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Role of winter food supplies in the population ecology of common British wading birds

By **J. D. Goss-Custard**

Institute of Terrestrial Ecology, Furzebrook
Research Station, Wareham, Dorset

Introduction

A number of suggestions have been made in recent years for developing several of the larger British estuaries for a variety of industrial purposes. Examples are provided by the proposals to build bunded reservoirs for storing fresh-water on the Wash and Dee estuaries and to construct a barrage across the Severn for generating electricity. Such schemes may remove substantial parts of the feeding areas used by large numbers of wading birds in winter and on passage. Studies on the Wash indicate that a reduction in feeding area on the scale envisaged could increase mortality outside the breeding season in several species (GOSS-CUSTARD 1977a, GOSS-CUSTARD et al 1977). However it is difficult at present to predict the effect of an increase in mortality on the overall numbers of birds because the factors determining population size are so poorly understood. This paper summarises recent research on the population ecology of the more common British waders. The conclusions from this review form the assumptions in a simple population model which is used to explore the role of mortality on British estuaries in determining overall numbers. The main conclusion is that, even if mortality outside the breeding season is low at present and the population is regulated by density-dependent production of young in the summer, a small increase in winter mortality could cause a considerable reduction in population size. Therefore we must be cautious when evaluating the effect of a loss of winter habitat on wader numbers.

There are two main review sections. The first considers factors affecting production, defined as the numbers of chicks raised to fledging. Factors which limit the number of pairs breeding and those which influence the number of young produced per pair are discussed separately. The second section examines the subsequent mortality of juveniles and adults. It considers how much mortality occurs on the passage and wintering areas in British estuaries and evaluates the importance of the food supplies. Within each section, the possibility that factors are density-dependent or density-independent is considered because this is important in understanding their role in determining numbers. Density-independent factors contribute to population fluctuations while density-dependent factors, according to their strength, may be either weakly or strongly regulatory or generate oscillations and fluctuations (VARLEY et al 1973, MAY 1976).

Production of young

Most of the studies mentioned in this review refer to species which are common on British estuaries in winter, although the particular group of birds studied may not actually visit there. Some reference is also made to species which do not normally occur in the British Isles.

Number of breeding pairs

Most species occupy territories on the breeding grounds, at least before the eggs hatch (e. g. *Haematopus ostralegus,* HARRIS 1967; *Charadrius hiaticula,* FERNS & MUDGE 1976; *Arenaria interpres,* NETTLESHIP 1973; *Tringa totanus,* GROSSKOPF 1959; *Calidris canutus,* NETTLESHIP 1974; *C. alpina,* SOIKKELI 1967; *C. alba,* PARMALEE 1970). Territorial behaviour may prevent potential breeders from nesting, as occurs in a variety of bird species. Several authors have noticed parties of non-breeding waders on the breeding grounds (GROSSKOPF 1959, HOLMES 1966, HARRIS 1967, PARMALEE 1970, NETTLESHIP 1973, 1974, FERNS & MUDGE 1976), but it is difficult by observation alone to distinguish non-breeders from failed breeders. However, removal experiments with *H. ostralegus* in Wales (HARRIS 1970) and *C. alpina* in the Arctic (HOLMES 1970) indicate that breeding birds in these study areas were quickly replaced, suggesting that territoriality did limit breeding density, at least locally. This may account for the relatively stable numbers of breeding birds recorded in several species, sometimes over many years (Fig. 1). In the case of *H. ostralegus* on Skokholm, breeding density remained unchanged when the numbers in an important wintering area for adults, the Burry Inlet, were experimentally reduced by almost half (HARRIS 1975). Similar territorial activity and the presence of non-breeding birds has been noted in island populations of *H. bachmani* in Canada (HARTWICK 1974) and *H. moquini* in South Africa (SUMMERS & COOPER 1977).

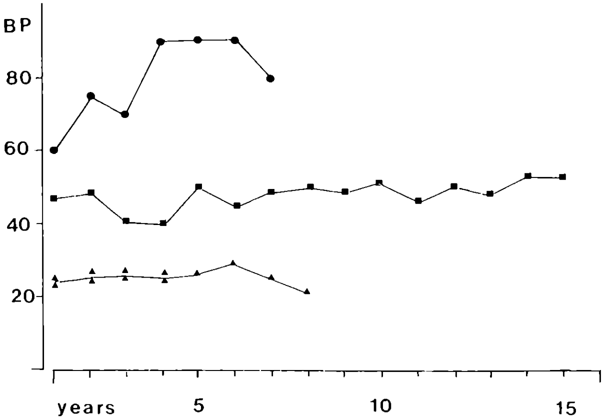

Fig. 1.

Number of breeding pairs (BP) in successive years in three study areas: (▲) *C. alpina* in Finland (SOIKKELI 1970), (■) *H. ostralegus* in Wales (HARRIS 1975), (●) *T. totanus* in Germany (GROSSKOPF 1970).

