



Competition for Food and Interference among Waders

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COMPETITION FOR FOOD AND INTERFERENCE AMONG WADERS

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1. INTRODUCTION

The simple idea behind this paper is illustrated in Fig. 1. We are trying to account for bird density which is the result of the three population processes of survival, production and dispersal. A

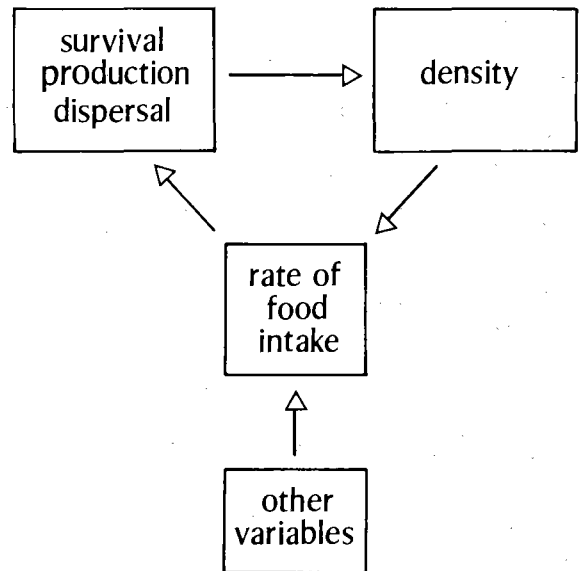


Fig. 1. The feed-back loop explored for waders in this paper.

main theme of this conference is how the feeding conditions, through their effect on the rate of food intake of individual birds, affects these population processes and so bird density. While factors uninfluenced by bird density (e.g. weather) will affect intake rate, the link between bird density and intake rate could be important to the dynamics of the population because it provides a potential feedback loop. The link may be either positive or negative *i.e.* an increase in bird density may either increase or decrease the rate of feeding. While positive effects may occur in nature, this paper is concerned only with negative effects. Testing for the existence of these in the field, let alone investigating the processes involved, is normally difficult because both the rates of food intake and food abundance are difficult to measure. Wading birds feeding on invertebrates on estuaries, mainly outside the breeding season, are good subjects for this kind of work because their activities are easily seen and the food supply is relatively simple to measure. This

paper reviews evidence that increasing wader density reduces intake rate and discusses what processes might be involved. This is followed by some speculations on the possible role of such phenomena in the dynamics of wader populations.

2. INTERFERENCE AND DEPLETION

A distinction can be made between two kinds of negative effect, depletion and interference. In depletion, intake rate decreases as bird density rises because more food is removed, so prey density goes down. Increased bird density may not reduce intake rate immediately because it may take some time for the birds to reduce prey density significantly. If half the birds are removed, intake rate does not immediately recover because the food supplies have already been reduced. However, the subsequent rate of decline in feeding rate will be slower than with the larger bird population. The change is irreversible, at least until the food recovers through growth and reproduction in the following spring. Interference is reversible because it is the presence of the birds themselves that, in one way or another, causes the reduced intake rate. In waders, there is also a difference in time scale between depletion and interference. The food is usually reduced only gradually during the winter so that depletion operates over a period of weeks and months. By contrast, interference occurs as a more-or-less immediate response to the increased bird density so that the time scale is much less.

3. INTERFERENCE

3.1. FIELD EVIDENCE

This section reviews the evidence for interference in the field and discusses some of the possible mechanisms involved.

The most comprehensive evidence for interference comes from studies of Oystercatchers, *Haematopus ostralegus*, feeding on a mussel, *Mytilus edulis*, bed in the Netherlands (R. Drent, pers. comm.). The density of Oystercatchers varied enormously as the tide ebbed and flowed and changed the area of bed available. There would have been little change in the abundance of

mussels during the short intervals involved, yet the birds' behaviour changed in two ways as their density increased. First, above approximately 125 birds per ha, an increasing proportion did not feed. Second, the numbers of mussels caught per hour of foraging decreased by up to 40 per cent as bird density increased. Increasing bird density artificially by putting out model Oystercatchers also decreased intake rate, although by not as much as an equivalent increase in the density of real Oystercatchers would have done. This suggests that it was the presence of the birds themselves, rather than the depletion of the food supplies, which was responsible.

In other studies, correlations between intake rate and bird density measured over such short intervals suggest that depletion is most unlikely to have been involved. Goss-Custard (1976) studied Redshank, *Tringa totanus*, feeding by sight on the amphipod crustacean *Corophium volutator* in a small area of mud within which bird density varied considerably (eight fold) and rapidly during a four hour watch. Fig. 2A shows

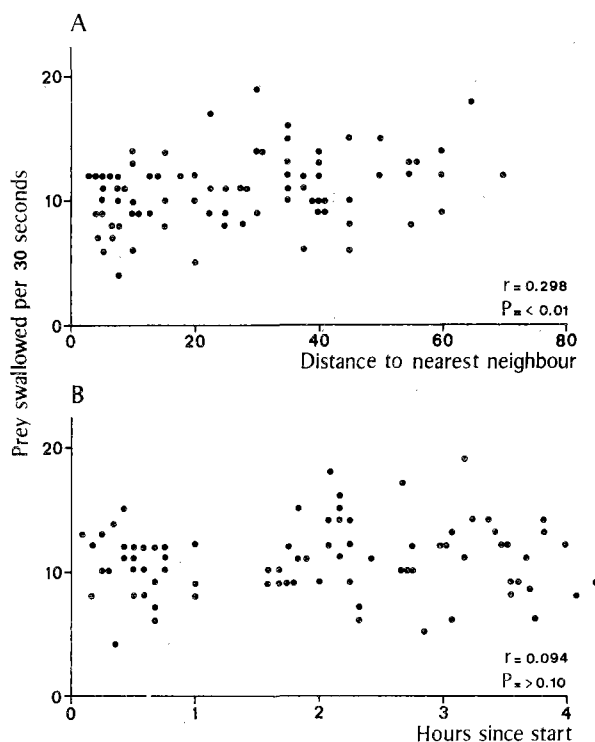


Fig. 2. Feeding rate of Redshank, *T. totanus*, in relation to (A) proximity of nearest neighbour (cm), and (B) the time that the flock had been feeding in the area.

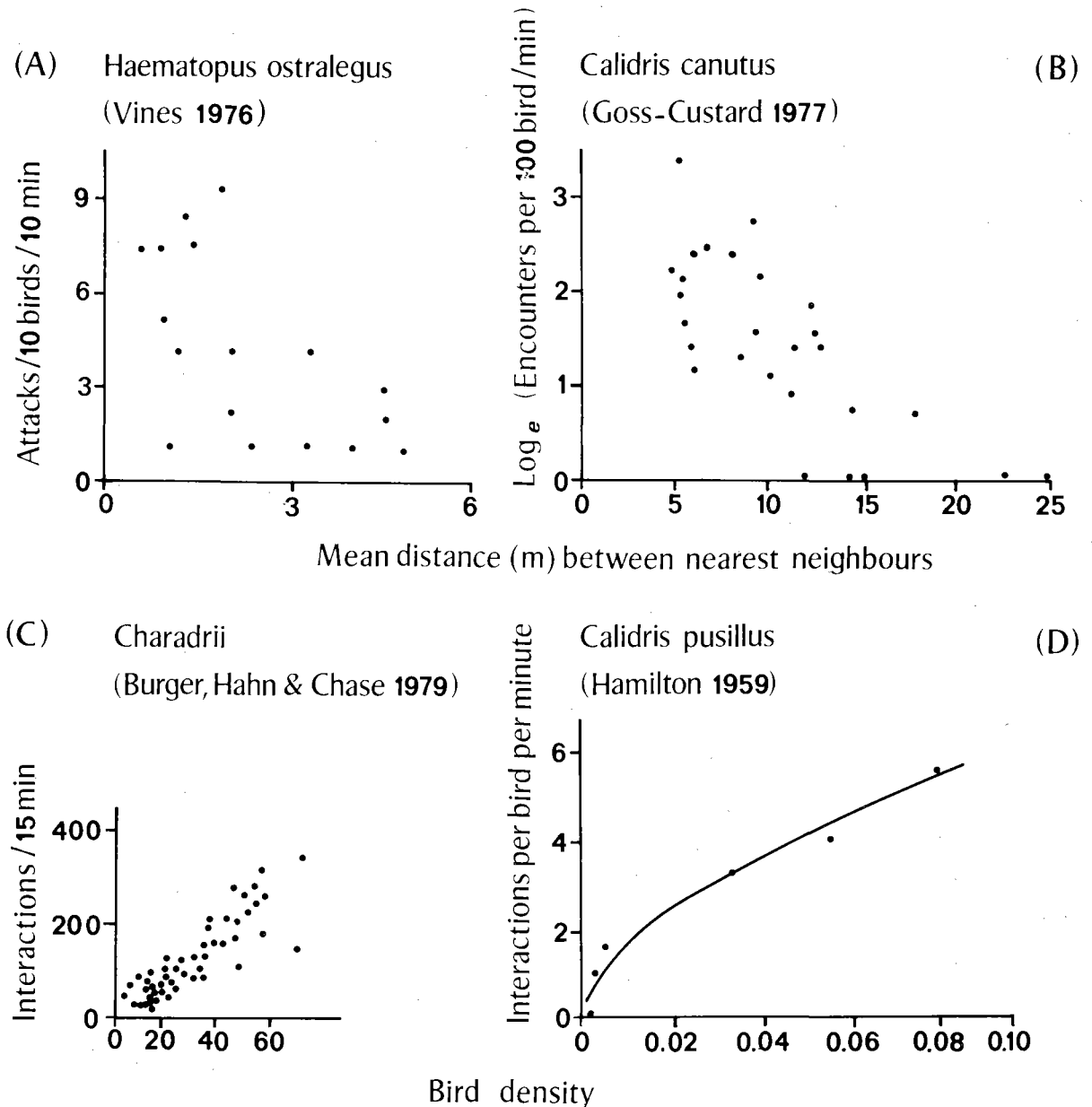


Fig. 4. The frequency of aggressive interactions between birds at different densities of waders. A. *Haematopus ostralegus* (Vines 1976); B. *Calidris canutus* (Goss-Custard 1977a); C. *Charadrii* (Burger *et al.* 1979); D. *Calidris pusillus* (Hamilton 1959).

bird lengths the values are 0.65 and 0.25 per cent respectively! Average gross intake rate is very little affected by the increased encounter rates at high bird densities in this case, though we do not know how net intake rate would be affected, because the energy expended in fighting has not yet been measured.

