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EFFECT OF HABITAT LOSS ON THE NUMBERS OF OVERWINTERING SHOREBIRDS

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ABSTRACT.—This paper discusses issues raised by attempts to predict whether the numbers of shorebirds using an estuary will decrease following industrial, agricultural, or recreational development of some of their feeding grounds. Within an estuary, most feeding is usually done in limited parts of the shore where the prey are most abundant. Hence, the siting as well as the size of a development scheme is important in evaluating its effects on particular shorebird species. Bird densities may be highest in those estuaries where prey densities are highest but it is not clear if this reflects a simple behavioral preference of individuals for the best feeding areas or results from disproportionately high mortality rates, or subsequently low reproductive output, in estuaries where food is scarcest, or is due to a mixture of both. Hence studies need to be designed to see if a loss of feeding grounds will lead simply to a redistribution of birds over the feeding grounds or to a reduction in overall numbers. Observations suggest that bird density may reach a ceiling level in preferred areas so that a loss of habitat would cause more birds to feed in the less favored areas or even to leave the estuary altogether. However, some increase in numbers in the preferred areas that remain may nonetheless take place. Several indirect lines of evidence suggest that food shortage may be a contributory factor to winter mortality, especially during very cold weather. Field studies indicate that all the ways in which birds might respond to a loss of feeding grounds within an estuary would reduce the rate at which they can feed and so exacerbate any food shortage. Some of the difficulties in predicting the effect of a loss of feeding areas on shorebird numbers are discussed.

This paper discusses some issues raised by attempts to predict whether the numbers of shorebirds using an estuary will decrease following a reduction in their feeding grounds when parts of the shore are developed for industrial, agricultural, or recreational purposes. It refers mainly to studies carried out in Britain where shorebirds occur in their greatest numbers outside the breeding season (August to May) and many of the estuaries are of international significance for migrating and overwintering birds (Prater 1975). The work was done on several estuaries along the east coast, but the paper focusses particularly on the Wash where a proposal has been made to build an impoundment on the shore for storing fresh water (CWPU 1976).

IMPORTANCE OF THE FEEDING AREAS

Shorebirds are not normally spread evenly over the intertidal flats of an estuary. Rather, some areas are used more than others. The most preferred feeding grounds may be the ones where the birds can feed at the fastest rate (Goss-Custard 1970a, 1977a, b), provided that they are not so far from the roosts occupied at high water that the amount of energy expended in reaching them renders less rich areas nearer to the roost more profitable to exploit (Zwarts 1974). On the Wash, for example, most species fed in only a small part of the intertidal flats and the areas used varied between species, largely according to the distribution of prey organisms. Consequently, a limited development on the shore would affect species to different extents. Figure 1 shows how one of the proposed reservoir schemes would remove a large part of the feeding grounds of the Knot, *Calidris canutus* (L.), but would leave the areas used by the Bar-tailed Godwit, *Limosa lapponica* (L.), virtually untouched (Goss-Custard et al. 1977a).

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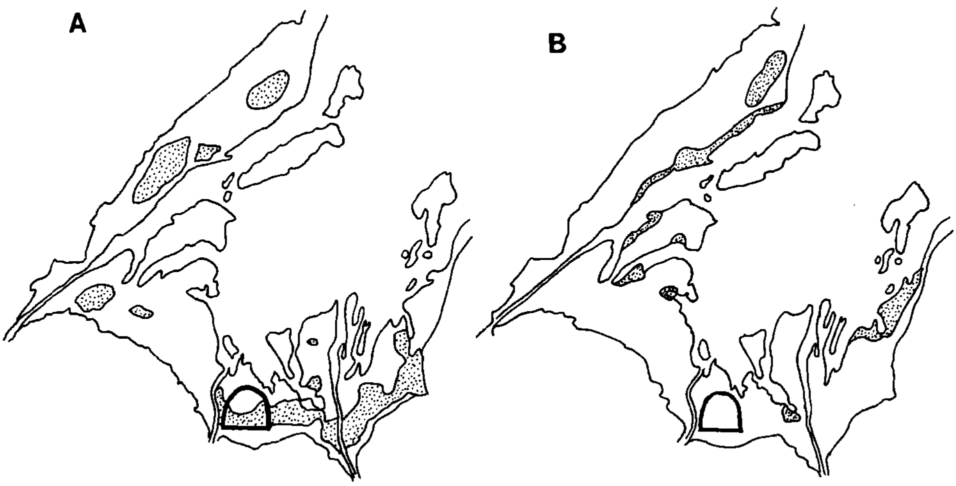

