The role of social behaviour in limiting the size of wildfowl populations and their output of young

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Social interaction within a population can be considered as an intermediate variable relating population size or output to some ultimate variable, such as food supply, and an alternative to direct competition for the resource itself.

Little information exists on the relationship between social behaviour and population variables in wildfowl, but some hypotheses can be suggested. Different types of dispersion pattern will be considered separately, since different kinds of social behaviour are likely to be involved.

In flocks of wildfowl a possible limiting mechanism is aggressive interaction leading to a dominance hierarchy. Murton (1968) has proposed a model for the Woodpigeon *Columba palumbus* in which subordinate birds are forced to leave the flock as food density decreases, so adjusting numbers to food supply. A variant of this (the immigration model) can be suggested, which requires that immigrants to an area should be low in rank. As numbers in (say) a wintering area rise towards a food or other limit competitive interaction would be concentrated on the low ranking new immigrants, which would be deterred from settling.

Dominance hierarchies have been demonstrated in several wildfowl species, including Shelduck *Tadorna tadorna* (Patterson, unpubl.), White-fronted Geese *Anser albifrons* (Boyd 1953) and Canada Geese *Branta canadensis* (Raveling 1970). In Shelducks, dominant birds were heavier and bred more successfully than subordinates (Patterson, unpubl.), and numbers remained constant throughout the winter although marked residents arrived progressively over the period, suggesting that others were leaving (Jenkins *et al.* 1975). It seems possible that a dominance hierarchy could limit the size of a breeding population by limiting further settlement by passage birds when a resource begins to become scarce.

The spacing of breeding pairs seems an obvious means to limit density. The social behaviour involved varies widely, from defence of a small area around the female, through 'chasing' and 'three-bird flights' (McKinney 1964) to true defended territory.

A density-limiting effect in addition to a dispersionary one requires that some potential breeders are excluded. In the Shoveler *Anas clypeata* there was no evidence of such exclusion (Poston 1969). In the Shelduck, when territorial pairs were removed, they were in some cases replaced by previously non-territorial birds (Young 1970; Williams 1973). Further such experiments are urgently needed.

Interaction at the nest may limit production of ducklings. Multiple clutches produced by a female laying in the nest of another of the same or different species, tend to be less successful than normal clutches (Weller 1959). This is due mainly to increased loss of whole clutches, probably by desertion. Jenkins *et al.* (1975) found that some nests deserted by Shelduck contained eggs probably laid by other females.

Since there is evidence that the incidence of multiple clutches increases with density (McLaughlin and Grice 1952) this behaviour will tend to reduce the output of ducklings with increasing population size.

Aggressive interaction associated with a hierarchy in the nesting grounds was related to hatching success in Shelducks (Patterson, unpubl.); only the dominant pairs succeeded in hatching their clutches. Although the mechanism is unknown, such behaviour could tend to limit output from a breeding area as numbers rise.

Aggressive interaction between broods may limit the number of broods which can be reared. Shelduck defend a large area around the brood and pairs interact vigorously when their broods converge. Williams (1973) found that young from different broods may mix during such interaction, and that ducklings involved in mixing had an increased mortality rate. It is likely that such brood interaction and associated mortality would tend to increase with increasing population size and so limit breeding output.

Although obvious, it should be emphasized that the various hypotheses which have been suggested here are very poorly supported by data and they are put forward merely to provoke discussion.

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Some factors affecting egg production in waterfowl populations

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Climatic factors

Low spring temperatures and late snow-melts in the arctic produce 'late seasons' in which typical responses by breeding birds are indicated by the following examples.

1. A delay in egg laying by up to 10 days—for example Ross's Goose *Anser rossii* (Ryder 1972), Lesser Snow Goose *Anser caerulescens*, Black Brant *Branta bernicla orientalis* (Barry 1962), Canada Goose *Branta canadensis*, Whistling Swan *Cygnus c. columbianus* (Lensink 1973), and Common Eider *Somateria mollissima* (Milne 1974).
2. A reduction in the proportion of laying females—Whistling Swans from about 35% to 17%, and Eiders from about 80% to about 50%.
3. A reduction in both mean egg size and mean clutch size—Whistling Swans and Eiders.
4. In extreme cases, when the season is very late, some species may not even attempt to nest—Lesser Snow Goose.

For any one breeding location, there appears to be a graded series in which swans are more affected than geese, and dabbling ducks more affected than diving ducks.

Food and body condition

The requirement of higher protein food for egg production has been demonstrated in the Pintail *Anas acuta* in which invertebrates increased their proportion of diet from 56% prior to laying, to 77% during egg laying and then dropped to 29% postlaying (Krapu 1974). Changes in habitat preference during the pre-laying and laying stages therefore may well reflect a change in food requirement rather than the state of the food supply previously being utilized. There is a real need for further work associated with food selectivity and the changing nutritional requirements during the annual cycle.

Prior to egg-laying, Eider females feed at 2–3 times their 'normal' over-wintering rate, whilst Harlequin *Histrionicus histrionicus* females spend 30% more time feeding (Bengtson 1972) and Shelduck *Tadorna tadorna* may spend up to 50% more time feeding (Buxton 1975). Bengtson's study (1971) of