Predicting how many wintering waterfowl an area can support

J. D. GOSS-CUSTARD AND K. CHARMAN

There is often a need to predict whether or not wintering waterfowl displaced from their normal feeding grounds by man's activities could be accommodated elsewhere. Two questions can be identified: (1) Are all the feeding areas that are used at the moment fully exploited? (2) Are there other feeding areas, not at present used, which could take birds? This short paper discusses and contrasts the methods adopted in studies of Dark-bellied Brent Geese *Branta bernicla bernicla* in south-east England (K.C.) and wading birds (Charadrii) and Shelduck *Tadorna tadorna* on the Wash (J.G-C.). Full reports are in preparation.

The feeding conditions to which migratory waterfowl return in the autumn vary spatially and can be thought of as a food gradient. For example, the density of the food of Redshank *Tringa totanus* may vary down the shore, between different regions of the same estuary (Goss-Custard 1970) and between different estuaries (Kay and Knights 1975). The abundance of available food is the most likely factor to determine feeding conditions, but others, such as the nearness of a suitable roost (Newton and Campbell 1973; Zwarts 1974), may also be important. Brent Geese contrast with many waders by the way in which they utilize and disperse themselves along food gradients. This fact had a considerable bearing on the way in which we predicted how many birds an area could support. An additional influence was the practical difficulty of measuring the availability of the prey of waders and shelduck.

Brent Geese

When Brent Geese return to southern England in the late autumn they feed almost exclusively on the *Zostera* beds of Foulness and Leigh, Essex. The food density they encounter in these sites seems to be high (60–70% of the mud surface covered with leaves). Large, dense flocks form which rapidly deplete the *Zostera* beds. The results from exclosure experiments suggest that the daily food intake of individual geese is not reduced until approximately 75% of the food has been removed. At this point, the majority of the birds leave these initially favoured feeding areas. They disperse to other estuaries and mudflats in south-east England to feed mainly on *Enteromorpha*. The small numbers of geese that remain on the depleted *Zostera* beds spread out, pace faster and spend longer feeding. They may turn to eating the roots if the leaf density declines sufficiently.

It is relatively easy to calculate the number of goose feeding-days the *Zostera* can support before this critical food density is reached. This is possible because all the leaves are in a position where they can be eaten by the geese. The calculation is made by simply dividing the total quantity of *Zostera* above the critical density by the daily ration of a single goose.

A similar pattern of food usage occurs on the *Enteromorpha* beds and similar calculations can be made. If in turn this food supply is greatly reduced, the birds leave Essex and move to feeding areas further along the south coast of England. Some may turn to feeding on winter cereals adjacent to the sea wall. Thus the effect of any reduction in the quantity of food available to these geese should be to advance their step-wise progression along the food gradient, although other factors such as disturbance and tradition may complicate the picture. This direct approach of simply measuring the amount of food present in an area enables us to predict with reasonable accuracy the number of goose-days an area could support.

Wading birds

In contrast, many waders are normally dispersed feeders. They tend to spread out over much of their food gradient early in the winter before any one food is seriously depleted. Their disperson then may be determined by the responses of the birds to their own density as well as to the feeding conditions. For example, any tendency to aggregate in a few very profitable areas may be offset by various forms of interaction. Consequently, as the numbers build up the birds may spread out (Zwarts 1974) along the food gradient in such a way that bird density becomes correlated with prey density (Goss-Custard 1970).

One consequence of such an early spreading over the food gradient may be that it sometimes results in relatively low rates of exploitation of the food so that birds can stay in an area throughout the winter. In contrast to the Brent Goose, simply measuring the abundance of food may give a serious overestimate of the number of bird/days an area can support because much food may re-

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main at the end of the winter. Studies of the factors and mechanism by which bird density is determined may be more appropriate in answering the two questions posed.

On the other hand, field studies may reveal that, in fact, the birds (and other predators) do seriously reduce their food supplies but, compared with the Brent Geese, it occurs much later in the winter. If this happens, we would expect to observe readjustments in the dispersion of the birds over the food gradient as areas become depleted. In these circumstances, measuring the initial quantity of food above this critical density may be an appropriate method for measuring the capacity of an area to support birds.

Unfortunately, seasonal and spatial variations in the availability of the invertebrate prey of waders often raises serious problems in making these measurements. A prey item is said to be available when it can be both detected and caught by the birds. Although the proportion in this condition can be determined by detailed studies (Smith 1974), it is often difficult and time-consuming. Availability may depend on factors that vary spatially (e.g. characteristics of the substrate) or seasonally (e.g. temperature) or, indeed, on bird density itself. This means that the feeding conditions at which a bird's rate of food intake is reduced may occur at very different food densities. Consequently, a simple measure of the abundance of food above a certain density may be quite inappropriate.

The difficulty, then, is that we can neither (1) adequately define the feeding conditions provided by an area (availability problem), nor (2) interpret this in terms of the number of birds that can utilize it throughout the winter (availability and bird interactions problem). Such questions cannot be tackled satisfactorily in the short time that is normally available for such studies. Consequently, an alternative approach is necessary. In the Wash project, we first asked whether or not there was a period of food shortage attributable to reduced food abundance or availability. If this was so, it would be unlikely that any areas existed within the Wash that were underutilized. It would then be assumed that any birds displaced would either leave the area completely or increase the bird density in existing feeding areas. Studies were then designed to indicate whether or not such an increase in bird density would worsen the period of food shortage.

Conclusions

We have tried to identify the main reasons why different methods were appropriate in our separate studies. Of necessity, we simplified the argument and omitted certain considerations, e.g. the complexity of the diet, long-term interactions between predator and prey, the effect of winter feeding conditions on the subsequent survival and breeding of the birds. However, it is our contention that, in short-term projects, the way in which the birds exploit food gradients has a major influence on the design of the study. Superimposed on this are the methodological problems raised by variations in availability. These do not appear to be so important in the case of Brent Geese but we recognize that severe weather conditions could render even these foods unavailable. Clearly, the contrasts we have drawn represent the extremes of a continuum. Further progress in making predictions of the kind discussed requires more research on the interactions between these birds and their food supplies and on their winter survival and breeding.

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Dr J. D. Goss-Custard and **K. Charman**, Institute of Terrestrial Ecology, Colney Research Station, Norwich.