FIGURE 1. The feeding areas of Knots (A) and Bar-tailed Godwits (B) on the Wash, east England. Shaded areas show the feeding grounds mainly used once the receding tide had exposed them. Thick black line shows the limits of one of the proposed reservoir schemes (Wingland).

Predictions on the effect of a loss of feeding area are required, of course, for those cases where large parts of the existing feeding areas would be lost and it is unlikely that new feeding grounds would accrete elsewhere to replace them. The problem, however, is that the role which these feeding grounds play in the population dynamics of shorebirds is not known, although there is some evidence to suggest that food abundance may be important in determining the numbers occurring in an estuary. The densities of Redshank, *Tringa totanus* (L.), and Curlew, *Numenius arquata* (L.), were correlated with the densities of their main prey species when nine estuaries and coastal flats in southeast England were compared (Goss-Custard et al. 1977b). Figure 2, for example, shows the relationship between (i) the mean winter density of Curlew based on monthly counts of each estuary from November to March, and (ii) the combined numerical densities of the two principal prey species, the polychaete worm *Nereis diversicolor* O. F. Müller and the bivalve mollusc *Scrobicularia plana* (da Costa).

Such a correlation may reflect a close adjustment of bird numbers to food abundance arising through disproportionately high rates of mortality, or subsequently low breeding output, amongst birds wintering where food is scarcest. In this case, a reduction in food abundance following a loss of habitat would probably lead to a further decrease in bird numbers. Alternatively, the correlations may simply reflect a preference by individual birds for the best feeding areas, as seems to occur within a single estuary (Goss-Custard 1970a, 1977a, b), so that the birds merely respond behaviorally to the different levels of food in the various estuaries. In fact, the association between bird and prey densities occurred in autumn as the birds returned from the breeding grounds at a time of year when British shorebirds seem to experience little difficulty in obtaining their food (Goss-Custard 1969, Heppleston 1971, Goss-Custard et al. 1977c). If this is the case, a loss of feeding grounds in one estuary may simply lead to a redistri-

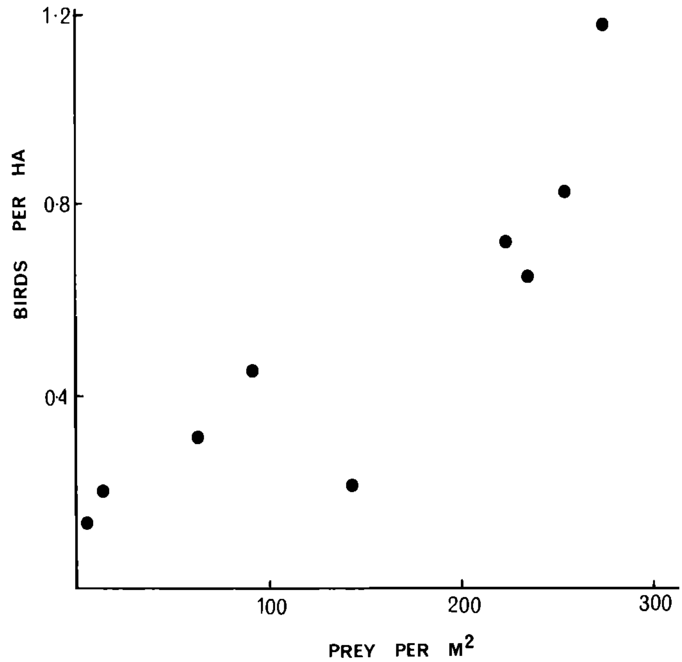

FIGURE 2. The mean winter density of Curlew on each of nine estuaries in relation to the combined densities of their main prey, *Nereis diversicolor* and *Scrobicularia plana*.

