UNIVERSITY OF SOUTHAMPTON

OYSTERCATCHER SPECIALISATION: FITNESS IMPLICATIONS AND POPULATION CONSEQUENCES

Sarah Elizabeth Aubin Le Vavasseur dit Durell

Thesis submitted for the degree of
Doctor of Philosophy

Centre for Environmental Sciences

January 2001

UNIVERSITY OF SOUTHAMPTON

ABSTRACT

FACULTY OF SCIENCE

ENVIRONMENTAL SCIENCES

Doctor of Philosophy

OYSTERCATCHER SPECIALISATION: FITNESS IMPLICATIONS AND POPULATION CONSEQUENCES

by Sarah Elizabeth Aubin Le Vavasseur dit Durell

The aim of this thesis was to investigate the fitness implications and the population consequences of individual feeding specialisations. In particular, it was concerned with how individual specialisations may affect the population consequences of habitat loss or change, a subject of particular relevance to conservationists. A review is made of individual feeding specialisation in shorebirds, the mechanisms involved in such specialisations and the different benefits and risks that may be associated with particular habitats or diets. Individual feeding specialisations were found to be widespread among many shorebird groups and most shorebird feeding specialisations were found to be constrained by differences in morphology, social status or individual skill. It is concluded that individuals or groups that are unable to change foraging area, diet or feeding method for social or morphological reasons would be the most vulnerable to any deterioration in their food supply.

Research into Oystercatchers Haematopus ostralegus overwintering on the Exe estuary, south-west England is presented and individual feeding specialisations described. Young birds and females specialised in different diets and feeding methods from adult males. Sex ratios changed with age such that 50% of immatures and 67% of adults were male. Individual fitness was measured in terms of body condition and mortality rates of ringed birds. Mussel-hammerers, the majority of which were male, had higher body condition indices and lower rates of mortality than mussel-stabbers and worm/clam feeders. Worm/clam feeders, the majority of which were females and young birds, had lower body condition indices and higher rates of mortality than mussel feeders. It is suggested that young birds and females on the Exe had higher rates of winter mortality because of the lower payoffs and/or higher risks associated with their feeding specialisations.

A modelling approach is used to predict the population consequences of differential mortality between age and sex groups. Increasing the mortality of young birds or females substantially reduced population size. Increasing female mortality resulted in a male biased population. Any increase in mortality which affected one sex more than the other resulted in a greater reduction in population size than if the increase affected both sexes the same. It is concluded that studies designed to predict the effect of habitat loss or change on shorebirds should be particularly aware of age and sex-related feeding specialisations that may lead to age and sex differences in mortality and age and sex differences in response to change.

CONTENTS

ACKNOWLEDGEMENTS

I would like to thank my supervisors, Professor Steve Hawkins and Dr Patrick Doncaster for all their help in the presentation of this thesis. I would particularly like to thank Steve Hawkins for arranging my studentship.

I am very grateful to Roger Swinfen and members of the Devon Wader Ringing Group for their expertise and assistance in catching and ringing birds on Dawlish Warren. I am also grateful to those of my colleagues who have helped with this research, particularly Dr Richard Caldow who helped with much of the fieldwork and Ralph Clarke who provided statistical advice and designed and built the Oystercatcher Population Dynamics model. Above all, I would like to acknowledge the instruction, encouragement, supervision and assistance given to me by Dr John Goss-Custard over many years. Thank you, John.

I would also like to thank the following for their very useful comments on various manuscripts: Dr Richard Caldow, Ralph Clarke, Dr Patrick Doncaster, Dr John Goss-Custard, Dr Richard Stillman and Professor Nigel Webb.

Chapter 1: INTRODUCTION AND LITERATURE REVIEW

This review has been published as:
Durell, S.E.A. le V. dit (2000) Individual feeding specialisation in shorebirds: population consequences and conservation implications. *Biological Reviews* **75**, 503-518.

I. INTRODUCTION

Individuals within a population can vary considerably in the way in which they exploit food resources used by the species as a whole. Such individual variations have important implications for the study of both animal fitness and animal numbers. Individuals can vary in the means by which they achieve certain goals and, because individuals vary in their adaptations, the risks of failing to reproduce or of dying are not distributed equally throughout the population. The aim of this thesis is to investigate these risks and the population consequences of individual feeding specialisation. In particular, it explores how individual specialisations may affect the population consequences of habitat loss or change, a subject of particular relevance to conservationists.

The study species used in this thesis is the Eurasian Oystercatcher *Haematopus ostralegus L.* The Oystercatcher is an extremely well-studied species which is well known for its individual differences in diet and feeding technique (see review in Sutherland *et al.* 1996). These specialisations have been related to age (Goss-Custard & Durell 1983) and to sex (Durell, Goss-Custard & Caldow 1993). If habitat loss or change occurs, some sections of the population will be affected more than others and the effects on population size might be very different from that predicted by models based on individual uniformity. In this review I look for evidence of individual feeding specialisation in all shorebirds. I then consider the possible population consequences and the conservation implications of any such specialisations.

Shorebirds (Order Charadriiformes) are widely distributed throughout the world and display a wide range of behavioural and ecological types. Shorebirds are also relatively large and easily recognised animals that tend to occupy open habitats such as wet grassland and estuaries. As such, they have made ideal study species for a range of ecological and behavioural investigations. Several studies have focussed on their breeding systems and on the evolution of sexual size dimorphism (Jehl & Murray 1986). Sexual size dimorphism in shorebirds ranges from species where males are the larger sex, through species where there is little size difference, to species where females are considerably larger. Shorebird breeding systems also cover the entire range of possibilities from monogamy to combined polygyny-polyandry (Jehl & Murray 1986).

Most shorebirds are also migratory species and many studies have used shorebirds in order to investigate migratory patterns and the energetics of migration (Pienkowski & Evans 1984; Kersten & Piersma 1987). Further studies have concentrated on foraging behaviour. Shorebirds, particularly on estuaries, are easy to follow when feeding and their invertebrate prey can be readily sampled, both qualitatively and quantitatively. Many of the theories developed for optimal foraging (Pyke, Pulliam & Charnov 1977) have been applied and tested in shorebird species (Goss-Custard 1984). Several studies have also been concerned with the impact that shorebirds have on their invertebrate prey, particularly when the prey is of commercial value to man (eg. Goss-Custard, McGrorty & Durell 1996).

Most work on shorebird foraging has been undertaken in the nonbreeding season and thus has often been concerned with the birds' overwinter survival. Many studies have investigated the role that winter food supplies play in determining shorebird distribution and shorebird numbers (several chapters in Evans, Goss-Custard & Hale 1984). More recently, attention has been focussed on the conservation aspects of shorebird distribution and numbers. In particular, as public awareness of the impact of habitat loss on animal numbers increases, studies have been concentrated on trying to predict the effect of habitat loss or change on shorebird populations (Goss-Custard & Durell 1990; Goss-Custard *et al.* 1991; Goss-Custard *et al.* 1995a; Goss-Custard & Sutherland 1997).

Most of the population models that have been developed in order to understand better the effect of habitat loss on population size have assumed that all individuals are affected in the same way and to the same extent (Goss-Custard & Durell 1990; Goss-Custard *et al.* 1995b,c). Even game-theoretic, individuals-based models, where individuals vary in their foraging efficiency and their social status, have all individuals competing for the same food resource (Sutherland & Dolman 1994; Goss-Custard *et al.* 1996c; Goss-Custard & Sutherland 1997). However, these models have shown that if better quality habitat is lost first, population decline is much more rapid than if the habitat lost was of average quality (Goss-Custard *et al,* 1996c). If individuals specialise in certain habitats or diets, the effect of habitat loss will depend on not only the quality of habitat lost, but also on which type of habitat is lost. Moreover, individuals with different feeding specialisations will be more or less susceptible to any increase in interference resulting from an increase in bird density.

II. INDIVIDUAL SPECIALISATION IN SHOREBIRDS

There are several possible mechanisms which may be responsible for individual differences in feeding behaviour. These mechanisms are not mutually exclusive, and it is often difficult to establish their relative importance in any given situation. Three mechanisms commonly quoted are: (1) difference in habitat use due to a patchy environment, (2) phenotypic differences, and (3) frequency-dependent selection (Partridge & Green 1985). In this review, I subdivide phenotypic differences into: (a) morphological differences, (b) individually acquired skills, and (c) differences in social status.

(1) Differences due to a patchy environment

Given that the nature of the food supply will vary in space or time, individuals may specialise in a particular diet because it is the only one that they encounter. Individuals within a species may occupy different geographic or microgeographic regions. Many studies of migratory birds have shown latitudinal differences in overwintering area between sex and age groups (Gauthreaux 1982; Ketterson & Nolan 1983; Van Eerden & Munsterman 1995). Generally speaking, adults and males tend to overwinter nearer to the breeding grounds than juveniles and females. As a male bias is frequently found in overwintering populations of shorebirds in higher latitudes (e.g. Greenhalgh 1968; Page 1974; Baker 1975; Atkinson *et al.* 1981; Page, Fearis & Jurek 1972; Buchanan *et al.*1986; Nicoll *et al.* 1988; Summers *et al.* 1990b; Durell & Goss-Custard 1996), it is often assumed that differential migration is common in this group of birds. However, there is very little conclusive evidence of age and sex differences in geographical distribution in overwintering shorebirds.

One reason for the lack of information on differential migration in shorebirds is the fact that it is often very difficult to distinguish between ages and sexes in the field. The majority of shorebird species tend to be monomorphic in plumage characteristics during the non-breeding season and any morphometric differences between the sexes are often slight and confused by size differences between races (Cramp & Simmons 1983). Extensive catching, measuring and ringing programmes are necessary, in most cases, to discover age and sex ratios within an overwintering population. To conduct such programmes on a geographic scale would involve considerable effort. Moreover, most research is concentrated at higher latitudes, and there is very little information on sex and age ratios amongst shorebirds overwintering closer to the equator. Nevertheless, a study of wader predation on fiddler crabs in Guinea-Bissau, West Africa, does mention a female bias in Bar-tailed Godwits *Limosa lapponica* and in Curlew *Numenius arquata* (Zwarts 1985). Also, Myers (1981) considered there to be sufficient evidence that males overwintered further north than females in Least Sandpipers *Calidris minutilla*, Western Sandpipers *Calidris mauri* and Ruff *Philomachus pugnax*. He also found no difference in distribution between the sexes in Sanderling *Calidris alba* and Grey Phalaropes *Phalaropus fulicarius* (Myers 1981).

On a more local scale, age and sex differences in distribution have been found in overwintering Purple Sandpipers *Calidris maritima* (Summers *et al.* 1990b), Oystercatchers (Swennen 1984; Durell, Ormerod & Dare 1996a) and Dunlin *Calidris alpina* (Clark 1983; Van der Have, Nieboer & Boere 1984). Differences were found in the distribution of ages and sexes between roost sites of Purple Sandpipers in Norway (Summers *et al.* 1990b). Overall there was a male bias, but males and females tended to predominate in different sites. The proportion of first-year birds found at each site also varied considerably, and those sites which contained the highest proportion of juveniles were also those which contained higher proportions of females (Summers *et al.* 1990b). Similarly, on the Burry Inlet, South Wales, UK, the roost site which contained a higher proportion of female Oystercatchers was also that which contained more immature birds (Durell *et al.* 1996b). Conversely, on the Wadden Sea, The Netherlands, roost sites which contained a higher proportion of immature Oystercatchers were those which contained more males (Swennen 1984). In both these Oystercatcher studies, it is concluded that the composition of birds at the roost sites reflects the distribution of ages and sexes foraging on nearby intertidal areas. Finally, with Dunlin, different age ratios were found at several roost sites on the Wadden Sea (Van der Have *et al.* 1984) and different age and sex groups tended to forage in different parts of the Severn estuary, UK (Clark 1983).

(2) Phenotypic differences: morphology

An individual's foraging strategy will be determined to a certain extent by their size, and the size and shape of their feeding apparatus. The two main sources of phenotypic variation are age and sex, and both can be associated with differences in morphology.

(*a*) *Age differences in morphology*

Juvenile shorebirds tend to be smaller than adults and their bills are shorter (Cramp & Simmons 1983), and probably still developing. One might expect, therefore, juveniles to specialise on smaller and more easily manipulated types of prey than adults. However, juvenile feeding specialisations have been noted in only three species of shorebird: Curlew Sandpipers, Crab plovers *Dromas ardeola* and Eurasian Oystercatchers. Juvenile Curlew Sandpipers (Puttick 1978) and Crab plovers (Fasola, Canova & Biddau 1996) took smaller prey types than adults. Juvenile Oystercatchers overwintering on the Exe estuary, south-west England, specialised in worm-feeding, whilst the majority of adults were mussel *Mytilus edulis* feeders (Goss-Custard & Durell 1983). Juvenile Oystercatchers also specialised in smaller prey size classes than adults (Goss-Custard & Durell 1987; Triplet 1989; Durell, Goss-Custard & Perez-Hurtado 1996a).

(*b*) *Sex differences in morphology*

Sex differences in body size are found in many animal species. This size dimorphism is frequently associated with differences in habitat use and in diet: for example in raptors and owls (Andersson & Norberg 1981) and in snakes (eg. Shine 1991; Shine *et al.* 1998) females can be much larger than males and specialise in larger prey. Differences in feeding apparatus are also found between the sexes, particularly in birds, where one sex may have a larger bill than the other (Selander 1972). This difference in bill size can result not only in different diets, but also in different foraging behaviour.

Many shorebird species are sexually dimorphic in body size and/or bill size (Table 1). Several different hypotheses exist to explain the selection pressures involved in size dimorphism in shorebirds, including those based on mating systems (Jehl & Murray 1986), parental care (Jönsson & Alerstam 1990) and aerial agility (Jehl & Murray 1986; Mueller 1989; Blomqvist *et al.* 1997). Whatever the mechanisms involved, the consequences are that, if the sexes differ in size, it is very likely that they will differ in their energetic requirements and in the way in which they meet their energetic needs. Moreover, if they differ in the size of their feeding apparatus, there will be differences in the size and the type of prey that they exploit.

Sex differences in diet or feeding technique have been found in at least 12 species of shorebirds, all of which have size differences between the sexes (Table 1). In all 11 Oystercatcher species, females tend to have longer, thinner bills than males. In the four Oystercatcher species that have been studied, females specialised in worm feeding whilst males specialise on hard-shelled prey (Hockey & Underhill 1984; Durell *et al.* 1993; Lauro & Nol 1995; Ens *et al.* 1996). Furthermore, when feeding on mussels or the Baltic tellin *Macoma balthica*, female Eurasian Oystercatchers specialised in 'stabbing', or taking the prey *in situ*, whilst males specialised in 'hammering' the prey open (Durell *et al.* 1993; Hulscher *et al.* 1996a). Oystercatchers which specialise on hammering bivalves, the majority of which are males, are those with relatively short and thick bills; Oystercatchers which specialise on worm feeding, the majority of which are females, are those with relatively long, thin bills (Hulscher & Ens 1992; Durell *et al.* 1993). Given this relationship between bill morphology and feeding specialisation, it would seem very likely that similar sex-related specialisations exist in all species of Oystercatcher.

Female Godwits are larger than males in all measurements, especially bill length. Bar-tailed Godwits *Limosa lapponica* at Lindisfarne, UK, tended to feed in single-sex flocks and females

Table 1. Numbers of shorebird species with sex differences in body size or bill size. M = male, F = female. The last column gives number of species with known sex differences in diet or feeding technique.

Family	Number of species	Body size		Bill size		No known difference in body or bill size	Known sex difference in feeding
		M > F	F > M	M > F	F > M		
Jacanidae: Jacanas	8	0	8	0	0	0	0
Rostratulidae: Painted snipe	2	0	2	0	2	0	0
Dromadidae: Crab plover	1	0	0	1	0	0	0
Haematopodidae: Oystercatchers	11	0	10	0	11	0	4
Ibidorhynchidae: Ibisbill	1	0	1	0	1	0	0
Recurvirostridae: Stilts	3	2	0	2	0	1	0
Avocets	4	0	0	3	0	1	0
Burhinidae: Stone curlews	9	0	0	0	0	9	0
Glareolidae: Coursers	8	2	1	0	0	5	0
Pratincoles	7	4	0	0	0	3	0
Chararadriidae: Lapwings	24	13	0	0	0	11	0
Golden & Grey plovers	4	0	0	0	0	4	0
Small plovers	37	0	2	1	1	35	0
Scolopacidae: Godwits	4	0	4	0	4	0	1
Curlews	9	0	9	1	7	0	1
Shanks & tattlers	15	0	14	0	5	1	0
Turnstones	2	0	2	0	0	0	1
Phalaropes	3	0	3	0	2	0	1
Woodcocks	2	0	1	0	2	0	1
Snipe	14	2	7	0	9	1	0
Dowitchers	3	0	3	0	2	0	0
Calidrids	24	4	19	4	17	1	4
Total	195	27	86	11	63	72	12

Sources: Hayman, Marchant, & Prater (1986); Cramp & Simmons (1983).

fed in deeper water than males (Smith & Evans 1973). Females also took larger worms than males (Smith & Evans 1973). In Guinea-Bissau, female Bar-tailed Godwits specialised on worms, whilst males selected small bivalves (Zwarts 1985). Dietary differences between the sexes have not been studied in the three other Godwit species.

Females are larger and longer billed than males in most Curlew species. The main exception is the Bristle-thighed Curlew *Numenius tahitiensis*, a rare Alaskan breeder, where females, although bigger, have shorter bills than males. In the Eurasian Curlew *Numenius arquata* on the Dutch Wadden Sea, there was little overlap between the sexes in diet (Zwarts 1979). Only the longer billed females took the clam *Mya arenaria*, whilst the shorter billed males specialised on worms. On the Tees estuary, UK, male Curlew specialised in field feeding whilst females fed on the mudflats (Townshend 1981). The shorter male bills were probably better adapted for field feeding, whilst females were better able to forage for larger, more deeply buried polychaete worms, particularly during the winter months (Townshend 1981; Davidson *et al.* 1986a). In a study of breeding Curlew, males caught significantly more surface-living invertebrates, whilst females caught more earthworms (Berg 1993).

In both species of Turnstones, females are larger than males, but do not have significantly longer bills. However, individual feeding specialisations have been identified in the Ruddy Turnstone *Arenaria interpres*, which, in some cases, are linked with sex (Whitfield 1990). The fact that 'stone-turning' was a more profitable foraging technique for female Turnstones was thought to be due to the females' larger size (Whitfield 1990). Other specialisations were linked with social status and will be dealt with in Section II(4).

Phalaropes are the most aquatic of the shorebirds, and often feed whilst swimming. Females are larger than males in all three species, and take little part in any breeding activities apart from laying eggs. Red-necked Phalaropes *Phalaropus lobatus* have no difference in bill size between the sexes and showed no sex differences in foraging (Rubega 1996). However, in the two other Phalarope species, females do have longer bills than males. In a study of breeding Grey Phalaropes *Phalaropus fulicarius*, females specialised in 'deep-feeding' in water, whilst males specialised in 'surface-feeding', which comprised a qualitatively different diet (Ridley 1980). This difference in feeding technique may be related to differences in bill size.

Woodcock are essentially crepuscular and nocturnal woodland birds. There is no difference in body size in the Eurasian Woodcock *Scolopax rusticola,* but female American Woodcock *Scolopax minor* are larger than males. In both these species, females have longer bills and sex differences in diet have been found in the Eurasian Woodcock (Fadat, Ferrand & Martinel 1979). Differences in foraging behaviour were not recorded, as dietary differences were established by the examination of stomach contents. However, male stomachs contained a higher proportion of adult beetle remains and female stomachs contained more earthworms and insect larvae. This supports the prediction that males would specialise in surface feeding, whilst females would specialise in probing in soft ground.

In most Calidrid shorebirds, females are larger than males and have longer bills. In four species, the Pectoral Sandpiper *Calidris melanotos*, the Sharp-tailed Sandpiper *Calidris acuminata*, the Buff-breasted Sandpiper *Tryngites subruficollis* and the Ruff *Philomachus pugnax*, males are larger and have longer bills. Only one species, the Surfbird *Aphriza virgata*, has no morphometric difference between the sexes. Several studies have shown sex differences in diet in this group of shorebirds. One of the best known studies is that on Curlew Sandpipers in South Africa, where male and female Curlew Sandpipers foraged in single-sex flocks and fed on a slightly different range of prey items (Puttick 1978, 1981). Sex differences in prey size have been found in breeding Pectoral Sandpipers and Dunlin (Holmes & Pitelka 1968), and sex differences in foraging technique in overwintering Dunlin (Clark 1983). Finally, longer billed Purple Sandpipers, the majority of which were females, took larger molluscs than shorter billed, mostly male birds (Summers *et al.* 1990a).

Many shorebird species have sexual size differences, particularly differences in bill size, and it would be surprising to find that there were no feeding differences between the sexes in these birds. Most shorebird foraging studies have not been concerned with sex differences, not least because of the difficulty of distinguishing between the sexes in the field in winter.

In most cases, extensive catching, measuring and ringing programmes, followed by intensive fieldwork, are necessary in order to ascertain sex differences in feeding in overwintering shorebirds. This is why I believe that sex differences in diet or foraging technique are probably even more common in shorebirds than is, at present, suspected.

There are three shorebird families, Burhinidae, Glareolidae and Charardriidae, where sexual size dimorphism is less common, and where it is less likely that sex differences in feeding exist (Table 1). Birds in all three families are more terrestrial than those in other families, with many inhabiting dry grasslands. Most of these birds are short-billed visual feeders, pecking prey items from the surface of the ground, rather than probing. Researchers concerned with the evolution of shorebird bill morphology hypothesise that surface pecking is the ancestral trophic condition and that the evolution of longer and thinner bills, along with an increase in the number of mechanoreceptors in the bill tip, are a later adaption for tactile feeding or probing (Zweers & Gerritsen 1997; Barbosa & Moreno 1999). It seems to be the case that sexual size dimorphism in bill length is more likely to occur in families, such as the Scolopacidae, which have evolved longer bills for tactile feeding. It is also probable that bill morphology is one of the most important determinants of individual feeding specialisation in shorebirds.

(*c*) *Morphological differences unrelated to age or sex*

Trophic polymorphisms also exist which are independent of age and sex (Partridge & Green 1985; Skulason & Smith 1995). Unlike sex- and age-related differences in morphology, such polymorphisms can be seen as adaptations for a varied and changing environment. For example, bill size polymorphism in the Hook-billed Kite was related to the available size ranges of its prey, terrestrial snails (Smith & Temple 1982). In both African finches (Smith 1987) and Darwin's finches (Gibbs & Grant 1987) bill size polymorphism was seen to be a genetic adaptation to an oscillating environment, where a particular bill size was the optimum in different years. No shorebird studies have mentioned morphological differences between individuals that are unrelated to their age or sex.

(3) Phenotypic differences: individually acquired skills

Some individuals are more efficient foragers than others, and less skilful foragers may have to compensate for lack of foraging efficiency by feeding in different habitats and by consuming different types or sizes of prey. Differences in foraging skills are frequently associated with age: there is considerable evidence that young animals are less efficient foragers than adults and that feeding efficiency improves with age (Wunderle 1991). There is also evidence that the greater the skill needed to handle prey, the less successful juveniles are in comparison with adults and the longer it takes for individuals to acquire that skill (Wunderle 1991). It is also possible that some individuals never acquire certain foraging skills.

Several shorebird studies have shown age-related differences in foraging ability. Juveniles were less efficient than adults feeding on the same prey in Ruddy Turnstones (Groves 1978), Black-necked Stilts *Himantopus mexicanus* (Burger 1980), Black-winged Stilts *Himantopus himantopus* (Espin, Mather & Adams 1983), Masked Lapwing *Vanellus miles* (Burger & Gochfield 1985), American Avocets (Burger & Gochfield 1986) and Eurasian Oystercatchers (Goss-Custard & Durell 1987). This difference in foraging ability may cause juveniles to specialise on different prey types or different feeding methods from adults. Juvenile Black-winged Stilts, unlike adults, did not forage by pecking items off the surface film of water, even though this was a more efficient feeding method (Espin *et al.* 1983). When feeding on mussels, no juvenile Oystercatchers were seen to use the hammering technique (Goss-Custard & Durell 1987). Mussel hammering is a skill which takes some individuals a long time to acquire and it is possible that some Oystercatchers, even when their bills are morphologically adapted to hammering, never manage to perfect this skill. Thus, particularly when a greater degree of skill is needed in order to find or to manipulate prey, some individuals, not only juveniles, may be restricted in their choice of prey or feeding method by their individual ability.

Individual experience will also influence feeding specialisations. It may be more profitable for an individual to persist with a particular type of prey or feeding method, rather than change to a potentially more rewarding diet, because of the skills they have already developed (Partridge & Green 1985). In an experiment designed to test this, individual captive Great Tits *Parus major* differed in their preference for feeding site, and this appeared to be the result of the birds' experience and learning during training (Partridge 1976).

In field studies, it is very difficult to distinguish between individual experience and other phenotypic mechanisms of feeding specialisation. However, individual differences in experience and/or skill, unrelated to other phenotypic differences, have been shown to be an important component of feeding specialisation in Ruddy Turnstone (Whitfield 1990). Differences in experience or skill may also be the reason why Oystercatchers specialise in hammering mussels open on either the ventral side or the dorsal side (Durell & Goss-Custard 1984; Sutherland & Ens 1987), and specialise in hammering *Macoma balthica* open on either the right or left valve (Hulscher 1982).

(4) Phenotypic differences: social status

Many studies have shown that subdominant individuals are excluded from preferred feeding areas (Wunderle 1991). With young animals, therefore, it is often difficult to establish whether their exclusion from preferred feeding areas is due to their poorer foraging ability or their lower social status. However, subdominant animals of any age may have their feeding opportunities restricted by more dominant individuals and be forced to feed on alternative prey (Partridge & Green 1985; Wunderle 1991). Sex differences in dominance are not uncommon, and can result in sex differences in habitat use: in a field experiment on Downy Woodpeckers *Picoides pubescens*, for example, males did not change their foraging areas when females were removed, but if males were removed, females moved into the feeding areas left vacant (Peters & Grubb 1983). This suggested that males were excluding females from the preferred feeding areas.

Several shorebird studies, cited above, have shown differences in the distribution of birds of different age and/or sex. Reasons for this differential distribution include differences in social status: less dominant individuals may be excluded from preferred overwintering areas, or from preferred feeding patches within one estuary. Young birds tend to be subdominant in Oystercatchers, and immature birds, which fed on preferred mussel beds throughout the summer, were displaced when the adults returned in the autumn (Goss-Custard *et al.* 1982b). These displaced birds either moved to less preferred mussel beds or changed diet altogether, feeding on mudflats and in fields (Goss-Custard & Durell 1983). In Redshank *Tringa totanus*, juveniles were excluded by adults from the mussel beds in one estuary (Cresswell 1994). The juveniles fed on saltmarsh where they not only took different prey, but were also subject to higher rates of predation (Cresswell 1994).

In Ruddy Turnstones, status had an important effect on feeding specialisation (Whitfield 1990). Routing for prey items appeared to be the preferred feeding technique and competition was greatest between routing birds. In the absence of interference, there was no difference in intake rates between high- and low-status birds when routing, but low-status birds suffered reduced intake rates with increased interference and high-status birds did not. Male turnstones tended to be dominant to females, so females, along with juveniles and other low-ranking birds, were more likely to probe rather than rout for prey items (Whitfield 1990).