3.2.2. Kleptoparasitism

Carion Crows, *Corvus corone*, and some gulls (Laridae), but particularly the Common Gull, *Larus canus*, also steal food found by waders. An increase in wader density could either increase or decrease the number of prey stolen from individuals depending on whether or not more klep-

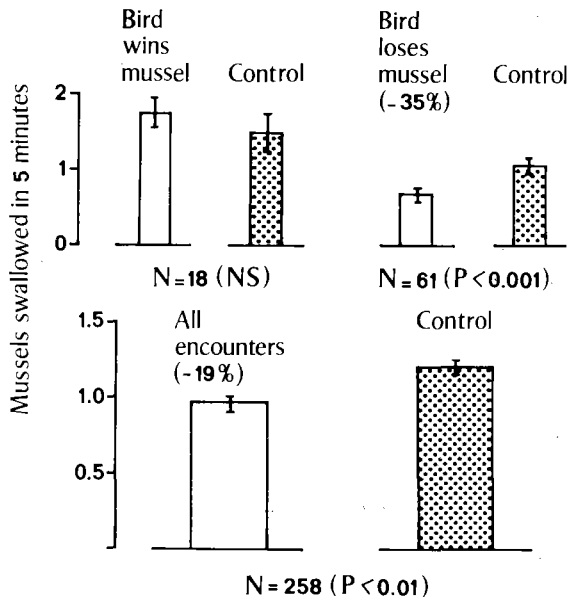


Fig. 5. The numbers of mussels consumed in five minutes by Oystercatchers, *H. ostralegus*, involved in various kinds of contests over mussels, compared with mussel consumption in control periods in which no encounters occurred. Top left: the bird steals a mussel from another. Top right: the bird has a mussel stolen from it by another Oystercatcher. Bottom: all encounters combined. N = number of observations. N.S. = not significant.

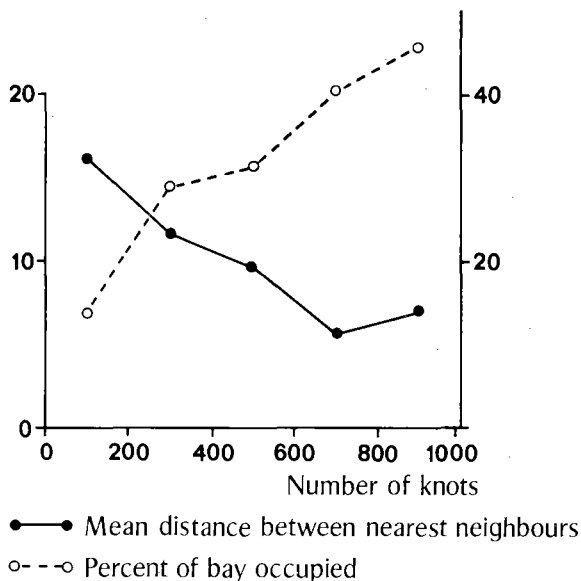


Fig. 6. The proportion (%) of a small bay used (right) by Knots, *C. canutus*, and the mean nearest neighbour distances (M) between them in relation to the numbers of birds in the area.

toparasites turned to attacking the waders. In one study, kleptoparasitism by gulls on individual Oystercatchers increased as wader density increased (R. Drent pers. comm.), but clearly more studies are desirable.

3.2.3. Disturbance in searching

The intake rate of Oystercatchers studied by Drent decreased even when the losses inflicted by the gulls had been taken into account. Neither these Oystercatchers or the Redshanks studied by Goss-Custard (1976) were aggressive towards conspecifics while feeding, yet feeding rate decreased as bird density increased.

Birds may vary their search path according to the dispersion of their prey, presumably in an attempt to maximise profitability (Krebs 1978). If waders do the same, the presence of other birds may deflect an individual from the route it would otherwise have taken so that it finds less food, especially as bird density rises. Model Oystercatchers may cause birds to alter their search path and feeding rate is reduced (R. Drent pers. comm.).

Other individuals might simply distract a bird from searching for prey. This is most likely to occur among birds hunting for prey by sight. Another bird always presents a threat because it may attack, and the nearer it is the more attention might be diverted away from looking for prey which are probably difficult to locate anyway. This could also explain why Redshank using visual clues fed more slowly when close together, because birds feeding on similar prey by touch did not interfere with each other's feeding even when very close together (Goss-Custard 1976).

3.2.4. Exploitation of available prey

Not all the prey in the mud are necessarily available to waders. Prey may be buried too deeply to be reached or, even if within reach, be inactive so they cannot be detected. If only a small proportion is available at any one time, the passage of birds over an area might cause a significant reduction in the density of the available fraction. Both the studies by Smith (1975) on Godwits, *Limosa lapponica*, eating the lugworm,

Arenicola marina, and Goss-Custard (1970a) on Redshank eating *C. volutator* suggest that only a small proportion is accessible at any one time, and there is no reason to think that turnover is increased when more are eaten by waders.

It is normally difficult to find out exactly when a prey is available to waders, but Smith (1975) showed that lugworms were vulnerable to Godwits when they backed up their burrows to defecate. Smith measured the area searched per minute by a Godwit, the numbers of worms eaten and the numbers of worms appearing per minute at the surface of the sand. The mean nearest neighbour distance (NNd) between Godwits was also determined, but I have converted these values to density from the expression (Clark & Evans 1954): $\bar{x}NNd = \frac{1}{2} \sqrt{MA}$ where MA is the mean area occupied by one bird within the flock. It is therefore possible to compare the impact of Godwits on the density of worms actually available to the birds.

Fig. 7 shows the numbers of worms coming to the surface per minute in (i) the mean area occupied by one bird at different densities of birds

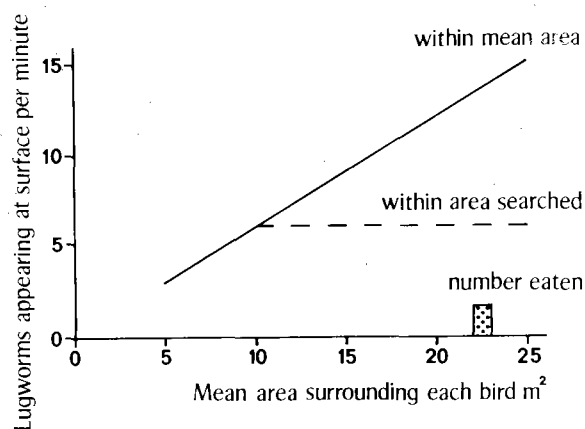


Fig. 7. Possible interference amongst Bar-tailed Godwits, *L. lapponica*, eating lugworms, *A. marina*. The dotted line shows the numbers of worms becoming available in one minute within the area searched in one minute by one Godwit. The stippled block shows the number eaten by one Godwit in one minute at the average density of Godwits recorded in the study: 25 per cent of those available were eaten. The solid line shows the numbers of worms available per minute within the area occupied by one bird as density changes from low (right) to high (left). As density rises from the average recorded to about double that value, mean area and area searched coincide and, presumably, twice as many worms would be eaten. Data from Smith 1975.

and (ii) the numbers appearing within the area foraged by one Godwit. The area actually searched by individual Godwits was about half of the mean area. On average, each bird removed about 25 per cent of the worms becoming available per minute within the area it searched so that, within the flock as a whole, only about one eighth of the available worms were taken. How much interference resulted from this impact depends on the degree of overlap between birds in the areas each searched, and on the effect of reduced prey density on intake rate. Since neither of these has been measured, it is not possible to calculate whether interference was occurring to a significant degree. On the other hand, remembering that the values given by Smith were average values and that overlap in foraging area may have occurred, the percentage reductions in prey density are not obviously so small that this form of interference can be entirely ruled out, so that further studies might be worthwhile.

3.2.5. Depression of prey availability

The density of available prey may be reduced by the prey themselves reacting to the presence of the birds on the surface. Goss-Custard (1970a) showed that walking Redshank cause *C. volutator* to disappear from the surface for several minutes, and this may explain why visually hunting Redshank feed more slowly when close together (Goss-Custard 1976). That Redshank locating food by touch were not affected is consistent with this suggestion because they can reach most prey this way even if they retreat down their burrows. The feeding rate of touch-feeding Knots on the Wash was also unaffected by the proximity of other birds in minutes during which no encounters occurred (Fig. 8). Indeed, waders feeding by touch may be in general less prone to various kinds of interference than visually searching birds (Goss-Custard 1970a), although more tests are required.