bution of birds between estuaries rather than to a reduction in overall numbers. However, it is possible that the correlations reflect both behavioural responses of individuals to spatial variations in prey density and area differences in survival related to food abundance, especially if different sections of the population behave in different ways. Thus, young birds wintering in a region for the first time may move between estuaries to find areas where the chances of survival are greatest: in fact, some movement of birds between estuaries in southeast England has been recorded (Prater 1971, Goss-Custard et al. 1977b). In contrast, older birds may return to the area where they successfully survived the previous winter, and survival may be higher in those estuaries where food is most abundant each year: this would account for individuals being recorded in the same estuary in different winters, both in southeast England (Goss-Custard et al. 1977b) and elsewhere (Ogilvie 1963, Dare 1970, Kelly and Cogswell this volume).

Although usually hindered by being of limited duration and restricted only to the estuary in question, much of the research in environmental impact studies is designed to distinguish between these possibilities. But at the present state of knowledge, predictions on the effects of a loss of habitat are necessarily made without a full understanding of the population biology of the species concerned and, in particular, of the role played by the food supplies outside the breeding season. Nonetheless, studies of (i) the behavioral responses of the birds to their own density and to that of their prey, and (ii) the possibility that some birds already have difficulty in obtaining their food requirements, may provide a basis for prediction.

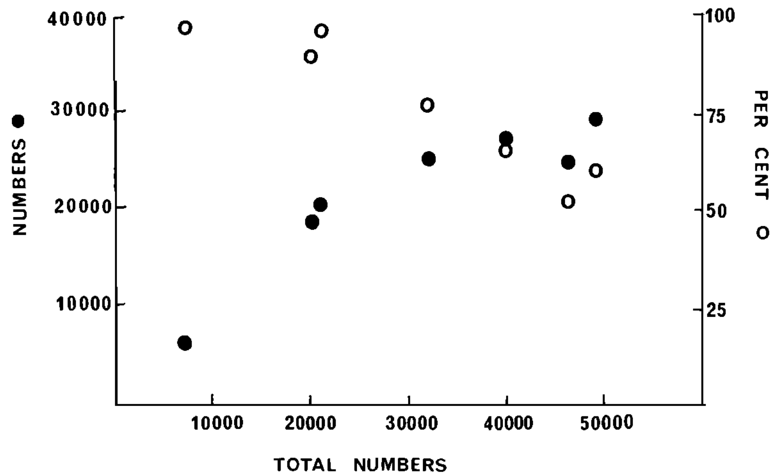

FIGURE 3. The numbers (●) and proportion (O) of Knots on the preferred feeding grounds in relation to the total numbers of birds present.

DENSITY-RELATED BEHAVIOR

Studies in Holland (Zwarts 1974) and in Britain (Goss-Custard 1977a, b) on the sequence in which shorebirds occupy their feeding grounds as their numbers increase suggest that the densities of several species may reach a maximum or ceiling level in the preferred parts of the habitat. For example, on the eastern half of the Wash, most of the small number of Knots present in late summer occurred in one place (Fig. 3). An increasing proportion fed in the less favored areas as the total numbers rose in the autumn, suggesting that there was a resistance to a further rise in density in the preferred areas. A linear increase in the proportion of birds feeding in the poorer areas means that the numbers in the preferred areas will eventually reach a ceiling level and, in fact, the numbers there did rise at a decelerating rate until substantial increases in overall numbers produced only a small rise in density.