Table 1. Clutch size, hatching success and main mortality agents.

					per pair		
H. ostralegus	Wales	15	2.5 — 3.3	44 — 82	1.2 — 2.1	Predation, failure to hatch, human interference	Harris 1967
	Scotland: (River valley)	3	2.9 — 2.9	36 — 75	0.7 — 1.2	Predation, human interference failure to hatch	Heppleston 1972
	(Sand dunes)	3	2.4 — 2.7	32 — 75	0.6 — 1.5		Heppleston 1972
	(fields)	2	2.6 — 2.8	38 — 53	0.6		Heppleston 1972
	Germany	1	3.0	79	2.4		Dircksen 1932
	Finland	1	2.9	92	2.7		Nordberg 1950
H. bachmani	Canada	3	2.0 — 2.1	25 — 46	0.5 — 1.1	Predation, weather	Hartwick 1974
C. alpina	Finland	8	3.0 — 4.0	56 — 84	1.7 — 3.4	Predation	Soikkeli 1967, 1970
	Canada	1	3.9	98	3.8	Predation	Jehl 1971
	Alaska	5	?	58 — 97	?	Predation failure to hatch	Norton 1973
C. canutus	Canada	1	4.0	38	3.3		Parmalee & MacDonald 1960
	Canada	1	3.7	54	2	Predation	Nettleship 1974
T. totanus	Germany	?	4.0	86	3.4	Predation, flood failure to hatch	Grosskopf 1958, 1959, 1970
A. interpres	Canada		4.0	78	3.1		Parmalee & MacDonald 1960
	Canada	1	3.5	53	1.9		Nettleship 1973
	Finland	1	4.0	85	3.4		Nordberg 1950
	Finland	1	4.0	72	2.9		Bergman 1946

Footnote: the following studies note main mortality agents, without recording hatching success:

H. ostralegus	England	Predation	Harrison 1967
	British Isles	predation, human interference, floods	Harris 1967
C. alpina	Canada	predation, weather	Baker & Baker 1973
C. alba	Canada	Predation	Parmalee 1970
C. alba	Greenland	Predation	Pienkowski & Green 1976

Competition for space may also be intense in high Arctic waders where a late snow melt may restrict the area available for breeding.

Clutch size and hatching success

Mean annual clutch size varies by a relatively small amount both within and between different populations (Table 1). Clutch-size in *H. ostralegus* on Skokholm declines

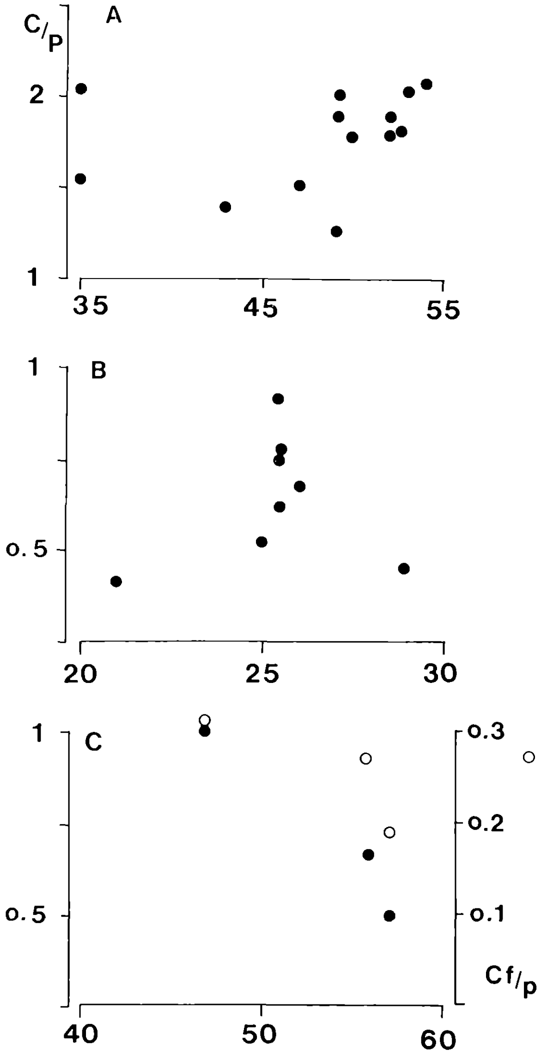

Fig. 2.

Number of chicks hatched per breeding pair (C/P) in relation to breeding density in (A) *H. ostralegus* (HARRIS 1967, 1970), (B) *C. alpina* (SOIKKELI 1967, 1970) and (C) *H. moquini* (HARTWICK 1974), where fledgling production (Cf/p) is also shown.

during the breeding season, perhaps because the females find it increasingly difficult to obtain food to form eggs as the season progresses (HARRIS 1969).

Hatching success is much more variable and may vary by a factor of two in different years in the same place (Table 1). The numbers of chicks hatched per pair may vary even more and even larger differences occur between areas.

Human interference, bad weather, tidal flooding and failure to hatch are frequently mentioned as important causes of egg loss but most authors suggest predation is the main factor (see Table 1, also *C. mauri* [HOLMES 1971, 1972], *C. minutilla* [BAKER & BAKER 1973], *C. bairdii* and *C. melanotus* [NORTON 1973] in North America). However, the possibility that the investigator himself increases the risk from predation cannot usually be ruled out.

The mortality from several of these factors is potentially density-dependent. Predators may concentrate their attention on the more common species and so destroy a greater proportion when nests are numerous. Alternatively, the proportion of clutches vulnerable to bad weather and flooding may be highest when many pairs are breeding and birds are forced into the less favourable areas. However, there is no indication that hatching success is related to nest density in *H. ostralegus, H. bachmani* or *C. alpina* (Fig. 2), though the range in breeding densities studied is very limited. JEHL (1971) came to the same conclusion for a variety of North American shorebirds and GROSSKOPF (1959), HOLMES (1966), NORTON (1973) and SOIKKELI (1967) have noted that the intensity of predation on wader nests depends on factors quite unrelated to nest density; for instance, the abundance of an alternative, more preferred prey or on the numbers of the predators themselves. It seems that the production of chicks is variable but unlikely to be density-dependent.