3.2.6. Increasing use of poorer areas

Food abundance varies considerably from place to place, with gradients occurring down the beach, along the length of an estuary and between estuaries (Goss-Custard 1970b, Goss-

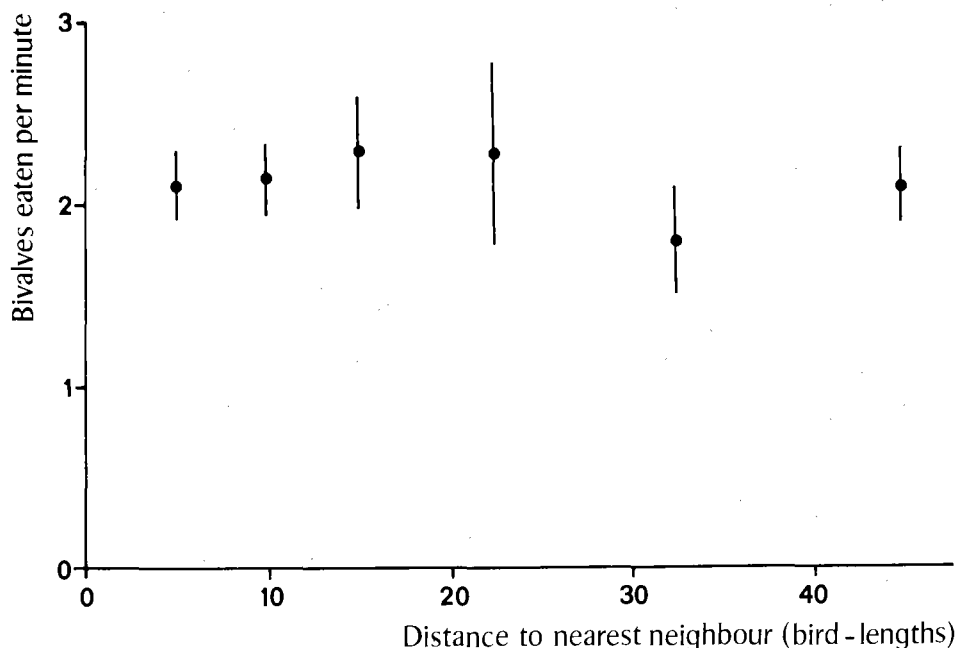


Fig. 8. The numbers of bivalves, mainly *C. edule* and *M. balthica*, consumed per minute by individual Knots, *C. canutus*, at different distances from the nearest neighbour. No overt aggressive encounters occurred during the intervals timed. Vertical bars are \pm S.E.

Custard *et al.* 1977). Studies on Oystercatchers (Goss-Custard 1977a) and Redshanks (Goss-Custard 1970b, 1977b) suggest that waders may often concentrate in areas where prey density, and so their rate of feeding, is high unless the food is made unavailable by a dry substrate. It seems that the distribution of waders over these gradients may vary according to the size of the population using them and in ways which could cause average feeding rate to decrease as population size increases.

Some areas are occupied before others as bird numbers increase on an estuary and so may be called "preferred". Recent studies (Zwarts 1974, 1976, Goss-Custard 1977a, b) suggest that bird density in these areas may eventually reach a ceiling, perhaps to prevent further increases in interference of the kind already discussed. As a result, an increasing proportion of the birds feed in the remaining, less preferred parts of the shore as population size increases further (Fig. 9).

While in some cases the preferred areas are those which are simply closest to the roost, in others they are those where food is most abundant and the birds can feed at the fastest

rate (Goss-Custard 1977b). Therefore, as population size increases, more birds feed in those parts of the shore where food abundance, and so intake rate, is lower. This should cause the average intake rate of the population as a whole to decrease, although by how much has yet to be determined.

3.3. CONCLUSIONS

Data from Oystercatchers, Curlew and Redshank suggest that increasing bird density may depress average feeding rate in the short-term, reversibly and without depletion of the prey populations occurring: hence interference can be said to occur. Several mechanisms have been postulated and include (i) fighting over food items, although this had a negligible effect in Knot, (ii) kleptoparasitism, which was important in Oystercatchers eating mussels, (iii) disturbance during searching, which perhaps occurs in Oystercatchers, Redshank and Curlews, (iv) depletion of the available fraction of the prey, perhaps important in Godwits eating lugworms, (v) depression of prey availability, perhaps important in Redshank, (vi) increasing use of

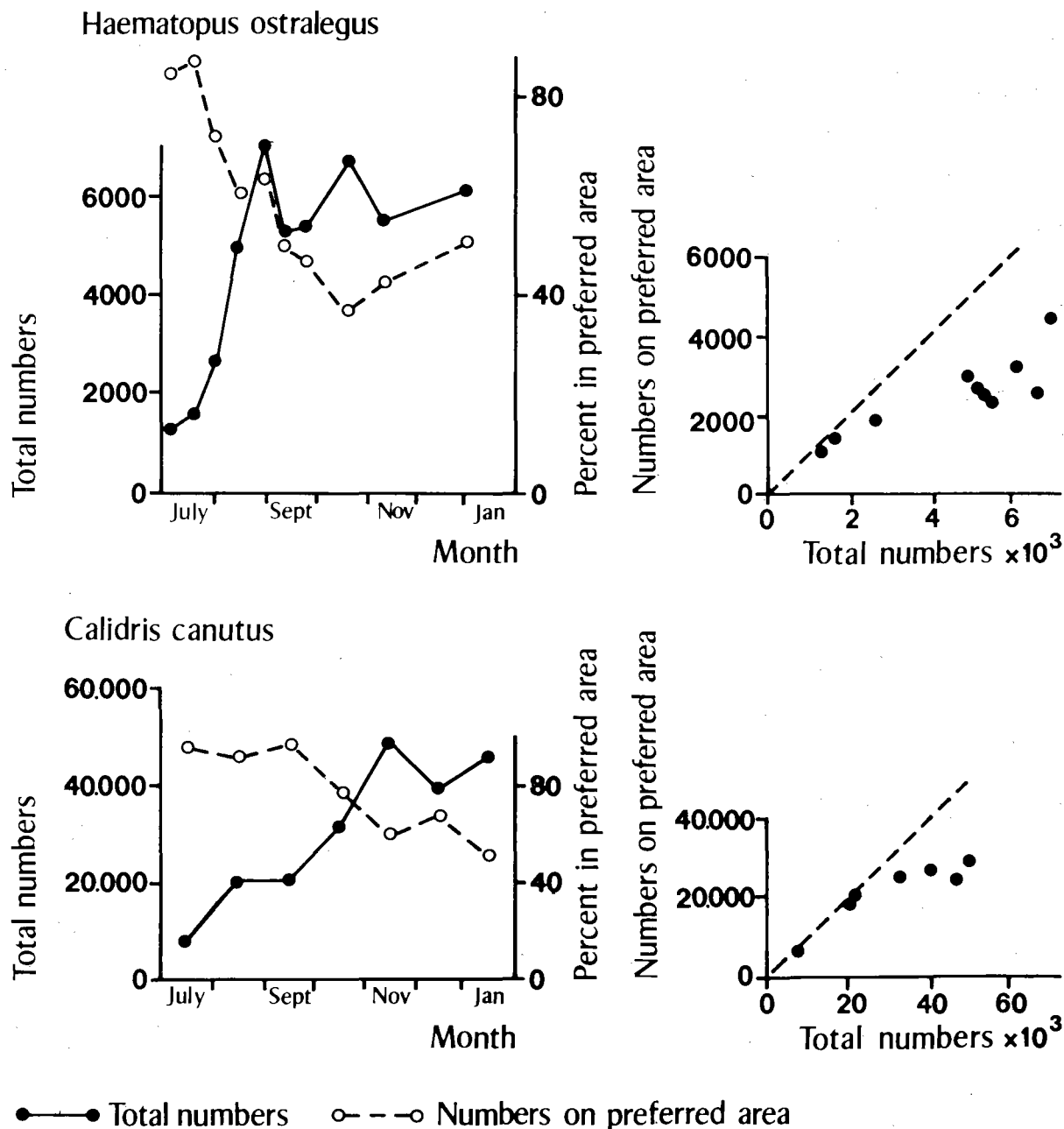


Fig. 9. The left-hand graphs show that the proportion of Oystercatchers, *H. ostralegus*, and Knots, *C. canutus*, in the preferred feeding areas decreased as the total numbers of birds available to feed there increased. The right-hand graphs show that the numbers of birds in the preferred areas tended to level off when large numbers were present: the dotted lines show what would happen if all the birds had fed in the preferred areas however many were present. From Goss-Custard 1977a.

poorer feeding areas, likely to be important in a number of species. Clearly, more tests on the mechanisms involved are required. Unfortunately, rather few studies have focussed on the

effects of the densities of both food and birds on food intake, despite the theoretical interest in both these factors for studies of population dynamics (Varley *et al.* 1973).

4 DEPLETION

4.1. CHANGES IN FOOD ABUNDANCE

Waders return to the estuaries in north-west Europe in late summer and autumn when the prey are still growing and reproducing. Because of growth of small animals into the size range taken by each wader species, the food supplies may continue to increase at this time of year despite increased losses due to waders (Goss-Custard *et al.* 1977). By winter, most growth has stopped in the more northerly estuaries, although some may continue in those further to the south and west. But in the main, the food will not be replaced until growth accelerates with the rise in temperature in spring, and substantial decreases in abundance may occur.