The mechanism underlying this apparent density limitation has not been investigated. However, it seems that the spreading out need not necessarily involve overt aggression between birds even though Knots did fight over food items and feeding sites at an increasing rate as their density increased (Goss-Custard et al. 1977c). On the Ythan estuary, for example, Redshank spread out from the most profitably exploited parts of the shore when large numbers of birds were present even though aggressive interactions were not seen (Goss-Custard 1977b). Apparently, birds simply avoided areas of high bird density, perhaps to reduce the various forms of interference which may occur when birds forage at high densities (Goss-Custard 1970b, 1976).

These observations imply that there would be a limit to the numbers of birds that could exploit any preferred feeding areas that remain after a development has taken place and indicate that more feeding would be done, presumably by subdominant individuals, in the less suitable areas. Indeed, a reduction in feeding area might result in birds leaving the estuary altogether. The extent to which birds do both these things would depend on how close densities already were to

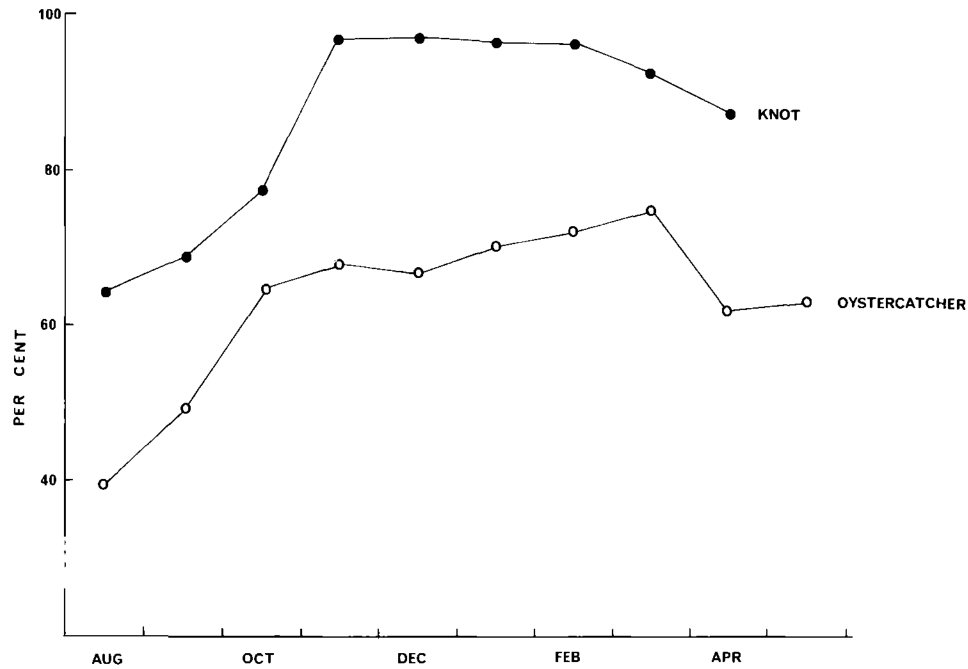

FIGURE 4. The proportion of the time during which feeding grounds were exposed in daylight that Oystercatchers and Knots spent feeding.

any ceiling levels that exist and this is likely to vary both between species and situations. Studies of Oystercatchers, *Haematopus ostralegus* L., and Knots on the Wash, for instance, showed that a decreasing proportion occurred in the preferred areas as overall numbers increased so that a reduction in habitat could lead to both a redistribution of birds within the Wash and to emigration from the area altogether. However, it is expected that some increase in density above present levels might also occur in the preferred areas because in neither species, but especially in Oystercatchers, was a clear ceiling density reached and, in any case, an increase in competition for space might force birds to tolerate higher densities. Consequently, some increase in densities would probably occur in all the remaining feeding areas.