(5) Frequency-dependent selection

The application of game theory (Maynard-Smith 1982) to animal behaviour has shown that different strategies can have equal payoffs and that a mixture of strategies may be maintained by frequency-dependent selection. Frequency dependence probably plays some role in the maintenance of feeding polymorphisms within a population. One example which has demonstrated this is the scale-eating cichlid fish *Perissodus microlepis* in Lake Tanganyika, Tanzania, where the frequency of right- or left-handed morphs oscillated around unity, probably through frequency-dependent selection exerted by the prey's alertness (Hori 1993).

It is also possible that, even when individuals have identical phenotypes, frequency-dependent feeding specialisations may develop (Davies 1982). There is little empirical evidence for this, particularly because of the difficulty in proving that different strategies have equal payoffs. However, there is little doubt that an individual's strategy will be influenced by the behaviour of others. It may be more realistic to assume that different strategies will not necessarily have equal payoffs, and that an individual's choice of strategy will be conditional upon its limitations in terms of, for example, size, foraging ability or social status (Gross 1996). Individuals will not only have different constraints, but also different priorities: for example, young animals may need to acquire extra nutrients for growth, and egg-laying females may need to acquire more nutrients prior to breeding. Thus, feeding specialisations may be frequency dependent, but the optimum strategy for a given individual will be conditional upon its specific priorities and constraints.

All studies of feeding specialisations in shorebirds have linked individual variation to differences in phenotype and differences in habitat. Apart from Whitfield (1990) and Sutherland *et al.* (1996), none has considered the possibility of an evolutionary stable strategy (ESS) type mixture of alternative strategies. Whitfield (1990) found no evidence for frequency-dependent selection in Ruddy Turnstone and Sutherland *et al.* (1996) pointed out that the different Oystercatcher feeding strategies did not appear to have equal payoffs. However, an individual's strategy must be influenced by the behaviour of others and frequency dependence must play some role in an individual's choice of feeding specialisation.

III. POPULATION CONSEQUENCES

Feeding specialisations can have important consequences for population dynamics. If different feeding strategies have different payoffs, then those individuals specialising in less profitable strategies may be at greater risk of failing to breed or of dying. Even if different feeding strategies are equally profitable, some may incur greater risks from, for example, parasites or predation. Moreover, some prey may be more variable than others, or more subject to changes in environmental conditions, such as drought or severe winter weather.

(1) Different payoffs

It is extremely difficult to compare the payoffs from different feeding strategies. Most studies record the benefits, in terms of food intake, but very few can measure the costs of different diets or feeding methods. However, in studies where subdominants are excluded from preferred feeding areas, and move into these areas as they mature or when dominant birds are removed, it is usually assumed that the preferred diet or feeding area is more profitable. Differences in mortality rates may also indicate differences in feeding success. Juvenile shorebird mortality is usually higher than adult's (Boyd 1962) and, although partly due to inexperience, this may be due to their feeding options being limited by more dominant birds. In Oystercatchers, higher mortality rates were recorded from poorer feeding areas (Swennen 1984).

Evidence that different strategies may have different payoffs has been provided by work on Oystercatchers overwintering on the Exe estuary (Durell *et al.* 2001). Birds that specialised on mussel-hammering had higher body weights and lower rates of winter mortality than mussel-stabbers. Mussel-hammerers were also less likely than mussel-stabbers to be seen supplementing their low water diet by feeding in upshore areas or in the fields at high water. Birds that specialised on worms and clams *Scrobicularia plana* had lower body weights and higher winter mortality than mussel feeders. All known worm/clam specialists were seen to use supplementary feeding at some stage during the winter, indicating that they were failing to meet their daily energy requirements during the low water period. It would appear, therefore, that the payoffs were highest for mussel-hammers and lowest for worm/clam feeders.

(2) Different risks

Different diets or habitats may incur different risks. One risk which can vary between diets is parasite loading. Infection by parasites may affect a bird's fitness and its ability to survive periods of stress. The intensity of parasite infection has been related to diet. For example, on the Exe estuary, cockles carried far more parasites than mussels and large cockles carried more parasites than small ones (Goater 1988; Goater 1993). Juvenile Oystercatchers had higher parasite infections than adults, and it is possible that this was related to the broader range of prey taken by juveniles. In particular, birds that fed in upshore areas and in the fields were thought to be more susceptible to infection than those that fed on low-level mussel beds (Goss-Custard *et al.* 1996a). A second risk which can vary between diets is risk of bill damage. Birds which specialise on hammering open hard-shelled prey will be more at risk from bill damage than birds that feed on soft-bodied prey.

Birds that feed on different habitats will be subject to different predation risks. Cresswell (1994) showed that juvenile Redshank were at greater risk from predation by Sparrowhawks *Accipiter nisus* because the saltmarsh on which they were feeding was closer to cover than the mussel bed where the adults fed. In general, birds that feed near the high water mark, and so closer to tree cover, are more at risk from raptors (Whitfield, Evans & Whitfield 1988; Cresswell & Whitfield 1994). Birds that feed in fields will also suffer higher predation rates, not only from birds of prey, but also from Foxes *Vulpes vulpes* and other mammalian predators. Birds that feed inland will certainly be more at risk from accidents, such as colliding with overhead wires, trains or cars, than birds feeding on intertidal areas. Amongst Oystercatchers that overwinter on the Exe estuary, 10% of recovered ringed birds (1976-1999) had the cause of death given as a road or rail accident (own data).

(3) Prey variability

Birds which specialise on prey which fluctuates greatly in abundance will be more at risk from loss of feeding sites when the prey population crashes or becomes unavailable. Some prey are subject to greater fluctuations in abundance than others, in either the short or long term. Populations of mussels (McGrorty *et al.* 1990), *Macoma balthica* and *Scrobicularia plana* (Zwarts *et al.* 1996) tend to be relatively stable from one year to the next, whilst cockles are subject to large fluctuations in abundance, largely through their susceptibility to frost (Zwarts *et al.* 1996) and also to eutrophication (Desprez *et al.* 1992; Rybarczyk *et al.* 1996). The polychaete worms *Lanice conchilega*, *Nephtys hombergii* and *Anaitides mucosa* are also susceptible to frost and numbers fluctuated widely from year to year on the Wadden Sea (Beukema *et al.* 1993). Within a prey population, the abundance of some size classes may vary more than others. In particular, smaller size classes may vary more because of variations in reproductive output and subsequent recruitment to the population (Beukema *et al.* 1993). Smaller size classes, particularly if they are less deeply buried, may also be more susceptible to frost.

One of the greatest sources of prey variability for shorebirds is prey availability. Tidal and seasonal patterns of prey activity affect their vulnerability to capture. Both the Lugworm *Arenicola marina* and the Ragworm *Nereis diversicolor* appear to burrow more deeply as the mud in which they live dries out and so become less accessible, particularly to shorter billed waders, as the tide recedes (Vader 1964). The prosobranch *Hydrobia ulvae* is only active, and easily detectable, when the mud is covered by a film of water, and buries itself when the mud dries (Newell 1962). Many of the small arthropod crustacea taken by shorebirds are only active in front of the advancing tide (Evans 1979). Other intertidal prey, such as mussels and cockles, are available throughout the period of tidal exposure, but are unavailable when covered by the tide. Terrestrial invertebrates are unaffected by any tidal regime, but those buried in the soil are only easily available when the soil is wet (Gerard 1967). All these factors may become critical during the winter, when birds' energetic needs are high and time available for feeding in daylight hours is short.

Many intertidal and terrestrial invertebrates become less available during periods of cold weather. *Macoma balthica*, *Scrobicularia plana* and *Nereis diversicolor* bury more deeply in the mud during cold weather, and are only reachable by the longest billed waders (Esselink & Zwarts 1989; Zwarts & Wanink 1989; 1991; 1993). Other prey, such as the polychaetes *Arenicola marina* and *Scoloplos armiger* (Evans 1979) and the amphipod crustacean *Corophium volutator* (Goss-Custard 1969), become less active as the temperature drops and so become harder to detect. Earthworms also become less active in cold weather and all terrestrial invertebrates become totally inaccessible when fields are frozen or covered with snow. Birds which specialise in prey which become less available in cold weather will be more likely to be adversely affected during periods of severe winter weather.

(4) Population consequences

The main impact of different feeding specialisations on population dynamics will be through differential mortality. In many circumstances, higher mortality amongst certain individuals will have little effect on the population size except, perhaps, on a local scale. However, if a whole section of the population, such as a particular age group or a particular sex, specialises in a diet which is associated with lower payoffs or higher risks, then the resultant differential mortality may have a marked effect on population structure and on population size. In particular, if a certain section of the population is more likely to be affected by catastrophic events, such as a prolonged period of severe winter weather, any differences in mortality between age groups or sexes may result in consequences more far reaching than the short-term reduction in population size.

As with most animals, juvenile shorebirds suffer higher mortality than adults (Boyd 1962; Evans & Pienkowski 1984). Whilst other factors will be involved, the fact that juveniles are usually subdominant to adults and thus often forced to feed in less profitable habitats and on less profitable prey must have an influence on their mortality rates, particularly during the winter. Juveniles will almost certainly be more susceptible to prolonged periods of severe winter weather. Although juvenile birds often make up only a small proportion of the population, population models have shown that increasing the mortality of this small and vulnerable minority of the population can have a substantial effect on stable population size (Goss-Custard & Durell 1984a; Goss-Custard & Durell 1990).

Amongst adults, if one sex suffers from higher mortality than another, this will affect the sex ratio of the whole population and also the number of potential breeding pairs. A male bias has been found in several populations of overwintering shorebirds (Greenhalgh 1968; Page 1974; Baker 1975; Atkinson *et al.* 1981; Page, Fearis & Jurek 1982; Buchanan *et al.* 1986; Nicoll *et al.* 1988; Summers *et al.* 1990a; Durell & Goss-Custard 1996). This may, in part, be due to differential migration, but may also be due to higher female mortality. Oystercatcher sex ratios on the Exe estuary changed with age and this could not be explained by differential immigration/emigration alone (Durell & Goss-Custard 1996). It was concluded that females had higher rates of mortality than males. This suggestion was supported by the fact that, in Holland, female Oystercatchers started to breed at an earlier age than males (Ens 1992).

Higher female mortalities have also been reported for Least Sandpipers *Calidris minutilla* (Miller 1983), Dunlin (Jönsson 1991), Semipalmated sandpipers *Calidris pusilla*

(Sandercock & Gratto-Trevor 1997) and Kentish Plovers *Charadrius alexandrinus* (Székely, Cuthill & Kis 1999). There is no evidence to suggest that these higher female mortalities were due to different diets or habitat use. However, female Oystercatchers on the Exe specialised in diets associated with higher rates of mortality (Durell *et al.* 2001). In particular, females specialised in field feeding which, as shown above, has higher risks from parasites and predation and is also more affected by severe winter weather. Other birds which specialise in field feeding, such as male Curlew, may also be more subject to higher rates of winter mortality.

Apart from the increased risk of dying, birds specialising in diets or feeding methods associated with lower payoffs will be more likely to be in poor condition. Female Oystercatchers on the Exe specialised in worm/clam feeding which was associated with lower body condition (Durell *et al.* 2001). If they are in poor condition when they return to the breeding grounds in the spring, it is likely that their chances of breeding success will be reduced. It is difficult to predict the population consequences of certain individuals failing to breed, but if a high proportion of one sex is in poor condition, it is possible that the breeding output would be less than it could be. Any factor which decreases reproductive output has a critical effect on equilibrium population size (Goss-Custard *et al.* 1996b). However, any variation in individual breeding success is likely to be balanced by density-dependent fledgling mortality (Goss-Custard *et al.* 1995c).

Finally, different sections of a population may be more susceptible to any increase in bird density resulting from either an increase in population size, or a decrease in available habitat. Birds which specialise in diets or feeding methods associated with longer handling times will be more susceptible to interference from other birds (Stillman, Goss-Custard & Caldow 1997). In Oystercatchers, mussel hammerers are more susceptible to interference than mussel-stabbers (Goss-Custard & Durell 1988; Stillman *et al.* 1996). At low bird densities mussel-hammerers had higher intake rates than mussel stabbers. However, as bird density increased, mussel-hammerer intake rates decreased below that of mussel-stabbers of the same social status (Goss-Custard & Durell 1988; Stillman *et al.* 1996). Those birds which are more susceptible to interference will probably be the first to be affected by density-dependent mortality resulting from increased bird densities. Conversely, if individuals specialising on diets or feeding methods with little interference are less affected by density-dependent mortality, increasing population densities could reach levels where the prey are seriously depleted, resulting in a population crash. This was demonstrated by simulations using an individuals-based model, when the Oystercatcher population consisted of mussel-stabbers only (Goss-Custard & West 1997).

IV. CONSERVATION IMPLICATIONS

One of the main concerns of conservationists is predicting the effect of habitat loss or change. If individuals within a population specialise in different habitats or diets, they will be affected to a greater or lesser degree by any change. It can be argued that individual variation will actually dampen the population response to change in that, if population densities increase, the more vulnerable individuals will die first, resulting in a gradual increase in mortality rates. Without individual variation, all individuals will survive until the food supply is so depleted that there will be a population crash. However, if individual variation is ultimately due to phenotypic constraints, and if those individuals that are affected represent a significant proportion of a certain section of the population, eg. juveniles or females, the effect on population size may be greater than that predicted from the actual loss of feeding area.

There are several different ways in which some individual shorebirds may be affected more than others by habitat loss or change. First, with differential migration, and on a geographic scale, development in one area may affect more of a particular age or sex group than another during the non-breeding season. Second, on a local scale, only one particular habitat may be affected. For example, removal of cockle beds will affect cockle-feeding birds or any change in agricultural practices will affect field-feeding birds. Third, only certain prey types may be affected by, for example, climate change, sea-level change or pollution. Birds will suffer if there is no alternative prey, or if they are unable, for morphological reasons, to switch prey types.

Finally, if feeding habitat is lost, there will be increased competition for the remaining resources. As shown above, if competition is already intense on certain habitats, then any increase in bird density may have a more marked effect on these habitats than on others. Particular diets or feeding methods are also associated with different risks from interference from other birds. Birds which specialise in these diets and feeding methods, particularly if they are of lower social status, will be the first to suffer from any increase in mortality resulting from increased competition. As shown in the review of shorebird feeding specialisations, such individuals are very likely to be of the same age, particularly young birds, or of the same sex.

Population models developed over the last decade have greatly increased our understanding of how population size is affected by habitat loss or change (Goss-Custard & Durell 1990; Goss-Custard *et al.* 1995b,c; Durell, Goss-Custard & Clarke 1997). However, most of these models have assumed that all individuals within a population are affected in the same way and to the same extent. Even game-theoretic, individuals-based models, where individuals vary in their foraging efficiency and their social status, have all individuals competing for the same food resource (Sutherland & Dolman 1994; Goss-Custard *et al.* 1996b; Goss-Custard & Sutherland 1997). In this thesis I shall use one of these population models to explore the effect on population size of age and sex-differences in response to habitat loss.

V. THESIS AIMS

The aim of this thesis is to investigate the fitness implications and population consequences of Oystercatcher feeding specialisation. In Chapter 2, I describe the methods used and some results from a long-term study of Oystercatcher feeding ecology, behaviour and population dynamics on the Exe estuary, south-east Devon. I have been involved in this research since 1979, as part of a team led by Dr John Goss-Custard. From the beginning, I played a major part in data collection and data analysis. In later years I was in charge of my own original research and led teams concerned with particular aspects of our work.

We found that Oystercatcher feeding specialisations were related to their age and their sex. If different feeding specialisations have different payoffs, this could mean that some individuals, and some age or sex groups, may be fitter than others. In chapter 3, I describe my research into Oystercatcher fitness, which involved measuring the body condition of overwintering Oystercatchers.

Different age and sex groups may also be more vulnerable to habitat loss or change. Population models have helped us to understand better the effect of habitat deterioration or loss on Oystercatcher populations. One of the main conclusions from these models is that the effect of habitat loss or change depends critically on the strength of winter density-dependent mortality. In chapter 4, I analyse data from colour-ringed adults, collected over a period of time when the Oystercatcher population on the Exe was increasing, for evidence of density-dependence in their winter mortality. In chapter 5, I use a population model to investigate the population consequences of age and sex differences in mortality and age and sex differences in response to habitat loss or change. Finally, in chapter 6, I discuss the conservation implications of my results.

Chapter 2: OYSTERCATCHER POPULATION BIOLOGY

I. INTRODUCTION

The research undertaken for this thesis was conducted as part of a long-term study of Oystercatchers *Haematopus ostralegus* overwintering on the Exe estuary, south Devon. This study started in 1976 and continues to the present day. I have been a member of the Oystercatcher research group since 1979, and in this chapter, I review the work done over the last 20 years. I provide some background information on the study species and the study area. I then describe some of the methods and results, most of which have already been published, which are relevant to the present work. I conclude with a section describing some of my work on modelling Oystercatcher population dynamics.

II. THE OYSTERCATCHER

The Oystercatcher is an ideal study species, being a large and conspicuous wader which is not too timid. It is an easy bird to watch whilst feeding, and it is relatively easy to identify the prey items it takes and to quantify its intake rates. A considerable amount of ecological and behavioural research has been undertaken on the Oystercatcher over the last three decades, mainly in Britain and the Netherlands (Goss-Custard 1996).

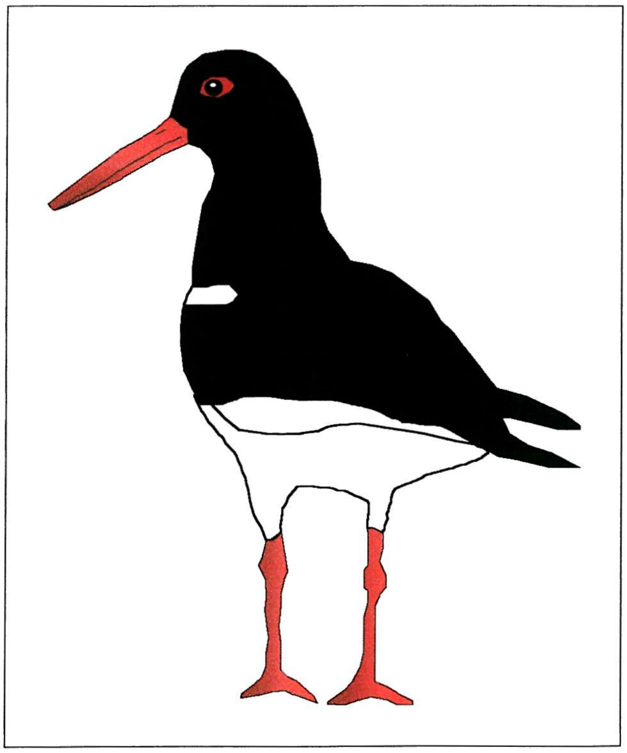


Fig. 2.1 Oystercatcher *Haematopus ostralegus*

The main feeding habitats of Oystercatchers are estuaries, rocky shores, beaches and inland fields. The range of prey taken by Oystercatchers is extremely broad, including bivalve and gastropod molluscs, arthropod crustaceans, polychaete worms, earthworms and insect larvae (Hulscher 1996). However, individual Oystercatchers tend to specialise on one or two particularly prey types over long periods of time (Hulscher 1996; Sutherland *et al.* 1996). One of the main features of Oystercatchers is their ability to open shellfish in order to consume the flesh inside. This means that Oystercatchers are able to exploit larger size classes of hard-shelled prey than those shorebirds which swallow their prey whole.

Oystercatchers are very long-lived birds, sometimes living in excess of 40 years, and they do not breed until at least their fourth year (Dare 1970; Ens *et al.* 1996b). Juvenile and immature birds remain on the overwintering grounds during the summer months and do not migrate to the breeding grounds until they mature (Ens *et al.* 1996b). Oystercatchers breed in coastal areas throughout north-west Europe and also inland in Britain, Denmark, Holland and Germany (Dare 1970; Hulscher *et al.* 1996b; Goss-Custard *et al.* 1996c). The overwintering population of north-west Europe is primarily found on estuaries in Britain, Denmark, north-west Germany, Holland and France (Dare 1970; Hulscher *et al.* 1996b). The Oystercatcher population overwintering in Britain has increased over the last few decades, probably as a result of an expansion of inland breeding during the latter half of this century (Cranswick, Kirby & Waters 1992; Goss-Custard *et al.* 1996c).

III. THE STUDY AREA

The Exe estuary was chosen as a study site because it is a relatively small estuary with easy access to the shoreline. This means that birds can easily be followed and counted and the prey populations are relatively easy to sample. The Exe estuary is also isolated from other sizeable estuaries and so the Oystercatcher population is relatively discrete. In the summer months, a few hundred immature Oystercatchers are found on the estuary. In August, they are joined by over two thousand adults returning from their breeding grounds in northern Britain, Norway and Holland. These adults remain on the estuary until their spring migration in late February or early March (Goss-Custard & Durell 1983).

The Exe estuary is approximately 10km long and mostly 2km wide (Fig. 2.2). The majority of Oystercatchers on the Exe feed on the mussel *Mytilus edulis* beds found in the lower reaches of the estuary. Most of these birds are mussel-feeders, although a small number feed on cockles *Cerastoderma edule*, periwinkles *Littorina spp.* or Ragworms *Nereis diversicolor*. The rest of the estuary consists of sand- and mudflats where Oystercatchers feed on cockles, Ragworms and clams *Scrobicularia plana*. Oystercatchers also feed along the coast at low water, where the majority take mussels and limpets *Patella spp.* from the rocks and bivalves *Spisula spp.* from sandy areas. As the winter progresses, increasing numbers of Oystercatchers are found feeding in fields adjacent to the estuary, particularly at high water. The type of field used most by Oystercatchers is permanent grassland, including recreational grassland, where they feed on earthworms *Lumbricus spp.* and insect larvae.

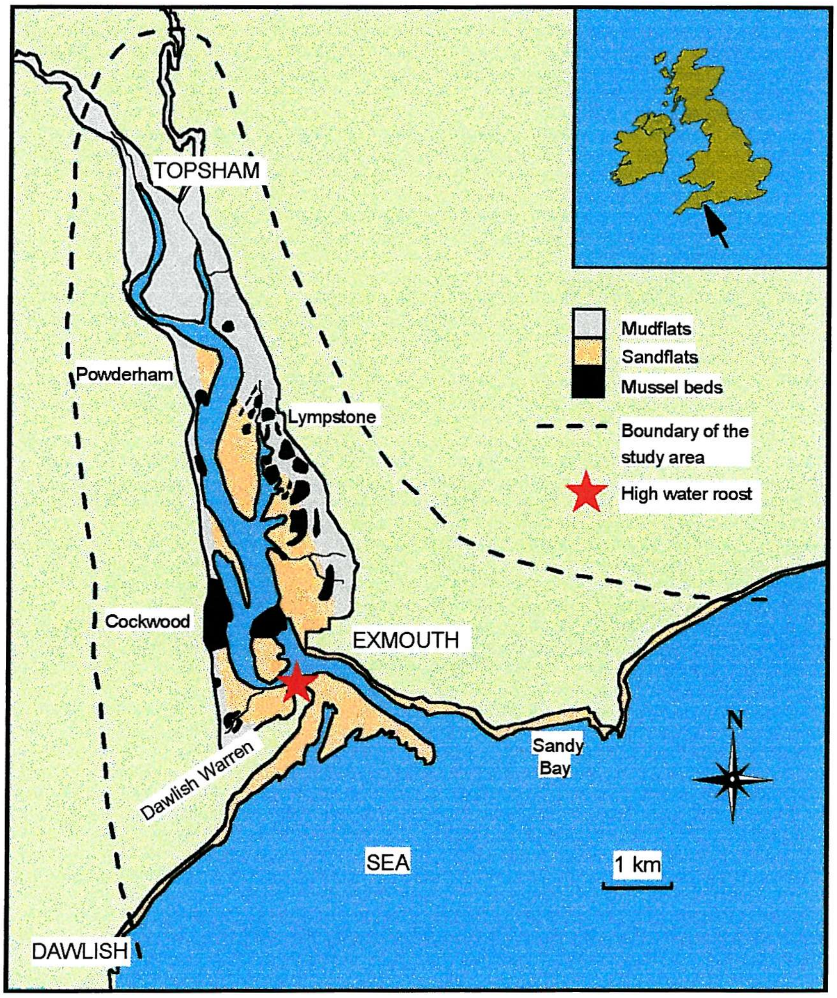


Fig 2.2 The Exe estuary

IV. METHODS

(1) Counts

Birds were counted on all habitats at low water on spring tides, using a x15-x60 telescope. The fields, coast and wider sections of the estuary were searched on foot, but some of the narrower parts of the estuary could be counted from the sea wall. Up to five low water periods were needed to complete a count, so movements between areas could have affected the results. However, there was a close correspondence between total numbers counted at low water and counts made at the roost at high water (Goss-Custard 1981). Birds were also counted at high water to find out how many were feeding in the fields. All the fields in the study area were counted within ±2.5 hrs of high water.

The age structure of the population was determined by scanning flocks at low and high water. As large a sample as possible was aged in each place and the total numbers present counted. Birds were aged as juveniles (in their first year), immature (second to approximately fourth year) and adult, employing the criteria given in Prater *et al.* (1977). Tests showed that errors in ageing at a distance (through a telescope) occurred in under 7% of cases (Goss-Custard & Durell 1983).

(2) Catching, measuring and ringing birds

Birds were caught at the roost at Dawlish Warren using mist-nets at night and cannon-nets during the day. All birds caught were aged (as above), and their weight, bill length and wing length measured. From 1989 onwards, several additional measurements were taken. These included keel length, tarsus length, head+bill length, bill depth halfway down, bill-tip width and bill-tip depth (Durell *et al.* 1993).

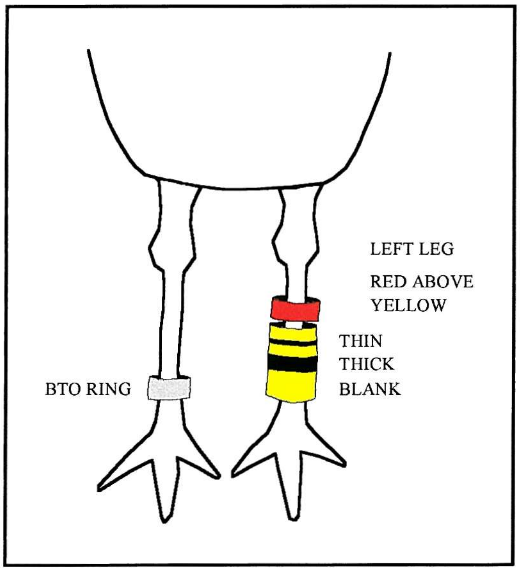


Fig. 2.3 Colour rings used on the Exe

In addition to the standard BTO numbered rings, a substantial proportion of birds caught were colour-ringed in order to identify individual birds. These colour rings were designed so that the whole combination could be placed on one leg, a great advantage when studying a bird which often stands on one leg only. To date, over 1000 birds have been colour-ringed.

The system of ringing, devised by Chris Mead, consists of two rings placed below the intertarsal joint on one leg (Fig. 2.3). One ring is a tall (22mm) 'wasp' ring which may have black bands engraved on it. These bands are either thin (1-1.5mm) or thick (4-5mm) and occur in one of three positions (top, middle, bottom) on the ring. Positions on the ring may also be left blank, giving 27 possible combinations. The second ring is small and uniformly coloured and may be placed either above or below the tall ring and both may be placed on either the right or left leg of the bird. A complete record, as in Fig. 2.3, would therefore read: left leg, small red over tall yellow, thin, thick, blank.

(3) Ring searches

The presence of individuals within the population was checked during a series of spring tides once or twice a month. The high water roost was checked at least three times during a spring tide series to ensure that most individuals present had been seen (Goss-Custard *et al.* 1982a). Flocks feeding in the fields at high water were also searched until we were confident that all the colour-ringed birds had been found. Records were also kept of any colour-ringed birds seen on the low water feeding grounds during counts and feeding studies.