The size of the winter decrease varies enormously between different parts of an estuary, and may depend on the abundance of food present at the start. Unless the prey migrate, the percentage loss is often much greater where initial stocks were high than where they were low, *i.e.* the predation rate is density-dependent (Hancock 1971, Goss-Custard 1977b, Goss-Custard *et al.* 1977). Since waders tend to concentrate their feeding where prey density is highest, the decrease in the food supply is most serious in their preferred feeding areas. But whether or not variations in wader density will give rise to significant variation in the winter depletion of the food supply depends on how much of the loss in different areas is due to waders themselves and how much to other mortality agents.

4.2. IMPACT OF THE WADERS

There are methodological problems in finding out how much impact the waders have on their food. As long as prey are sedentary, exclosures which keep only waders out may indicate the mortality due to these predators. However, such estimates may be highly biased because the removal of predation by waders within the exclosure causes prey density there to be high relative to that on the surrounding mudflats, so other predators move in to reap the reward. The food supplies may then go down equally inside and out, giving the mistaken impression that waders are not important at all. Where mortality

is likely to be compensatory in this way, exclosures may lead to serious errors.

A second approach is to count the birds in plots, estimate the daily consumption of individuals and compare their total consumption over the winter with the amount of food in the mud. Unfortunately, many waders feed at night, often in places and on foods different from those used during daylight (Goss-Custard 1969, 1977a). Measuring the proportion of the daily intake actually obtained within the study areas is difficult, even with modern night-viewing devices. Furthermore, wader counts in small plots are extremely variable so that confidence limits can be extremely high. So, both these approaches have serious problems, and the results now presented must be viewed in this light.

Fig. 10 summarises data from studies in which the depletion of food over the winter has been measured and the proportion taken by waders estimated with the method shown. Some estimates refer to small areas of uniform prey density, which were either important or subsidiary feeding areas, while others refer to a large part of an estuary which could contain areas of both types.

The proportion of food disappearing over the winter is highly variable, but the amount taken by waders in the important feeding areas (A and C) is estimated at between 25 and 45 per cent. It seems that waders may indeed remove substantial proportions of their winter food supply.

4.3. EFFECT OF DEPLETION ON RATES OF FOOD INTAKE

What effect does this impact have on the waders' own ability to obtain their food requirements, especially within the preferred feeding areas where prey is dense and most feeding is done? The effect of a 25–45 per cent decline in food abundance on intake rate can be estimated for Redshank eating *C. volutator* and the polychaete worms *N. diversicolor* and *Nephtys hombergi* and for Oystercatchers eating *C. edule*. From the lines relating intake rate to prey biomass shown on the left-hand side of Fig. 11, the decline in intake rate resulting from different percentage reductions in food supply can be calculated. The graphs on the right in Fig. 11 show

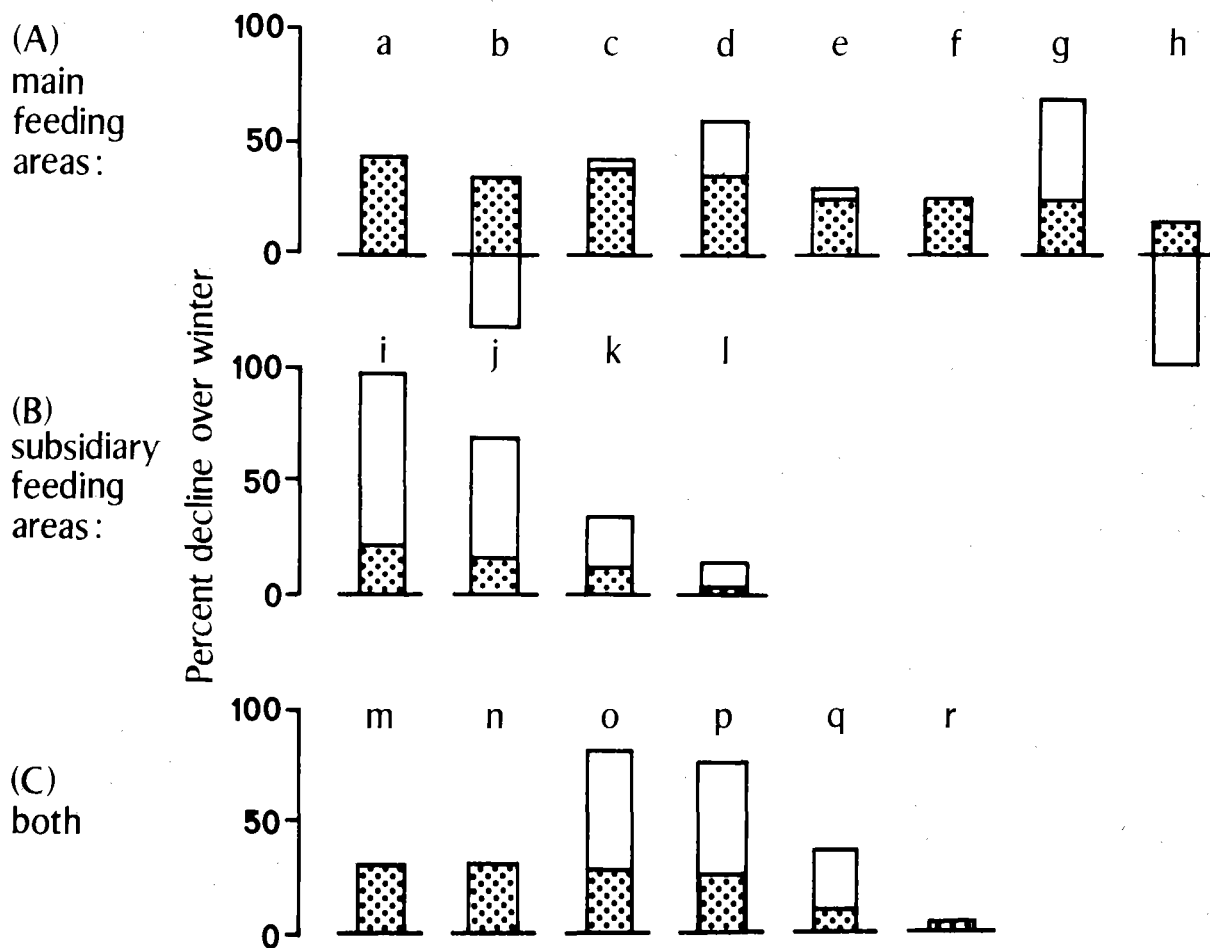


Fig. 10. The percentage of food loss during the winter (open histogram) and that part caused by wader predation (stippled histograms), in (A) main feeding areas, (B) subsidiary feeding areas, and (C) both combined. Histograms below the line indicate food increases due to immigration. The studies cited, species involved and methods used to measure the impact of waders are as follows:

- (a) *Lanice conchilega* eaten by *P. squatarola*, *N. arquata* and *L. lapponica*. Enclosure.
- (b) Several invertebrates eaten by all waders present. Counts.
- (c) *C. volutator* eaten by *T. totanus*. Counts.
- (d) *C. edule* eaten by *C. canutus*. Counts.
- (e) Several invertebrates eaten by all waders present. Counts.
- (f) *A. marina* eaten by *L. lapponica*. Counts.
- (g) *M. balthica* eaten by *C. canutus*. Counts.
- (h) *C. edule* eaten by *H. ostralegus*. Counts.
- (i) *C. edule* eaten by *H. ostralegus*. Counts.

- (j) Several invertebrates eaten by all waders present. Counts.
- (k) *C. edule* eaten by *H. ostralegus*. Counts.
- (l) *C. edule* eaten by *C. canutus*. Counts.
- (m) *M. edulis* eaten by *H. ostralegus*. Counts.
- (n)-(q) *C. edule* eaten by *H. ostralegus*. Counts.
- (r) *M. balthica* eaten by *C. canutus*. Counts.

References: a, b, d, e, g, h, i, j, k, l: Goss-Custard 1977a. c: Goss-Custard 1969. f: Smith 1975. m: Goss-Custard *et al.* 1980. n-q: Horwood & Goss-Custard 1977. r: Prater 1972.

this for two levels of initial density of each prey type. The reduction in intake rate varies according to the slope, and shape, of the relationship between intake rate and prey abundance and according to the initial density of prey chosen. A depletion of 25–45 per cent reduces

average intake rate by 5–30 per cent over the winter. So an increase in the density of waders, within areas not already at capacity, is likely to cause a significant decrease in the average rate of food intake unless, of course, there is a compensatory relaxation in some other mortality agent.

