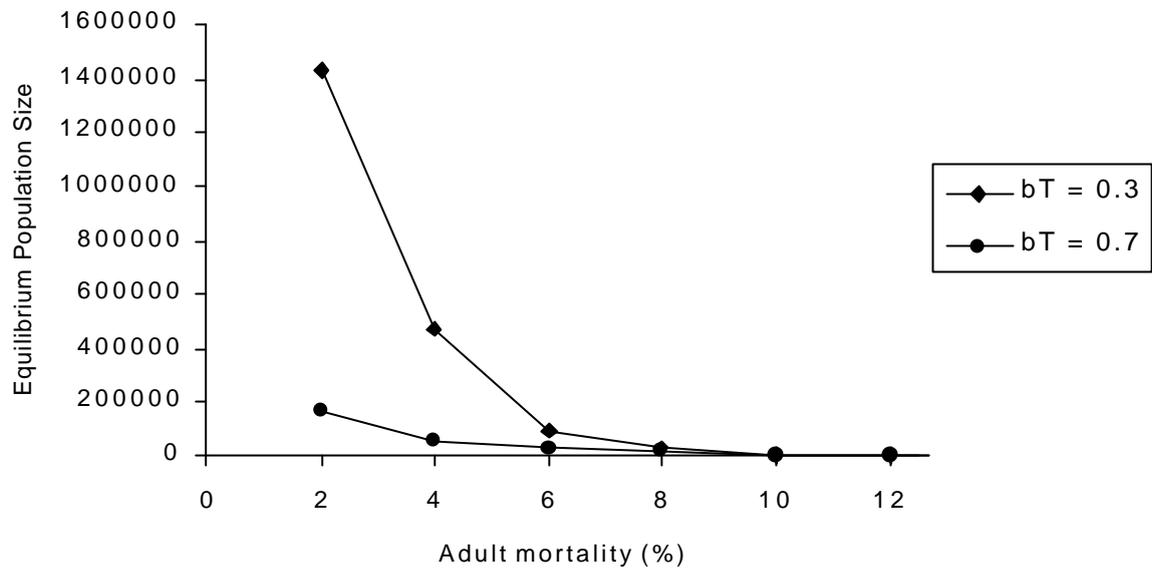
Figure 73 The equilibrium population size of a bird species as a function of its adult mortality rate in winter and the strength of the density dependence (bT) occurring on the breeding grounds in summer: with bT = 0.3, the density dependence is weak; with bT = 0.7, it is strong, though not perfectly compensating (from Goss-Custard 1980). Adult mortality rate is very low, or absent, during the breeding season.

Appendix 1 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 hours
Number of tidal stages		2 (no upshore) or 4 (upshore present)
Duration of spring-neap cycle		14.5185d = 28 tidal cycles
Time of first high-water on full spring tides		6.25 h after midnight
Duration of tidal stages (all tides)	No upshore	High water, 6.2222 h; Low water, 6.2222 h
	Upshore included	High water, 3.2222 h; receding tide, 1.5000 h; low water, 6.2222 h; advancing tide, 1.5000 h
Duration of longest and shortest days at latitude of S. Devon (including the hours of twilight)		18.11 h on 21 June and 9.25 h on 21 December
Mean daily temperature at Exeter airport 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)

Food patches

Parameter and source	Simulation type	
Number of patches	Normal	1
	Upshore	2
	Food preference	2
	Food preference with upshore	4
	Heterogeneous food	5
Proportion of each patch exposed at each tidal stage (high water, receding tide where applicable, low water, advancing tide where applicable).	Normal	Downshore 0.0, 1.0
Values were the same for spring and neap tides.	Upshore	Downshore 0.0, 0.0, 1.0, 0.0; Upshore 0.0, 1.0, 1.0, 1.0
	Food preference	Both downshore 0.0, 1.0
	Food preference with upshore	Both downshore 0.0, 0.0, 1.0, 0.0; Both upshore 0.0, 1.0, 1.0, 1.0
	Heterogeneous food	All downshore 0.0, 1.0
Energy density of food flesh (Zwarts *et al.* 1996)		22.4 kJ g^{-1}
Number of size classes		1
Width of size classes (mm)		1-200
Density (m^{-2}) of food at the start of winter	Redshank	37-29000
	Dunlin	25-10000
	Curlew	80-32000
Ash-free dry mass at start of winter (mg)	Redshank	20
	Dunlin	10
	Curlew	50
Over-winter non-bird mortality		0
Over-winter decrease in ash-free dry mass	Food decline	50%
	Other	0%

Birds

Parameter and source	Simulation type	Values
Range of feeding efficiencies (coefficient of variation)	FE = 5%	5%
	FE = 15%	15%
	FE = 25%	25%
	All other	15%
Asymptote (a) and 'slope' (b) of functional response	Redshank sight-feeding	a = 0.7484, b = 0.2152
	Redshank touch-feeding	a = 0.9914, b = 8.8346
	Dunlin sight-feeding	a =0.4729, b = 0.0168
	Curlew sight-feeding	a =1.4618, b = 1.6256
Daytime feeding efficiency	All types	1.0
Night-time feeding efficiency	All types	1.0
Strength of interference	Food depression	-0.25
	Kleptoparasitism	0 to -0.5 (depending on dominance)
Aggregation factor	Aggregation	2 - 10
	All other	1
Temperature-related food availability	All	Food fully available at all temperatures
Mass on 1 September (g)	Redshank	146.5
	Dunlin	50
	Curlew	798
Starvation mass (g)	Redshank	88
	Dunlin	39
	Curlew	489
Target mass (days since 1st September, target mass (g))	Redshank	30, 160.7, 61, 163.4 , 91, 165.6, 122, 164.8, 153, 147.5, 181, 142.6
	Dunlin	30, 51.1, 61, 52.3, 91, 55.6, 122, 55.1, 153, 48.9, 181, 48.6
	Curlew	30, 894, 61, 832, 91, 881, 122, 752, 153, 863, 181, 871
Energy expenditure - non-thermoregulatory	All	a = 10.5, b = 0.681

Parameter and source	Simulation type	Values
Lower critical temperature ($^{\circ}$C)	Redshank	15.7
	Dunlin	20.8
	Curlew	8.8
Energy expenditure - thermoregulatory (kJ $^{\circ}$C^{-1} day^{-1})	Redshank	13.89
	Dunlin	8.34
	Curlew	39.7
Food assimilation efficiency	All	0.75
Energy density of fat reserves (kJ g^{-1})	All	33.4
Fat storage efficiency	All	1.0
Fat usage efficiency	All	1.0