Individual colour-ringed birds were followed at low water and their location, habitat and behaviour noted. Feeding birds were watched to see what prey were being taken and, in the case of mussel feeders, which feeding method was being used. It was easy to identify most prey and, as birds usually only ate one kind of prey in one location for long periods, it was usually only necessary to watch until two or three prey were eaten (Goss-Custard & Durell 1983).

In two winters, 1989/90 and 1990/91, intensive searches were made for colour-ringed birds on upshore areas as the tide advanced and receded, and in the fields at high water, in order to ascertain the frequency with which birds were supplementing their low water diets during the winter months (Caldow *et al.* 1999).

(4) Feeding and behavioural studies

(a) Mussel feeders

One of the primary aims of our work was to develop a model of the Oystercatcher population in relation to their main prey, mussels. Most of the work on Oystercatcher feeding and behaviour was, therefore, concentrated on mussel-feeding birds. We measured the relationship between individual intake rate and bird density in order to establish their foraging skill and their susceptibility to interference (Fig. 2.4). A bird's foraging skill, the intercept in Fig. 2.4, measures how fast it can feed in the absence of competitors, or its 'interference free intake rate' (IFIR). A bird's susceptibility to interference, the slope in Fig. 2.4, measures how its intake rate is depressed as the number of competitors increases. We looked at the relationship between these two attributes and a bird's age, dominance, feeding method and sex (Goss-Custard & Durell 1987a,b,c; Goss-Custard & Durell 1988; Caldow *et al.* 1999).

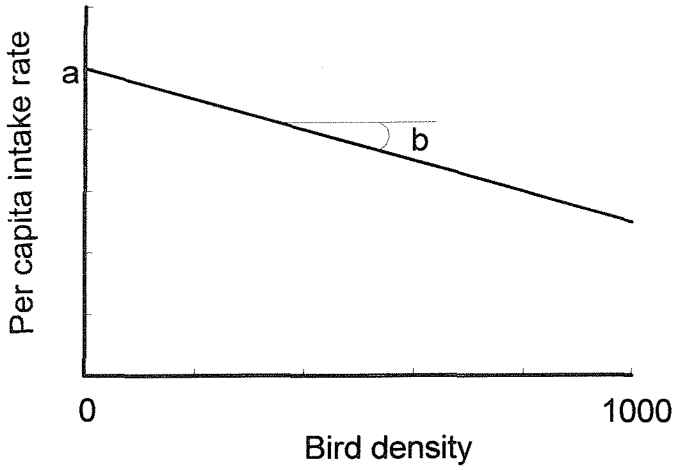


Fig. 2.4 A hypothetical interference curve illustrating how foraging efficiency (the intercept, a) and susceptibility to interference (the slope, b) were measured. From Goss-Custard & Durell (1987a).

Observations of feeding Oystercatchers were made on mussel beds which had been marked out in 25 x 25m squares with bamboo canes. Bird density was measured by counting the number of foraging and resting birds in the square occupied by the focal bird at the beginning and end of five minute periods and taking the mean. Observations were made from elevated hides using a x15-x60 telescope. These hides were entered on the receding tide before the mussel bed was exposed and the birds had arrived and observations were made throughout the tidal cycle. Intake rate varies through the tidal cycle, so when individually marked birds were being followed, twelve five minute observations were obtained for each bird during each hour of the tidal cycle over a period of two winters. When comparisons were being made between adult and juvenile foraging, observations were taken as a series of matched pairs, watching a young bird and then an adult in the same place. In addition, several environmental variables were measured in order to include them in statistical analyses. These were mean tide height for that day, days since 1 August, day length, mean and maximum air temperature and mean airflow.

Foraging birds were watched for five minute periods and their feeding method and behaviour noted. Numbers of mussels opened and swallowed, and the time taken to do so, were recorded. The length of each mussel was estimated by comparison with the bird's bill (Goss-Custard *et al.* 1987). The biomass of flesh consumed was later calculated from the relationship between mussel length and ash-free-dry-mass (AFDM) obtained from mussel samples (see below). Intake rate was expressed as mg of dry flesh consumed per five minutes of foraging.

All interactions of the focal bird with other birds were recorded, including the age of the opponent, which bird initiated the attack, whether or not a mussel was involved and what the outcome was. With individually marked birds, a bird's dominance was defined as the proportion of interactions that it won, a measure which accurately predicts an individual's position in the linear dominance hierarchy occurring on a mussel bed (Ens & Goss-Custard 1984).

(b) Worm feeders

Intake rates were also measured in Oystercatchers feeding on Ragworms on the mudflats during the autumn in two years (Durell *et al.* 1996b). Matched pairs of juveniles and adults were watched, through a telescope, from the sea wall throughout the tidal cycle. Bird density was measured by estimating the nearest neighbour distance, in bird lengths, of the two nearest birds at the beginning and end of each five minute period and taking the mean. Birds were selected at random and watched for five minutes, the number and length of worms eaten was recorded and all interactions with other birds noted. Worm length was estimated as the fraction of a mean bill length of 75mm for juveniles and 83mm for adults (Durell *et al.* 1993). The reliability of worm length estimation was tested, and a correction factor obtained, by estimating, through a telescope, the length of measured worms held next to the bill of a model Oystercatcher at a distance of 40m (Boates & Goss-Custard 1989). Worm biomass consumed was calculated from the relationship between worm length and ash-free-dry-mass (AFDM) obtained from worm samples. Intake rates were expressed as mg dry flesh consumed per five minutes of foraging.

(5) Prey sampling and measuring

(a) Mussels

Spatial and annual variations in the supply of mussels on a study mussel bed were measured by taking 10 cores (20 x 20 cm) from each 25 x 25m square and measuring all the mussels over 20mm long, the size range taken by Oystercatchers. Mussels were kept in a deep freeze until they were processed. Prey quality was measured by taking a subsample of over 40 mussels from each square. The length of these mussels was measured, all the flesh extracted from the shell and placed in a crucible and dried in an oven at 90 °C until a constant weight was reached (usually after 48 hours). After weighing, the samples were placed in a muffle furnace at a temperature of 550 °C for approximately two hours until all organic matter had been burnt off, and then left in a desiccator to cool before reweighing. The difference in weight between a dry sample and an ashed sample gave us the ash-free-dry-mass (AFDM) for that particular mussel. The relationship obtained between mussel length and AFDM for each sample was used to calculate intake rates (Fig. 2.5). The calculated AFDM for a mussel of 45mm, the mean size taken by Oystercatchers, was used as a measure of the mussel quality in that square.

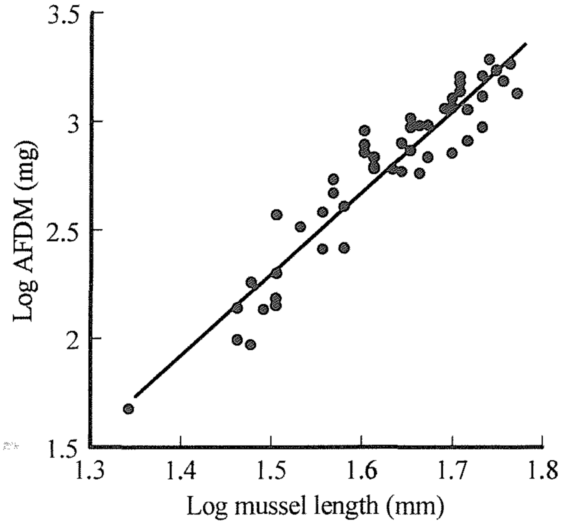


Fig. 2.5 An example of the relationship between log10 mussel length (L) and log10 AFDM (AFDM) from a sample of 50 mussels taken from a square on mussel bed 20. $L = 0.965 + 0.238AFDM$, $R^2 = 89.4$, $P < 0.0001$)

Shell thickness was also measured, using the mussels subsampled from each square. The ventral thickness and dorsal thickness of one valve from each mussel was measured using a micrometer (Fig 2.6). Ventral hammerers select mussels which are thinner on the ventral surface, whilst dorsal hammerers select mussels which are thinner on the dorsal surface (Durell & Goss-Custard 1984).

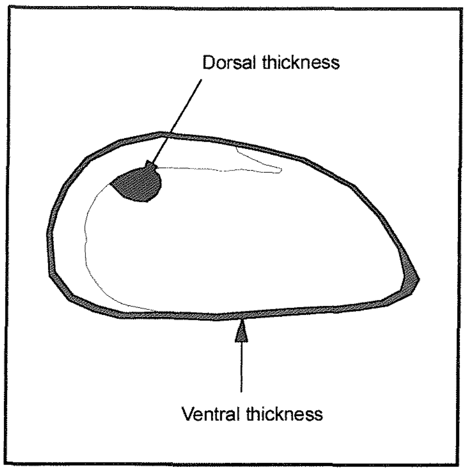


Fig. 2.6 Where dorsal and ventral shell thickness is measured. From Durell & Goss-Custard (1984).

The relationship between mussel length and shell thickness was used to obtain a shell thickness value for a mussel of 45mm for each part of the mussel bed.

(b) Worms

Samples of 35 Ragworms were obtained from mud cores taken at each of the two study sites where observations of feeding Oystercatchers had been made. Worm length was measured when the worms were still alive, then samples were killed by freezing. Worm AFDM was obtained using the same techniques as for mussel flesh. The relationship between worm length and AFDM was used to calculate the intake rate of worm-feeders (Durell *et al.* 1996b).

V. RESULTS

(1) Habitat use

Most of the immature Oystercatchers present on the Exe estuary at the end of the summer fed on the two most preferred mussel beds (Goss-Custard *et al.* 1982b). When the adults arrived back from the breeding grounds at the end of July, the number of mussel feeders increased fourfold (Fig. 2.7). As the mussel feeding population spread out over the estuary, 75% of the young birds on the preferred mussel beds moved away to less preferred mussel beds and to other habitats altogether (Goss-Custard *et al.* 1982b). From September onwards numbers on the mussel beds decreased slightly as some birds moved to feed on the coast and in the fields (Fig. 2.7).

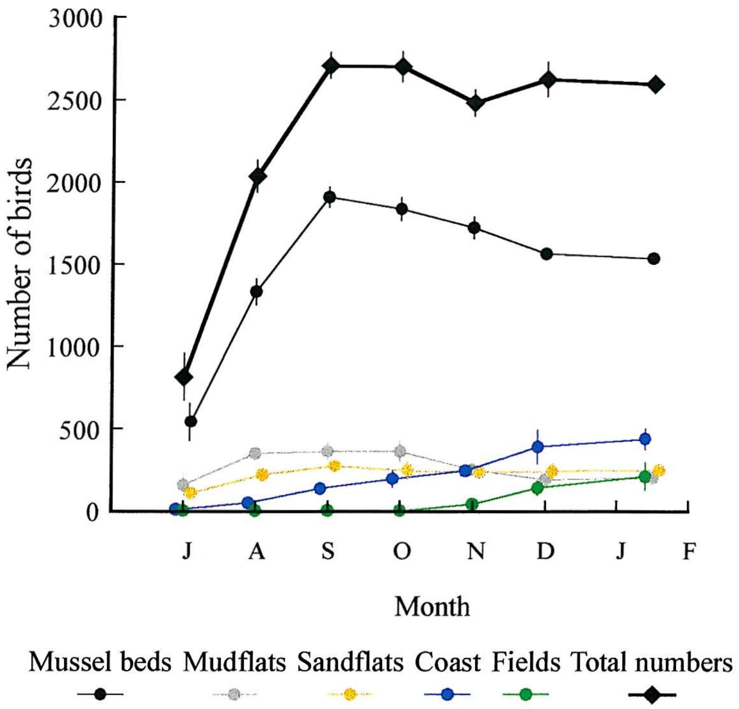


Fig. 2.7 The mean (± 1SE) number of Oystercatchers counted on each habitat throughout the winter. Counts are from the years 1976-1983.

Approximately 400 birds fed on the mudflats in the autumn, decreasing to around 200 birds in late winter as birds increasingly fed in the fields at low water (Goss-Custard & Durell 1983). Numbers of birds on the sandflats, most of which were cockle feeders, remained fairly constant throughout the winter, whilst those feeding on the coast and in the fields gradually increased. Few birds fed on the coast in late summer because of disturbance. No birds fed in the fields in the autumn months.

(2) Age distribution

Approximately 75% of the overwintering population of Oystercatchers on the Exe were adults, 20% immatures and 5% juveniles. The age groups were not evenly distributed between habitats (Goss-Custard *et al.* 1980) (Fig. 2.8). In September, adults formed 78% of birds on the mussel beds and only 41% of birds on the mudflats (Durell & Goss-Custard 1996). In January the proportion of adults on the mussel beds had increased to 88% on the mussel beds and 62% on the mudflats, whilst 55% of those birds feeding in the fields were immatures and juveniles (Fig. 2.8b).

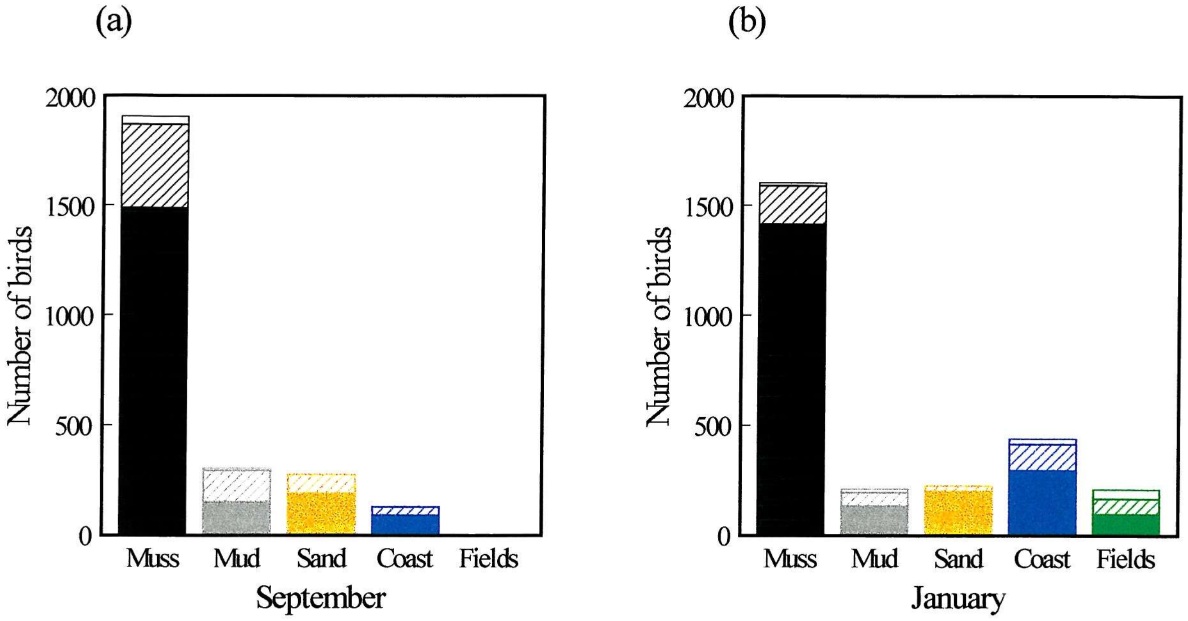


Fig. 2.8 The numbers of adults (solid colour), immatures (diagonal shading) and juveniles (no fill) on each habitat in (a) September and (b) January. Data from Durell & Goss-Custard (1996).

In the summer and autumn, all birds went to the roost at Dawlish Warren at high tide. As the winter progressed, however, increasing numbers of birds were found feeding in the fields at high water (Goss-Custard & Durell 1983). The proportion of young birds seen in flocks in the fields at high water was higher than that found at the main roost (Goss-Custard & Durell 1983). Thus, more young birds than adults fed in the fields, both at low and high water.

(3) Individual behaviour

(a) Site fidelity

Most Oystercatchers that spent one winter on the Exe were likely to return there the next (Goss-Custard *et al.* 1982a). We found no evidence of emigration amongst adult birds; no colour-ringed adults that disappeared from the Exe were seen overwintering elsewhere. We felt confident, therefore, that any adult birds that disappeared had died. However, there was emigration amongst immature birds, with several colour-ringed individuals which disappeared from the Exe being reported overwintering on other estuaries. Immatures that emigrated to other estuaries were last seen on the Exe during early summer, indicating that emigration took place during the summer months.

(b) Diet and feeding method

Data from colour-ringed birds showed that individuals tended to feed on the same habitat, and even the precise locality, for long periods (Goss-Custard *et al.* 1980; Goss-Custard *et al.* 1982c). Many adults returned to the same mussel bed, and even the same part of a mussel bed for many years running (Goss-Custard *et al.* 1982c). Individual specialisation was, therefore, determined to some extent by where a bird fed. However, even within one habitat, individuals consistently selected different prey (Goss-Custard *et al.* 1980). Whilst most birds feeding on mussel beds were taking mussels, some individuals on the same mussel beds specialised in winkles, cockles or worms.

This does not mean that birds were restricted to one prey type only. Many birds, particularly young birds, were seen taking different prey types over both the long and short term. Thus, several young birds that fed on mussels in the autumn switched to worm feeding as the winter progressed (Goss-Custard *et al.* 1980). Birds that fed on the mudflats switched from taking Ragworms to taking clams in late autumn and winter (Boates & Goss-Custard 1989). Some mussel-feeders were seen supplementing their diet in late winter with cockles, clams or worms on upshore areas as the tide advanced and receded (Goss-Custard *et al.* 1996a). Mussel-feeders were also seen feeding on earthworms in the fields at high water (Goss-Custard *et al.* 1996a).

The differential age distribution between habitats was reflected in a change in the diet of individual birds with age (Goss-Custard *et al.* 1980). Most juveniles specialised in worm/clam feeding in their first winter. Some maintained this specialisation into adulthood, but the majority changed to mussel feeding in their second or third winter (Goss-Custard & Durell 1983). Only young birds made long-term changes in feeding specialisation. Once they reached adulthood, no birds were seen to change their feeding specialisation.

Mussel-feeding birds specialised in one of three different feeding methods: ventral hammering, dorsal hammering or stabbing (Goss-Custard *et al.* 1982c). Again, there was a change in feeding method with age. All juvenile mussel-feeders were stabbers and some persisted with this feeding method into adulthood (Goss-Custard & Durell 1987a). However, the majority changed to mussel hammering in their second, third or even fourth winter. No adult mussel-feeders were seen to change their feeding method.

(4) Individual differences in feeding efficiency and susceptibility to interference

(a) Mussel-feeders

Bird densities were high on the preferred mussel beds and aggressive interactions between birds were common (Goss-Custard, Clarke & Durell 1984). Adults were dominant to immatures, and it was the least dominant immatures that left the preferred mussel beds when the adults returned in the autumn. Bird densities were lower on the less preferred mussel beds and aggressive encounters less common (Goss-Custard *et al.* 1984).

In all feeding method groups, intake rates at low bird densities were unrelated to dominance ranking (Goss-Custard & Durell 1988). However, foraging efficiency was related to age (Goss-Custard & Durell 1987a) and to feeding method (Goss-Custard & Durell 1988). In the absence of interference, young birds averaged lower intake rates than adults and stabbers averaged lower intake rates than hammerers.

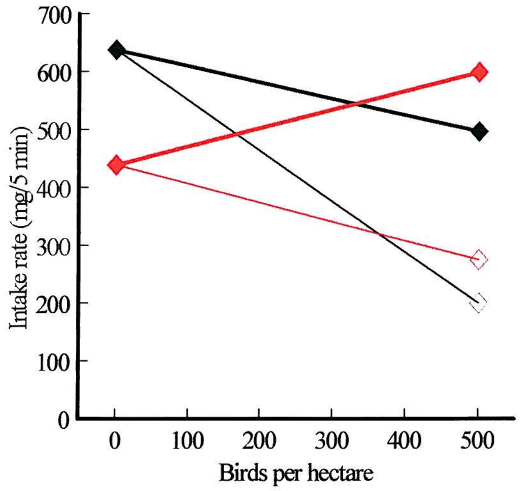


Fig. 2.9 Predicted mean intake rate for the most dominant (solid symbols) and least dominant (open symbols) hammerering (black symbols) and stabbing (red symbols) Oystercatchers over a range of densities of foraging birds. From Goss-Custard & Durell (1988).

An individual's susceptibility to interference was related to its dominance and to its feeding method (Goss-Custard & Durell 1988). Less dominant birds suffered most when bird density was high, whilst the intake rates of the most dominant birds could actually go up with increasing bird density as there were greater opportunities for them to steal mussels from others (Fig. 2.9). Hammerers were more susceptible to interference than stabbers, but this difference was insufficient to override the initial difference in foraging efficiency, so hammerers still averaged higher intake rates than stabbers.

(b) Worm-feeders

Bird densities on the mudflats were much lower than on the mussel beds and aggressive interactions between birds were far less common (Durell *et al.* 1996b). Bird density, as measured by nearest-neighbour distance, had no effect on either adult or juvenile intake rates. Moreover, juvenile worm-feeders averaged the same intake rates as adults. Unlike mussel-feeders, therefore, there were no age differences in foraging efficiency or in susceptibility to interference.

(5) Diet, feeding method and bill-tip shape

Swennen *et al.* (1983) distinguished three main forms of bill tips in Oystercatchers: pointed, chisel-shaped and blunt. The same three categories of bill-tip shape were found on birds on the Exe (Fig. 2.10). Bill-tip measurements confirmed our visual estimation of bill-tip shape (Durell *et al.* 1993).

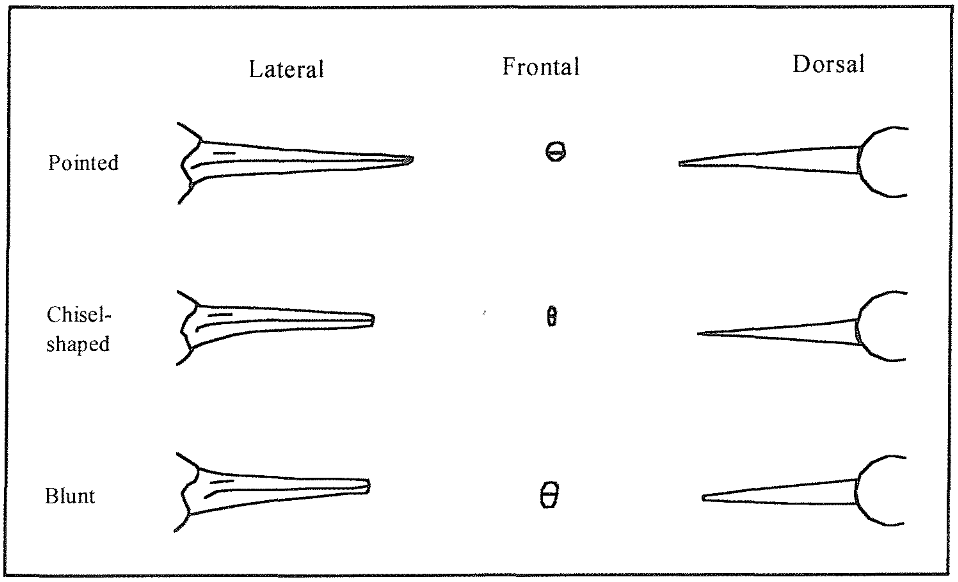


Fig 2.10 Lateral, frontal and dorsal views of the three main bill-tip shapes of Oystercatchers on the Exe estuary. After Swennen *et al.* (1983).

Observations of colour-ringed birds showed that the three different bill-tip shapes corresponded with three different types of feeding (Durell *et al.* 1993). Birds with pointed bills fed on the mudflats on Ragworms and clams, birds with chisel-shaped bill tips were mussel-stabbers and birds with blunt bill-tips were mussel-hammerers (Table 2.1). We could, therefore, use bill-tip shape to establish the diet or feeding method of birds when we ringed them.

Table 2.1 Diet and feeding method of colour-ringed birds according to their bill-tip shape (number of birds). From Durell *et al.* (1993).

	Bill-tip shape		
Diet/feeding method	Pointed	Chisel	Blunt
Worms/clams	32	0	0
Mussel-stabber	3	50	1
Mussel-hammerer (dorsal)	0	0	34
Mussel-hammerer (ventral)	0	0	27
Cockles	0	4	3
Winkles	0	0	1

(6) Sex determination

Oystercatchers have no external characteristics that readily permit sexual identification, even in the hand. Bill measurements have been used successfully for sexing Oystercatchers by discriminant analysis, although different discriminant scores were obtained not only for different species of Oystercatcher (Baker 1974), but also for different populations of the same species (Heppleston & Kerridge 1970). I took external measurements of 77 Oystercatcher corpses, collected from the Exe and sexed by gonad examination, to establish which measurements were the most useful for discriminating between the sexes in our population (Durell *et al.* 1993).

I found no differences between the sexes in body size in terms of wing, keel or tarsus length. There were, however, significant differences in bill measurements. Bill depth halfway down the bill was the best single correlate with sex in juveniles and adults, and bill length was the best single correlate in immatures. Male Oystercatchers tend to have thicker and shorter bills than females. The best combination of measurements for discrimination for all age groups were bill depth and head+bill length. As there was no age difference in the ratio of bill depth to head+bill length, I was able to combine the age groups to increase the sample size (Fig. 2.11). Complete separation of the sexes was not achieved, so the probability of any new individual being male was estimated using the discriminant function shown in Fig. 2.11. When processing live birds, only those birds with a 90% probability of being either sex were assumed to be of that sex.

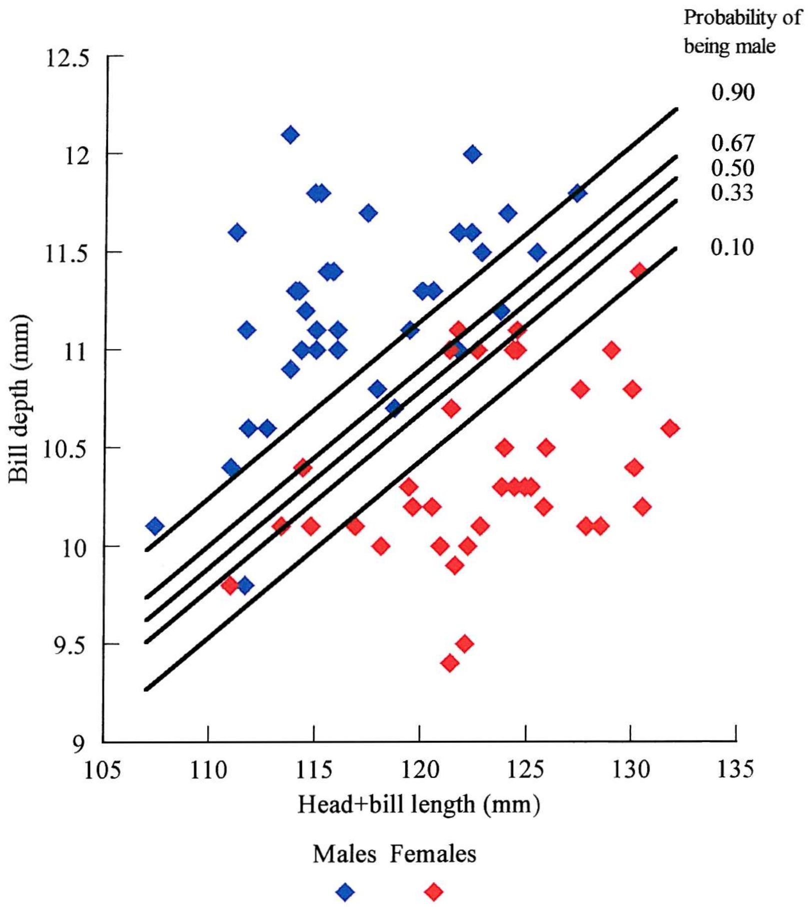


Fig. 2.11 Bill depth and head+bill length of male (blue) and female (red) Oystercatchers, with a contour plot of the probability of being male based on the discriminant function *S*. $S = 0.187 + 6.152$bill depth - 0.555head+bill length. From Durell *et al.* (1993).