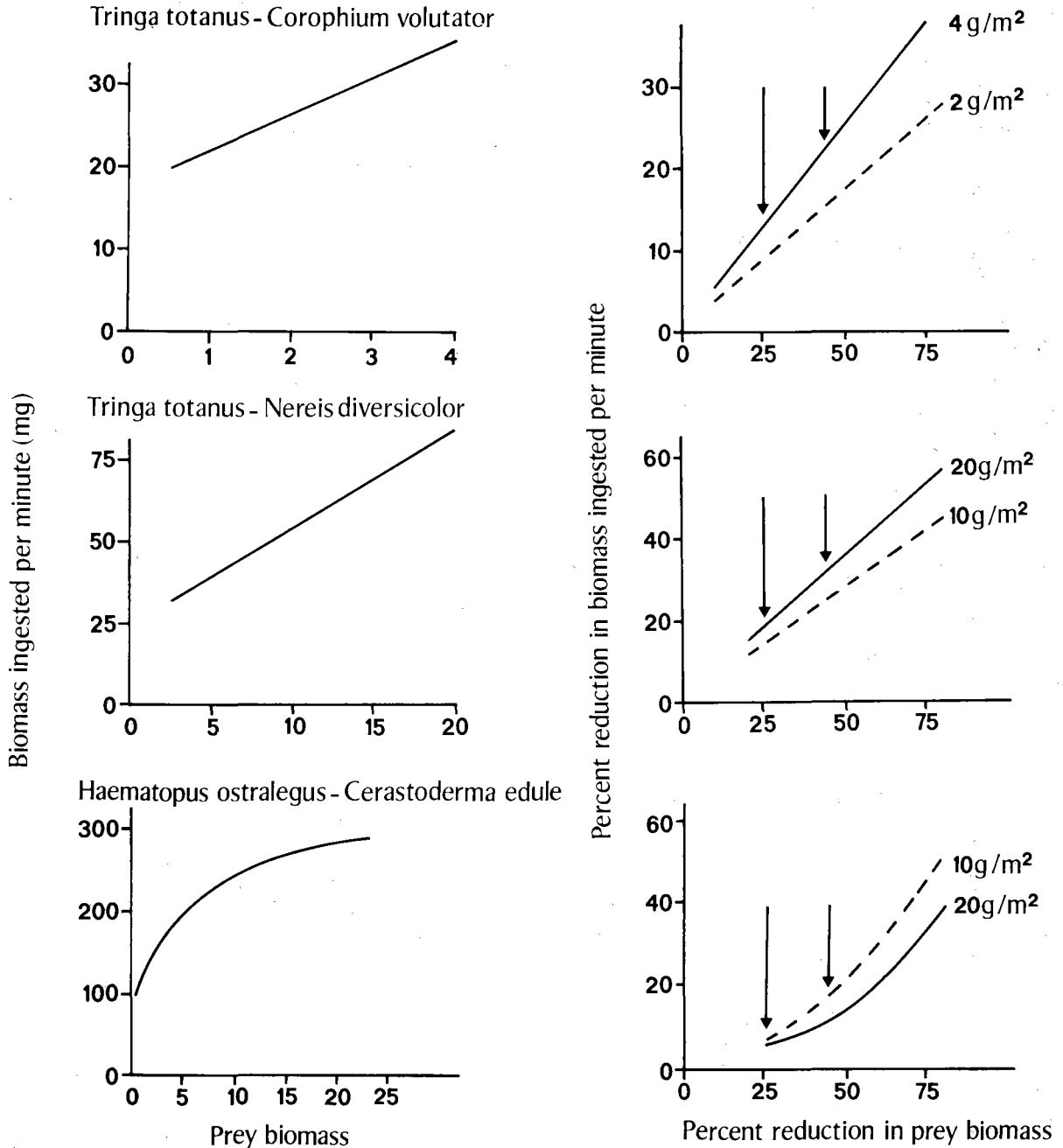


Fig. 11. The left-hand graphs show the line relating intake rate to prey biomass in three studies: A. *T. totanus* eating *C. volutator* (Goss-Custard 1970b), B. *T. totanus* eating *N. diversicolor* (Goss-Custard, et al. 1977), C. *H. ostralegus* eating *C. edule* (Goss-Custard 1977a). The right-hand graphs show the percentage reductions in intake rate that would follow from the percentage declines in prey biomass shown. These reductions in intake were calculated from the lines shown in the left-hand graphs, and values for high and medium initial values of prey biomass are shown. The arrows show the range in the impact of waders on their main winter food supplies in the field.

4.4. CONCLUSIONS

The food supply of waders decreases sharply during the winter, especially in places where it is initially abundant and the birds prefer to feed. The waders themselves may consume 25–45 per cent of the food in such areas. Present indications are that this could reduce the birds' feeding rate during the winter by between 5 and 30 per cent, depending on the species of prey and wader considered. Hence feeding rate may decline significantly more in winters when waders are abundant because of the additional depletion of the food supplies.

5. INDIVIDUAL DIFFERENCES

5.1. INTRODUCTORY REMARKS

The review suggests that average intake rate may decrease as wader density increases because of both interference and food depletion, although by how much is uncertain. However, it is unlikely that all members of a population would suffer equally. While such individual differences are to be expected from our knowledge of birds as a whole, little has been done on waders themselves. Therefore, the following discussion of how the effects of interference and depletion may be distributed unequally between individuals is necessarily rather speculative, and so brief.

5.2. INTERFERENCE

5.2.1. Encounters over food

Individuals may vary considerably in the probability that they will win or lose contests over food. So even if average intake rate is little affected by increased fighting over food as bird density rises, that of some individuals may be. Sub-dominants particularly may be attacked more as density rises, and their intake rate suffer disproportionately as a result.

Individual differences have not been studied but there are data on attack and success rates for different age classes (e.g. Harrington & Groves 1977). On the Exe estuary, for example, most Oystercatchers eat mussels (Goss-Custard 1978). Some birds in their first winter (juveniles) occur on the mussel beds, but most of the birds there are in their second or third winter (immatures) or

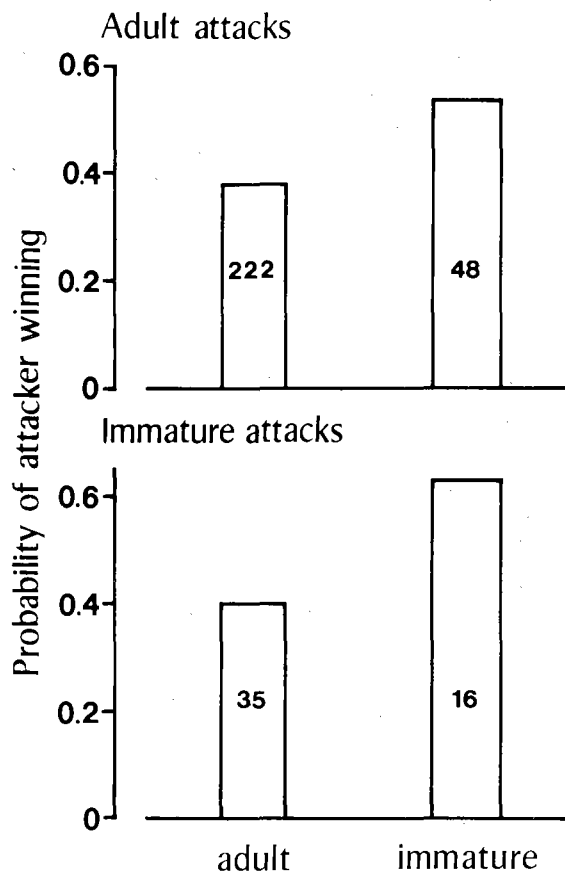


Fig. 12. The probability that an adult or immature attacking an adult (left) or immature (right) Oystercatcher, *H. ostralegus*, will win. Values in the histograms show sample size.

are adults. They were studied by watching, for five minutes, individuals chosen at random on a representative sample of beds. Fig. 12 shows that, as expected, adults tend to win contests over mussels with immatures. Table 1 shows that immatures are much more likely than adults to lose mussels to other Oystercatchers, but perhaps a little more likely to steal from others themselves. The net effect, however, is that immatures are 2–3 times more likely to lose any mussels they have found, and they do not make up the loss by searching harder (Fig. 6).

5.2.2. Disturbance in searching, exploitation and depression of available prey

Even though waders prone to any of these forms of interference may forage in loose flocks to minimise the effect (Goss-Custard 1970a,

Table 1. The numbers of mussels lost to other birds or stolen from other birds by adult and immature Oystercatchers in 212 periods of 5 minutes. The incidence of fighting over mussels and the proportion of immatures present varied between seasons and beds. To ensure comparability, each observation period for immatures had been matched with the nearest one obtained for an adult on the same bed. The observations were seldom made more than twenty minutes apart, and were usually adjacent

	Number of occasions:		Net loss
	(i) mussel lost to Oystercatcher	(ii) mussel stolen from Oystercatcher	
Adults	7	2	5
Immatures	24	7	17

1976), birds at the rear of the flock may nonetheless suffer a reduced rate of feeding. If certain individuals tend to feed in these positions consistently (cf. Woodpigeons, *Columba palumbus*: Murton *et al.* 1966), the interference would be distributed unequally amongst the population.

5.2.3. Increasing use of poorer areas

If individuals mainly feed within a limited area, some may consistently feed in good places while others may feed in poorer ones. On the Exe estuary, individual Oystercatchers tend to feed in the same area for long periods. For instance, in a study of 28 marked individuals, an average of 80 per cent of the sightings of each bird was made on the same bed. Since a greater proportion of the birds feed in the less preferred parts of the estuary as the population increases, an increasing number of individuals feed for most of their time in these areas as numbers rise.

5.3. DEPLETION

Some individuals may track the changing position of the best food supplies more effectively than others, either because they are better adapted or because they compete successfully for the best feeding areas, but so far, there are no published reports.

5.4. CONCLUSIONS

The idea that the deleterious effects of increasing population size is distributed unequally amongst the individuals in the population has been little studied, but seems a strong possibility. It is easy to envisage mechanisms for this with all

the forms of interference so far conceived, and with depletion. There is some evidence from Oystercatchers eating mussels that young birds lose more mussels to other Oystercatchers than do adults, which suggests that increasing population size could particularly affect them. But so far, the magnitude of any inequality has not been measured, and this remains an important area for future research.

6. WINTER FEEDING CONDITIONS AND POPULATION PROCESSES

6.1. INTRODUCTORY REMARKS

The discussion so far may be summarised as follows. Average intake rate is likely to decrease as population density rises in winter because of (i) an immediate increase in interference, and (ii) the longer term depletion of food. Particular individuals, or young birds, may suffer disproportionately. Thus the intake rate of some or all birds is likely to be related to wader density.