Fledging success

Most data are from *Haematopus* spp (Table 2 & 3) which may be untypical because parents feed their young. Fledging success is less variable than hatching success but has been measured over fewer years. Although difficult to study, most authors again stress the importance of predation. The risk of young *Haematopus* spp being taken may be higher when food is scarce (HARRIS 1967, SAFRIEL 1967). Bad weather may also kill many chicks, especially in the first few days when they are most vulnerable to chilling and disappear at the fastest rate (PARMALEE 1970, HEPPLESTON 1972, SOIKKELI 1967). Bad weather may also reduce the availability of food to chicks and so reduce their survival (HOLMES 1966, HOLMES & PITELKA 1968). PRATER (1975) has suggested that greater annual differences in weather may make the production of young in the Arctic more variable than in the temperate zone and argues that this accounts for the greater variation in the numbers of Arctic breeding waders overwintering in Britain.

Conclusions

The data are few and come from a limited range of species so any conclusions are necessarily provisional. But for the purposes of developing a working hypothesis, it is concluded that (i) territoriality limited the density of breeding pairs in two very diffe-

Table 2. Mortality of chicks before fledging.

Species	Area	Year	Percent mortality	Main mortality agents	Authority
H. ostralegus	Wales	1963	66	Predation in relation to food shortage	Harris 1967, Safriel 1967
		1964	41		
		1965	58		
	Scotland: River valley	1966	83		Heppleston 1972
		1967	67	Predation	
		1968	73		
	Sand dunes	1966	55	Predation	Heppleston 1972
		1967	65		
		1968	59		
	Fields	1966	46	Predation	Heppleston 1972
		1967	52		
H. bachmani	Canada	1970	38	Predation weather	
		1971	37		Hartwick 1974
		1972	28		
C. alpina	Finland	1963	36		Casen & Hilden in Soikkeli 1967

Footnote: the following studies note main mortality agents, without recording fledging success.

C. alpina	Finland	Predation and weather	Soikkeli 1967
	Alaska	Weather, predation, food	Holmes 1966
	Canada	Predation	Baker & Baker 1973
C. canutus	Canada	Predation	Nettleship 1974
C. alba	Canada	Predation and weather	Parmalee 1970
T. totanus	Germany	Predation	Grosskopf 1963
A. interpres	Canada	Predation	Nettleship1973
Several species	Greenland	Weather	Ferns & Mudge 1976
	Greenland	Predation	Larson 1960
	Canada	Predation	Jehl 1971

Table 3. Fledged young produced per pair.

Species	Area	Year	Fledged young per pair	Authority
H. ostralegus	Wales	1963	0.9	
		1964	1.5	HARRIS 1967,
		1965	0.8	SAFRIEL 1967
	Scotland:			
	River valley	1966	0.45	
		1967	0.71	HEPPLESTON 1972
		1968	0.64	
	Sand dunes	1966	0.13	
		1967	0.44	HEPPLESTON 1972
		1968	0.50	
	Fields	1966	0.65	HEPPLESTON 1972
		1967	0.85	
H. bachmani	Canada	1970	0.27	
		1971	0.19	HARTWICK 1974
		1972	0.31	

rent species, and (ii) the numbers of young produced per breeding pair varied considerably, though independently of breeding density. Despite the second conclusion, preventing some birds from breeding by territoriality gives rise to density-dependent production when this is expressed as a function of the whole population of both breeders and non-breeders. Therefore it is assumed in the model that the production of young is density-dependent because of the territorial behaviour of nesting birds.

Annual mortality

Magnitude

BOYD (1962) estimated mean annual mortality of adult waders from ringing returns of long-distance migrants. GROSSKOPF (1964), HARRIS (1967), SOIKKELI (1967), and BOTKIN & MILLER (1974) suggested that, through ring loss, these estimates may be too high and argued that the annual return rate of adults to their nest areas may be a more accurate measure. Even this will overestimate mortality if some adults do not breed every year, as is the case in *H. ostralegus* (HARRIS 1975) or if birds breed outside the immediate study area. Therefore there is some doubt about the magnitude of annual mortality, although both methods of calculation indicate that the rate decreases with body size (Fig. 3).

The mortality of *H. ostralegus* and *C. alpina* varies by up to three-fold in different years (Table 4) but whether it is density-dependent or density-independent has not been examined. The mortality rate of juveniles in the first year after fledging is higher than in adults (Table 5) but annual variations have not been measured.

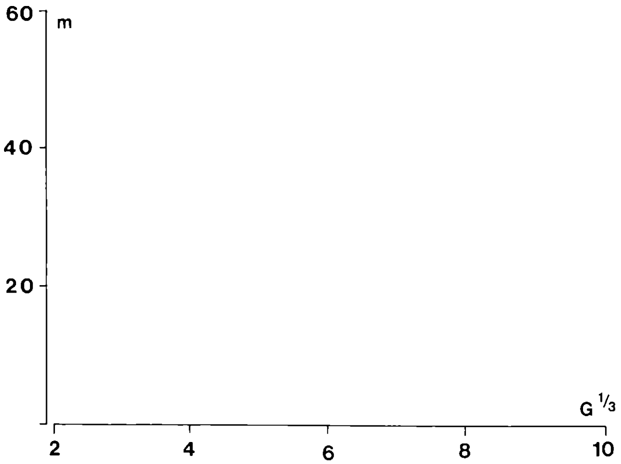

Fig. 3.
Annual adult mortality (m) in relation to body size: (o) data from Boyd (1962), ● data from GROSSKOPF (1964), SOIKKELI (1967), HARRIS (1975). Body weight $^{1}/^{3}$ = G $^{1}/^{3}$

Table 4. Annual variations in adult mortality.

