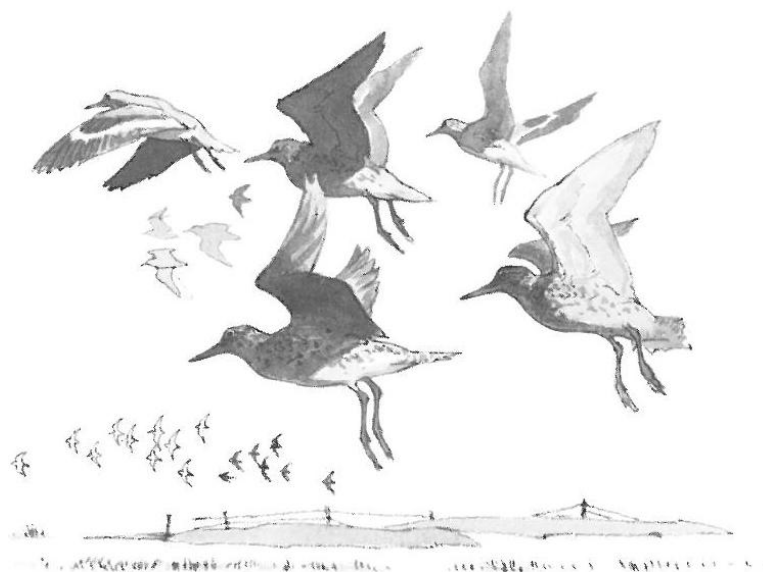


ESTUARY BIRDS

of Britain and Ireland

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stage most of the birds moved to *Enteromorpha* beds elsewhere in south-east England. The few geese that remained on the depleted *Zostera* beds spread out, walked faster, and spent longer feeding. The *Enteromorpha* beds were similarly treated and, on depletion, were abandoned, with further dispersal to other sites in England or with birds moving on to cereals on adjacent land.

SHOREBIRDS IN MID-WINTER

Body size and energy reserves

There are theoretical reasons for believing that larger birds have proportionally greater energy reserves against food shortages than have smaller species (Calder 1974) and smaller birds do in fact feed more intensively than larger species (Fig. 2:15). The figure shows also that birds of a given size hunt about twice as intensively in mid-winter as in autumn, with birds lighter than about 150 g feeding for nearly all of the time available. Birds have higher metabolic rates at low temperatures and need more food as fuel, and their problems are compounded by the shorter days of midwinter and by the reduced activity (Fig. 2:14) and deeper burrowing of potential prey. The bivalve *Macoma balthica* in the Wash, for example, undergoes a vertical migration annually, to the upper layers of the mud in June and to deeper levels in December. Consequently, only 4% of the *Macoma* are accessible to the bills of Knot in December and hardly more than 25% at any time between September and April, the major period for Knot on the Wash. The migration is apparently triggered by day-length but its function is unknown (Reading and McGrorty 1978).

The shortness of winter day-lengths may be more important to shorebirds than the low temperatures. Bar-tailed Godwits have been shown to carry more fat in December, when days are shortest, than in January, when days are on average coldest (Evans and Smith 1975). It is, however, very difficult to separate the effects of one weather or seasonal factor from another in the face of normal seasonality, for the foraging success of shorebirds is also affected by wind and tide conditions (Evans 1976). Strong winds can cause wind chill (by forced ventilation of the body surface) and alter feeding conditions (by drying the substrate, forcing prey deeper, and by disturbing the water surface). In consequence, the birds may move to sheltered but less food-rich bays. Similarly, feeding rates may fall if low tides coincide with darkness. Grey Plover taking ragworm *Nereis diversicolor* averaged only 3.5 pecks/minute at night compared to 5.5–5.8 pecks/minute by day on the same mudflat (Evans 1976). The seasonal variation between neap and spring tides also influences the availability of prey.

Adverse weather

These effects are six-fold, (1) reduction in feeding time due to ice covering the upper shore, which is the first to be uncovered and last to be covered by the tide, (2) fewer available prey on the unfrozen areas since invertebrates are less active at the surface in low temperature (above), (3) killing the prey and so eventually reducing their abundance (Hauser 1973), (4) perhaps increasing the density of birds in the reduced feeding area, so increasing interference between them (Goss-Custard 1976, 1977a), (5) reducing supplementary feeding in the coastal fields at high water (Dare 1966, Goss-Custard 1969, Heppleston 1971), and (6) increasing energy demand. These points have been discussed fully in a recent review (Goss-Custard 1980).

Severe winters with prolonged periods of frost are few in Britain, the most

50 *Patterns of shorebird feeding*

memorable recently being the 1947–48 and 1962–63 winters, though less severe spells of frost occur approximately every five years. Waders are killed by such severe winters (Dobinson and Richards 1964, Heppleston 1971, Goss-Custard et al 1977); the smaller species such as Dunlin, Knot and Redshank are especially vulnerable (Ash and Sharpe 1964, Pilcher et al 1974), and emaciated birds are frequently found, whether as a result of starvation or of starvation exacerbating a disease condition being unknown (Pilcher et al 1974). Heppleston (1971) estimated that 25% of Oystercatchers 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 a less profitable part of the shore (O'Connor and Brown 1977). On the other hand even brief cold spells have been uncommon in the last ten years, and mortality from severe weather is not normally a winter hazard on British estuaries. Even the 1962–63 severe winter depressed the population of the species most affected for only a few years (Pilcher et al 1974, Tubbs 1977).

Winter mortality

Few studies have estimated winter mortality rates in waders. However, Goss-Custard (in press) concluded that wader deaths on the Wash must normally be well below 10%. He found that waders were ten times less likely to be found dead during mild winters than in the 1968–69 winter when there was a cold spell lasting several days (Table 2:3). Unless normal mortality had been below 10% an increase of this magnitude during a moderately cold winter would have wiped out the entire population in the absence of extensive movements. Simulation studies of wader populations have, however, shown that even quite low levels of winter mortality may have quite profound effects on the longer term population size, particularly if this mortality is brought about by density-dependent competition for food (Goss-Custard 1980).

SUMMARY

Estuarine birds in Britain forage mostly on the exposed intertidal flats. A few common invertebrates are taken by many shorebirds but most are taken by those species with appropriate adaptations. Shorebirds generally concentrate on the most profitable prey (food gained per unit time) rather than on the largest available prey but this may be modified by the time required to locate and/or to identify prey. The density of shorebirds within and between estuaries is largely determined by the distribution of prey though physical characteristics of the estuary and interactions between birds may have some influence. Feeding routines vary tidally and seasonally and may be modified by prey behaviour. Young birds are less effective at foraging than adult birds but may be supported by living in family groups. Foraging success amongst shorebirds hunting live prey by visual cues is reduced by flock densities but touch feeders and grazers are unaffected. Energy demands, particularly on the smaller species, are greatest in midwinter, and most severe when icing occurs. Winter mortality is generally low but is sensitive to reduced feeding rates.