The important question, though, is whether an increase in bird density increases winter mortality and dispersal or decreases subsequent breeding success. Feeding conditions may normally be so good that large reductions in intake rate can occur without any of these processes being affected. If this is not so, these three processes are likely to be density-dependent because feeding conditions probably deteriorate as population density rises. What evidence is there to suggest that any of these three processes are affected by food shortage in winter?

6.2. WINTER MORTALITY

Mortality outside the breeding areas seems to be highest in winter and early spring in several species on the Wash (Goss-Custard *et al.* 1977) and in *H. ostralegus* in west Britain (Goss-Custard in press). The timing of this peak indicates that food shortage may be involved, either directly or by increasing the risk of birds dying through injury, predation or disease. Many waders spend a very high proportion of the time feeding in winter, especially the smaller species (Goss-Custard *et al.* 1977). Food may be more difficult to find then because (i) daylength is short, and feeding at night may be less profitable, (ii) the abundance and food value of each prey

may decrease from autumn to spring because little growth and recruitment occurs, and (iii) the food may be deeper in the mud in winter and also less available at low temperatures. Thus food shortage may be at least a contributory factor to normal winter mortality, although the evidence is circumstantial.

The size of the mortality may vary considerably between years, however. Large mortalities are recorded in prolonged periods of severe frost (Pilcher *et al.* 1974). Birds found then are very thin, apparently having died from starvation. Cold weather could do this (i) by reducing the time available for feeding on the shore by covering the upper levels of the shore with ice, (ii) by reducing the availability of prey on those areas of the shore that are not covered by ice (Goss-Custard 1969, Smith 1975, Goss-Custard *et al.* 1977), (iii) by increasing interference in feeding areas reduced in size by ice, (iv) by preventing birds from supplementing their diet in the fields at high water (Goss-Custard 1969, Heppleston 1971), and (v) by increasing energy demand. Heppleston (1971) estimated that 25 per cent of *H. ostralegus* on the Ythan estuary died during a cold spell lasting 22 days. Juveniles were much more likely to die than adults, perhaps because they were less effective at feeding or because they were forced by the adults to feed in the less profitable parts of the shore. Dead birds are usually found after three days of hard frost (R. Berry pers. comm., Heppleston 1971). However, cold spells, even of this short length, are uncommon in many areas so that such large mortalities may be unusual.

What is the size of mortalities occurring in more usual circumstances? Very few corpses are normally found, even in north Scotland (Goss-Custard 1969, Heppleston 1971). Waders on the Wash were ten times less likely to be found dead during four mild winters than during the winter of 1968/69 when there was a cold spell lasting several days (Goss-Custard *et al.* 1977). Unless considerable movements occur, mortality must normally be below 10 per cent otherwise a ten-fold increase during a cold winter would have wiped out the entire population! Similarly, only 6 of 45 (13 per cent) juvenile Oystercatchers ringed on the Exe before December in three years had

disappeared (including 2 known to have died) by the following May, suggesting that even this presumably most vulnerable segment of the population has a high survival rate. It appears that winter mortality is usually rather light, but its possible density-dependence has not yet been investigated.

6.3. DISPERSAL

Waders may leave an estuary when the feeding conditions deteriorate sufficiently, either because the food is frozen over (Goss-Custard 1969) or scarce anyway (Davidson 1966). They may disperse themselves between estuaries according to the abundance of the food. The densities of Curlew and Redshank on nine estuaries and coastal flats in south-east England are correlated with food density (Goss-Custard *et al.* 1977), and the regular movement of birds between estuaries suggests that this is brought about at least in part by dispersal, although its magnitude had not been measured.

6.4. BREEDING SUCCESS

The winter food supply may influence the subsequent production of young through its effect on the condition of adults. MacLean (1969) suggests that the breeding densities of *Calidris melanotos* in Alaska depend on the feeding conditions encountered in winter and on passage. The idea is difficult to test but data from Harris (1967, 1975) and Horwood & Goss-Custard (1977) suggest that the fledging production of *H. ostralegus* on Skokholm was unrelated to the abundance of their main food *C. edule* in the Burry Inlet where many adults spend the winter (Goss-Custard in press).

6.5. CONCLUSIONS

Although mortality can be high in some species in severe winters, it is normally rather slight. Apart from severe weather, there is only circumstantial evidence that mortality is related to food. But given that individuals probably differ in their abilities to obtain food and that, on average, birds of many species feed for a very high proportion of the time in winter, it is likely that a few individuals do experience chronic shortages, and either die or leave. There is as yet no evidence

that winter feeding conditions affect breeding success, but tests are difficult in these highly migratory birds. Dispersal may be related to feeding conditions but, when considering population dynamics, may be ignored in these very mobile birds if the unit of population size considered is large enough. Therefore, the remainder of this paper considers only the population consequences of a slight winter mortality, possibly related to food shortage.

7. POPULATION CONSEQUENCES OF WINTER MORTALITY

7.1. INTRODUCTORY REMARKS

What role then, does a slight winter mortality play in the population dynamics of waders? We cannot examine this empirically at present because observations and experiments on population processes are difficult in these migratory birds. I have therefore had to resort to a simulation exercise with a simple theoretical model of wader population dynamics in the hope that this might give insights into the way in which the population size is affected by winter mortality. The assumptions of the model are based on a review of wader literature (Goss-Custard in press) and are as follows.

7.2. MODEL OF POPULATION DYNAMICS

7.2.1. Derivation of assumptions

Clutch size, hatching success and fledging success of waders in general are variable between places and between years but there is no evidence that the mortalities at any stage are related to the density of breeding pairs, even though many deaths are due to predators. However, it is likely that the production of young is density-dependent when one considers the whole population, not just the segment that is breeding. This is because territoriality may limit breeding density so that a part, sometimes as high as 60 per cent of the population fails to breed. Many studies report sightings of non-breeders, and two have shown that breeders removed by shooting are quickly replaced (Harris 1970, Holmes 1970). It is assumed in the model that territoriality limits breeding density and that annual production per

breeding pair varies up to three fold, but independently of nesting density.

Annual mortality is highest in the small species, but is unlikely to exceed 35 per cent on average and is probably very much less. Mortality in the larger species, such as Oystercatchers, is normally under 10 per cent. The mortality of juveniles is higher than in adults. Three-fold variations in annual mortality of Oystercatchers have been recorded, but it is not known whether they are density-dependent. Adults die on the breeding grounds, either as they arrive on breeding areas still under snow or later on when taken by predators on the nest. Mortality during migration is difficult to study and no measures of it have yet been reported. As discussed above, winter mortality seems usually to be slight except during very severe weather.

The main assumptions in the model are therefore (i) territoriality limits breeding density, (ii) annual production per breeding pair varies two or three fold, but independently of nesting density and winter feeding conditions, (iii) annual mortality does not exceed 35 per cent, and (iv) winter mortality is usually low. For simplicity, I also assume that breeding starts at one year, although many waders may start to breed in their second or even fourth or fifth years. Sex ratio is assumed to be equal, although little is published on this.

7.2.2. The model

Territoriality is strongly density-dependent if the number of pairs breeding is roughly constant despite wide variations in the total number available to breed. However, the numbers trying to settle may influence breeding density (Patterson 1965, Krebs 1970), even though some are always prevented from getting a territory. Vines (1979) showed that territory size in Oystercatchers could be compressed up to a limit as the numbers of birds trying to settle in an area increased. Breeding density of *C. alpina* in southern Finland was affected by the numbers of young produced two years previously (Soikkeli 1970), suggesting that the numbers of potential breeders influenced density. The possibility that the number available to breed affects breeding density is included in the model. A convenient

way of doing this is to express the proportion failing to obtain a territory in the same way that mortality is defined in key-factor analysis (Varley & Gradwell 1960), *i.e.*:

$$k = \log N - \log B$$

where N is the number of potential breeders and B is the number able to obtain territories. If a constant number (B) of birds breeds each year and k is plotted against $\log N$, the slope (b) is 1; this is illustrated in Fig. 13. The number breeding in this case is determined solely by the point at which the line crosses the X-axis *i.e.* the level of the intercept. Reducing the slope of the line below unity means that the numbers attempting to breed influences the numbers actually establishing territories *i.e.* competition for space compresses the size of the average territory taken up. In this case, then, the numbers breeding depends on both the slope and the intercept, as well as the numbers attempting to breed. To illustrate these points, Fig. 13 shows the numbers of birds breeding and the proportion not breeding at various population levels for two values of b , but with the same intercept. Some birds are always prevented from breeding, but the numbers involved depends on the total population size where $b = 0.4$, but not where $b = 1$.