Species	Area	Years studied	Annual percentage mortality	Authority
H. ostralegus	Wales	10	4.2 — 14.1	HARRIS 1975
	Germany	5	2.5 — 11.0	GROSSKOPF 1964
C. alpina	Finland	7	12.1 — 37.0	SOIKKELI 1970
	Finland	6	30 — 65	HELDT (from SOIKKELI 1967)
T. totanus	Germany	3	25 — 31	GROSSKOPF 1959

Table 5. Mortality rates of adults and juveniles after fledging. Only estimates considered reliable by the original author are given.

Species	Adult	Immature	Authority
H. ostralegus	16	36	BOYD 1962
	11	40	HARRIS 1967, 1975
C. hiaticula	42	61	BOYD 1962
N. arquata	25	62	BOYD 1962
C. alpina	38	75	BOYD 1962
	26	72*	SOIKKELI 1970
	30	70	HOLMES 1966

* N. B. from shortly after hatching, not fledging.

Mortality in the breeding areas

Adults die on the breeding grounds from a number of causes. Mortality may be heavy at the start, especially if the weather is bad and food short (PEDERSEN 1942, SOIKKELI 1967, MACLEAN 1969, MORRISON 1975). There may be a premium on early breeding (HOLMES 1966, SAFRIEL 1967, SOIKKELI 1967, MACLEAN 1969, HARRIS 1969, GROSSKOPF 1970) and much energy and time is expended during a limited period on defending a territory (MERCER 1968) and in producing eggs (GROSSKOPF 1958, MERCER 1968, HARRIS 1969, MAC LEAN 1969, SUMMERS & COOPER 1977). Birds are taken by predators during incubation, (GROSSKOPF 1959, 1963, DARE 1966, SOIKKELI 1967), but how severe the mortality is subsequently on the breeding grounds and during migration, in both adult and juvenile birds, has been difficult to establish. SOIKKELI (1967) calculated that 27 % of the adult annual mortality of *C. alpina* took place during incubation, but it is not yet possible for any population to estimate the proportion of deaths which occur during the breeding season as a whole.

Mortality on British estuaries

Noticeable mortalities occur in prolonged periods of severe frost (DOBINSON & RICHARDS 1964, PILCHER 1964, HEPPLESTON 1971, Pilcher et al 1974, GOSS-CUSTARD et al 1977), especially amongst the smaller species *C. alpina, C. canutus* and *T. totanus* (ASH 1963, PILCHER et al 1974). Birds are found in an emaciated condition apparently having died from starvation, perhaps exacerbated by disease (PILCHER et al 1974, but cf ASH & SHARPE 1964). Cold weather has this effect (i) by reducing the time available for feeding on the shore by covering with ice the top levels of the beach, which are the first to be uncovered and last to be covered by the tide, (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 killing the prey and so eventually reducing their abundance (HAUSER 1973), (iv) perhaps by increasing the density of birds in the reduced feeding area, so increasing interference between them (GOSS-CUSTARD 1976, 1977a), (v) by preventing birds from supplementing their diet in the fields at high water (DARE 1966, GOSS-CUSTARD 1969, HEPPLESTON 1971), and (vi) by increasing energy demand. HEPPLESTON (1971) estimated that 25 % 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 (O'CONNOR & BROWN 1977).

Mortalities from cold weather do not appear to have a serious long-term effect on the populations of most species because severe winters do not occur sufficiently often (WILLIAMSON 1972). Dead birds are usually found after three days of hard frost (R. BERRY pers. comm., HEPPLESTON 1971) and cold spells, even of this short length, have been uncommon in the last decade. The populations of most species which are thought to have suffered heavy mortalities during the 1962/63 freeze-up recovered within a few years (PILCHER et al 1974, TUBBS 1977).

It is more important to evaluate the magnitude of mortalities occurring in typical winters, but this is not easy to do. Even when population counts are sufficiently accurate to detect a change in numbers, decreases due to death, emigration or increased feeding in adjacent fields cannot be separated. Similarly, the absence of a decline in numbers does not necessarily mean that few birds are dying because birds that die may simply be replaced by immigrants from uncounted areas (Goss-Custard 1969). However, very few corpses are found on the shore in normal winters, even in north Scotland (Goss-Custard 1969, Heppleston 1971). Waders on the Wash were, on average, 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 (Table 6). The mortality in this area must normally be well below 10 % otherwise a ten-fold increase during a moderately cold winter would have wiped out the entire population unless considerable movement occurred. The data suggest, then, that winter mortality is usually rather slight.

Table 6. Risk* of waders being found dead along a 5.63 km section of the Wash in winter (November — March) and at other times of year (August — October and April — May). Adapted from Goss-Custard et al (1977).