OCCURRENCE OF FOOD SHORTAGE

An increase in bird density may not affect survival unless birds already have difficulty in obtaining their food requirements at some time between August and May. On the Wash, shorebirds were between 3 and 10 times more likely to be found dead in winter than in autumn and spring, as were Oystercatchers elsewhere (Heppleston 1971). In contrast to some North American estuaries (Page and Whitacre 1975), predation on shorebirds in Britain seems to be of minor significance so that food shortage may indeed be implicated in the winter peak of mortality either directly or by reducing resistance to disease. Strong evidence of this is difficult to obtain, but the following kinds of indirect evidence, mainly from the Wash (Goss-Custard et al. 1977c), are suggestive.

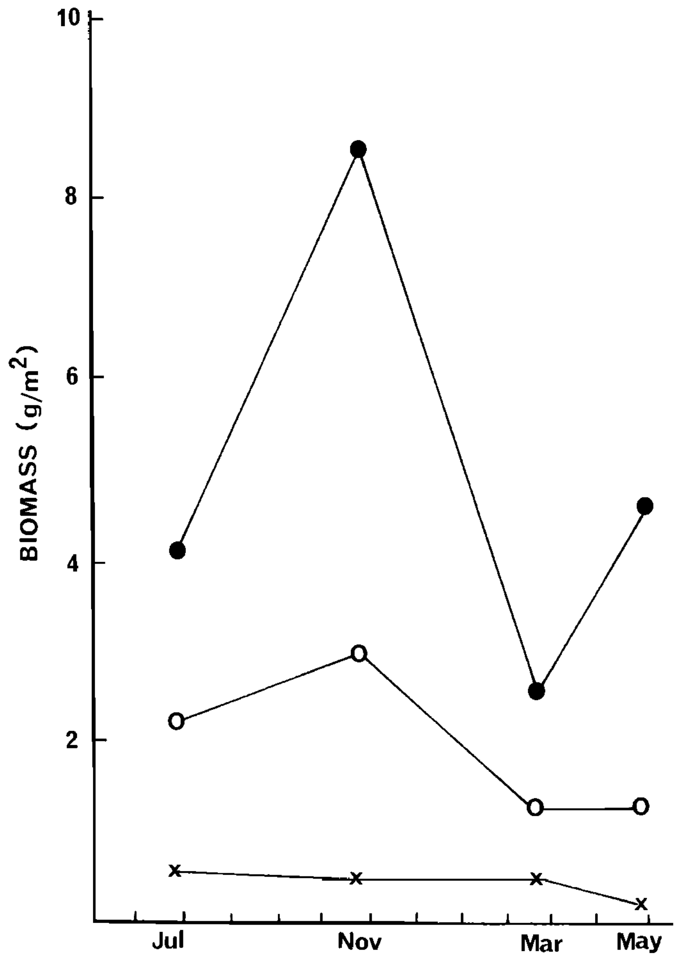

FIGURE 5. The biomass density of the size range of *Macoma balthica* taken by Knots on the Wash (6–15 mm) in three areas sampled in July (as the birds began to return from the breeding grounds), in November and March (at the start and end of the winter), and in May (when birds leave to breed).

(i) In daylight in winter, most species fed for a very high proportion of the time when the feeding grounds were exposed by the tide (Fig. 4). Indeed the small waders, such as Knots, Dunlins, *Calidris alpina* (L.), and Redshanks, fed all day on neap tides when some feeding areas were available throughout the tidal cycle, even at high water. In contrast, the birds spent a considerable time resting in spring and particularly in autumn. Shorebirds can feed at night but on the Wash we were unable to determine whether or not most did so. Consequently, feeding may have seemed more intense in winter simply because the birds preferred to feed in daylight and had to compensate for the reduced daylength. However, studies elsewhere along the east coast of Britain on Redshanks (Goss-Custard 1969), Oystercatchers (Heppleston 1971) and Bar-tailed Godwits (Smith 1975) suggest (a) that many waders may feed at night in winter because they fail to obtain