(7) Age and sex differences in bill-tip shape

Because diet and feeding method changed with age, the proportion of live birds caught with different bill-tip shapes also changed (Durell *et al.* 1993). Juveniles had mostly chisel-shaped or pointed bills, immature birds had mostly chisel-shaped and blunt bills, whilst the majority of adults had blunt bills (Table 2.2). In other words, juveniles were mainly worm-feeders or mussel-stabbers, immatures were mainly mussel-stabbers and mussel-hammerers, whilst the majority of adults were mussel hammerers.

Table 2.2 The proportion (%) of each bill-tip shape within age groups and sex ratios within bill-tip shapes. P, pointed; Ch, chisel-shaped; Bl, blunt. Data from Durell *et al.* (1993).

	n	%	%Male	%Female
Juveniles				
P	19	46	26	74
Ch	22	54	50	50
Immatures				
P	23	18	26	74
Ch	47	37	55	45
Bl	56	44	88	12
Adults				
P	22	24	27	73
Ch	21	23	52	48
Bl	50	54	88	12

I also found sex differences in bill-tip shape (Table 2.2). In all age groups, over 70% of birds with pointed bills were females, whilst nearly 90% of the birds with blunt bills were males. The sex-ratio in chisel-shaped bills was almost exactly 50:50. This meant that, whilst mussel-stabbers were equally likely to be male or female, the majority of worm/clam feeders were females and the majority of mussel-hammerers were males.

(8) Sex ratios

As the majority of adult Oystercatchers on the Exe were mussel-hammerers, and nearly 90% of mussel-hammerers were male, it seemed likely that males outnumbered females on the estuary as a whole. Using data on bird numbers, age distribution, habitat use and feeding methods, in conjunction with the sex ratios found within birds having particular bill-tip shapes, I estimated the sex ratio of the entire overwintering population (Durell & Goss-Custard 1996). The estimated proportion of males was 36-38% in juveniles, 50-53% in immatures and 66-67% in adults (Table 2.3).

Table 2.3 Estimated numbers, and standard error (*SE*), of each sex to be found on the Exe estuary in September and January. From Durell & Goss-Custard (1996).

	September				January			
	Males	Females	*SE*	%males	Males	Females	*SE*	%males
Adults	1271	637	191	67	1396	733	147	66
Immatures	346	301	38	53	223	227	14	50
Juveniles	47	76	3	38	39	70	6	36
Total	1664	1014	196	62	1658	1030	196	36

The predominance of females amongst juvenile Oystercatchers, and the change in sex ratios with age such that the majority of adults were male, indicated that there was a marked decrease in the proportion of females within each cohort from one year to the next. There are three possible explanations for this. First, female Oystercatchers that initially overwinter on the Exe may be more likely than males to overwinter elsewhere as they get older. Second, there may be disproportionate immigration of young males. Third, females may be subject to higher mortality than males during their immaturity or throughout their lives. All three possibilities were examined using a simple population model (Durell & Goss-Custard 1996).

I found that disproportionate emigration of young females and immigration of young males would have had to be at unrealistically high levels in order to achieve the sex ratio found amongst adults. I also found that young female mortality would have had to be 15% higher than in males to achieve the same results. I suggested, therefore, that both disproportionate emigration/immigration and higher female mortality in young birds must occur, and that there is probably higher female mortality amongst young adults.

VI. MODELLING OYSTERCATCHER POPULATION DYNAMICS

(1) Introduction

In order to understand the behaviour of migratory bird populations, and to predict how they might respond to major habitat loss or change, we built and parameterised models based on the Oystercatcher (Goss-Custard & Durell 1984a, 1990; Goss-Custard *et al.* 1995b,c; Goss-Custard *et al.* 1996c; Durell *et al.* 1997). These models were designed to investigate how density-dependent processes affecting reproduction and mortality may vary in their strength and in their interaction, and how, in combination with density-independent processes occurring throughout the year, they determine the population size and its response to habitat change.

(2) Density-dependent processes

One of the main sources of density-dependence in our population dynamics models is competition for breeding territories in the summer. As the number of potential breeding pairs increases, an increasing proportion either fails to obtain a territory, or breeds in poorer quality habitats. In the model, below a threshold density of breeding pairs (c_T), all potential breeders find a territory and breed (Fig. 2.12a). Above this threshold, the possibility that territories can be compressed as competition intensifies was incorporated by expressing the proportion of birds prevented from breeding as a k-value (Varley *et al.* 1973), and by varying the slope (b_T) of its relationship with the logarithm of the total numbers of birds available to breed (Fig. 2.12a). When $b_T < 1$, territories can be compressed further so that more pairs breed as the number of potential breeding pairs increases, even though an increasingly large proportion is excluded. When $b_T = 1$, territories cannot be compressed so that a constant number breed, irrespective of any further increase in numbers attempting to do so. As very few estimates are available for the parameters b_T and c_T, we used a range of values in all our simulations. We also thought it likely that, in reality, the shape of the relationship would be curvilinear, with b_T gradually increasing as the number of potential breeders increases (Klomp 1980; Goss-Custard 1993). We therefore explored the effect of varying the function shape.

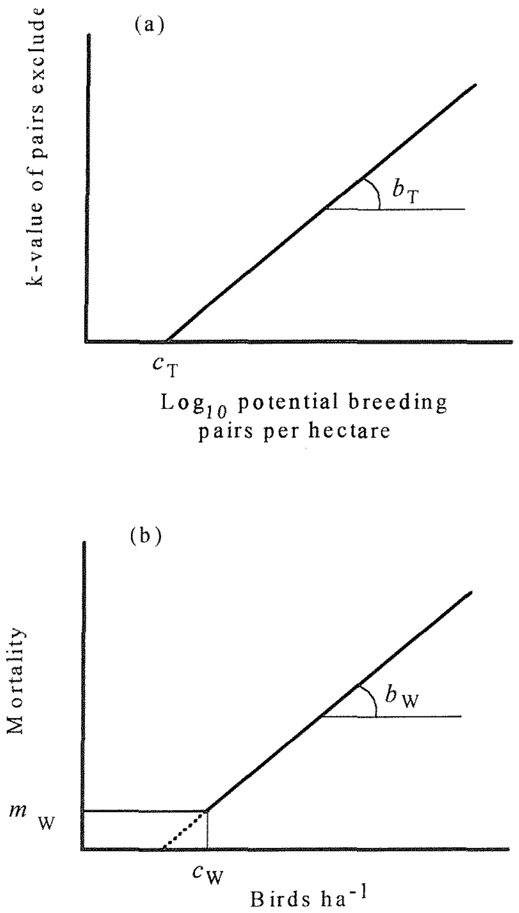


Fig. 2.12. How density dependence is represented in the model. (a) Competition for breeding territories. Below the threshold density of c_T, all pairs obtain territories. Above c_T, the proportion of potential breeding pairs failing to obtain a territory, expressed as a k-value, increases at a rate b_T. (b) Competition for winter food supplies. Below the threshold density of c_W, overwintering birds die at the density-independent rate m_W. Once densities exceed c_W, the probability of dying increases at a rate of b_W for every bird per hectare increase in total bird density. From Durell *et al.* (1997).

The other main source of density-dependence was density-dependent winter mortality (Fig. 2.12b). Below a certain bird density (c_W), there was no competition for food resources, so that any increase in bird density did not affect the density-independent proportion of birds (m_W) that die. Eventually, however, a point is reached (c_W), where mortality begins to increase and so becomes density-dependent. From then on, mortality increases at a rate of b_W for every unit increase in bird density. We used a range of values of c_W and b_W in all simulations. We also explored the effect of making the shape of b_W curvilinear. In particular, we investigated how the values of c_W and b_W affected the impact of winter habitat loss on the equilibrium population size of the global population of the European subspecies of the Oystercatcher *Haematopus ostralegus ostralegus* (Goss-Custard *et al.* 1995c).

(3) Parameter values and simulation procedure

Mean parameter values were obtained from a review of Oystercatcher field studies (Goss-Custard *et al.* 1995b). These were age of first breeding (four years old), clutch-size, hatchling and fledgling mortality, mortality rates of breeding and non-breeding birds in summer and mortality rates of immatures and adults in the winter. All these values were assumed to be density-independent and, in the first models, fluctuated at random with a range of values. Later models also introduced density-dependent fledgling mortality.

Table 2.4 Parameter values used in the European Oystercatcher population model. Apart from clutch size, values are for mean annual mortality. Standard deviations (SD) are the same across all four subpopulations and refer to annual variation. From Goss-Custard *et al.* (1995b)

	Atlantic		Continental		SD
	Coastal	Inland	Coastal	Inland	
Clutch size	2.604	2.750	2.840	2.986	0.0062
Egg mortality	0.682	0.598	0.518	0.435	0.0040
Chick mortality	0.445	0.445	0.796	0.796	0.0046
1st & 2nd winter	0.200 above adult rate				
3rd & 4th winter	Same as adult rate				
Adult winter	0.091	0.091	0.039	0.039	0.0025
Additional winter	0	0	0.07-0.15	0.07-0.15	0
Adult summer	0.010	0.010	0.010	0.010	0
2nd-4th summer	0	0	0	0	0

In the European population model, the population was divided into the Atlantic and Continental regions (Fig. 2.13), largely because of the difference in winter climate and because there is little interchange of birds between them (Hulscher *et al.* 1996b). A further subdivision was made between those birds which bred on the coast or inland, with all birds from one region overwintering together on the coast. Table 2.4 gives the parameter values used in this model for each of the four subpopulations of breeding birds. These values were mean annual values which were varied annually at random within ± 2 SD of the mean. We also introduced an effect of severe winter weather, where additional mortality was varied at random within the range of 1-15%.

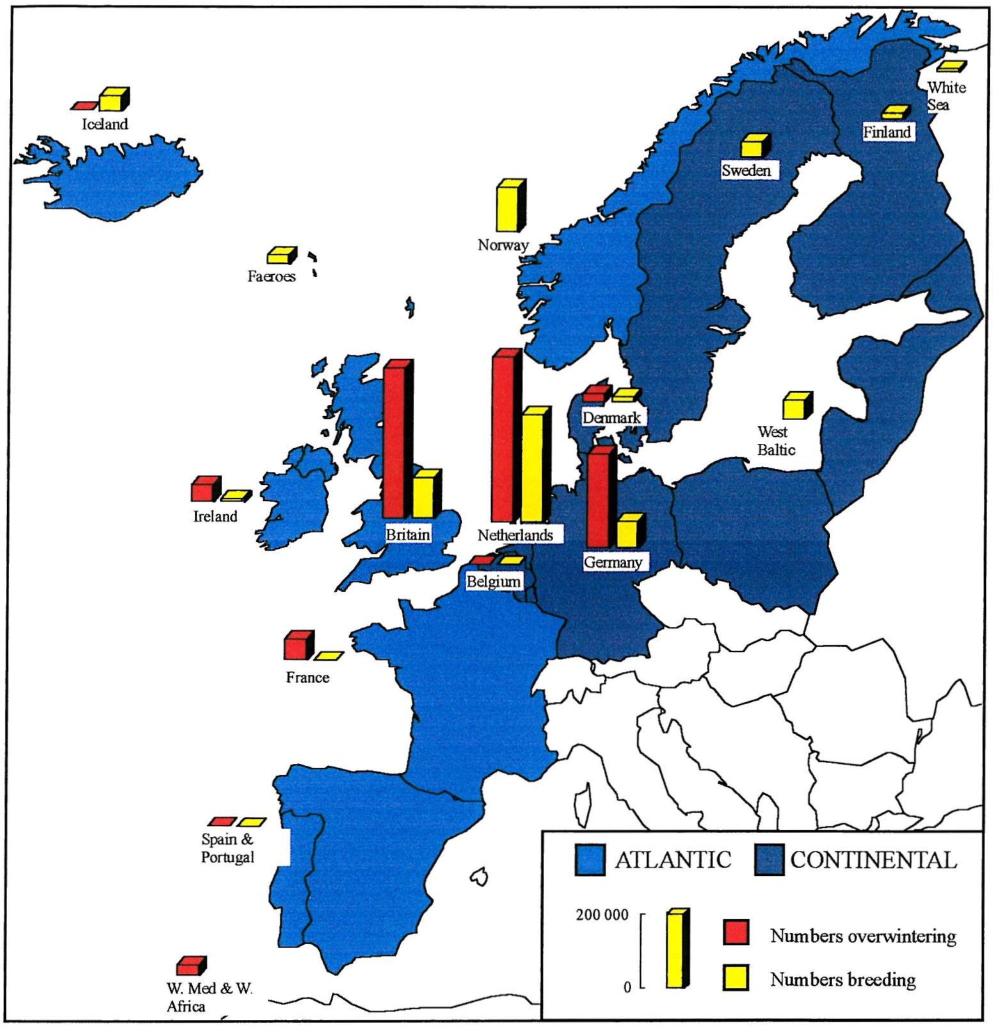


Fig 2.13. The division into Atlantic and Continental regions used in the European population model, with the numbers of Oystercatchers recorded as breeding and wintering in each country shown as histograms. From Goss-Custard *et al.* (1996c).

Simulations were run until the equilibrium population size had been reached, i.e. there was no trend in numbers either up or down, and this usually happened within 100 years. Habitat loss simulations were run for 1000 years to ensure stability had been reached, and output averaged over the final 100 years. After the first run, winter habitat was reduced by 10% in each subsequent run until 90 % of the winter habitat had been removed.

(4) Factors affecting the equilibrium population size

Equilibrium population size was critically affected by how compressible territories were during the breeding season (Goss-Custard & Durell 1990; Goss-Custard *et al.* 1995b; Goss-Custard *et al.* 1996c). It was also greatly influenced by the threshold (c_W) and the strength (b_W) of density-dependent winter mortality. However, it was not just density-dependent factors which influenced population size. All populations were sensitive to the production rate of fledglings, the survival of young birds during their first and second winters and to the adult mortality rate (Goss-Custard *et al.* 1996c). Population size was particularly sensitive to these density-independent rates at lower values of b_T, i.e. when the strength of regulation during the breeding season was weak. In all simulations we used a range of values for b_W and b_T.

(5) Responses to winter habitat loss

We first examined the affect of winter habitat loss in terms of increasing the mortality of juveniles only (Goss-Custard & Durell 1990). Even when regulation during the breeding season was strong, the equilibrium population size was greatly reduced when only juvenile mortality rates increased in winter as a result of an increase in bird density.

With the European model, we assumed that birds of all ages would be affected by increasing bird densities (Goss-Custard *et al.* 1995b). Simulations over a range of probable parameter values showed that the density at which winter mortality becomes density-dependent (c_W) simply determined the point at which population size was affected as habitat was gradually removed. Importantly, habitat loss began to have an effect earlier in the more fluctuating Continental population (which had the additional mortalities from severe winter weather) because winter densities began periodically to exceed c_W earlier in the process of habitat removal. Winter habitat loss would, therefore, be expected to affect population size sooner in populations that fluctuate widely than in ones that do not.

Once enough habitat had been lost to increase bird density above c_W, the magnitude of the impact then depended on the slope (b_W) of the density-dependent winter mortality function (Goss-Custard *et al.* 1995b). The reduction in population size increased sharply as b_W increased (Fig. 2.14a). The percentage reduction in population size never exceeded the percentage reduction in habitat loss, but they were roughly equivalent at the higher values of b_W (Fig. 2.14b).

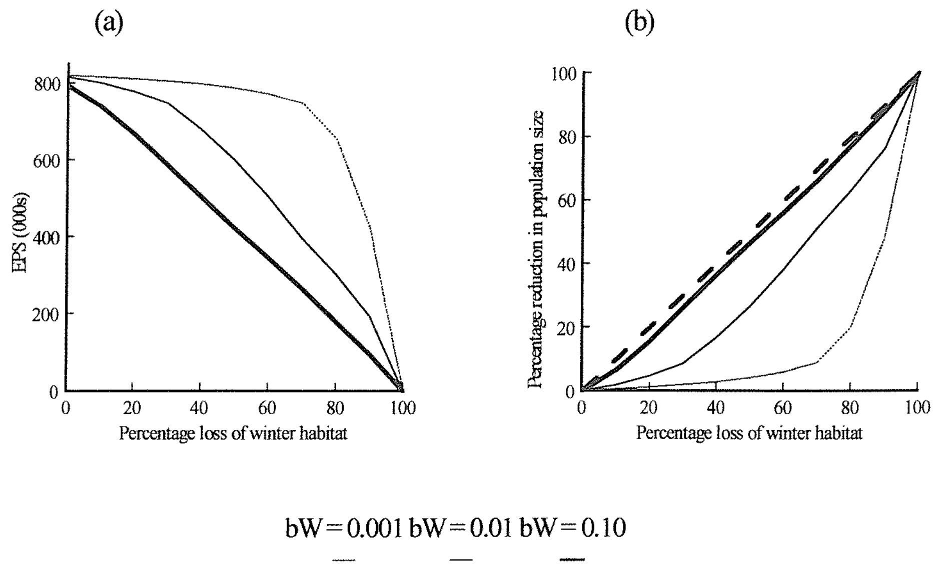


Fig. 2.14 The effect of winter habitat loss on the European Oystercatcher population as predicted by the model. (a) Equilibrium population size (EPS) and (b) percentage reduction in population size following different percentage reductions in winter area at a given value of b_W. The diagonal dashed line in (b) represents proportionality, where a given percentage reduction in habitat results in the same percentage reduction in population size. In all cases $b_T = 0.5$ and $c_W = 1.0$.

Further simulations were run to test how sensitive these conclusions were to the values of other model parameters. Varying the strength and the shape of b_T, the slope representing competition for breeding territories, made little difference to our results (Goss-Custard *et al.* 1995b). Similarly, changing the winter density-dependent function from linear to curvilinear had little effect, although if the curve was made strongly concave, population loss was delayed, as initial habitat loss had very little effect (Goss-Custard *et al.* 1996c). Introducing density-dependent fledging success greatly reduced the predicted effects because the elevated winter mortalities resulting from habitat loss were partly compensated by the increased fledgling production at low breeding densities (Goss-Custard *et al.* 1996c). Our main conclusion was that only in a very limited set of circumstances did the effect of removing winter habitat of average quality result in a proportional reduction in population size. At all other times, the reduction in population size was 'subproportional'.

(6) Removal of best and worst habitats

However, there were circumstances when the reduction in population size was 'supraproportional'. All the simulations above used the same density-dependent winter mortality function throughout the various stages of habitat loss, as if habitat of average quality was removed at every stage. In reality, the first habitat to be removed may be of above or below average quality. This would mean that the shape and the parameter values of the density-dependent function will change as habitat loss proceeds. In order to explore this idea, we parameterised a model for the Exe estuary population. We investigated how the density-dependent function would change if habitat of above or below quality was removed by using an individuals-based, physiologically-structured game theoretic model of Oystercatchers feeding on the mussel beds (Goss-Custard *et al.* 1996d). In this model, the area of the mussel beds was gradually reduced in steps of 10%, starting with either the best or worst beds. Unsurprisingly, the predicted density-dependent mortality functions were much steeper when the better areas were removed first (Goss-Custard *et al.* 1996c).

When the density-dependent function from the removal of best habitat was used in the population model, the reduction in population size occured much sooner than when average habitat had been removed (Fig. 2.15). In fact, the effects of habitat loss became 'supraproportional'. In contrast, removing habitat of below average quality had much less effect on population size and was 'subproportional' throughout (Fig. 2.15).

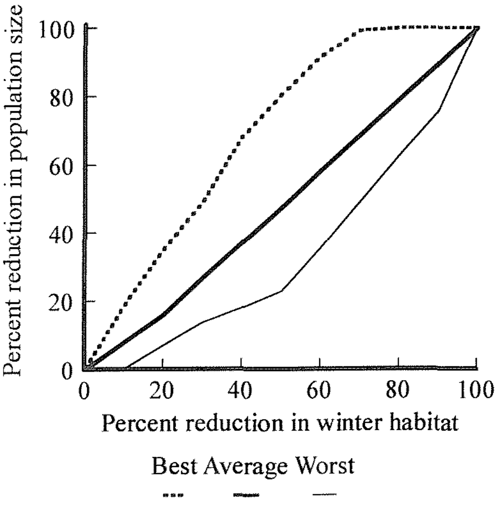
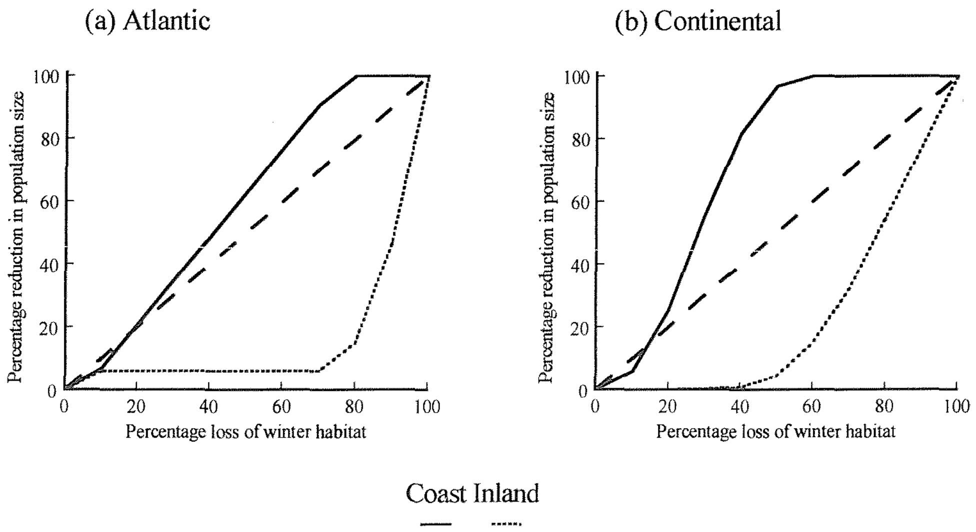


Fig. 2.15 The predicted effect of successively removing 10% of the best, worst or average mussel beds on population size. From Goss-Custard *et al.* (1996c).

(7) Inland and coastal breeding subpopulations

In the European Oystercatcher model, breeding parameters were different for inland and coastal birds (Table 2.4). Both continental and atlantic inland breeding birds have higher reproductive rates than those breeding on the coast (Goss-Custard *et al.* 1995b). As a result, inland subpopulations were intially less affected by winter habitat loss than the coastal subpopulations that they overwintered with (Fig. 2.16). Again, the percentage reduction in population size of coastal breeding birds was 'supraproportional'.


(a) Atlantic

(b) Continental

Fig. 2.16 The effect of removing winter habitat on the size of the coastal and inland breeding populations that share it. (a) Atlantic population and (b) Continental population. The diagonal dashed line represents proportionality. From Goss-Custard *et al.* (1996c).

We were not sure what caused this difference in response between subpopulations, and I investigated the phenomenon using a simplified version of the population model (Durell *et al.* 1997). This model contained either two or four subpopulations overwintering in the same place. As in the original model, density-dependence arose because of competition for breeding territories in summer and for food in winter. Within each subpopulation, pairs that bred produced the same number of fledged young each year and, as with all rates used in this model, there was no annual variation in fledgling production. In all the simulations, fledgling production in the least productive sub-population was set at 0.40 fledglings per breeding pair. In the other subpopulations, the constant fledgling production was set at between 0.41 and 0.70 per pair. Once fledged, birds died only in winter and they start breeding at the age of five.

When each subpopulation was given the same size of breeding area, equilibrium was reached at different numbers of birds in each subpopulation because of the different fledgling production rates. In case this difference in initial equilibrium population size affected subpopulation response to winter habitat loss, I also ran simulations in which the starting equilibrium subpopulation sizes were the same. This was achieved by modifying the breeding area available for each subpopulation.

Whether the initial equilibrium population sizes were the same or different, all subpopulations were affected in the same way up to a certain point (Fig. 2.17a). Beyond this point, which I called the 'divergence point', the lines of proportional population loss diverged. The reduction in size of the slowest breeding subpopulation became 'supraproportional', whilst the reduction in size of the fastest breeding subpopulation remained 'subproportional'. When subpopulations started with the same equilibrium population size, the divergence point was always at 50 % habitat loss. When subpopulations had the same breeding area, and different starting population size, the divergence point occurred at lower and lower proportions of habitat loss as the difference between subpopulations in their reproductive rate increased.

I found that the divergence point was also the point when, for the first time, all the potential breeders in the slowest breeding subpopulation were able to obtain a breeding territory (Fig. 2.17b). Before this point, the numbers of breeding pairs in all subpopulations had declined in parallel because all were equally affected by increasing competition on the breeding grounds (Fig. 2.17c).

In all subpopulations there was a pool of non-breeding adults available to replace the breeding birds that died in winter. However, once the subpopulation size was reduced to the level where all adults were breeding, production was insufficient to replace breeders that died. At the same time, winter mortality rates remained high as winter densities were sustained by birds from other subpopulations. Further habitat loss after this critical point, therefore, resulted in a sharp decrease in the number of breeding pairs and in the total reproductive output of the least productive population. This rapid decline in one subpopulation temporarily relieved the pressure in winter on the other subpopulations, so the rate of their population decline slowed down. As winter habitat continued to be lost, however, increasing winter mortality (Fig 2.17d) eventually reduced the numbers in these subpopulations, in their turn, to the point at which all adults were breeding. As each subpopulation reached this point, its population decline accelerated as it had for the least productive subpopulation.

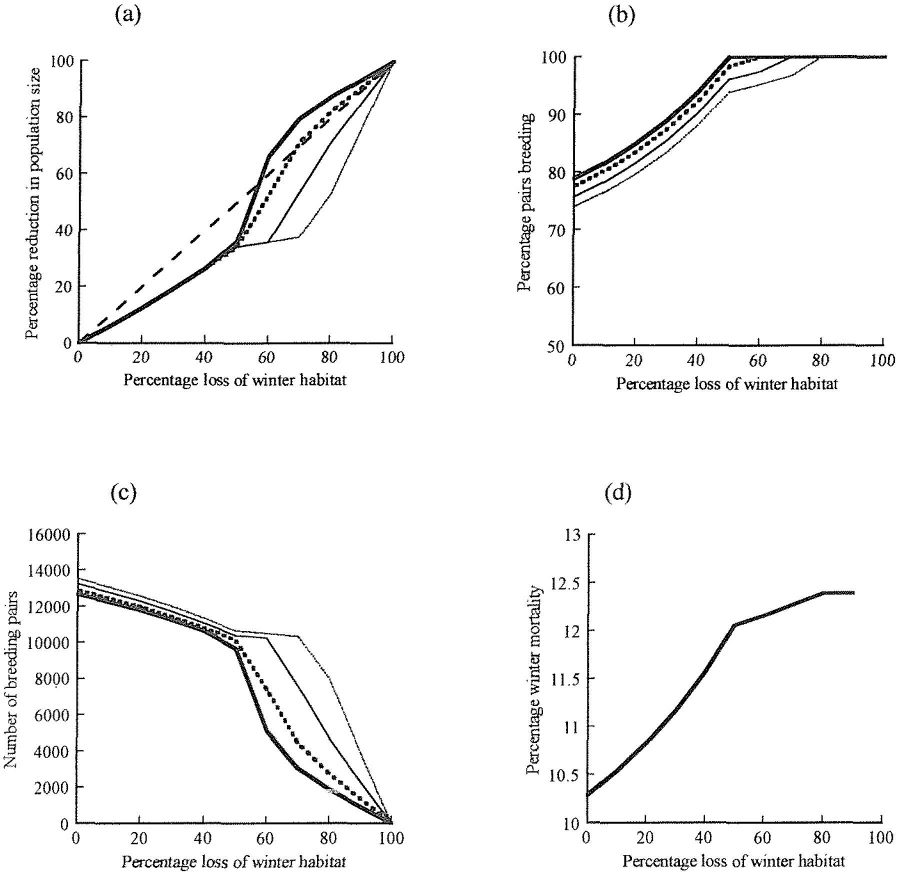


Fig. 2.17 How the divergence point between four subpopulations with different reproductive rates (0.40, 0.41, 0.42 and 0.43 fledglings per breeding pair) was determined. All graphs show the effect on each subpopulation of increasing habitat loss. (a) The proportionate reduction in population size; (b) the percentage of potential breeding pairs that breed; (c) the numbers of breeding pairs and (d) the rate of winter mortality. $b_T = 0.5$, $b_W = 0.05$. From Durell *et al.* (1997).