	1969		1970-1974	
	Winter	Autumn/ Spring	Winter	Autumn/ Spring
H. ostralegus	0.21	0.07	0.08	0.05
C. alpina	0.16	0	0.02	0.01
C. canutus	0.15	0.02	0.04	0.02
T. totanus	9.37	0.05	0.34	0.04
A. interpres	1.35	0	0.34	0.07
N. arquata	0.72	0	0.22	0.08
L. lapponica	0.15	0	0.08	0.02
P. squatarola	0	0.19	0.07	0.05
Mean	1.51	0.05	0.15	0.04

* N. B. Risk was calculated as: $\frac{\text{Number of corpses found per period}}{\text{Total numbers of birds present on the Wash}} \times 1000$

Winter food supplies

While it is obvious that many birds die in cold winters from starvation, the contribution which food shortage makes to mortality in milder years is unclear. However a winter and early spring peak of mortality in several species on the Wash (Table 6) and of *H. ostralegus* in west Britain (Fig 4) indicates that food shortage may be involved, either directly or by reducing their resistance to disease and predation. Food may be more difficult to obtain at that time of year because (i) daylength is short, and feeding at night may be less profitable (Prater 1972, Greenhalph 1976), (ii) the food value (Hancock & Franklin 1972, Beukema 1974, Chambers & Milne 1975a, b, Dare & Edwards 1975, Goss-Custard et al 1977) and abundance (Dales 1951, Goss-Custard 1969, Hughes 1970, Hancock 1971, Beukema 1974, Chambers & Milne 1975a, b, Goss-Custard et al 1975, McGrorty & Reading in prep.) of the prey may decline substantially from autumn to spring because little growth and recruitment occurs, and (iii) the prey may burrow

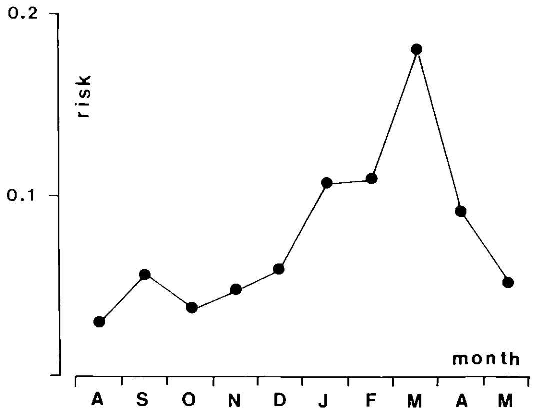

Fig. 4.
The risk that adult *H. ostralegus* along the west coast of England and Wales will be found dead at different times of year. Risk is calculated by dividing the total numbers of corpses found per month prior to 1973 (P. J. Dare pers. comm.) by the numbers of birds recorded each month from 1970-1974 by Estuaries Enquiry counters (Prater 1975).

deeper in the mud in winter (Reading & McGrorty 1978) and also be less accessible to waders at low temperatures (Goss-Custard 1969, Smith 1975, Goss-Custard et al 1977). Compared with autumn and spring, many waders spend a very high proportion of their time feeding in winter, especially the smaller species (Goss-Custard et al 1977). Thus food shortage may be at least a contributory factor to normal winter mortality.

Unless birds are able to expand their wintering range, the effect of more industrial development of feeding areas will be to increase the density of birds on our estuaries. Even if food-linked mortality is slight at present, such an increase in density could introduce density-dependent mortality for the following reasons: (i) The proportion of birds feeding in the most preferred parts of the shore may decline as total numbers increase, apparently because of social interactions between birds (Zwarts 1974, Goss-Custard 1977a, b). Consequently, more birds will feed in the less preferred areas where the ingestion rate is likely to be relatively low (Goss-Custard 1970, 1977a, b). An increasing proportion of birds would be expected to feed at relatively low rates as bird numbers increase, so exacerbating any period of food shortage. (ii) Waders may already consume a large proportion of their food supply during the winter, expecially in those areas where food is most abundant initially and the birds congregate (Goss-Custard 1969, 1977, Hughes 1970, Horwood & Goss-Custard 1977). An increase in the density of birds and other predators such as fish, will further deplete the food supply and so reduce the ease with which food is collected. This applies even when food shortage results mainly from the reduced availability of prey at low temperatures, for instance, since it is presumably the interaction between actual abundance and availability which determines the effective food density to the birds. (iii) The feeding rate of some birds may decrease when bird densities rise either because there are more contests over food items (Goss-Custard 1977a) or because more subtle forms of interference increase in intensity (Goss-Custard 1976).

Conclusions

There is no evidence that a considerable proportion of the annual mortality of waders normally occurs when they are on British estuaries, although many may die of starvation during occasional severe winters. However some birds die there, particularly in winter, and this may be linked to the relatively poor feeding conditions occurring at that time of year. There seems to be a risk that the continuous removal of feeding areas for industrial development would increase winter mortality from food shortage because it may be density-dependent.

Winter food supply and subsequent production

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 *C. melanotus* 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 (Table 7) of *H. ostralegus* on Skokholm was unrelated to the abundance of their main food *Cerastoderma edule* in the Burry Inlet where many adults spend the winter (Harris 1975).

Table 7. Production of fledging *H. ostralegus* on Skokholm in relation to the food supply in the Burry Inlet in the preceeding winters (from Harris 1967, Saffriel 1967, Hancock 1971).

Year	Clutch size	Chicks fledged per pair	Abundance of 2nd & 3rd winter cockles in preceeding winter*
1963	3.0	0.9	358
1964	3.0	1.5	35
1965	2.8	0.8	860

* N. B. Expressed in "cockle units" where, based on weight, 2nd winter cockle = 1 unit and a 3rd winter cockle = 1.9 units (Hancock & Franklin 1972).