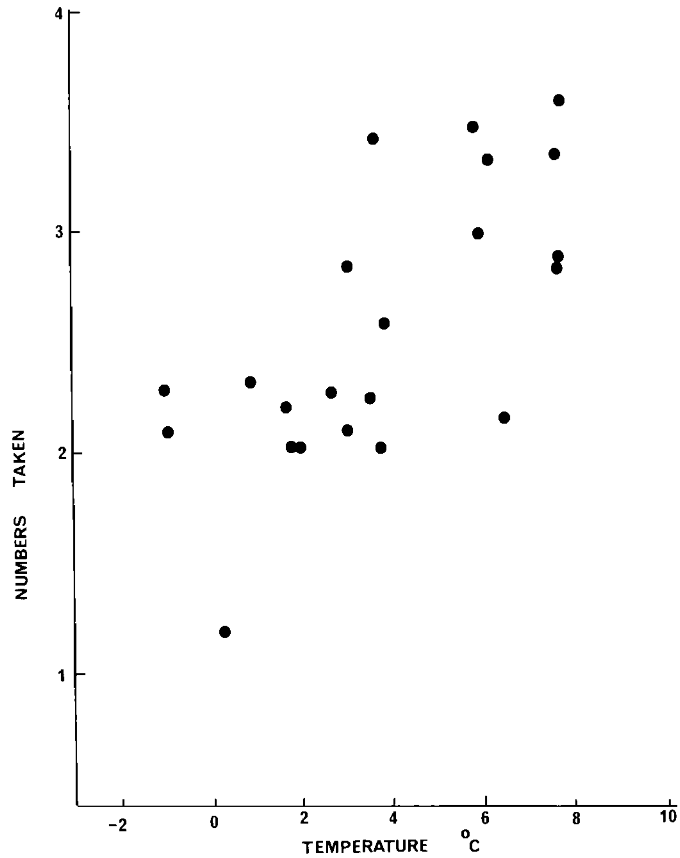

FIGURE 6. The numbers of bivalve molluscs taken per minute by Knots in relation to the temperature of the mud.

enough food during daylight and (b) that feeding at night occurs when the birds are also feeding intensively during the day.

(ii) The abundance of available food for several species declined during winter, suggesting that food may be relatively difficult to collect at that time of year. The decline was due to two factors. First, the actual biomass density of several important prey species decreased from a late summer or autumn peak to reach a low level by late winter or spring and the biomass of food consumed per unit time by waders depends in part on prey biomass (Goss-Custard 1970a, 1977a, b, Goss-Custard et al. 1977b). This winter decline was particularly marked in the preferred feeding areas where prey abundance was initially highest (Fig. 5). The decline can be attributed to (a) mortality (and perhaps emigration) of the restricted size range taken by shorebirds at a time when little replacement by growth from smaller size classes occurred, and (b) a decline in the biomass of individuals of a particular size: for example, some bivalves lost up to 40% of their weight during the winter. Second, the prey were least available or accessible to shorebirds in winter. The size classes of the bivalve mollusc, *Macoma balthica* L., taken by

Knots were buried much deeper in the mud in December than in autumn or spring and over 80% of the biomass present was below the depth at which the birds could reach it (Reading and McGrorty 1978). There were also more short-term variations in availability, superimposed on this long-term seasonal shift, which would make food more difficult to obtain in winter. The numbers of bivalves taken per minute by knots decreased sharply as mud temperature decreased (Fig. 6), presumably because the prey became less active and so more difficult to locate.