I found that, for a given rate of fledgling production, the point at which all adults were breeding always occurred at the same rate of winter mortality, i.e. when the mortality rate balanced the recruitment rate. This meant that any change in the overall rate of winter mortality, such as increasing the value of the base density-independent mortality rate or the slope b_W, caused the divergence point to occur at lower amounts of winter habitat loss.

I concluded that, when more than one population of a migratory animal is wintering in the same area, there are circumstances in which differences in their breeding output may give one subpopulation an advantage over another when winter habitat is lost. I considered that there were two main implications from this for conservation management. First, the decline in some, but other, local breeding subpopulations may not be due to a deterioration in their breeding habitat, but to a reduction in quality of their shared wintering grounds. In these circumstances, looking for local causes of subpopulation decline could be fruitless. Second, at a global scale, the early cumulative effects of winter habitat loss on population size may be difficult to detect across a species range because of the difficulty of estimating population size at the scale required. In contrast, it is relatively straightforward to monitor population size in a sample of breeding areas amongst which the *per capita* rate of reproduction differs. My results suggested that conservationists should pay special attention to monitoring breeding numbers in local subpopulations with below average rates of reproduction because it is here that the first signs of the effect of winter habitat loss would be expected to show up.

Chapter 3: BODY CONDITION AND SURVIVAL IN OYSTERCATCHERS

This chapter has been published as:
Durell, S.E.A. le V. dit, Goss-Custard, J.D., Caldow, R.W.G., Malcolm, H.M. & Osborn, D. (2001) Sex, diet and feeding method-related differences in body condition in the Oystercatcher *Haematopus ostralegus. Ibis* **143**, 107-119.

I. INTRODUCTION

The benefit to birds of maintaining high fat reserves during the non-breeding season has long been recognised, particularly as an insurance against periods of high energy requirements but low food availability (Newton 1969; King 1972; Blem 1976; Owen & Cook 1977; Dugan *et al.* 1981; Davidson 1981, 1982: Davidson *et al.* 1986b; Blem 1990; Castro *et al.* 1992) and, in the case of migratory birds, as a means of fuelling migration back to the breeding grounds in the spring (Blem 1976; King 1972; Dare 1977; Pienkowski *et al.* 1979; Blem 1990). Low weights in some birds, therefore, may reflect an inability to accumulate the same amount of reserves as others. However, as there may be mass-dependent costs associated with avian fat storage (Lima 1986; McNamara & Houston 1987, 1990; Witter & Cuthill 1993; Gosler *et al.* 1995), birds may vary in their fat storage strategy. Differences between individuals may, therefore, reflect either (i) differing abilities to achieve the same target weight or (ii) differing target weights according to their individual needs. For example, female Oystercatchers tend to be heavier than males (Cramp & Simmons 1983; Dare 1977). This weight difference is not due to any difference in body size (Cramp & Simmons 1983; Dare 1977; Durell, *et al.*1993; Zwarts *et al.* 1996b), but to a higher fat loading in females (Zwarts *et al.* 1996b). Are females heavier because they are more efficient feeders than males due to differences in their feeding apparatus (females have longer, thinner bills than males) or, alternatively, do females have a particular reason for maintaining higher levels of reserves?

Zwarts *et al.* (1996b) used body weight, standardized for body size by wing length, in order to investigate age and sex differences in Oystercatcher body condition throughout the year. In this study, we also used body weight and wing length to measure body condition in

Oystercatchers overwintering on the Exe estuary, south-west England. Oystercatchers are well known for their individual specialization on different diets and feeding techniques (Dare & Mercer 1973; Dare 1977; Goss-Custard & Durell 1983; Goss-Custard & Durell 1987b; Durell *et al.* 1993), and we wanted to explore the possible fitness consequences of such specializations. Having found differences in body condition, we investigated whether they were due to some birds failing to reach a common target weight, or to individual differences in fat storage strategy.

II. METHODS

(1) Oystercatcher corpses

Over the period January 1986 to February 1991, 63 Oystercatcher corpses were collected from the Exe estuary (Durell *et al.* 1993). We used these corpses to determine which measurements would be most useful for measuring body condition in live birds. Ten corpses were used to test the repeatability, within and between two observers, of three measurements of structural size: tarsus length, keel length and wing length (Durell *et al.* 1993). The same corpses were used to test the accuracy and repeatability of measuring the thickness of the pectoral muscles at a fixed point at the anterior end of the sternum by using an ultrasound flaw detector (Sears 1988) and comparing these measurements with those obtained by insertion of a hypodermic needle at the same place.

All corpses were weighed when they were collected and aged as juvenile (in their first year), immature (second to approximately fourth year) or adult (Prater *et al.* 1977). Tarsus length, keel length and wing length were measured and sex was established by gonad examination. We tested the use of thickness of the pectoral muscles as a method of measuring a bird's protein reserves by measuring this thickness at a set point using ultrasound. We also scored skin colour at the same fixed point to obtain an index of subcutaneous fat as follows: 1: blue, 2: yellowy blue, 3: bluey yellow, 4: yellow. The protein and fat content of the pectoral muscles were then measured by dissecting out the pectoral and supracoracoides muscles on one side. These were weighed, dried to constant weight and the fat removed using Soxhlet extraction

(Horwitz 1965, Jones & Ward 1976) to obtain the lean dry muscle weight. The total fat content of the muscles (superficial and interstitial) was measured as the difference between the dry and lean dry muscle weights. The total fat content of the flight muscles has been shown to provide a good estimate of total body fat in Oystercatchers (Zwarts *et al.* 1996b).

(2) Live birds

All the birds were caught at the high water roost at Dawlish Warren (50° 36' N, 3° 25' W) and almost all by cannon net. As cannon net catches were always made at the same stage of the spring/neap tidal cycle and always at the highest point of the daily tidal cycle, all birds would have been caught at approximately the same stage in their daily feeding routine. In other words, all the birds would have stopped feeding at least two hours before they were caught. As birds continue to lose weight after capture (Wilson & Davidson 1982; Davidson 1983; Zwarts *et al.* 1996b), we recorded time of capture and time of weighing.

From 1989 onwards, additional measurements were made when ringing. These were (a) head+bill length and bill depth, to determine a bird's sex by discriminant analysis and (b) bill tip width and bill tip depth, to establish a bird's diet and feeding method (Durell *et al.* 1993). Durell *et al.* (1993) established that the majority of birds with blunt bills on the Exe were mussel *Mytilus edulis* hammerers, the majority of birds with chisel-shaped bills were mussel stabbers and birds with pointed bills fed on the mudflats on worms and clams *Scrobicularia plana*.

(3) Colour-ringed birds

As the winter progresses, Oystercatchers increasingly supplement their low water diets by feeding on upshore areas on the receding and advancing tides, and in fields at high water (Goss-Custard *et al.* 1996a, Hulscher 1996, Caldow *et al.* 1999). This use of supplementary feeding areas is an indication that birds are failing to meet their energy intake requirements on their low water feeding grounds (Goss-Custard *et al.* 1996a). Caldow *et al.* (1999) have shown that individual variation in the use of supplementary feeding is related to individual variation in foraging efficiency, i.e. birds with lower intake rates at low water are more likely to be seen using supplementary feeding areas. Caldow *et al.* (1999) only analysed data on mussel-feeders so, in this study, we examined the use of supplementary feeding by both mussel-feeding and worm/clam-feeding colour-ringed Oystercatchers.

Extensive colour-ring searches were made at low and high water from 1976/77 to 1983/84 and from 1988/89 until 1990/91. Data on the death and disappearance of colour-ringed birds during these 11 years were used to estimate rates of mortality in adults (Durell *et al.* 2000). In this study, we analysed the data for all age groups in order to investigate differences in mortality between the sexes and between birds with different diets and feeding methods.

In 1989/90 and 1990/91, intake rates, dominance and feeding efficiency of colour-ringed birds were measured on the mussel beds at low water (for methods see Caldow *et al.* 1999). Most of these birds were of known sex and, in this study, we analysed the data to determine whether any difference between the sexes in body condition was associated with either their dominance or their feeding efficiency.

III. RESULTS

(1) Choice of measurements in corpses

Of the three external structural size measurements (tarsus length, keel length and wing length), tarsus length had the highest variability within observers and keel length the poorest match between observers (Table 3.1). Wing length proved to be the most consistent measure, both within and between observers. Wing length is a standard measurement taken by bird ringers and has been considered by many workers to be an accurate indicator of structural size in several bird species (Ward 1969; Mascher & Marcstrom 1976; Owen & Cook 1977; Pienkowski, Lloyd & Minton 1979; Davidson 1983; Gosler *et al.* 1998), including Oystercatchers (Zwarts 1996b). We decided, therefore, to use wing length to represent and control for body size in all analyses.

Consistent repeat measurements of the thickness of the pectoral muscles were obtained by using an ultrasound flaw detector. Indeed, this method was less variable than the method using a hypodermic needle, which was used to verify the ultrasound readings (Table 3.1).

Table 3.1. Comparison of variability within observers of repeat measurements made on Oystercatcher corpses and comparison between observers of mean values obtained. The first two columns show, for each observer, the average variance (as a percent of the mean) of three repeat measurements of 10 corpses. The last two columns show the 95% confidence intervals for the intercept and slope of regressions of observer 1 means against observer 2 means for each bird (n = 10).

	Average variance within observers (%)		Regression of observer 1 against observer 2 (95% CI)	
Measurement	Observer 1	Observer 2	Intercept	Slope
Tarsus length	1.99	1.85	-10.2: 21.6	0.56: 1.22
Keel length	0.57	1.44	- 8.9: 53.9	0.24: 1.14
Wing length	0.18	0.91	-17.5: 26.5	0.91: 1.07
Pectoral: needle	13.15	18.13	-12.0: 17.4	-0.04: 1.80
Pectoral: ultrasound	3.14	1.90	- 5.2: 5.8	0.69: 1.27

Lean dry pectoral muscle weight was significantly correlated with thickness of the pectoral muscles, as measured by ultrasound, ($r_{61} = 0.50$, $P < 0.0001$) (Fig. 3.1a), but also with total body weight ($r_{59} = 0.72$, $P < 0.0001$) (Fig. 3.1b). There were no statistically significant differences between age groups in the slopes of either of these relationships, but there were slight differences in the intercept: for a given muscle thickness or total body weight, lean dry muscle weight increased with age. Allowing for age, the relationship between lean dry muscle weight and total body weight had a higher value of r (0.564) than that between lean dry muscle weight and muscle thickness (0.374). Total fat (superficial and interstitial) extracted from the pectoral muscles was significantly correlated with both fat score ($r_{61} = 0.62$, $P < 0.0001$) (Fig.3. 1c) and total body weight ($r_{59} = 0.47$, $P < 0.0001$) (Fig. 3.1d). There were no statistically significant differences between age groups in either of these relationships. As total body weight is a single measurement which was as good a predictor of both protein and fat reserves, and because weight is a standard measurement made when ringing birds, we decided that total body weight was the most useful measure of body condition in live birds.

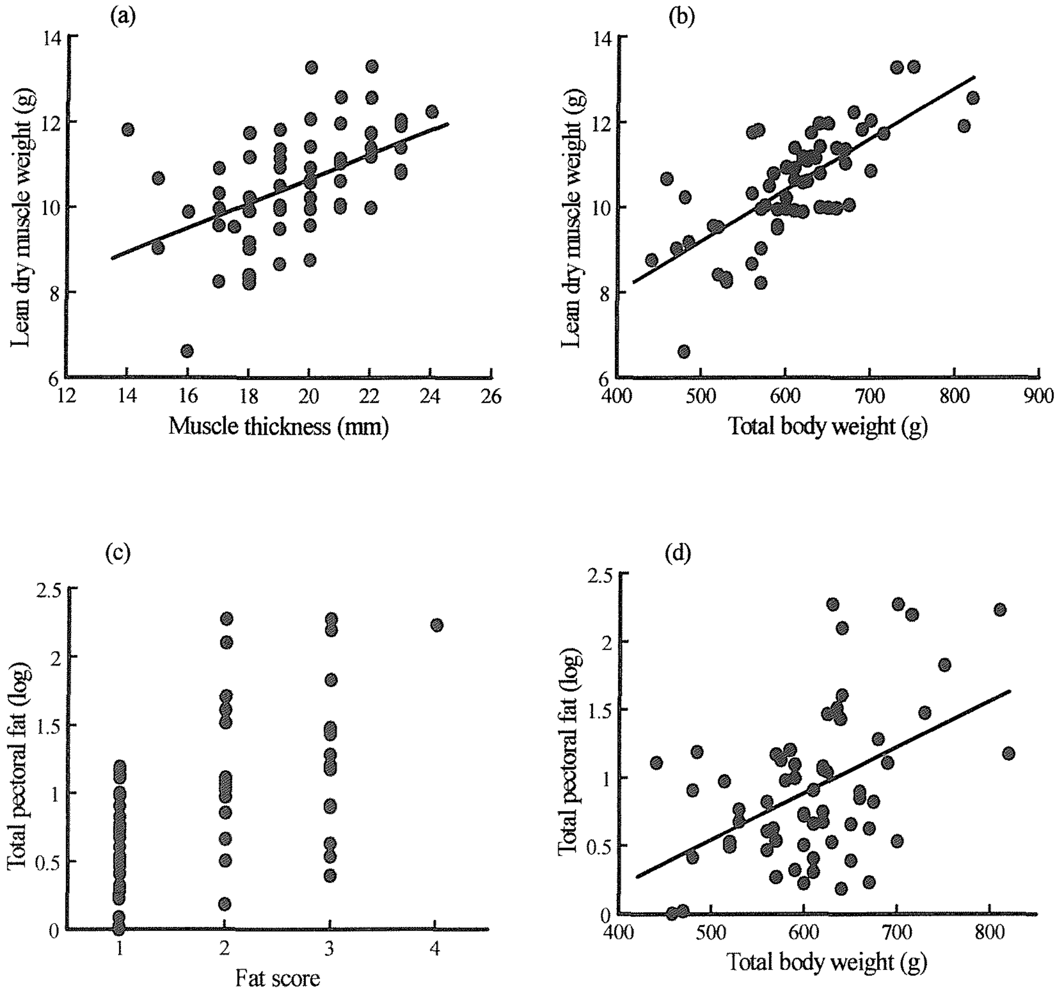


Fig. 3.1. The relationship in Oystercatchers between (a) the lean dry weight of the pectoral muscles and muscle thickness as measured by ultrasound ($y = 4.93 + 0.286x$, $R^2 = 0.24$), (b) lean dry muscle weight and total body weight ($y = 3.20 + 0.012x$, $R^2 = 0.52$), (c) total pectoral fat ($\log_e$) and fat score (adjusted R^2 from oneway ANOVA = 0.37) and (d) total pectoral fat ($\log_e$) and total body weight ($y = -1.15 + 0.003x$, $R^2 = 0.22$).

(2) Body condition in live birds

(a) Wing lengths

As found elsewhere (Dare 1977; Zwarts *et al.* 1996c), the mean wing lengths of Oystercatchers on the Exe increased with age. Wing lengths were significantly longer in adults (mean = 265 mm, sd = 6.4) than in immatures (mean = 262 mm, sd = 6.6) ($t_{1223} = 8.25$, $P < 0.0001$) and significantly longer in immatures than in juveniles (mean = 257 mm, sd = 5.9) (t_{610}

= 9.44, $P < 0.0001$). In the subset of birds that were sexed by discriminant analysis, there was no significant difference in wing lengths between the sexes in any age group (Table 3.2).

Table 3.2. Mean wing lengths (mm), with standard error (SE) for Oystercatchers of each age group sexed by discriminant analysis. t = Student's t-test of male against female within age groups.

	Males			Females				
Age	n	mean	SE	n	mean	SE	t	*P*
Adults	118	263	1.0	41	262	1.2	0.56	NS
Immatures	64	261	0.8	53	261	0.9	0.57	NS
Juveniles	18	255	1.6	19	254	1.5	0.52	NS

(b) Body weights

We controlled for differences in body size by using the residuals of ($\log_e$) body weight regressed against ($\log_e$) wing length. Differences in mean residuals between age groups through the winter are shown in Fig. 3.2. Adults and immatures had higher reserves than juveniles throughout most the overwintering season (Fig. 3.2). All age groups lost weight in the autumn and then increased weight in early winter. Adults continued to increase in weight throughout the winter, but immatures and juveniles did not. The relationship between ($\log_e$) body weight and ($\log_e$) wing length was thus different according to age and month, but was always linear: an example is shown in Figure 3.3.

Using the residual, for each bird, of the relationship between ($\log_e$) body weight and ($\log_e$) wing length for each age and month, weight loss followed the same non-linear curve for all ages in all months (Fig. 3.4). When expressed as a quadratic relationship, the resulting curve gave an unrealistic increase in weight shortly after capture, so we chose to use the cubic polynomial function shown in Figure 3.4, which described an initial plateau of no weight loss.

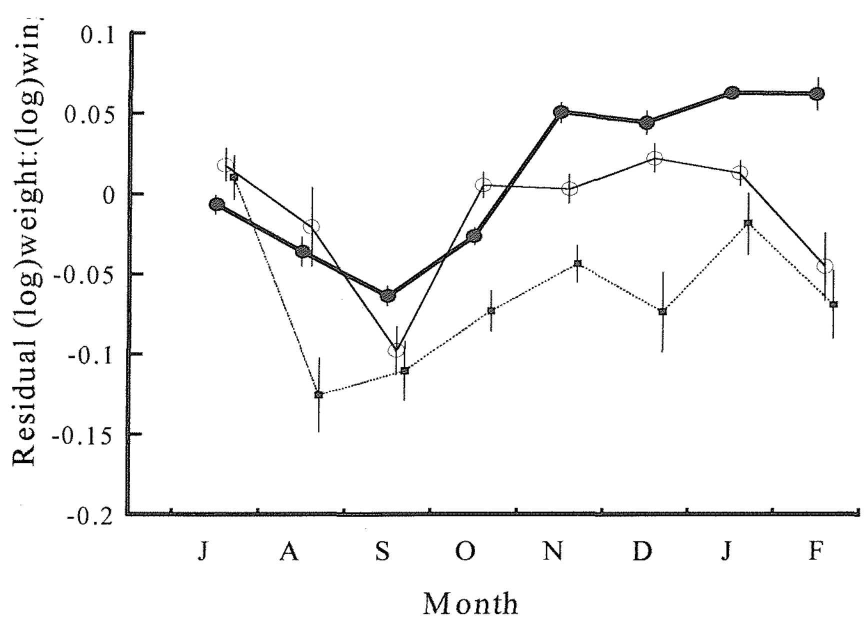


Fig. 3.2. Oystercatcher weight change through the winter. Plotted are the monthly means of individual residuals of ($\log_e$) body weight against ($\log_e$) wing length for adult (closed circles), immature (open circles) and juvenile (closed squares) Oystercatchers caught on the Exe estuary. Vertical bars show one standard error.

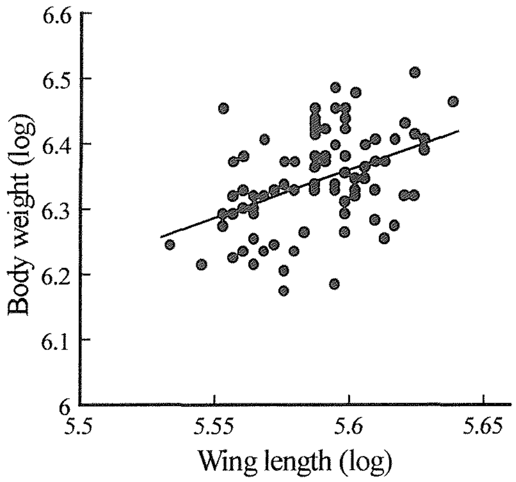


Fig. 3.3. The relationship between ($\log_e$) body weight and ($\log_e$) wing length in adult Oystercatchers caught in December ($y = -1.83 + 1.46x$, $R^2 = 0.18$).

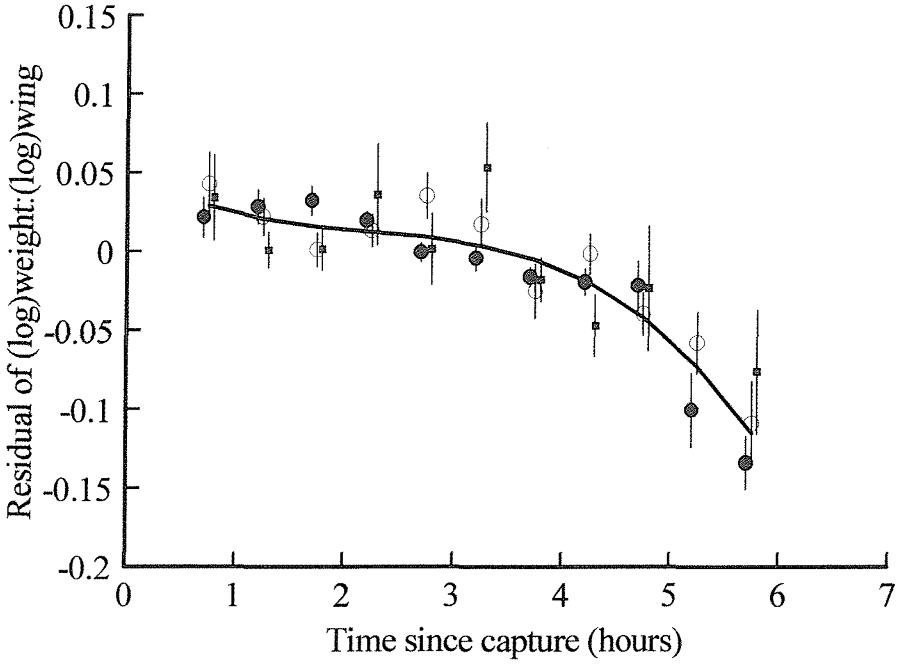


Fig. 3.4. The shape of weight loss over time since capture. Plotted are the means, for each time period, of the residuals of the regression of ($\log_e$) body weight against ($\log_e$) wing length for each age group in each month. Solid circles = adults, open circles = immatures, solid squares = juveniles. Vertical bars show one standard error. The solid line shows the cubic polynomial function, for all ages combined, of the mean residuals against time since capture.

(c) Body condition index

Body condition was therefore modelled using a general linear model of ($\log_e$) body weight against ($\log_e$) wing length, and also included factors allowing for differences due to age and month and a cubic polynomial function of time since capture. No statistically significant differences were detected in the slopes of the relationship between ($\log_e$) body weight against ($\log_e$) wing length between either the ages or months. However, there were differences in the intercepts between ages, months and their interaction, highlighting the fact that body weight for a given wing length varies between age groups and over the winter. The resulting model was:

$$\text{LogWT} = A_{ij} + b(\text{LogWL}) + c_1(\text{TSC}) + c_2(\text{TSC})^2 + c_3(\text{TSC})^3 \qquad \textbf{eqn 3.1}$$

where WT = body weight, WL = wing length and TSC = time since capture. A_{ij} = the constant term for age i in month j, b = +1.2085, c_1 = -0.0325, c_2 = +0.0060, c_3 = -0.0011.

The body condition index (BCI) for each bird was calculated as its residual from this model and was therefore equivalent to the log of the ratio of observed to predicted body weight. For example, for an adult bird (age i = 5), wing length 264mm, body weight 580g, weighed 3 hours after capture in December (month j = 6), $A_{5\,6}$ = -0.3292, and hence the predicted body weight (PW) would be as follows:

$$\begin{aligned} \text{LogPW} &= -0.3292 + 1.2085(\text{LogWL}) - 0.0325(3) + 0.0060(3^2) - 0.0011(3^3) \qquad \textbf{eqn 3.2} \\ &= -0.3292 + 6.7385 - 0.0975 + 0.0539 - 0.0297 \\ &= 6.336 \\ \text{PW} &= 564\text{g} \end{aligned}$$

The body condition index (BCI) is the difference between the observed body weight and the predicted body weight, as follows:

$$\text{BCI} = \text{Log}(580) - \text{Log}(564) = 6.363 - 6.336 = 0.027$$

When comparing mean body condition indices between diets and feeding methods we used an initial oneway ANOVA F-test, followed up, when significant and when there were more than two groups involved, by pairwise t-tests.

(3) Body condition in autumn

As we expected birds to be under greater stress as the winter progressed, analyses were conducted separately for birds caught in the autumn (September and October) and winter (November - February). In autumn, there was no significant difference in body condition between birds of the same age with different diets and feeding methods (Table 3.3). There was also no significant difference in body condition between the sexes when all diets and feeding methods were combined (Table 3.3). Nor could we find any significant difference between the sexes amongst birds of the same diet and feeding method, but sample sizes in many cases were small, so confidence limits for the differences were wide.