This is a useful way to model the effect of territoriality on breeding density and, therefore, the production of young by the whole population. The higher the value for b , the stronger is the density-dependent limitation on the number of pairs, and therefore the numbers of young being produced. The main characteristics of two theoretical populations in which the slope of k against $\log N$ is either 0.4 or 1 are shown in Fig. 14, and some examples of the calculations made are given in Appendix 1. The production of young per breeding pair varies randomly between 0.5 and 1.5 and a 25 per cent density-independent mortality acts on the combined numbers of breeding and non-breeding adults and juveniles after the young have fledged. Each population is regulated by territoriality and reaches the same level whether the initial population is high or low (although this is only shown for one of them). When $b = 1$, only 10 birds are able to breed however many there are able to do so. When $b = 0.4$, more birds breed but the population

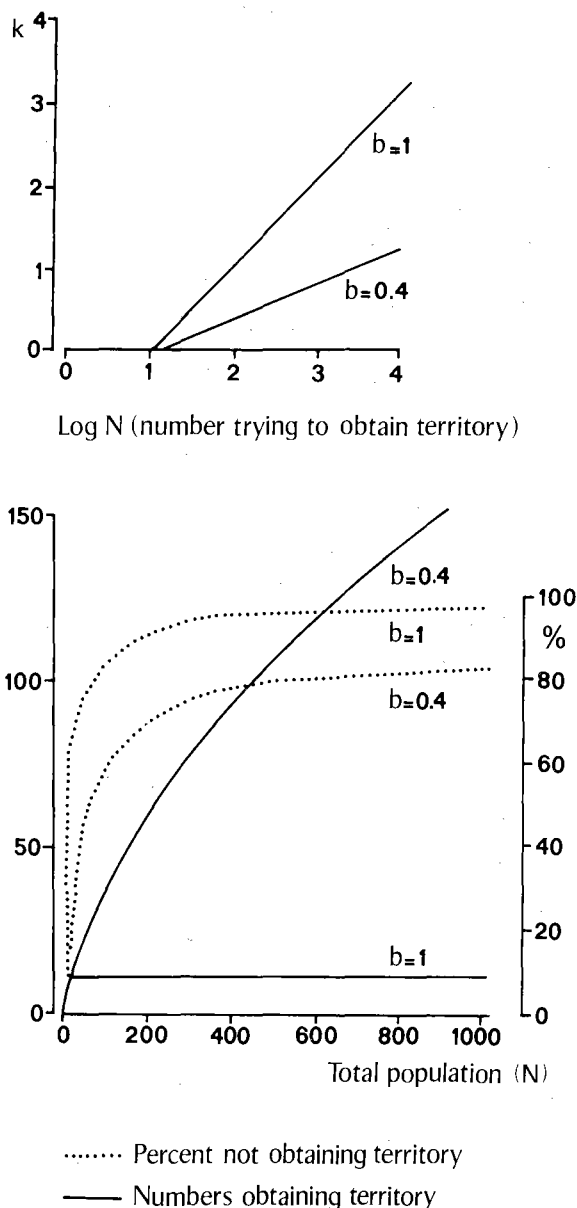


Fig. 13. How the numbers of birds excluded from breeding by territoriality is incorporated into the model. Top: two examples of the proportion failing to obtain a territory (expressed as a k -value) as a function of the total population size. Values of b refer to the slope of the line. Bottom: the numbers of birds obtaining a territory and the percentage failing to do so with the slopes of 1 and 0.4 shown in the top graph. When $b = 1$, the numbers of birds obtaining a territory is unaffected by how many are trying to breed over most of the range, whereas with a slope of 0.4, this is not so.

In this case, more birds breed as population size increases, but an increasingly large proportion is excluded so breeding production is still density-dependent.

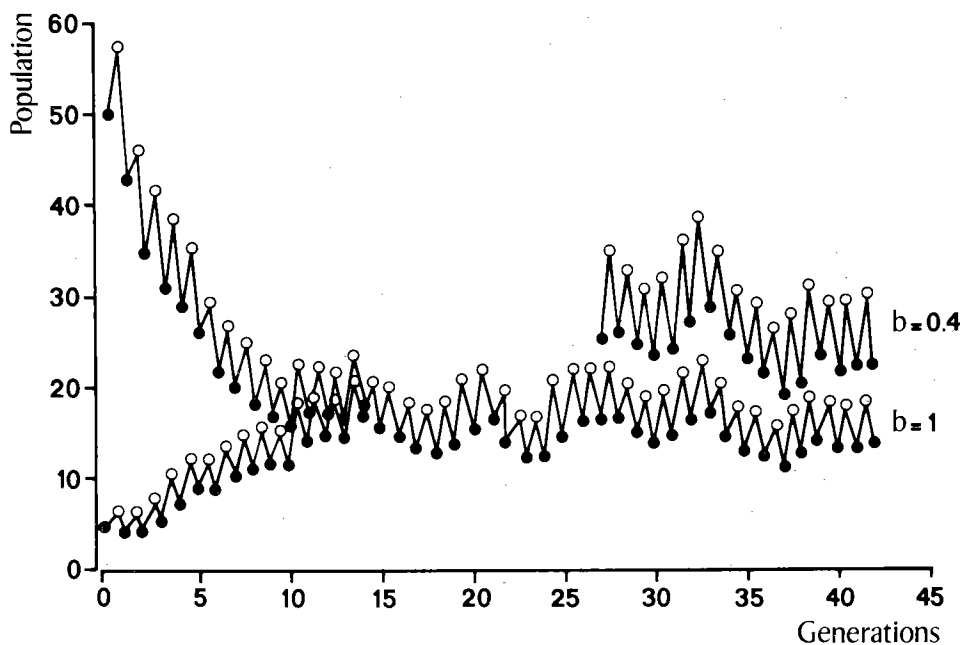


Fig. 14. The dynamics of two populations regulated entirely by territoriality with different degrees of density-dependence. Production of young varies randomly between 0.5 and 1.5 per breeding pair and an 25 per cent density-independent annual mortality operates. Solid dots: potential breeders at the end of the winter. Open circles: total number of birds after the breeding season, including breeders, non-breeders and fledged young.

still stabilises, though at a higher and more variable level. Both populations fluctuate from year to year because the numbers of young produced per breeding pair vary, but the population in which $b = 0.4$ will fluctuate more because the numbers breeding also varies according to how many are trying to obtain territories. These populations stabilise, of course, when the average percentage mortality of the whole population from the end of one breeding season to the beginning of the next is the same as the average number fledged, which is itself fixed by the number of pairs allowed to breed.

7.3. ROLE OF MORTALITY

Although regulation may only occur through spring territoriality, the size of a density-independent mortality (M) operating at other times of year has, of course, a considerable effect on population size. Fig. 15 shows the population size at stabilised levels for different values of M and b : production per breeding pair (P) is 1.2 in all cases. Population size is very sensitive to changes in the magnitude of a density-independent mor-

tality because the population stabilises when mortality and natality are equal.

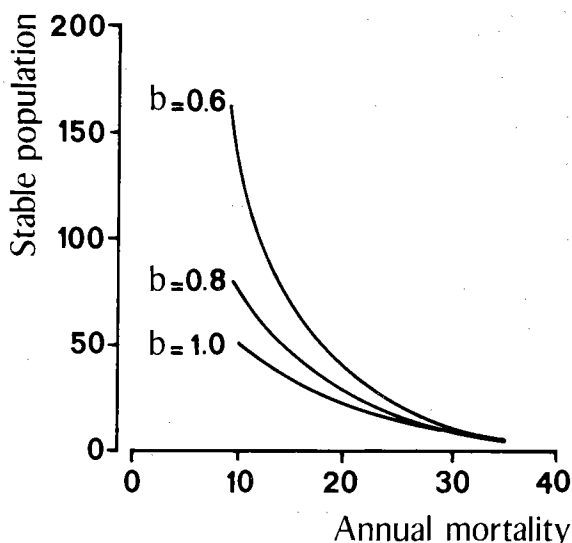


Fig. 15. Stable population size with different strengths of density-dependent limitation on production through territoriality ($b = 1, 0.8$ or 0.6) and different density-dependent annual mortalities (per cent).

Table 2. Population size at stability under different amounts of summer and winter regulation

Strength of territoriality on the breeding grounds	Average Population size in spring		
	With no winter mortality	With weak winter regulation*	Average winter mortality observed with weak winter regulation
0.6	42	23	9
0.8	30	20	7
1.0	24	18	6

* N.B. Winter mortality is expressed as k values (Varley & Gradwell 1960) where
 $k = \log N_A - \log N_S$

and N_A and N_S are the population sizes in autumn and spring before and after the mortality acts. Mortality is density-independent if k varies independently of $\log N_A$ but is density-dependent when k increases as $\log N$ increases. The slope of the line (b) relating k to $\log N_A$ defines the strength of a density-dependent factor (Varley *et al.* 1973) and in this example it is very weak ($b = 0.1$).

The limited data on wader populations suggest that winter mortality, though slight, might be density-dependent. Does introducing a weak density-dependent winter mortality have a significant effect on population size?

Table 2 shows the size of populations strongly regulated by territoriality in the breeding season ($b = 0.6, 0.8$ or 1) but also weakly by density-dependent mortality in winter. Population size without any winter mortality is also shown. P is again 1.2 and there is a 20 per cent density-independent mortality between fledging and arrival on the wintering grounds. The introduction of a relatively small winter mortality can have a surprisingly large effect on population size, especially when b on the breeding grounds is small. This is true even though it is superimposed on a high density-independent mortality that occurred before.

7.4. CONCLUSIONS

Studies of the dynamics of wader populations are in their infancy because of the considerable practical difficulties involved in making them. The assumptions used in this model of population dynamics are therefore provisional, and so the conclusions reached should be regarded as tentative. The interesting point to emerge from the exercise, however, is that we should perhaps not immediately dismiss as unimportant a small, possibly density-dependent, winter mortality. Even though most regulation and most of the mortality occurs at other times of year, a winter mortality of this magnitude could be quite significant.

8. DISCUSSION

8.1. POPULATION DYNAMICS

There is evidence that as wintering wader populations increase, food is collected more slowly. Whether this increases mortality rate, or decreases breeding success, is in doubt. Simulations suggest that, even if this mortality is small, it should not automatically be dismissed as having only a trivial effect on population size. Therefore, studies of food shortage and winter mortality, and the possibility that this mortality is density-dependent and so contributes negative feed-back to population growth, constitutes an important area of enquiry in wader population dynamics.