Population model

Simulation experiments with mathematical models of populations can yield valuable insights into the way in which population fluctuations and mean levels are determined (Williamson 1972, Varley et al 1973, May 1976). Such models are best constructed from field data, but this is not possible for waders due to lack of information. The properties of a simple theoretical model are explored here in an attempt to understand the effect of an increase in winter mortality on population size. The main assumptions in the model are derived from the review and are (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 may be as high as 35 %, and (iv) winter mortality is usually low. These are taken to be the most likely possibilities given the limited data available. For simplicity, I also assume that breeding starts at one year, although many waders may breed in their second (SOIKKELI 1967, GROSSKOPF 1959) or even fourth or fifth years (HARRIS 1970). Sex ratio is assumed to be equal, although little is published on this.

Strength of territoriality

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 in. For example, 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. Therefore, if territoriality limited breeding density in Finland as it seemed to in this species in Alaska (HOLMES 1970), its effect on production may not be strongly density-dependent. The possibility the number available to breed affects breeding density is included in the model. This is done by expressing the number excluded by territoriality (Nb) in the same way that mortality is defined in key-factor analysis (VARLEY & GRADWELL 1960), i. e.:

$$N_b = \log_{10}N - \log_{10}B$$

where N is the number of potential breeders and B is the number allowed to breed. If a constant number of birds breeds each year and Nb is plotted against log N, the slope (b) is 1. The slope of the line is reduced if the numbers attempting to breed influences the numbers establishing territories (Fig 5). The numbers breeding and the proportion not breeding at different population levels are shown in Fig 6 for several values of b.

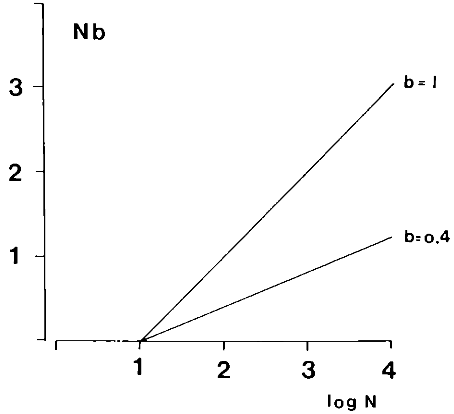

Fig. 5.
The way in which the numbers of birds prevented from breeding by territoriality is expressed in the model. Two theoretical examples, with different slopes (b), are shown.

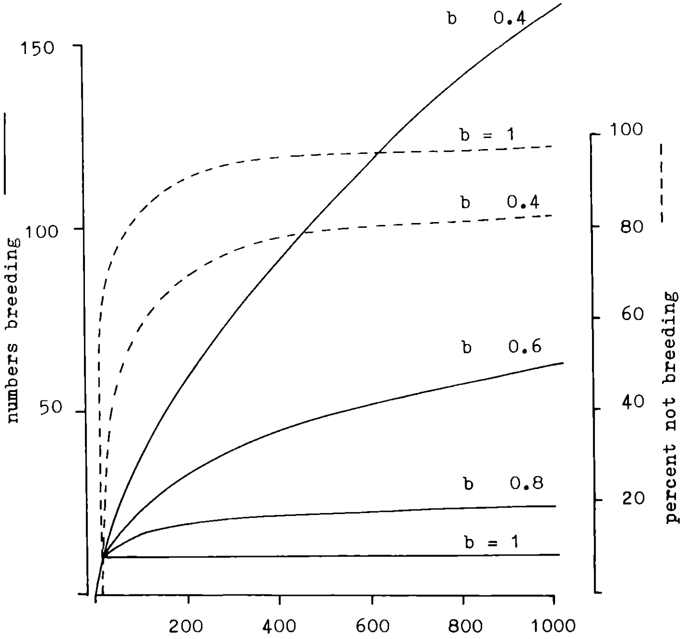

Fig. 6.
Numbers of birds breeding, and the proportion prevented from breeding, in relation to total population size for different values of b.

This is a convenient way to quantify 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 restriction on breeding density. Fig 7 compares the main characteristics of two theoretical populations in which the slope of Nb against log N is either 0.4 or 1. In both cases, the production of young per breeding pair varies randomly between 0.5 and 1.5 and a 25 % density-independent mortality acts on the combined numbers of breeding and non-breeding adults and juveniles sometime after the young have fledged. Both populations are regulated by territoriality and eventually reach stable levels whether large or smaller numbers are present at the start, though this is only shown for one population. When b = 1, production is constant at 5 young because only 10 birds are able to breed. When b = 0.4, more birds breed but the population still stabilises, though at a higher and more variable level. Stable population size is of course reached when the percentage mortality of the whole population is equivalent to the average number fledged, which is itself fixed by the number of pairs allowed to breed.

Although regulation by strong or weak territoriality may occur only during the breeding season, the magnitude of a density-independent mortality (M) operating at other times of year has a considerable effect on the size of the stable population. Fig 8 shows the stable population for different values of M and b: production per breeding pair (P) is 1.2 in all cases.