Table 3.3. Oystercatcher body condition indices in autumn by age, sex and diet/feeding method. x = insufficient data. NB only a subsample of birds, caught since 1989, were sexed.

a) Adults

	Males			Females			All birds		
Diet/ FM	n	mean	SE	n	mean	SE	n	mean	SE
Hammerers	19	-0.021	0.016	2	0.045	0.004	49	0.015	0.011
Stabbers	9	-0.002	0.018	4	-0.003	0.053	27	0.022	0.013
Worms/clams	x	x	x	x	x	x	14	0.046	0.014
All birds	31	-0.019	0.012	7	0.015	0.035			

b) Immatures

	Males			Females			All birds		
Diet/ FM	n	mean	SE	n	mean	SE	n	mean	SE
Hammerers	17	0.024	0.017	4	-0.002	0.010	23	0.020	0.013
Stabbers	14	-0.012	0.014	13	-0.005	0.023	30	-0.010	0.011
Worms/clams	2	0.027	0.092	11	0.015	0.020	21	0.003	0.019
All birds	34	0.005	0.012	28	0.003	0.013			

c) Juveniles

	Males			Females			All birds		
Diet/ FM	n	mean	SE	n	mean	SE	n	mean	SE
Hammerers	x	x	x	x	x	x	x	x	x
Stabbers	6	0.034	0.022	2	0.014	0.093	11	0.008	0.025
Worms/clams	3	0.012	0.067	8	-0.008	0.018	32	-0.003	0.012
All birds	13	0.023	0.019	11	-0.010	0.019			

Table 3.4. Oystercatcher body condition indices in winter by age, sex and diet/feeding method. x = insufficient data. Asterisks in superscript indicate a significant difference between the particular diet/feeding method and any others. Asterisks between the male and female columns indicate significant differences between sexes. * $P < 0.05$, ** $P < 0.01$. NB only a subsample of birds, caught since 1989, were sexed.

a) Adults

	Males				Females			All birds		
Diet/ FM	n	mean	SE		n	mean	SE	n	mean	SE
Hammerers	51	0.062^{**}	0.012		8	0.054	0.032	85	0.053^{**}	0.010
Stabbers	26	-0.011	0.021	*	11	0.077	0.021	43	0.012	0.015
Worms/clams	x	x	x		9	-0.026^{*}	0.022	14	-0.029	0.023
All birds	81	0.034	0.011		29	0.035	0.016			

b) Immatures

	Males				Females			All birds		
Diet/ FM	n	mean	SE		n	mean	SE	n	mean	SE
Hammerers	13	-0.004	0.016		4	-0.029	0.020	19	0.001	0.015
Stabbers	8	-0.009	0.017	*	11	0.053^{**}	0.020	21	0.028	0.015
Worms/clams	3	-0.022	0.055		9	-0.015	0.019	20	-0.017^{*}	0.015
All birds	26	-0.006	0.011		24	0.014	0.014			

c) Juveniles

	Males				Females			All birds		
Diet/ FM	n	mean	SE		n	mean	SE	n	mean	SE
Hammerers	x	x	x		x	x	x	x	x	x
Stabbers	8	-0.040	0.021		5	0.016	0.024	22	-0.029	0.016
Worms/clams	x	x	x		x	x	x	29	0.026^{*}	0.015
All birds	8	-0.040	0.021	*	8	0.035	0.021			

(4) Body condition in winter

In winter, there were significant differences in body condition between groups of birds (Table 3.4). Amongst adults as a whole, there were significant differences between different diets and feeding methods ($F_{2, 139} = 6.16$, $P < 0.01$), with mussel hammerers having significantly higher body condition indices than both mussel stabbers ($t_{126} = 2.35$, $P < 0.05$) and worm/clam feeders ($t_{97} = 3.14$, $P < 0.01$). Among immatures, differences were not significant when all diet/feeding methods were included ($F_{2, 57} = 2.36$ ns), but worm/clam feeders had significantly lower body condition indices than mussel stabbers ($t_{39} = 2.13$, $P < 0.05$). The situation was reversed in juveniles, with worm/clam feeders having higher body condition indices than mussel stabbers ($F_{1, 49} = 5.94$, $P < 0.05$).

When the sexes were considered separately, and when sample sizes were adequate, differences between birds of different diets and feeding methods were also apparent (Table 3.4). Adult male mussel hammerers had significantly higher body condition indices than male mussel stabbers ($F_{1, 75} = 10.34$, $P < 0.01$). Both adult ($F_{1, 18} = 11.1$, $P < 0.01$) and immature ($F_{1, 18} = 5.96$, $P < 0.05$) female mussel stabbers had higher body condition indices than female worm/clam feeders .

When birds of all diets and feeding methods were combined, there was no significant difference in body condition between males and females in either adults or immatures (Table 3.4). Amongst juveniles, there was a significant difference between the sexes, with females having a higher mean BCI ($F_{1, 14} = 6.00$, $P < 0.05$).

As the majority of mussel hammerers are males, and the majority of worm/clam feeders are females, only amongst mussel stabbers were sample sizes large enough to compare the body condition of males and females with the same diet or feeding method. In adults ($F_{1, 35} = 6.46$, $P < 0.05$) and immatures ($F_{1, 17} = 4.95$, $P < 0.05$), female mussel stabbers had significantly higher BCI scores than male mussel stabbers (Table 3.4). The mean BCI for juvenile female mussel stabbers was also higher than for males, but was not statistically significant.

(5) Body condition and bill structure

As birds were sexed by differences in their bill structure (bill depth/head+bill length), we investigated whether any sex differences in feeding apparatus could account for the sex differences in body condition of stabbers in winter. It is possible that longer, thinner bills are an advantage to mussel stabbers, and this is the reason why female stabbers were heavier than males. We therefore looked at the relationship between the bill index (ratio of bill depth:bill length) and body condition. Results for immatures and juveniles were similar and, as there is no difference in bill index between the age groups (Durell *et al.* 1993), we combined juveniles and immatures to increase sample size.

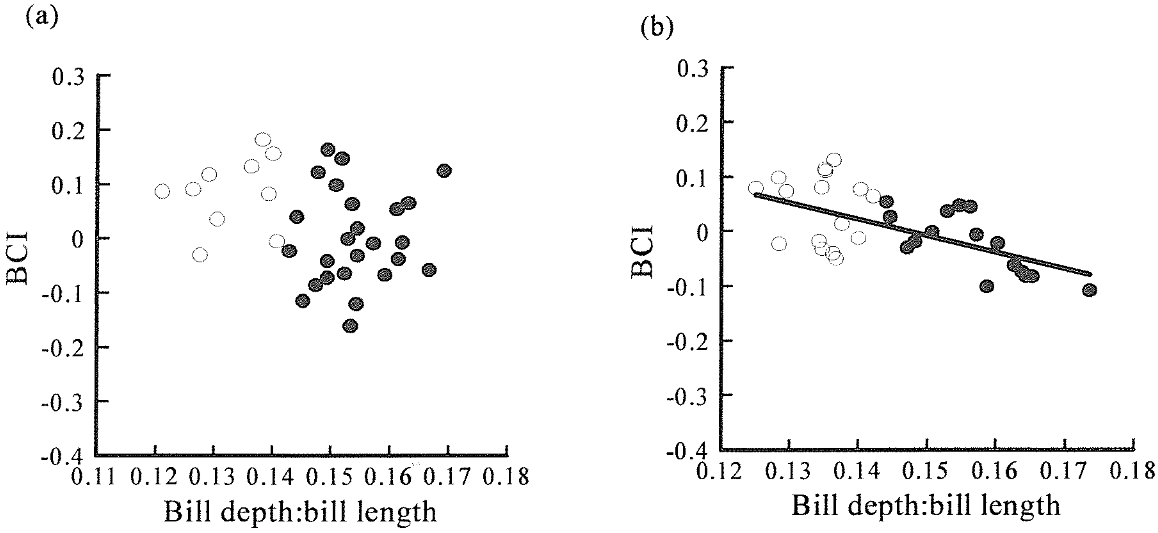


Fig. 3.5. The relationship between the ratio of bill depth:bill length and body condition index (BCI) in (a) adult stabbers (NS) and (b) immature and juvenile stabbers ($y = 0.444 - 3.02x$, $R^2 = 0.23$). Open circles = females, closed circles = males.

With adult stabbers in winter, there was no significant relationship between body condition and bill index, either with sexes combined or separately (Fig. 3.5a). When both sex and bill index were included in a multiple regression analysis, only sex was significant (partial $F_{1,32} = 5.63$, $P < 0.05$) and not bill index (partial $F_{1,32} = 2.20$, ns). However, with immature and juvenile stabbers in winter, the reverse was the case: there was a significant correlation between body condition and bill index, both with the sexes combined ($r_{37} = -0.503$, $P < 0.01$) and with males separately ($r_{14} = -0.744$, $P < 0.01$) (Fig. 3.5b). Birds with longer thinner bills had higher values of BCI. Moreover, when both bill index and sex were included in a multiple regression analysis, sex was no longer significantly correlated with body condition (partial $F_{1,29} = 0.45$, ns).

(6) Supplementary feeding in relation to diet and feeding method

Data on colour-ringed birds seen supplementing their diet were expressed as the proportion of birds within each subgroup which were never seen feeding on the upper mudflats as the tide advances and recedes or in the fields at high water (Table 3.5). All worm/clam feeders in all ages groups were seen supplementary feeding at some stage during the winter. Amongst mussel feeders, significantly fewer hammerers supplemented their diet than stabbers in adults ($\chi^2_1 = 5.95$, $P < 0.01$) but not in immatures ($\chi^2_1 = 0.93$, NS).

Table 3.5. Percent of colour-ringed Oystercatchers of each age and diet/feeding method never seen supplementary feeding in 1989/90 and 1990/91. x = insufficient data.

	Adults		Immatures		Juveniles	
Diet/FM	n	%	n	%	n	%
Hammerers	201	41.3	49	20.4	x	x
Stabbers	73	19.2	57	12.3	10	0
Worms/clams	38	0	21	0	9	0

(7) Winter mortality in relation to sex, diet and feeding method

Table 3.6 shows percent mortalities for birds of different age, sex, diet and feeding method. The number of bird-years is the sum of the number of colour-ringed birds of that category that were present on the Exe in each year over which statistics were calculated. Percent mortality was calculated using the total number of birds found dead or disappearing in winter over the same period. Data on known sex birds and on birds of different feeding methods was only available for the period 1988/89-1990/91, when winter mortality was higher than in earlier years (Durell *et al.* 2000). This explains why mortalities for known sex and feeding method birds tend to be higher than those for all birds and all mussel feeders.

In most cases, the number of birds dying were too few to enable statistical analysis of the data, particularly when trying to compare mortality between the sexes. With all adults combined, however, mussel-feeder mortality was significantly lower than that of worm/clam feeders ($\chi^2_1 = 5.05$, $P < 0.05$). When adults and immatures were combined, the mortality of mussel hammerers was significantly lower than that of mussel stabbers ($\chi^2_1 = 3.75$, $P < 0.05$).

Table 3.6. Winter mortality (%) for Oystercatchers of different age, sex, diet and feeding method. Numbers in brackets = number of bird/years. x = insufficient data.

	Adults			Immatures			Juveniles		
	M	F	all	M	F	all	M	F	all
Hammerers	2.6 (76)	0 (3)	1.2 (344)	2.6 (38)	0 (7)	3.7 (54)	x	x	x
Stabbers	11.8 (17)	5.6 (18)	2.3 (128)	14.3 (21)	18.8 (16)	7.8 (64)	0 (3)	0 (3)	5.0 (40)
All mussel feeders	4.3 (93)	4.8 (21)	1.4 (1915)	6.8 (59)	13.0 (23)	2.9 (272)	0 (3)	0 (3)	5.0 (40)
Worm/clam feeders	0 (6)	11.1 (9)	3.1 (323)	20.0 (5)	20.0 (10)	4.1 (122)	0 (3)	20.0 (5)	5.4 (56)
All birds	4.0 (99)	6.7 (30)	1.4 (2238)	7.8 (64)	15.2 (33)	3.6 (394)	0 (6)	12.5 (8)	5.2 (96)

(8) Sex, dominance and feeding efficiency

With 96 well-watched Oystercatchers, only age was found to have a significant effect on dominance (Caldow *et al.* 1999). Controlling for age, there was no significant difference between the sexes in dominance (partial $F_{1,60} = 0.04$, NS). Feeding efficiency, which was unrelated to dominance, was related to a bird's age and feeding method (Caldow *et al.* 1999). Controlling for age and feeding method, there was no significant difference between the sexes in feeding efficiency (partial $F_{1,60} = 0.06$, NS).

IV. DISCUSSION

On the Exe estuary in autumn, there was no significant difference in body condition between same age Oystercatchers of different diets or feeding methods. Nor did the sexes differ significantly in their body condition at that time of year. In the winter months, however, body condition differed significantly between a) birds that fed on mussels and those that fed on worms/clams and b) between mussel feeders using different feeding methods. Furthermore, in winter, females that opened mussels by stabbing were significantly heavier than males using the same technique. How can these seasonally-dependent differences in body condition amongst groups of Oystercatchers be understood?

(1) Body condition, diet and feeding method

There is considerable evidence that birds maintain reserves below the maximum that is attainable, and observed variations in fat storage over space and time are consistent with the hypothesis that birds are able to regulate their reserves in response to their needs (see review in Witter & Cuthill 1993). Moreover, data from passerines suggests that birds with predictable food supplies carry lower reserves than those with unpredictable food supplies (Rogers 1987; Ekman & Hake 1990; Ekman & Lilliendahl 1993; Gosler 1996), an explanation that has also been put forward to explain weight variation in Oystercatchers (Zwarts *et al.* 1996b). We do not know whether the predictability of the food supply differs for mussel hammerers and mussel stabbers, or for mussel-feeders and worm/clam feeders on the Exe estuary in winter. However, if the birds were adjusting the levels of their reserves in response to food predictability, one would expect consistent weight differences between diets and feeding methods across age groups. This was not the case: birds with the highest mean BCI in adults were mussel hammerers, in immatures mussel stabbers, and in juveniles, worm/clam feeders.

On the other hand, there is evidence that differences in body condition between Oystercatchers with different diets and feeding methods were due to the inability of some birds to meet their energetic requirements on the estuary at low water. In autumn, very few Oystercatchers appear to have difficulty in obtaining their energy requirements (Goss-Custard *et al.* 1996a). Most individuals feed for only a fraction of the time available over the low water period (Stillman *et al.* 2000) and very few supplement their diet by feeding on upshore prey as the tide ebbs and flows and in the fields at high water (Goss-Custard & Durell 1983; Caldow *et al.* 1999). Later in the winter, however, many birds appear to be hard-pressed because they feed for most of the low tide period and make extensive use of supplementary feeding (Caldow *et al.* 1999). The increased energy demands associated with inclement weather coincides with a deterioration in the food supply, making winter a difficult time for Oystercatchers to meet their food requirements (Goss-Custard *et al.* 1996a). Any differences between birds in their ability to attain target body weights would, therefore, be expected to emerge in winter, rather than in autumn.

Differences between Oystercatcher groups in their foraging behaviour are consistent with the hypothesis that some are less able than others to reach their target weights in winter. First, in adults, mussel hammerers have higher intake rates than stabbers at low water (Goss-Custard & Durell 1987b, Goss-Custard & Durell 1988, Stillman *et al.* 1996) and it is the mussel hammerers that had the heaviest weights. Immature hammerers were not heavier than stabbers, but birds usually change from mussel stabbing to mussel hammering when they reach their second or even third winter (pers. obs.), suggesting that success at mussel hammering is only achieved by older birds. Second, Caldow *et al.* (1999) showed that birds with low intake rates were most likely to be involved in supplementary feeding. Accordingly, both stabbers and worm/clam feeders were more likely than mussel hammerers to supplement their low water diet by feeding upshore as the tide ebbed and flowed and in the fields at high water.

Stabbers and worm/clam feeders also had higher winter mortality than mussel hammerers. On the assumption that most birds that die in the winter die from starvation (Durell *et al.* 2000), this also suggests that stabbers and worm/clam feeders were finding it more difficult than hammerers to maintain their target body mass during the winter. In adults, the relationship between body condition, supplementary feeding and mortality follows the expected pattern: birds with lower weights were more likely to be recorded feeding on supplementary foods and had higher winter mortality rates (Fig. 3.6). Thus, the change from autumn to winter in the feeding conditions for all Oystercatchers, the differences in winter in intake rates, foraging time budgets and in mortality rates are all consistent with the idea that the differences in body condition between different diet and feeding method groups reflect differences between them in their ability to achieve the same target weight.

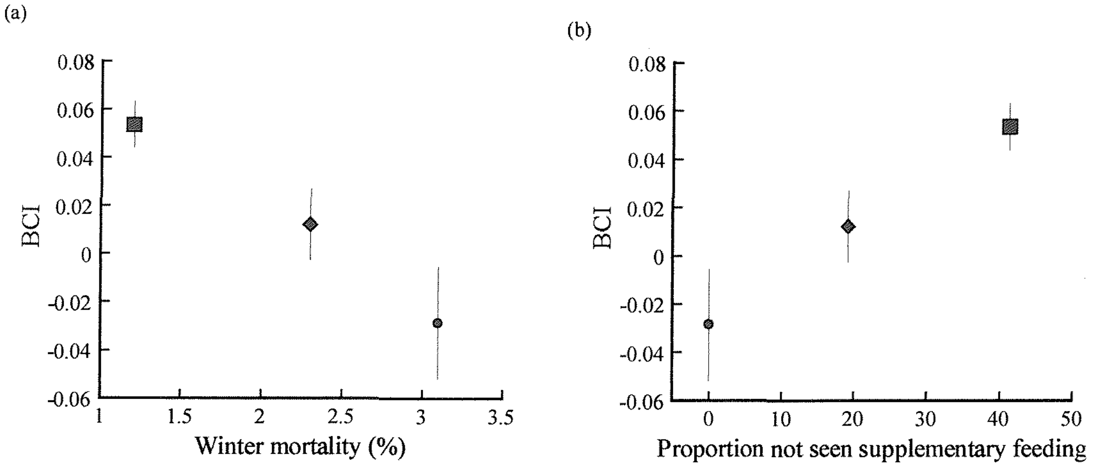


Fig. 3.6. Mean body condition index (BCI) in adult mussel hammerers (squares), mussel stabbers (diamonds) and worm/clam feeders (circles) against a) winter mortality and b) proportion of birds never seen supplementary feeding. Vertical bars show one standard error.

(2) Body condition in male and female mussel stabbers

Nevertheless, we do not think that this argument holds true for the sex difference in body condition in adult mussel stabbers. In all age groups, female stabbers were heavier than male stabbers, even though we found no difference in intake rates between the sexes at low water. It is possible that female stabbers, with their longer, thinner bills, could have an advantage when feeding in upshore mudflats and in fields at high water. This seemed to be the case with immature birds, where bill structure, and not sex, correlated best with body condition. However, in adults, there was no correlation between body condition and bill structure. This suggests that there is a different reason for adult female stabbers being heavier than males.

Why should adult female Oystercatchers be heavier than males? There is some evidence that dominant birds store less fat than subdominants because they have a more predictable food supply or a higher mean energetic gain (Witter & Cuthill 1993; Gosler 1996), and Zwarts *et al.* (1996a) suggest that female Oystercatchers on the Wadden Sea may have been heavier than males because they were subdominant. However, we found no evidence that body condition was related to a bird's social status. Caldow *et al.* (1999) found no difference in dominance between mussel hammerers and mussel stabbers and also no relationship between dominance and supplementary feeding. In a more recent study, 12 colour-ringed birds were caught and then watched in subsequent weeks on one mussel bed but no correlation was found between dominance and body condition (J.D. Goss-Custard pers. obs.). In this study, we also found no difference in dominance between the sexes. We think it extremely unlikely, therefore, that weight differences between the sexes are due to differences in dominance.

We think that adult female Oystercatchers may have a different target weight from males in the winter because they have a different pre-migratory and pre-breeding strategy. In adults, there was no weight difference between the sexes in the autumn, but as the winter progressed, as also found by Dare (1977), adult females put on more weight than adult males of the same diet or feeding method. There is no evidence that female Oystercatchers accumulate more reserves because they migrate further to breed. This is supported by the fact that, in this study, the sexes did not differ in wing length (Table 2), since Oystercatchers breeding further north tend to have longer wing lengths (Dare 1977; Cramp & Simmons 1983). It may, however, be of greater advantage for females to arrive at the breeding grounds with higher levels of reserves. In birds, female energy expenditure during reproduction is often greatest during prelaying and egg production (Ricklefs 1974, Brunton 1988a,b), and the timing of egg laying has been related to female body condition (Ward 1969; Perrins 1970; Jones & Ward 1976; Fogden & Fogden 1979). Oystercatchers start to breed very early in the year, with adults starting to leave the Exe in mid-February and, in northern Britain where they breed, starting to lay in early April (Hepplestone 1972). Oystercatchers that breed early tend to fledge the most young (Harris 1967; Hepplestone 1972; Ens *et al.* 1992). It is possible, therefore, that those females which arrive on the breeding grounds with higher levels of reserves will be the most successful breeders. We also think that this is the most likely reason why adult female Oystercatchers are heavier than males.

(3) Fitness consequences for female Oystercatchers

If it is true that females arriving at the breeding grounds with higher levels of reserves will be the most successful breeders, then one would assume that all adult females would be trying to achieve higher target weights prior to migration. On the Exe, however, female specialization in diets and feeding methods associated with lower weights meant that, overall, female weights in winter were not significantly greater than males. Female stabbers were able to attain the same BCI as male hammerers, but only through extensive use of supplementary feeding which would expose them to an increased risk of predation and parasite loading (Goss-Custard *et al.* 1996a). Female worm/clam feeders, on the other hand, were significantly lighter than mussel feeders in winter. This could mean that female worm/clam feeders are at a disadvantage when they arrive at the breeding grounds, resulting in a poorer breeding performance.

On the Exe, there is a male bias amongst adult Oystercatchers (Durell & Goss-Custard 1996). Durell & Goss-Custard (1996) showed that this sex bias, and the change from 50% females in immatures to 33% females in adults, could not be explained by disproportional emigration/ immigration alone, but must also have been due to higher female mortality. In this study, female mortality did appear to be higher than male mortality (Table 6). In addition, adult worm/clam feeders had higher mortalities than mussel feeders and, when adults and immatures were combined, stabbers had higher mortality than hammerers. As the majority of adult females are worm/clam feeders and mussel stabbers, the indications are that adult female mortality is, indeed, higher than male mortality. Thus, females overwintering on the Exe may not only be at a disadvantage in terms of breeding success but also in terms of life expectancy.

Chapter 4: DENSITY-DEPENDENT MORTALITY

This chapter has been published as:
Durell, S.E.A. le V. dit, Goss-Custard, J.D., Clarke, R.T. & McGrorty, S. (2000) Density-dependent mortality in Oystercatchers *Haematopus ostralegus. Ibis* **142**,132-138.

I. INTRODUCTION

When considered on a scale large enough to disregard immigration and emigration, population size results from a combination of density-dependent and density-independent processes affecting breeding and mortality. For shorebirds, density-independent factors, particularly those related to weather, can be catastrophic and, as a result, have become the focus of attention (Goss-Custard *et al.* 1977, Baillie 1980, Clark 1982, Davidson & Evans 1982, Evans & Pienkowski 1984, Davidson & Clark 1985, Hulscher 1990, Clark 1993, Camphuysen *et al.* 1996, Zwarts *et al.* 1996c). The effect of density-dependence on mortality has been less well studied, not least because it is harder to detect. There are three main reasons for this. Mortality is often difficult to measure in such highly mobile species and errors can occur in estimating mortality from missing birds or from ringing recoveries (Harris 1967; Evans 1980). Mortality may also vary considerably at any given population density due to density-independent factors, making any underlying density-dependence difficult to isolate. Lastly, if a population is relatively stable, population size may not vary enough over a period of study for the effect of density-dependence to be apparent.

Population models of the Oystercatcher *Haematopus ostralegus* have shown that the shape (linear or non-linear) and the strength (slope) of density-dependent functions are critical for predicting the effect of habitat deterioration or loss on shorebird populations (Goss-Custard & Durell 1990, Goss-Custard *et al.* 1995a,b,c, 1996, Sutherland 1996a, 1996b). Density-dependence on the breeding grounds has been identified and described (see review in Goss-Custard *et al.* 1995b). Potential breeding pairs compete for a limited supply of suitable territories, so that an increasing proportion is excluded from breeding altogether, or forced to nest in poor quality habitats, as the number of pairs attempting to breed increases. There is also some evidence of density-dependent reduction in fledging success (Goss-Custard *et al.* 1995b). However, the possibility that adult mortality is also density-dependent has not yet been demonstrated.

The Oystercatcher population overwintering in Britain has increased over the last few decades (Cranswick, Kirby & Waters 1992; Goss-Custard *et al.* 1996), probably as a result of an expansion of inland breeding by Oystercatchers during the latter half of this century (Goss-Custard *et al.* 1996a). The size of our well-studied Oystercatcher population wintering on the Exe estuary in south Devon similarly increased over the period 1976-1991. In this paper we test for density-dependence in Oystercatcher mortality over this period.

II. METHODS

Oystercatchers have been caught and individually colour-ringed on the Exe estuary since 1976 (for methods see Goss-Custard *et al.* 1980). Regular searches were made for colour-ringed birds at low and high water each winter until 1983/84 (see Goss-Custard *et al.* 1982a) and again from 1988/89 until 1990/91. In addition, colour-ringed birds seen elsewhere were reported to us by the Wader Study Group and any dead birds found on the Exe or elsewhere were reported to us through the British Trust for Ornithology ringing scheme.

This analysis was restricted to adult birds because (i) more data were available for adult birds and (ii) emigration to other estuaries is fairly common amongst younger birds. With young birds, therefore, we could not be sure whether a bird that had disappeared had emigrated or died. No evidence of emigration was found in adults. Adults that failed to return to the Exe the following winter were never seen in subsequent winters, nor were they seen or recovered dead elsewhere in subsequent years. We assumed, therefore, that any absent adult birds had died. This assumption was supported by the fact that 12.4% of colour-ringed birds that disappeared were recovered. This figure is very close to the cumulative 12% chance that a dead ringed bird would be recovered, estimated in Goss-Custard *et al.* (1982a). Only birds that were regularly seen in the first winter after ringing were included in the analysis.

Annual mortality and winter mortality were analysed separately. Annual mortality included all birds failing to return to the Exe the following winter. Winter mortality included those birds found dead on the Exe between 1 September and 31 March and those birds that disappeared before the end of January. As adults start leaving the Exe for the breeding grounds in early February, we could not tell whether any bird missing after that time had died on the Exe or elsewhere.

Oystercatchers on the Exe estuary specialize on different diets, although the majority are mussel *Mytilus edulis* feeders (Goss-Custard *et al.* 1980). In this analysis, we examined mortality first in all adults and, second, in known mussel-feeders only. As we did not count the total numbers of oystercatchers on the estuary in all months in all winters, analyses involving all adults used the Wetland Bird Survey (WeBS) counts for the Exe estuary. We assumed that the total area of the Exe estuary remained constant over the study period and used the mean of WeBS counts for the winter months October-February for each year as the relevant total population density that could affect mortality. There was no seasonal trend in Oystercatcher numbers over these winter months (Goss-Custard *et al.* 1980). For analyses of mussel feeding birds, we used Oystercatcher densities on the mussel beds. Numbers of Oystercatchers on the main mussel beds of the Exe estuary were counted each month for all 11 of the study winters (Goss-Custard *et al.* 1982b). Mussel bed areas were measured in September for 1976-1983 and again in November 1992 (for methods see McGrorty *et al.* 1990). Mussel bed areas for 1988-1990 were estimated by a regression of mussel bed area against year. Population density used was the mean bird density on the mussel beds in the winter months October-February.

In order to control for the severity of the winter weather, data were obtained from the monthly Meteorological Office reports for Exeter Airport, a weather station approximately five miles from the estuary. Variables included in the analyses were mean daily temperature, mean minimum daily temperature, number of days of air frost and number of days of grass frost. These were calculated over two time periods, October- February and December-February.

The relationships between mortality, bird density and winter weather were explored by regression. Because the colour-ringed birds on which mortality estimates were based formed only a part of the total population size, errors in estimates of mortality and population density were effectively independent. They were, therefore, free of statistical problems associated with relating mortality values to population density (Ito 1972). The relationships between mortality and population density often appeared curvilinear. The curvilinearity was not adequately described by quadratic relationships as predicted mortality increased at low population densities, but was best represented by a linear relationship between $\log_e$ mortality and $\log_e$ population density. This transformation to $\log_e$ mortalities also made the residual variance in mortality about all regression lines roughly independent of the predicted value (an assumption of standard regression analyses), and this approach was applied to all the regression analyses in this study.

III. RESULTS

(1) Annual mortality

(a) All adults

The mean number of colour-ringed adults present on the Exe estuary each year, over the 11 years studied, was 234 birds, with the total number of bird-years being 2576. Of these bird-years, a total of 282 birds went missing, giving an average annual mortality of 10.9%. This compares with the range of 4% - 13.5% given in Goss-Custard *et al.* (1982a).