The migratory habits of waders make it difficult to study these possibilities in an easily defined population. Birds wintering on one estuary may disperse to huge breeding areas. The importance of natality and mortalities at different times of year may have to be explored with population models as was done here. Hopefully, these models will be based increasingly on field studies. Simulation exercises are useful in deciding which aspects of natality and which mortalities may be most important because they show how a population might behave were any one mortality, or combination of mortalities, to be removed or increased.

This is the equivalent of field experiments in which the magnitude of factors thought to be limiting are either increased or decreased and the effect on population size monitored. Such experiments may be possible at certain times in the waders' annual cycle; for instance, nest pre-

dation could be decreased or increased. But the difficulty is that the effect of this on population size is hard to follow through because of their complex and extensive migratory habits. This is where models will be able to play a valuable role, especially as the parameters incorporated in them become increasingly well defined. If removing nest predation does increase production significantly, for example, the consequences of such an increase for the population size as a whole could be explored in the model.

Another feature of studies of wader population dynamics is that we are as interested in accounting for population size in winter as at any other time. This is partly because many waders are least accessible to us when they breed and partly because they excite most interest, and concern for their conservation, in the winter. We do not therefore consider the density of breeding pairs as being the main feature of the population to be explained, especially as the proportion of non-breeders in the population may be large (up to 60 per cent in some island populations of Oystercatchers) and their survival seems to be high. We are forced to examine birth and death rates amongst all sections of the population and, with mobile birds, this is a difficult task. But one way to explore the relative importance of different factors acting on birth and death rates in different places at different times of year is to sample these rates in as many areas as possible and to explore their combined effects with a general population model of the kind described earlier.

8.2. COMPETITION, INTERFERENCE AND DEPLETION

The definition of competition had stimulated some debate in the past but it is now generally recognised that it may be defined either in terms of a measurable effect or in terms of a process operating within the population. Thus Milne (1961) defines competition as the endeavour of two or more animals to gain a particular requirement, or to gain the measure each wants from the supply of a requirement, when that supply is not sufficient for both (or all). This definition is widely accepted where a definition by process, rather than by effect, is preferred. On this defi-

nition, individual waders may compete to minimise the effect of depletion and interference on themselves because, with the possible exception of kleptoparasitism, individuals can probably do better than the average at the expense of others. Williamson (1976), however, rejects this definition on the grounds that it introduces too many unmeasurable and undefinable notions e.g. "endeavour", "wants" etc. He defines competition as occurring when the size of two populations occurring together is less than both would have been in the absence of the other, and thus favours a definition by effect. While this definition cannot be strictly applied to individuals within a population, it can be modified by substituting for population size some presumably important goal of individuals, e.g. maximising breeding success or food intake. Individuals would be expected to compete to minimise the effect of increased bird density on their own rate of feeding because predators as a whole (Krebs 1978) and waders in particular (Goss-Custard 1970, 1977b, c) may forage so as to increase feeding profitability. On this definition, this paper has been concerned largely with competition for food because it discussed how intake rate may decrease as bird density rises.

The two mechanisms involved in this decrease, namely interference and depletion, were distinguished on grounds of process but characteristics enabling each to be identified where studies of processes are impractical were also suggested. Thus, interference occurs where intake rate decreases as a reversible response to increased bird density, whereas depletion is irreversible, at least until growth and reproduction of the food restores it to the original level. The two can be distinguished in the field on the basis of time scale and sequence. Interference occurs when intake rate goes up or down as a more-or-less immediate response to changes in bird density and there is no trend for intake rate to decrease the longer the birds have been feeding in an area. Depletion occurs in waders over a longer time scale and intake rate continues to decrease because the food is becoming scarcer. Most interference processes postulated here are likely to operate rapidly: if half the birds fly away, the remainder should benefit immediately from reduced

stealing, increased density of available prey and reduced disturbance in searching. The response may be less rapid where birds are now able to move to the better feeding areas, but how long such a readjustment would take may depend on the size of feeding area in question.

The disadvantage of distinguishing interference and depletion this way is that it lumps together processes which on other, common sense, criteria are clearly separable. Thus interference includes kleptoparasitism which involves interactions with other species. The justification for doing this is the presumed association between increasing wader density and kleptoparasitism and the difficulty in distinguishing how much of the decrease in intake rate is due to kleptoparasitism and how much to the waders themselves. The same difficulty applies with other definitions by effect: for instance, the population size of two species may decrease when together because they attract a generalist predator in addition to the one specialist predator each attracts when alone. This is not competition in terms of the process we think of when we use the word, but defined by effect, it is. But as research on the processes of competition, depletion and interference proceed, it should be possible to define them more by process than by effect which, I think, is what many workers would prefer.

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10. SUMMARY

This paper discusses how the rate of food intake of wading birds may decrease as their density increases. It distinguishes two main processes, depletion and interference. Interference is the more-or-less immediate, and reversible, reduction in rate when wader density increases. It occurs because the actual presence of other birds themselves in some way interferes with feeding. In depletion, the reduction in the food supplies themselves reduces feeding rate. Field evidence is reviewed for interference in *Haematopus ostralegus*, *Tringa totanus* and *Numenius arquata*. Although little studied, interference may occur because, as wader density increases, (i) birds fight more for food or feeding sites, (ii) kleptoparasitism increases, (iii) birds disturb or distract each others' searching more frequently, (iv) the available fraction of prey is depleted more, (v) the prey retreat more into the mud, or (vi) more birds are forced into the poorer feeding areas. The evidence for each of these possibilities is discussed, but few conclusive

data have been published to date. Depletion of the food may be considerable during the winter, with waders taking 25–45 per cent of the food present in their main feeding areas. Such reductions could reduce average feeding rate by up to 30 per cent in *T. totanus* and *H. ostralegus*.

The deleterious effects of interference and depletion could be distributed unequally amongst the population so that some individuals bear the brunt of the decrease. Field evidence suggests that, in most winters, mortality is slight but that the relatively poor feeding conditions at that time of year may be involved: in very cold winters, starvation and heavy mortalities do occur. Since intake rate is depressed by increased population density, a greater proportion of birds are likely to be at risk as population density rises. Though slight, winter mortality linked to poor feeding conditions could thus be density-dependent, although more field studies are required to test this possibility. Using a theoretical population model in which most regulation is through territoriality in the breeding season and the population is subject to a larger density-independent mortality in the summer, it is shown that the introduction of a weakly density-dependent winter mortality of only a few per cent could decrease stable population size by 25–45 per cent. Therefore we should be cautious before dismissing such a mortality as trivial. The use of models like this in studies of the population dynamics of these migratory birds is discussed. Competition, interference and depletion may be defined in terms of some effect and by the process involved. With the possible exception of kleptoparasitism, competition is probably involved in interference and depletion however terms are defined.

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12. APPENDIX

Some examples to illustrate how the population model works. In all cases, the production per breeding pair is set at one fledged young and the post-breeding population of breeders, non-breeders and fledged young is subjected to a 25% density-independent mortality before the next breeding season begins. All that varies in these examples is the strength of the territorial limitation on breeding density (between cases 1 and 2) and the size of the initial population (between examples A and B).

Case 1

The slope (b) of the line of k-value (proportion excluded from breeding) against log N (population size at the start of the breeding season) is 1 and crosses the x-axis (as in Fig. 13) at 1 so that the intercept on the y-axis is -1. From the general formula for a straight line ($y = a + bx$), the equation here is $k = -1 + 1(\log N)$.

Example A:

$N = 50$

$k = -1 + 1(\log 50) = -1 + 1.699 = 0.699$.

$\log B$ (breeding population) = $\log N - k = 1.699 - 0.699 = 1$.

therefore $B = 10$ birds, or 5 pairs,

therefore NB (non-breeding population) = $50 - 10 = 40$ birds.

P (production of young) = $5 \text{ pairs} \times 1 \text{ per pair} = 5 \text{ young}$.

PB (post-breeding population) = $P + B + NB = 5 + 10 + 40 = 55$.

M (post-breeding mortality) = 0.25, therefore $55 \times 0.25 = 13.75$ birds die.

Therefore N for next year is $55 - 13.75 = 41.25$, so the population is declining.

Example B:

$N = 10$

$k = -1 + 1(\log 10) = -1 + 1 \times 1 = 0$.

$\log B = 1 - 0 = 1$.

$B = 10$ birds, i.e. 5 pairs.

$NB = 10 - 10 = 0$

$P = 5 \times 1 = 5$

$PB = 5 + 10 + 0 = 15$

$M = 0.25 \times 15 = 3.75$

$N = 15 - 3.75 = 11.25$, so the population is rising.

Case 2

The slope of k on $\log N$ is now 0.4. The line crosses the x-axis at 1, so intercepts the y-axis at -0.4, therefore $k = -0.4 + 0.4(\log N)$.

Example A:

$N = 50$

$k = -0.4 + 0.4 \times 1.699 = 0.280$

therefore $\log B = 1.699 - 0.280 = 1.419$

$B = 26.24$, i.e. 13.12 pairs

$NB = 50 - 26.24 = 23.76$

$P = 13.12 \times 1 = 13.12$

$PB = 13.12 + 26.24 + 23.76 = 63.12$

$M = 0.25 \times 63.12 = 15.78$

$N = 63.12 - 15.78 = 47.34$, so the population is declining but more slowly than in Case 1.

Example B:

$N = 10$

$k = -0.4 + 0.4 \times 1 = 0$, so all birds breed as in Case 1, Example B, and the remainder of the calculation is the same as in that example.