Fig 9 shows the number of non-breeding adults to be expected with various values of M (b = 1). A high proportion are non-breeders when mortality is low. This may ap-

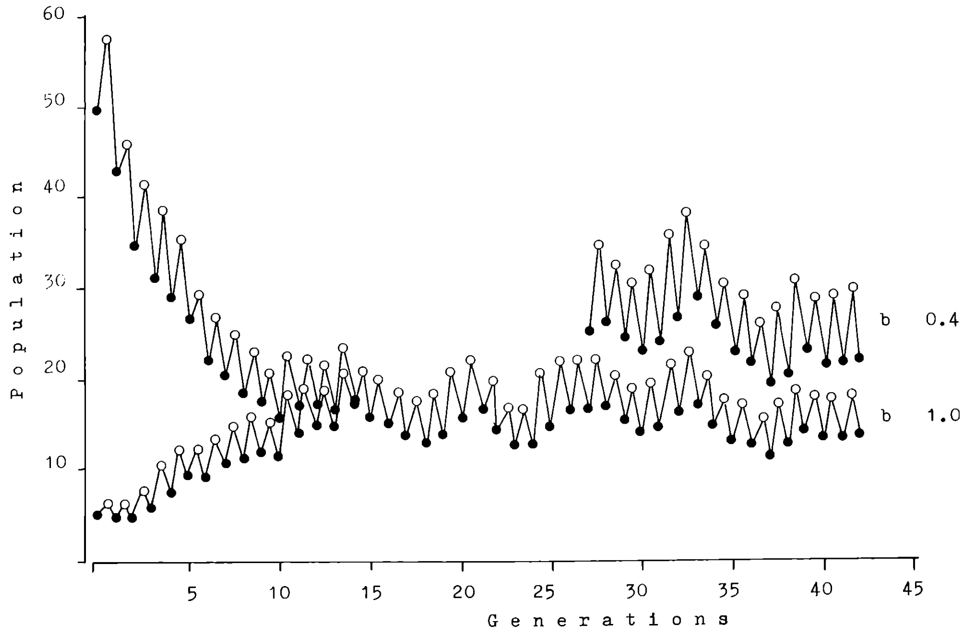

Fig. 7.

Two theoretical populations regulated by territoriality but with different values of b. The population with b = 1 starts at either a high or low point but reaches the same level. Only the stable population is shown in the other case. ● = pro-breeding population; ○ = post-breeding population.

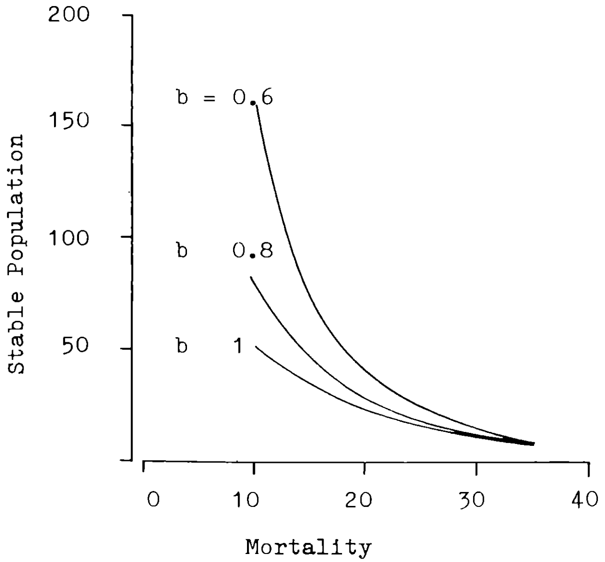

Fig. 8.

Stable population size in populations regulated by territoriality (b = 1 to 0.6) and subject to different density-independent annual mortalities.

proximate the situation in *Haematopus* spp where M is less than 15 % and non-breeders make up a large part of the population (e. g. 63 % in the population of *H. moquini* studied by Summers & Cooper [1977]). The proportion of non-breeders decreases, of course, as M increases and quite low numbers of non-breeders are found when mortality is at the typical rate for small waders of 25 %. Therefore a population may be regulated entirely by territorial behaviour, even though only a few non-breeding adults are seen e. g. *C. alpina* in the Arctic (Holmes 1966).

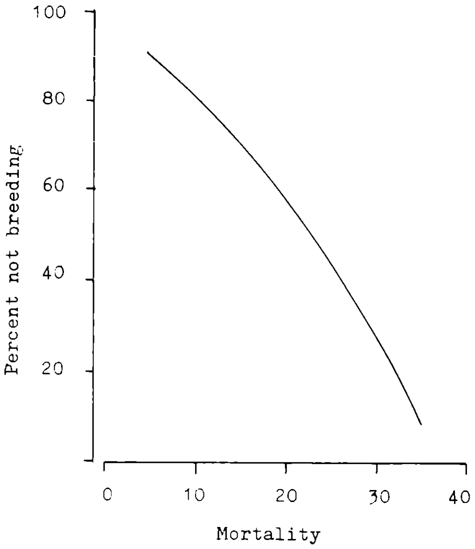

Fig. 9.
The proportion of non-breeders in a territorial population (b = 1) with different values of annual mortality.

The role of winter mortality

Fig 10 explores the effect of apportioning different amounts of a density-independent annual mortality between summer and winter. Summer mortality (m) is set at 10 or 20 % and occurs after the young have fledged; perhaps most deaths are of inexperienced young birds either prior to or during migration. Winter mortality is between 0 and 15 % of the birds arriving in the wintering area, and the populations are regulated by territoriality on the breeding grounds (b = 1). Stable population size is reduced by 64 % (m = 10) or 47 % (m = 20) as winter mortality increases from 0 to 15 per cent.

Table 8 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 from food shortage in winter. Population size without any winter mortality is also shown. P is 1.2 and there is a 20 % density-independent mortality between fledging and arrival on the wintering grounds. Again, the introduction of a relatively small winter mortality can have a large effect on stable population size, especially when b on the breeding grounds is smal l.