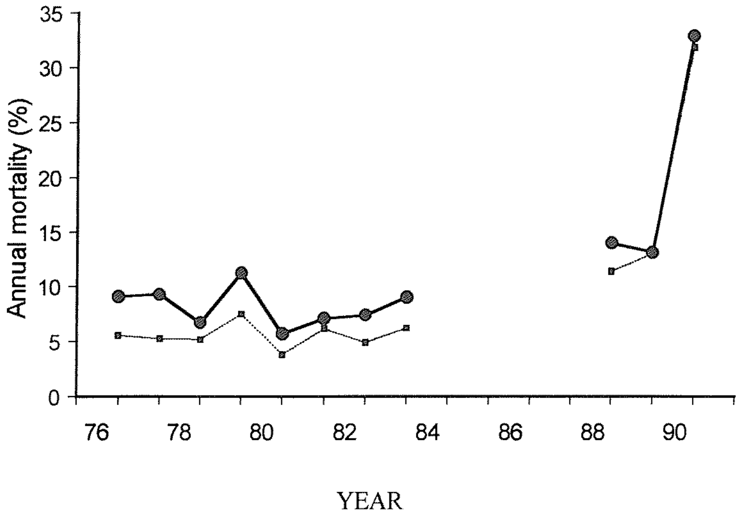


Fig. 4.1. Annual mortality of all adult Oystercatchers (circles) and adult mussel-feeders (squares) over the study period.

Annual mortalities increased over time ($r_9 = 0.688$, $P < 0.02$) (Fig. 4.1). This trend was still significant after data for 1990/91, the last year of the study, and a year of very high mortality, was excluded from the analysis ($r_8 = 0.639$, $P < 0.05$). Mean WeBS counts (October-February) also increased over this period ($r_{13} = 0.671$, $P < 0.01$) (Fig. 4.2).

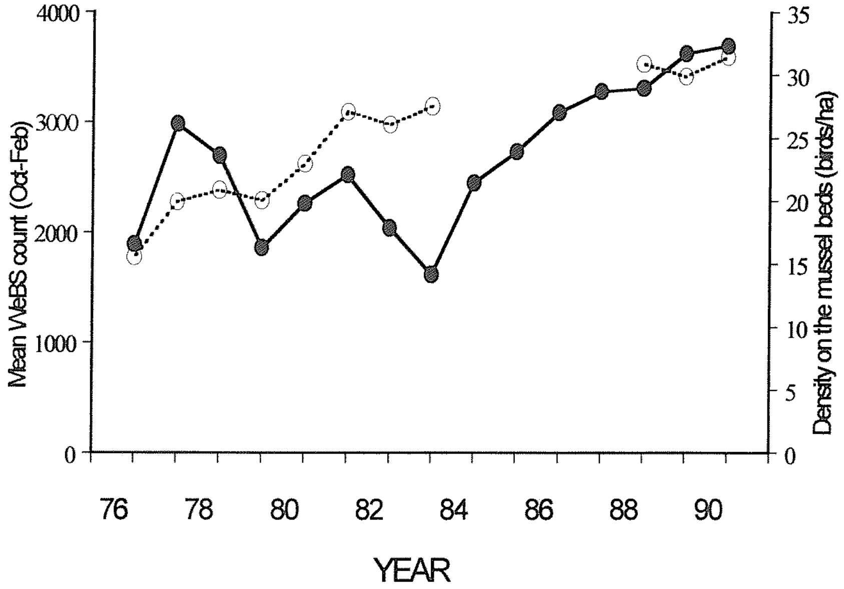


Fig. 4.2. Mean (October-February) WeBS whole estuary Oystercatcher count (closed circles) and mean (October-February) bird density on the mussel beds (open circles) over the study period.

Individually, the relationship between ($\log_e$) annual mortality and ($\log_e$) population density was almost significant ($P = 0.075$, Table 4.1)(Fig. 4.3a). There was no significant relationship between ($\log_e$) mortality and any of the weather variables used (Table 4.1), but when the number of days of grass frost in late winter (December- February) was included in a multiple regression, the relationship between ($\log_e$) annual mortality and ($\log_e$) population density became significant ($P < 0.05$, Table 4.2). This relationship was partly dependent upon a single point of high mortality, occurring in a winter of higher than average number of days of frost (Fig. 4.3a). As a further test, therefore, the multiple regression relationships were re-assessed using a general randomisation significance test proposed by ter Braak (1992), based on the repeated ($n = 5000$) randomisation of multiple regression residuals, implemented using the RT software package described in Manly (1997). The randomisation tests supported the suggestion of density-dependent annual mortality in all adults ($P < 0.05$, Table 4.2).

Table 4.1. The individual effect of ($\log_e$) population density and number of days of grass frost on ($\log_e$) adult annual mortality. b = estimated coefficient, SE = standard error of b, t = t-value, P = regression significance, r = Pearson correlation, r_s = Spearman rank correlation coefficient (* $P < 0.05$)

		b	SE	t	P	r	r_s
All adults	Population density ($\log_e$)	0.9412	0.4680	2.01	0.075	0.558	0.482
	Days of frost	0.0113	0.0200	0.56	0.587	0.372	-0.187
Mussel-feeders	Population density($\log_e$)	1.5224	0.7175	2.12	0.063	0.577	0.609*
	Days of frost	0.0098	0.0247	0.40	0.699	0.132	-0.078

Table 4.2. The combined effect of ($\log_e$) population density and number of days of frost in late winter on ($\log_e$) adult annual mortality. b = estimated partial coefficient, SE = standard error of b, t = partial t-value, P = significance using multiple regression, P_r = significance using randomisation test.

		b	SE	t	P	P_r
All adults	Population density ($\log_e$)	1.1406	0.4660	2.45	0.040	0.035
	Days of frost	0.0237	0.0168	1.41	0.196	0.167
Mussel-feeders	Population density($\log_e$)	1.6235	0.7404	2.19	0.060	0.057
	Days of frost	0.0174	0.0210	0.83	0.431	0.403

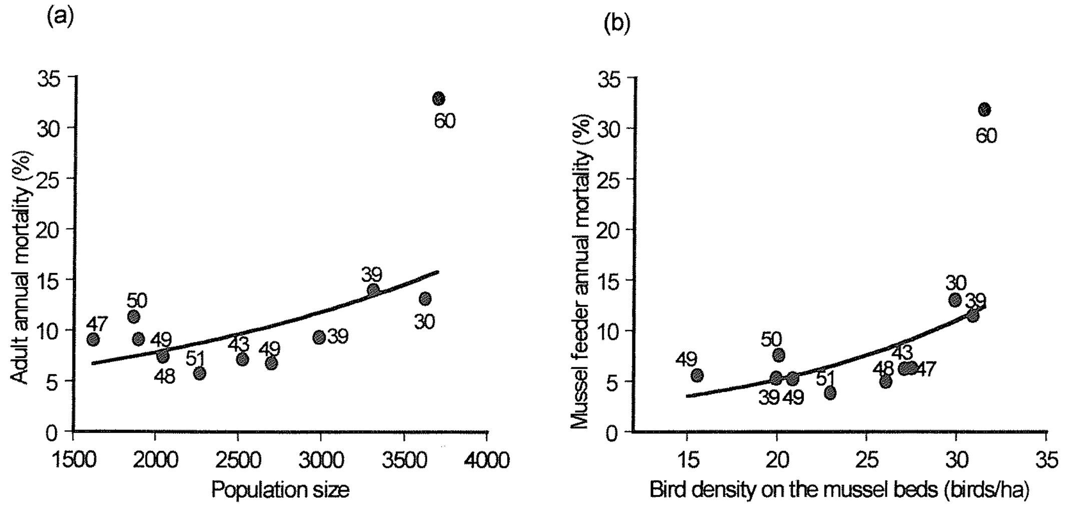


Fig. 4.3. (a) Observed annual mortality (M) in all adults against WeBS mean winter count (D) for that year (logM = -9.661 + 0.94121ogD, $R^2 = 0.31$). (b) Observed annual mortality (M) in adult mussel-feeders against mean winter bird density (birds ha^{-1}) on the mussel beds (D) (logM = -7.422 + 1.5224logD, $R^2 = 0.33$). Numbers beside each data point on both plots are the number of days of grass frost in December-February for that year.

(b) Mussel-feeders

On average, 174 colour-ringed adult mussel-feeders were present per year over the 11 study winters, with a total of 1915 bird-years. 176 of these birds disappeared, giving an average annual mortality of 9.2%.

As with all adults, annual mortality in mussel-feeders increased over time ($r_9 = 0.716$, $P < 0.01$) (Fig. 4.1). Oystercatcher densities on the mussel beds also increased over the study period ($r_9 = 0.905$, $P < 0.0001$) (Fig. 4.2). The regression of ($\log_e$) mussel-feeder annual mortality and ($\log_e$) bird density was almost significant ($P = 0.063$, Table 4.1) (Fig. 3b). There was no significant correlation between ($\log_e$) mussel-feeder annual mortality and any of the weather variables used (Table 4.1). Using Spearman rank correlation, the relationship between ($\log_e$) mussel-feeder annual mortality and ($\log_e$) bird density was significant (Table 4.1). The three highest mortalities occurred during the period 1988-91 when the bird density on the mussel beds was also highest (Fig 4.3b). The exceptionally high mortality during 1990-91 also coincided with the worst winter for frost, but the randomisation test using multiple regression residuals, allowing for possible correlations with the extent of cold weather, offered some support for the suggestion of density-dependent annual mortality of mussel feeding adults ($P = 0.057$ in Table 2).

(2) Winter mortality

(a) All adults

36 adults went missing or were found dead on the Exe during the winter over the study period, giving an estimate of 1.4% winter mortality. This is close to the 1.5% winter mortality given in Goss-Custard *et al.* (1982b). Unlike annual mortality, the correlation between winter mortality and year was not significant ($r_9 = 0.391$, n.s.). No significant relationship was found between ($\log_e$) winter mortality and ($\log_e$) population density (Fig. 4a) or any of the weather variables, either individually or in combination.

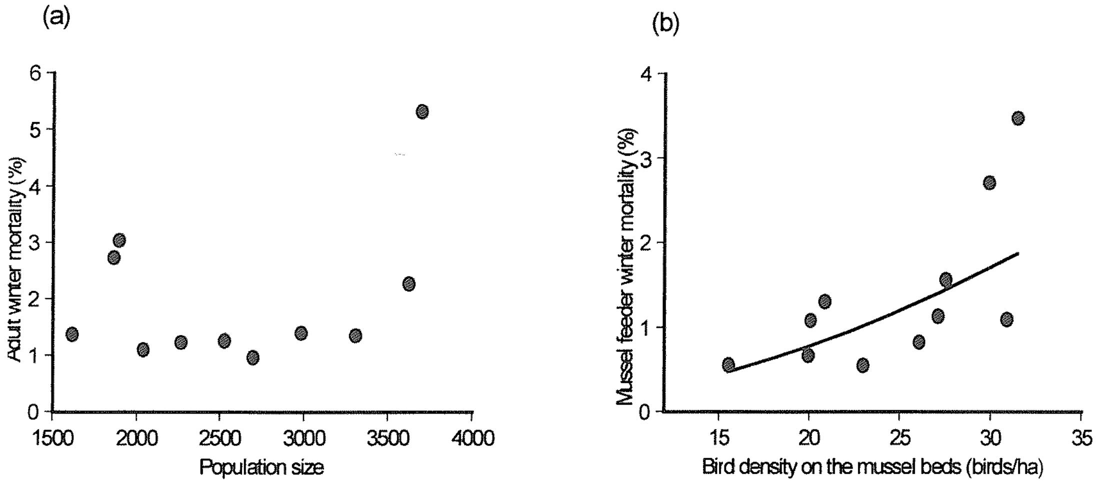


Fig. 4.4. (a) Observed winter mortality in all adults against WeBS mean winter count for that year. (b) Observed winter mortality (M) in adult mussel-feeders against mean winter bird density (birds ha^{-1}) on the mussel beds (D) ($\log M = -10.707 + 1.9514\log D$, $R^2 = 0.51$).

(b) Mussel-feeders

26 mussel-feeders went missing or were found dead on the Exe during the winter over the study period, also giving a mean winter mortality rate of 1.4%. With mussel-feeders, the

correlation between winter mortality and year was significant ($r_9 = 0.794$, $P < 0.01$), and was still significant when 1990/91 was excluded ($r_8 = 0.698$, $P < 0.05$). There was a significant positive correlation between ($\log_e$) mussel-feeder winter mortality and ($\log_e$) bird density on the mussel beds ($r_9 = 0.715$, $P < 0.02$, Spearman rank correlation = 0.764, $p < 0.05$) (Fig. 4.4b). This relationship was still significant when winter 1990/91, the year of highest mortality, was excluded from the analysis ($r_8 = 0.655$, $P < 0.05$). None of the weather variables was significant on their own, or in combination with bird density.

IV. DISCUSSION

In this study, we have demonstrated density-dependent winter mortality amongst mussel feeding Oystercatchers on the Exe estuary. The fact that we were able to find a significant density-dependent effect in the winter mortality of mussel-feeders, but not in all adults, could be due to three reasons. First, it could be argued that the increase in mortality over time was due to something other than density-dependent factors, the most likely being the food supply. However, the mussel beds on the Exe estuary were sampled from 1976-1983 and again in 1992, and there is no evidence that the density or the quality of the mussel food supply decreased over the study period (Goss-Custard *et al.* 1998). Secondly, it may be that our counts of birds on the mussel beds provided a more accurate measure of the relevant bird densities affecting competition. In other words, there was a density-dependent increase in mortality in all adults but we were unable to detect it due to errors in estimating population density. Lastly, however, it is likely that the increased competition resulting from an increase in bird density would be felt more acutely amongst mussel feeding birds. Indeed, it was only with mussel-feeders that winter mortality, as opposed to annual mortality, increased over the period of study. It is certainly true that bird densities are higher on the mussel beds than on other habitats on the Exe estuary. Bird density on the mussel beds in this study ranged from 15.5 to 31.4 birds ha^{-1}, whereas mean bird densities on the intertidal flats range from 0.2 to 1.8 birds ha^{-1} (Goss-Custard *et al.* 1991). It is also true that interactions between birds are far more frequent on the mussel beds (Boates & Goss-Custard 1992), indicating that competition is already intense between mussel-feeding birds. The low bird densities found on other habitats may be the reason why winter mortality amongst birds other than mussel-feeders remained unaffected by any increase in population size.

Although we suspect that there was also a density-dependent effect operating on annual mortality, this study shows how difficult it can be to detect. Intuitively, one would expect density-dependence to operate only above a certain threshold density, and our plots of annual mortality (Fig. 4.3) appeared to fit this expectation. However, there were too few years of higher bird densities to prove this. In addition, one of these years had even higher annual mortality than expected, almost certainly because of the severity of the late winter weather. Although we partialled out the effect of weather, this year remained crucial to any significant results we obtained.

In contrast to studies on the Continent (Camphuysen *et al.* 1996, Hulscher *et al.* 1996b, Zwarts *et al.*1996b), the effect of weather was not strong in any of our analyses, probably because winters on the Exe are relatively mild. The only weather variable to have any effect was the number of days of grass frost in late winter (December-February). However, the influence of this variable was only found in analyses involving annual, not winter, mortality. Mortality occurring away from the overwintering area is most likely to happen on spring migration or on arrival at the breeding grounds (Marcström & Mascher 1979, Watson 1980, Lambeck & Wessel 1991, Hulscher *et al.* 1996b). It is possible that there is a correlation between late winter weather on the Exe and that experienced elsewhere in spring, and that the relationship between frosts in late winter and annual mortality is not causal. However, we think that spring mortality will also be influenced by conditions experienced before departure: if the birds leave the Exe in poor condition they may be less likely to survive the rigours of migration.

Using our data on mussel-feeder annual and winter mortality, we can estimate mortality occurring in spring (Fig. 4.5). Our measures of winter mortality on the Exe were underestimates because birds that died in February and March would not have been included.

Goss-Custard & Durell (1984b) extrapolated winter mortality from 1.5% to 3.2% to include mortality on the Exe up to 31 March. We used this calculation to obtain a correction factor (*3.2/1.5) to estimate whole-winter mortality. Summer mortality on the breeding grounds is low, and has been estimated at 1% (Harris 1967, Safriel *et al.* 1984, Ens 1992). Subtracting this figure and whole-winter mortality from predicted annual mortality gives us a value for mortality in spring. As can be seen in Fig. 4.5, our prediction is that spring mortality is higher than winter mortality, and also density-dependent. On the assumption that annual mortality is density-dependent, our hypothesis is that increased competition on the wintering grounds results in more birds being less fit when they migrate in early spring. It is these birds that will be more likely to die if they encounter adverse conditions on migration, or on arrival on the breeding grounds.

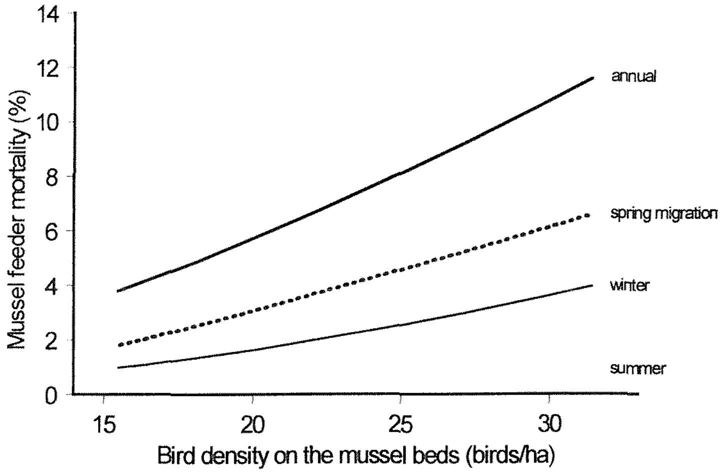


Fig. 4.5. Estimated mortalities for adult mussel-feeders for winter, summer and spring separately and their sum, total annual mortality, in relation to bird density (birds ha^{-1}) on the mussel beds.

V. POSTSCRIPT

The following has been accepted for publication in *Ibis* as:
Durell, S.E.A. Le V. dit, Goss-Custard, J.D., Stillman, R.A. and West, A.D. (in press) The effect of weather and density-dependence on Oystercatcher *Haematopus ostralegus* winter mortality.

In a previous paper we demonstrated the effect of density-dependence on the winter mortality of adult mussel-feeding Oystercatchers *Haematopus ostralegus* (Durell *et al.* 2000). In our analyses, we found no significant relationship between Oystercatcher winter mortality and winter temperatures or number of days of frost on the Exe estuary. However, a recent development has led us to re-examine our data. We were investigating the difference between the observed winter mortality of adult Oystercatchers and that predicted by a behaviour-based model (Fig. 4.6).

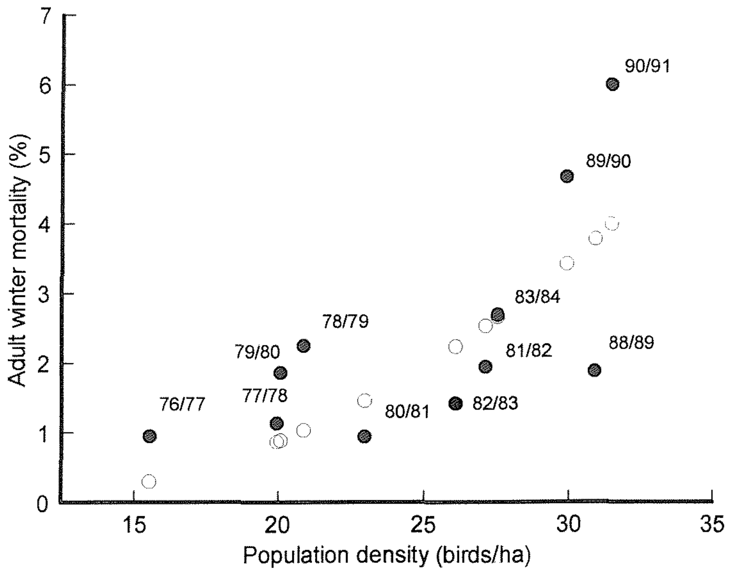


Fig. 4.6. Observed (closed circles) and predicted (open circles) winter mortality of adult mussel-feeding Oystercatchers plotted against mean winter bird density on the mussel beds. Observed mortality is from Durell *et al.*(2000) but has been corrected to account for mortality in February and March (*3.2/1.5: Goss-Custard & Durell 1984), and reduced by the estimated proportion of deaths resulting from accidents (0.188: unpublished data). Predicted values were obtained using the behaviour-based model described in Stillman *et al.* (2000). Values given next to each observed data point indicate the year.

As with observed mortality, there was no significant relationship between the difference in mortalities and number of days of frost or mean minimum temperatures in late winter. However, when data on the total number of days of gales from December to February was added to a multiple regression, both mean minimum temperature ($t_{10} = -3.61$, $P < 0.01$) and number of days of gales ($t_{10} = 2.99$, $P < 0.05$) were significant. Two-thirds of the variation between observed and predicted mortality was explained by these two weather variables ($r^2 = 0.67$). It was clear, therefore, that we should have included data on gales in our analysis of Oystercatcher overwinter mortality, and we present this analysis here.

The methods used to calculate winter mortality and bird densities are given in Durell *et al.* (2000). Data on winter mortality were available for 11 winters between 1976 and 1991. This analysis concerns mussel-feeding birds only and bird densities used are Oystercatcher densities on the mussel beds. Previous analyses had indicated that weather conditions in late winter (December-February) were more likely to influence Oystercatcher mortality than conditions for the winter as a whole (October-February) (Durell *et al.* 2000). This is understandable as the birds are more likely to be under stress at this time of the year (Goss-Custard *et al.* 1996a). In the present analysis we used mean daily temperature, mean minimum temperature and number of days of frost for the period December-February. Data were obtained on the total number of days of gales (December-February) at Exmouth, a weather station adjacent to the mouth of the Exe estuary.

Relationships between mortality, bird density and winter weather were explored by regression. Mortality and bird density data were $\log_e$ transformed (Durell *et al.* 2000). When mean minimum temperature was added to the regression of ($\log_e$) winter mortality against ($\log_e$) bird density, r^2 increased from 0.51 to 0.55 and temperature was not significant ($t_{10} = -1.41$, ns). However, when the number of days of gales was added to this regression, whilst bird density remained the most significant variable, minimum temperature also became a significant predictor of winter mortality and the r^2 increased from 0.55 to 0.80 (Table 4.3). When included as a linear variable, the number of days of gales was not quite significant (Table 4.3a). However, when included as a binary variable, where 0 = years with less than 7 days of gales and 1 = years with 7 or more days of gales, number of days of gales was a significant predictor of Oystercatcher mortality (Table 4.3b).

Table 4.3. The combined effect of ($\log_e$) population density, mean minimum temperature and number of days of gales in late winter on ($\log_e$) adult mussel-feeder winter mortality. *b* = estimated partial coefficient, SE = standard error of *b*, *t* = partial t-value, *P* = significance using multiple regression. (a) with number of days of gales as a linear variable and (b) number of days of gales as a 01 variable where 0 = less than 7 days of gales and 1 = 7 or more days of gales.

(a)

	b	se	*t*	*P*
Population density ($\log_e$)	1.4979	0.4848	3.09	0.018
Mean minimum temperature (°C)	-0.5595	0.1873	-2.99	0.020
Number of days of gales	0.0704	0.0304	2.32	0.053

(b)

	b	se	*t*	*P*
Population density ($\log_e$)	1.6633	0.4484	3.71	0.008
Mean minimum temperature (°C)	-0.3002	0.0937	-3.20	0.020
Number of days of gales (01)	1.1492	0.3776	3.04	0.019

Plotting the residuals from the regression of ($\log_e$) winter mortality against ($\log_e$) bird density against mean minimum temperature revealed that the inclusion of gale frequency explained the outlying point when mortality was higher than expected in a relatively mild winter (Fig. 4.7).

Although we expected winter temperatures to affect Oystercatcher mortality, we were not surprised when, in our initial analyses, winter weather appeared to have no significance. Winters on the Exe estuary are relatively mild and prolonged periods of frost occur infrequently. During the 15 year period of this study, severe frosts occurred in only one winter (1990/91), when Oystercatcher mortality was higher than average (Durell *et al.* 2000).

Furthermore, the availability of mussels is not affected by cold weather in that, unlike some other invertebrate prey, they do not burrow deeper in the mud. However, it now appears that, even in an area with mild winters, winter weather does have a significant effect on Oystercatcher survival. Even without severe frosts, lower temperatures in winter will increase the birds' energetic requirements and so increase the probability that they will fail to meet these needs and starve to death.

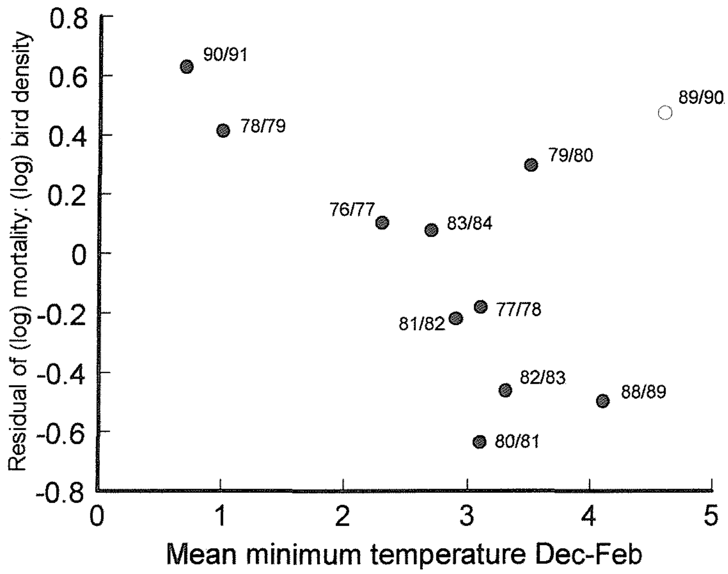


Fig. 4.7. The residuals of ($\log_e$) observed winter mortality against ($\log_e$) bird density plotted against mean minimum temperature (^{0}C) in late winter. The open circle denotes the only year when gale frequency was more than seven days. Values next to each data point indicate the year.

The reason we failed to detect the influence of temperature on Oystercatcher mortality was primarily because of one mild winter with higher than expected mortality. This was also a winter when gale frequency (15 days) was more than three times the average (4.6 days). High winds also increase the birds' energetic needs, particularly when combined with low temperatures (Goss-Custard *et al.* 1996a). Oystercatchers on the mussel beds have also been seen to stop feeding and to take shelter during periods of very strong winds (pers. obs.). In this case, it is also probable that the gales at Exmouth prevented the tide from emptying the estuary so that the intertidal feeding areas were available for a much shorter period. This reduction in feeding area, and feeding time, can be critical in late winter when the birds' energetic requirements are high (Goss-Custard *et al.* 1996a). By including gale frequency, along with mean minimum temperature in late winter and mean bird density on the mussel beds, we are now able to explain around 80% of the yearly variation in the winter mortality of adult mussel-feeding Oystercatchers on the Exe estuary.

Chapter 5: *POPULATION CONSEQUENCES OF OYSTERCATCHER FEEDING SPECIALISATIONS*

This chapter has been submitted for publication in *Oikos* as:
Durell, S.E.A. Le V. dit, Goss-Custard, J.D. & Clarke, R.T. (submitted) Population consequences of age- and sex-related differences in mortality in a migratory shorebird.