A decline in feeding rate at low mud temperatures has been observed in several other shorebirds (Goss-Custard 1969, Smith 1975). Along with the freezing over of large areas of mudflats, this tendency probably accounts for the large numbers of shorebirds found dead on many British estuaries during occasional prolonged periods of very cold weather (Dobinson and Richards 1964, Pilcher 1964, Pilcher, Beer, and Cook 1974, Goss-Custard et al. 1977c). While starvation is clearly implicated on these occasions, it is not yet apparent if such severe weather introduces acute difficulties which shorebirds do not normally experience or simply exacerbates a chronic condition of winter food shorage. Although requiring more research, the circumstantial evidence from the Wash and elsewhere indicates that at least a proportion of the birds of some species may have difficulty in obtaining food in winter, even in the absence of prolonged severe spells. By analogy with other groups of birds, it can be speculated that younger individuals, through being both inexperienced and subdominant to adults and so being harassed more and forced to feed in the less profitable areas, may be the ones most at risk.

EFFECTS OF INCREASED DENSITY ON SURVIVAL

The preceding two sections may be summarized as follows: (i) Following the loss of feeding areas in an estuary, some birds may move elsewhere but it is likely that bird density would nonetheless increase, especially in the less favored feeding areas. (ii) Shorebirds appear to have most difficulty in finding food in winter and food shortage may be at least a contributory factor to the winter peak of mortality, especially during very cold weather. This section discusses whether an increase in density on the feeding grounds would exacerbate the shortage of food and so increase mortality. In effect, this is really asking whether winter mortality is density-dependent, a possibility difficult to investigate directly because mortality is not easily measured. Consequently, studies are needed on the ways in which a rise in bird density could increase the birds' difficulties in finding enough food. Three possibilities can be identified.

(i) More feeding will probably be done in the less preferred parts of the shore where the rate of food intake may be relatively low. For example, on the Wash, most Oystercatchers fed where the biomass density of their main prey, the cockle, *Cerastoderma edule* L., was highest and the birds were able to obtain food at the fastest rate (Goss-Custard 1977a). Thus average feeding rate would decrease if birds fed more in the less favored parts of the shore.

(ii) A rise in bird density would be expected to increase the sometimes considerable impact which shorebirds (and other predators) may already have on their food supplies. On the Wash, shorebirds alone removed between 14 and 43% of the food supplies in the main feeding areas during the winter (Goss-Custard 1977a) and similar high rates have been recorded in other estuaries (Goss-Custard