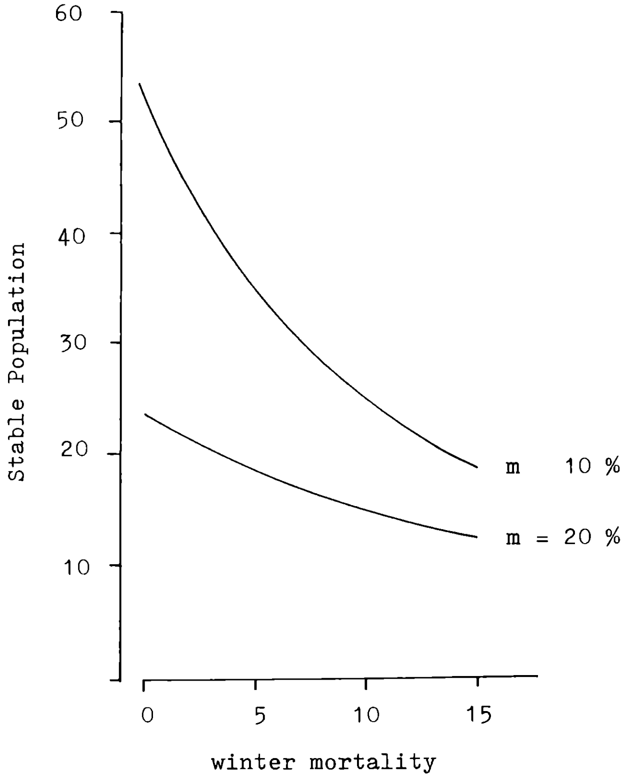

Fig. 10.
Stable population size in populations regulated by territoriality (b = 1) but with different density-independent summer (m) and winter mortalities.

Table 8. Stable population size under different amounts of summer and winter regulation.

	Stable population size		
Strength of territoriality on the breeding grounds	No winter mortality	Winter regulation (b = 0.1)*	Mean winter mortality %
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

$$k = \log N_{10} - \log_{10} N_{+1}$$

and N and N_{+1} are the population sizes before and after the mortality acts.
Mortality is density-independent if k varies independently of log N but is density-dependent when k increases as log N increases. The slope of the line (b) defines the strength of a density-dependent factor (Varley et al 1973) and in this example it is very weak (b = 0.1).

Conclusions

Major gaps exist in our knowledge of the size and variation in the mortalities occurring in most stages of the annual cycle of wading birds and of the extent to which any of them is density-dependent. However it is clear that all the population processes, i. e. mortality as well as natality, do not occur solely on the breeding grounds. Therefore, in order to understand the effect of reduced habitat on numbers, we need to consider the role which mortalities outside the breeding season play in determining population size.

The main finding is the degree of caution we should exercise in dismissing even small increases in winter mortality as unimportant. Low mortalities in winter can have disproportionately large effects on stable population size even if the strongest regulation occurs when the birds are on the breeding grounds, as the present very limited data suggest is likely. TUBBS' (1977) suggestion that a relaxation in shooting pressure has resulted in a considerable increase in wader numbers is consistent with this point. Similarly, the introduction by loss of habitat of even a weak density-dependent mortality factor in winter could have a large effect on bird numbers. The population is still secure because it is mainly regulated on the breeding grounds, but people in Europe would see far fewer birds.

Finally, more research is required, particularly on the role territoriality may play in determining breeding density and making production density-dependent. Only two species have been studied and most work has been done on island populations where the capacity for range extension and occupation of sub-optimal habitats is limited. Studies on the size, annual variation and density-dependence in mortality rates experienced at different times of year and in different parts of species' ranges are also highly desirable. It is important that more precise estimates are obtained so that, by modelling, we are able to obtain a better understanding of the effects of increased mortality rates in winter.

Summary

There are many threats to the feeding areas of wading birds overwintering on British estuaries. This paper discusses the role of these areas in determining population size. The factors affecting the production of young in the summer and the subsequent mortality of post-fledglings at different times of year are reviewed. The possible role of winter mortality in determining population size is then explored with the aid of a simple population model.

Waders which are common on British estuaries in winter are territorial on the breeding grounds. Removal experiments with two contrasting species suggest that territoriality limits breeding density, at least locally. The numbers of chicks or fledged young produced per pair varies by a factor of two or three in different years. Although there is no evidence that production per pair is related to breeding density, the exclusion of potential breeders by territorial behaviour may cause overall production to be density-dependent.

Annual adult mortality varies between species and years and is highest in separate juveniles. It is not known whether mortality is density-dependent. Many waders die in very cold winters but present evidence suggests mortality in less severe years may only be slight. Birds are more likely to die in winter than in autumn and spring and this mortality may be related to food shortage. The removal of feeding areas by industrial development could increase winter mortality.

The limited data available suggest that winter food supplies do not influence subsequent breeding success in *H. ostralegus.*

These findings provided the assumptions in a simple population model whose properties were explored. Although the population may only be regulated by territoriality in the breeding season, the magnitude of density-independent mortality operating at other times of year has a considerable effect on population size. With a mortality on the breeding grounds of 10 or 20 %, an increase in winter mortality from only 0 to 15 % decreases stable population size by 64 and 47 % respectively. The introduction of a weak density-dependent mortality by removal of winter feeding areas would also have a large effect. It is concluded that we must be cautious before dismissing even small increases in winter mortalities as unimportant.

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