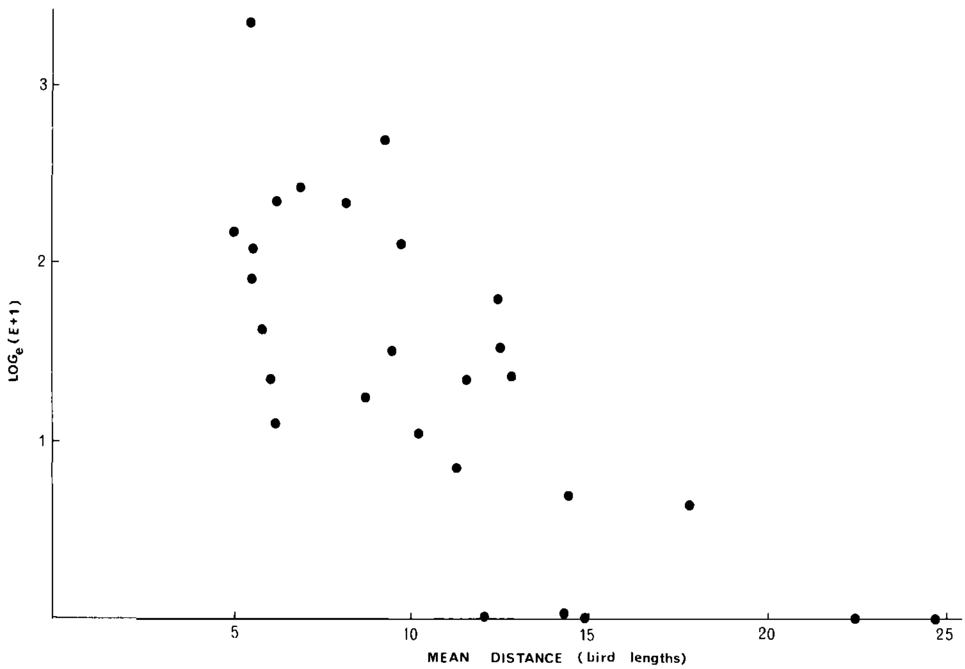

FIGURE 7. The numbers of encounters between Knots for food items on feeding sites in relation to their density. Encounter rate is expressed as number of encounters per 100 bird-minutes, and density as mean nearest neighbor distance.

1969, Smith 1975, Horwood and Goss-Custard 1977). Thus food abundance, and so the rate at which birds can feed, would probably decrease still further if an increase in bird density occurred. While the more rapid growth of individuals might enable the prey populations to some extent compensate for this added loss in autumn and spring, this is unlikely to occur in winter when growth usually ceases. The long-term effects of an increase in bird numbers are particularly difficult to evaluate, but studies in the Burry Inlet, South Wales, suggest that any sustained increase in predation by Oystercatchers would substantially decrease the abundance of cockles in the long term (Horwood and Goss-Custard 1977).

(iii) A rise in bird density would probably increase any interference that occurs between feeding birds. Interference may happen in two ways. First, birds may fight over food items or feeding sites. For example, on the Wash Knots contested bivalve molluscs, principally *Macoma,* at a rate which increased as their own density increased (Fig. 7). Although the evidence that such fighting significantly reduced average feeding rate is equivocal, the effects of an increase in fighting may fall disproportionately on subdominant individuals so that their ability to collect sufficient food is decreased still further. A second form of interference may take place amongst some visually searching birds even when no overt interactions occur. Feeding rate may be reduced because the proximity of other birds is distracting or because many birds reduce the density of available prey by driving them beneath the surface or by removing the accessible fraction faster than it is replenished (Goss-Custard 1970b, 1976), a phenomenon recently termed "resource depression" by Charnov et al. (1976). In either case, an increase in bird density could further increase the difficulties of collecting sufficient food.

CONCLUDING REMARKS

To conclude, where food shortage is already a contributory factor to winter mortality and an increase in bird density is likely to occur after part of the habitat is removed, a reduction in the feeding grounds seems likely to make an already difficult situation worse. This is because all the ways in which the birds seem likely to respond to the changed circumstances would reduce the rate at which they can feed. First, packing into the preferred feeding areas which remain, assuming that this is in any case possible, would reduce food abundance and may decrease feeding rate still further through increased interference. Second, feeding more in the less favored parts of the shore would mean that the birds would feed less profitably. Third, feeding on a wider range of size classes of prey would probably lead to a reduction in ingestion rate because the birds may already select the prey sizes which maximize the rate at which they collect food (Goss-Custard 1977c, this volume).

The reliability of this approach to making predictions about the effects of a loss of habitat on bird numbers depends a great deal on the evidence that birds already experience food shortage, and this is not easily obtained in short-term environmental impact studies. Furthermore, the degree to which food scarcity is a contributory factor to mortality is likely to vary both between estuaries, because food abundance varies considerably (Goss-Custard et al. 1977b), and between species within the same estuary. Hence each situation has to be examined in depth. One advantage of the approach is that it is unlikely that birds would be able to respond successfully to the reduction in food supplies: hungry birds would be expected to have already tried all available means of securing enough food. A disadvantage is that the approach fails to predict by how much survival and reproductive rates might be affected by a loss of feeding grounds. Furthermore, problems arise where food shortage does not occur at present. In such cases, it is necessary to predict at what point survival and reproductive rates will be affected by successive reductions in the food supplies, and whether or not birds that leave the estuary could utilize new grounds further into, or even beyond, the existing winter range of the population. Such difficulties underline the extent to which our present attempts at prediction need to be improved.

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