I. INTRODUCTION

Detailed studies of one shorebird species, the Eurasian Oystercatcher *Haematopus ostralegus,* have revealed individual differences in habitat use and diet, and in feeding technique on one particular diet (see review in Sutherland *et al.* 1996). These specialisations have been related to age (Goss-Custard & Durell 1983) and to sex (Durell, Goss-Custard & Caldow 1993). A recent review (Durell 2000) concluded that individual feeding specialisations were widespread among many shorebird groups and that most shorebird feeding specialisations were constrained by differences in morphology or social status. These constraints were usually age- or sex-related. For example, juveniles of many species specialised in different habitats and diets because they were subdominant to adults. Sex differences in diet could also be related to dominance, but were more frequently related to differences in morphology, particularly bill size.

There is evidence to suggest that there are fitness consequences associated with the different Oystercatcher feeding specialisations (Durell *et al.* 2001). Durell (2000) described how, even if different feeding strategies were equally profitable, they may have different benefits and different risks. For example, some diets may incur greater risks from parasites or predation. Some prey may be more variable than others, or more subject to changes in environmental conditions, such as drought or severe winter weather. Individuals specialising in different habitats and diets may thus be subjected to different rates of mortality and be affected to a greater or lesser degree by any change.

In many circumstances, higher mortality amongst certain individuals will have little effect on population size except, perhaps, on a local scale. However, if a whole section of the population, such as a particular age group or a particular sex, specialises in a diet which is associated with lower payoffs or higher risks, then the resultant differential mortality may have a marked effect upon population structure and population size. In addition, any catastrophic event and any habitat change or habitat loss which affects one particular age or sex group more than another may have a greater impact on population size than would be predicted if all animals were affected equally. Age or sex groups that are unable to change foraging area, diet or feeding method for social or morphological reasons will be the most vulnerable to any deterioration in their food supply.

On the Exe estuary, south Devon, young Oystercatchers and adult female Oystercatchers specialised in those diets and feeding methods that were associated with lower body condition and higher rates of winter mortality (Durell *et al.* 2001). Moreover, birds specialising in these diets and feeding methods made extensive use of surrounding fields at high water to supplement their low-water diet in late winter (Durell *et al.* 2001). Birds feeding in fields will not only be at greater risk from parasites and predation (Goss-Custard *et al.* 1996), but will also be more susceptible to severe winter weather: earthworms become less active as temperatures drop and become inaccessible when the fields freeze or are covered in snow (Edwards & Lofty 1977). It is likely, therefore, that young birds and females, by relying on field-feeding, may also suffer higher mortality than males during periods of severe winter weather.

In this study, we used a modelling approach (Goss-Custard *et al.* 1995b; Durell, Goss-Custard & Clarke 1997) to investigate the effect of varying the winter mortality of young birds and females on population size, population structure (i.e. the age and sex composition of the population) and population response to habitat loss. We also investigated the effect of age and sex differences in response to sporadic additional winter mortality caused by, for example, severe winter weather.

Previous modelling studies have shown that when a wintering population comprises a mix of separate breeding subpopulations (as is often the case), the effects of winter habitat loss on a given subpopulation can be exacerbated by competition with other subpopulations with a greater reproductive power to compensate for higher winter mortality (Durell, Goss-Custard & Clarke 1997). Therefore, we explored the consequences of varying the mortality of young and female birds within an overwintering population which consisted of two separate breeding subpopulations with different reproductive characteristics.

II. METHODS

(1) The model

The population dynamics model is described in Goss-Custard *et al.* (1995b) and in Durell, Goss-Custard & Clarke (1997). In the model, density-dependence arises because of competition for breeding territories in the summer and for food in winter. In summer, below a certain threshold density of potential breeders (c_T), all potential breeding pairs obtain a territory and breed. Above this threshold density, the proportion of potential breeding pairs which fail to obtain a territory increases at a rate of b_T for every pair ha^{-1}. The threshold (c_T) and the slope (b_T) of breeding territoriality were varied as they have a strong influence on population size (Goss-Custard *et al.* 1995b). However, as initial population size had no effect on our results, they were set at the intermediate values of $c_T = 0.10$ and $b_T = 0.5$ for all simulations presented here. Both breeding subpopulations were given the same territoriality function.

The breeding parameters used were those obtained for the coastal and inland breeding subpopulations of the Atlantic Oystercatcher population (Table 2.4). These give a mean reproductive rate of 0.46 fledglings per pair for coastal breeders and 0.61 fledglings per pair for inland breeders. In simulations, mean values were varied annually at random within ± 2SD of the mean.

In winter, mortality is density-independent below a threshold value of total population density (c_W). Above this threshold, the probability of dying increases at a rate of b_W for every bird ha^{-1} increase in total bird density. Both density-independent and density-dependent winter mortality were varied in the simulations. The threshold density (c_W) was set at 5 birds ha^{-1}, but the winter area was varied so that density-dependent mortality did not occur before habitat was lost, but always had an effect when the winter area was reduced. This was to ensure that the separate effects of density-independent and density-dependent mortality could be distinguished.

The model also allowed for additional winter mortality to take place, representing sporadic deterioration in overwintering conditions, such as severe winter weather. Simulations were run with and without additional winter mortality. In previous versions of the model, additional mortality affected all age and sexes to the same extent. In this version, the additional mortality could be varied for different age and sex groups separately.

(2) Simulation Procedure

The model was run for 100 years to ensure that population size had reached equilibrium. Population statistics were averaged over the next 200 of 300 years. In simulations concerned with the population response to habitat loss, 10 runs were made, with the winter area being reduced by 10% in the second and each subsequent run until 90% of the winter habitat had been removed. Results were plotted as the percentage reduction in population size as a function of the percentage reduction in winter feeding area.

We explored the effect of increasing the winter mortality of young birds and females by increasing a) density-independent mortality b) density-dependent mortality and c) the additional severe winter weather mortality. Mortality rates were only varied within realistic limits, estimated from field data collected from north-west Europe (Goss-Custard *et al.* 1995b; Durell *et al.* 2000, 2001). One of our assumptions was that, whilst mean adult mortality may be known for a given population, the mortality rates of young birds may not be so well known. Thus, when increasing the mortality of young birds, no change was made to the mortality of other age groups. However, when increasing female mortality, male mortality was adjusted so that mean adult mortality rates remained the same. Although it was female mortality which was increased, the results would have been the same whichever sex had been used.

III. RESULTS AND DISCUSSION

(1) Density-independent mortality

Realistic increases in the density-independent mortality of first and second year birds resulted in much lower population sizes than occurred when all groups had the same winter mortality (Fig. 5.1a). However, against expectation, increasing the mortality of young birds only slightly reduced the proportion of all birds that were adults (Fig. 5.1b). This was because Oystercatchers are long-lived birds and so young birds always represent a small fraction of the total population. The reduction in population size resulting from higher mortality in young birds meant that there were fewer potential breeding pairs and so a higher proportion of potential breeding pairs actually bred (Fig. 5.1c). However the proportion of breeding pairs was still below that recorded for Oystercatchers in north-west Europe (Goss-Custard *et al.* 1995a).

Increasing the density-independent mortality of females also resulted in lower population sizes than occurred when all groups had the same mortality (Fig. 5.2a). This was in spite of the fact that male mortalities had been correspondingly reduced so that there was no increase in mean adult winter mortality. As an increase in female mortality resulted in a male-biased population (Fig. 5.2c), and male mortality was lower than females, the mean adult mortality actually decreased (Fig. 5.2b). A male bias amongst birds of breeding age meant that the number of potential breeding pairs was reduced for a given population size (Fig. 5.2d). With fewer potential breeding pairs, fewer pairs actually bred and so breeding output was reduced. Increasing female mortality also increased the proportion of pairs that bred, such that the percent of pairs breeding was similar to that recorded for Oystercatchers in north-west Europe (Fig.5. 2e). Only by increasing female mortality could the proportion of breeding pairs in the model be made to match these field estimates.

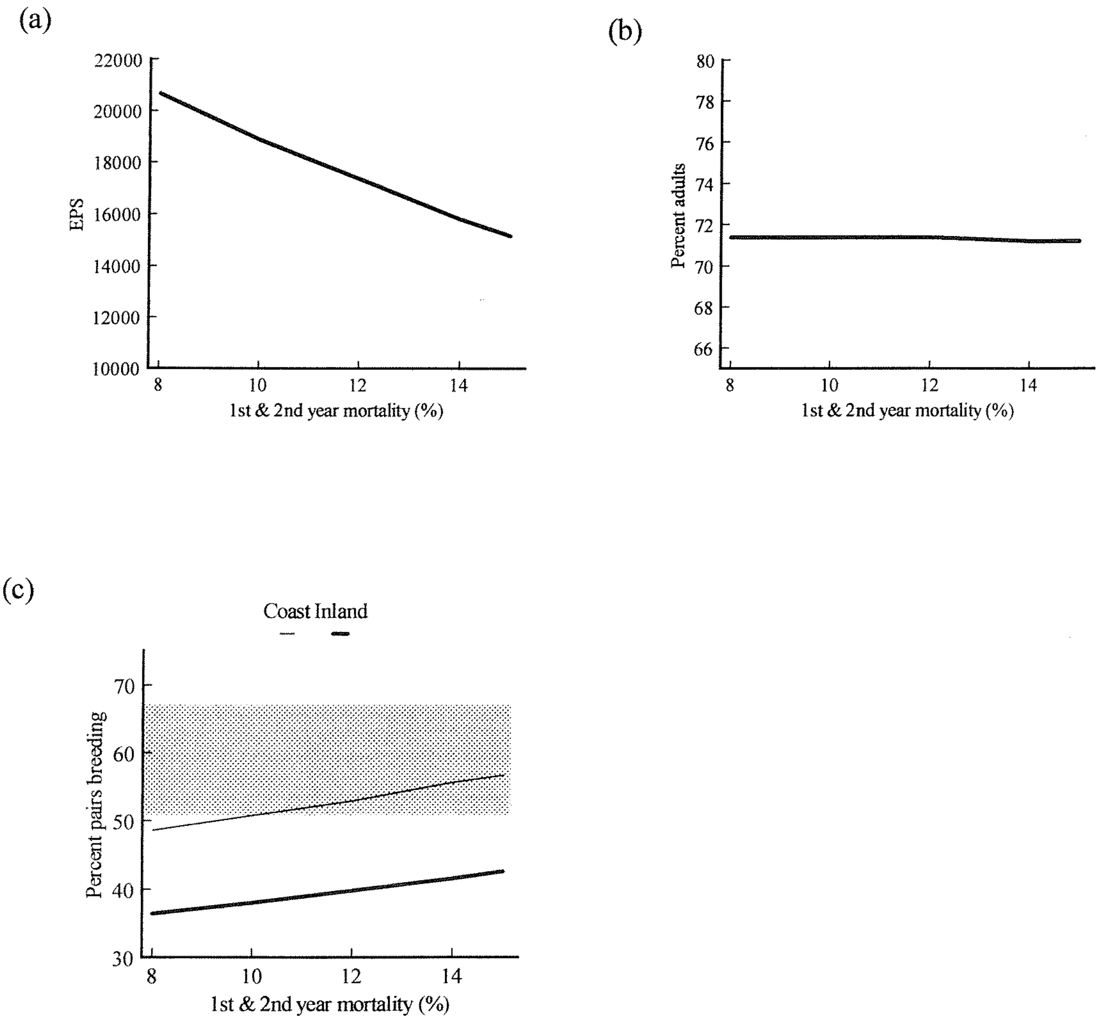


Fig. 5.1 The effect of increasing the density-independent winter mortality of first and second year birds on (a) equilibrium population size (EPS), (b) Percent of adults in the population and (c) the proportion of potential breeding pairs that actually breed. Mortality of birds of three years and above was set at 8%. The shaded area in (c) represents the range of values recorded for Oystercatchers in north-west Europe.

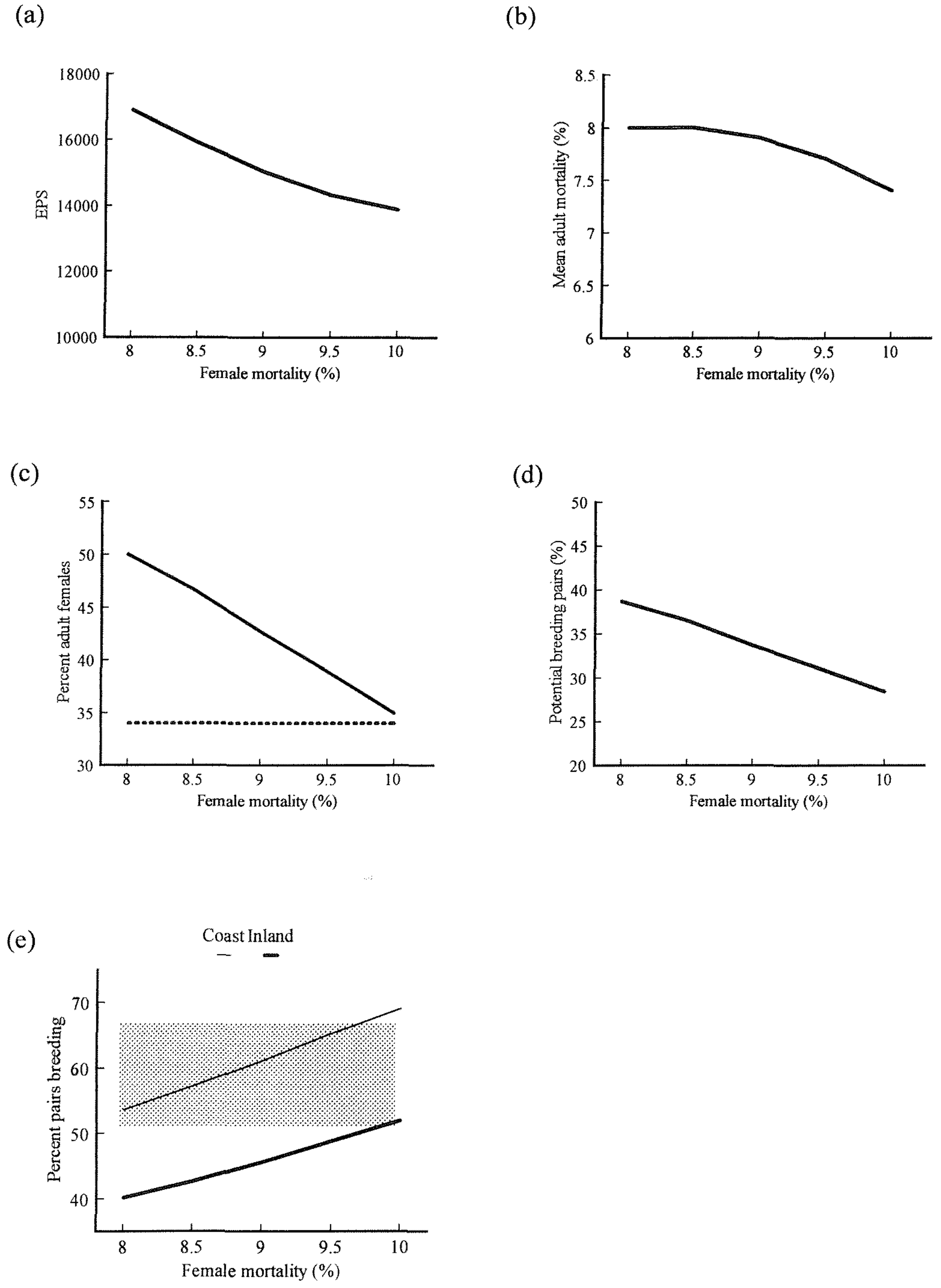


Fig. 5.2 The effect of increasing female density-independent mortality on (a) equilibrium population size (EPS), (b) mean adult mortality, (c) percent females in the adult population, (d) potential breeding pairs as a proportion of the total population and (e) the proportion of potential breeding pairs that bred. Juvenile mortality was set at 15% and second year mortality at 10%. Male mortality was reduced by the same amount as female mortality was increased, so that mean adult mortality at the start of each simulation was 8%. The horizontal dashed line in (c) represents the proportion of females found in the adult population of Oystercatchers on the Exe estuary, UK. The shaded area in (e) represents the range of values recorded for Oystercatchers in north-west Europe.

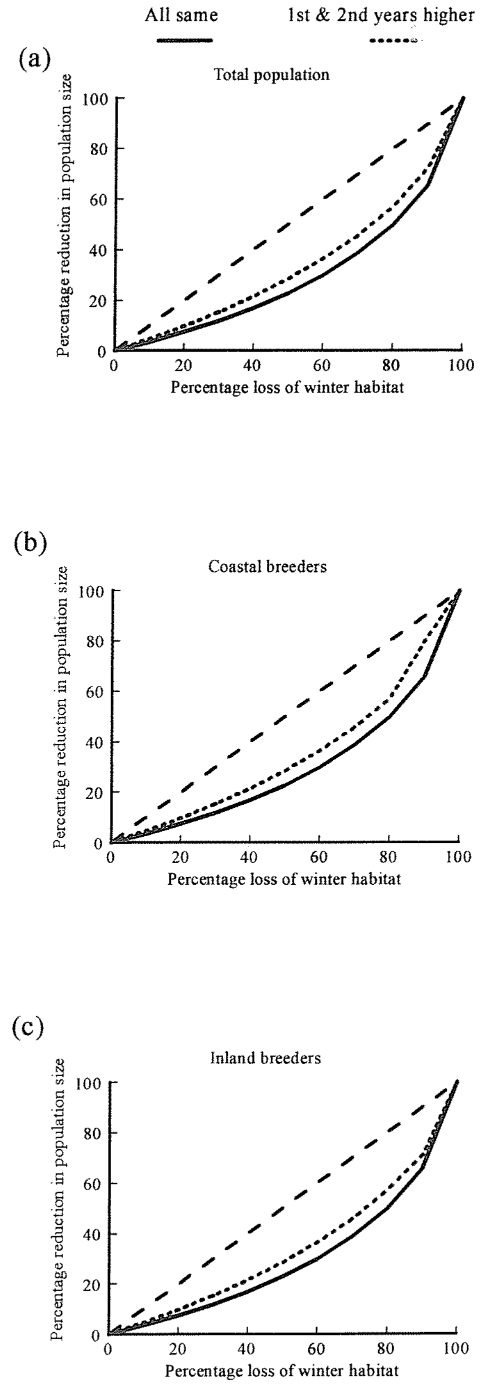


Fig. 5.3 The effect of increasing the strength of density-dependent winter mortality in first and second year birds on the population response to habitat loss of (a) the total population, (b) the coastal breeding subpopulation and (c) the inland breeding subpopulation. The slope (b_W) of density-dependent mortality in first and second year birds was increased from 0.003 to 0.009. The diagonal line represents proportionality.

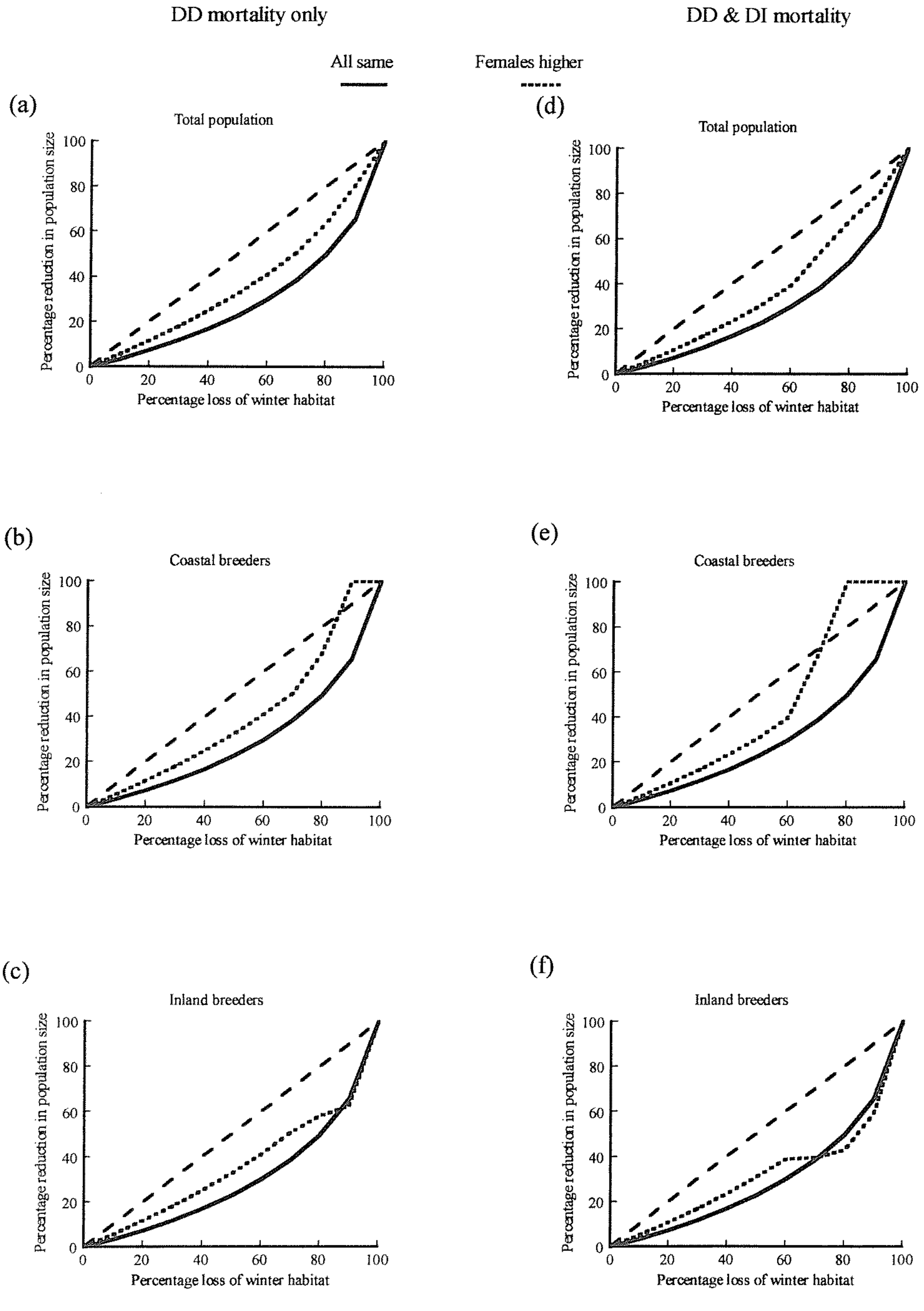


Fig. 5.4 The effect of increasing the strength of density-dependent winter mortality in females on the population response to habitat loss of (a & d) the total population, (b & e) the coastal breeding subpopulation and (c & f) the inland breeding subpopulation. (a-c) sex difference in density-dependent (DD) mortality only, (d -f) sex difference in both density-dependent (DD) and density-independent (DI) mortality (female DI mortality 10%, male DI mortality 6%). The slope (b_W) of density-dependent female mortality was increased from 0.005 to 0.009. The diagonal dashed line represents proportionality.

(2) Density-dependent mortality

Increasing the strength of first and second year density-dependent mortality caused a greater reduction in population size as habitat was lost than if all birds were affected to the same extent (Fig. 5.3). Increasing female density-dependent mortality had the same effect, even though male density-dependent mortality had been correspondingly reduced (Fig. 5.4). In addition, increasing female density-dependent mortality caused the coastal breeding subpopulation to be affected more by habitat loss (Fig. 5.4b) and the inland population less (Fig. 5.4c). Durell, Goss-Custard & Clarke (1997) explain how, when two distinct breeding subpopulations overwinter and compete as one population, the subpopulation with the lower reproductive rate will crash when there are no non-breeding birds available to replace those adults that die, in other words when 100% of pairs are breeding. By decreasing the density of potential breeding pairs, increasing female mortality relative to males caused this point to be reached at a lower rate of winter mortality (Table 5.1), and thus at a lower amount of winter habitat loss (Fig. 5.4b). When the coastal breeding subpopulation goes into a rapid decline, this relieves the pressure in winter for the inland breeding subpopulation, and the rate of population decline for this subpopulation is slowed down (Fig. 5.4c). If both female density-independent and density-dependent mortality were increased, the differential response of the coastal and inland populations was even more marked (Fig. 5.4d-f). This was because the additional female winter mortality relative to males had increased still further the male bias amongst breeding birds, so reducing even more the density of potential breeding pairs for a given population size and lowering further the level of winter mortality at which the critical point of 100% breeding pairs was reached in the coastal breeding subpopulation (Table 5.1).

Table 5.1 The winter mortality rate (%) at which the coastal breeding subpopulation reached the point where all pairs were able to obtain a territory and breed. When this point is reached, there are no non-breeding adults available to replace breeding birds that die and so the subpopulation declines rapidly. DI = density-independent mortality, DD = density-dependent mortality. Mean additional mortality was 10%, probability of occurring 10%.

Sex differences in DI & DD mortality	No additional mortality	No sex difference in additional mortality	Sex difference in additional mortality
DI & DD same	12.3	12.3	11.6
DI same, DD different	11.0	11.0	10.6
DI different, DD same	10.2	10.2	9.3
DI & DD different	9.0	9.0	8.8

(3) Additional severe winter weather mortality

Introducing any additional severe winter weather mortality into the model caused a reduction in equilibrium population size; the magnitude of the effect depending on the frequency and the intensity of the events (Fig. 5.5). If the additional mortality incurred by first and second year birds was increased relative to older birds, there was no effect on population size (Fig. 5.5). This was because, in this case, we reduced the additional mortality in older birds such that the mean additional mortality for all birds remained the same. However, if female additional mortality was set higher, the equilibrium population size was reduced more than if the additional mortality affected all classes of birds equally (Fig. 5.5). By reducing breeding output, the additional female mortality reduced the speed with which the population was able to recover from a catastrophic event (Fig. 5.6). Thus, if the severe weather occurred frequently, the population remained at a lower equilibrium population size (Fig. 5.7).

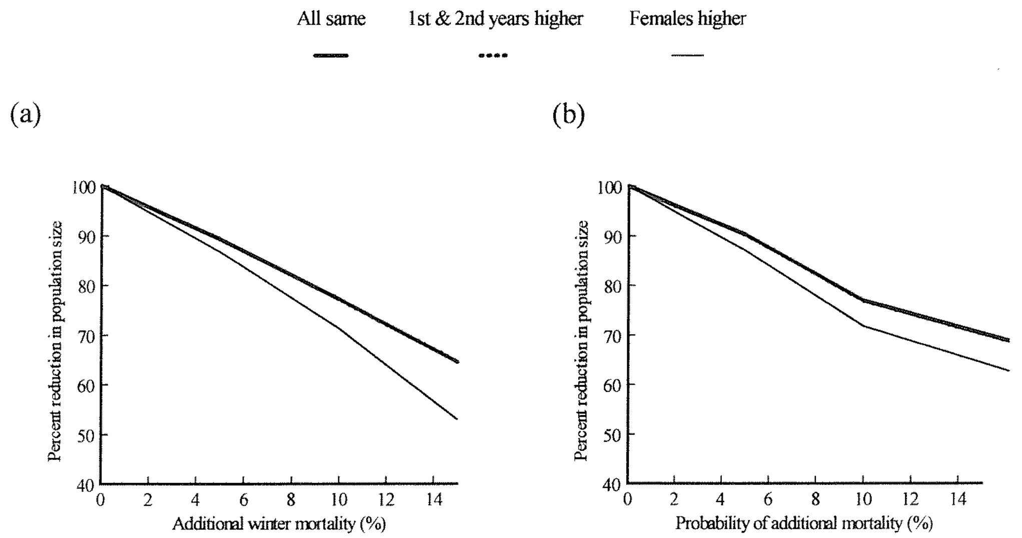


Fig. 5.5 The effect of additional severe winter weather mortality on equilibrium population size with additional mortality affecting all groups the same, first and second years more and females more. (a) increasing the amount of additional mortality, probability of occurrence = 10%, (b) increasing the probability of occurrence, additional mortality = 10%.

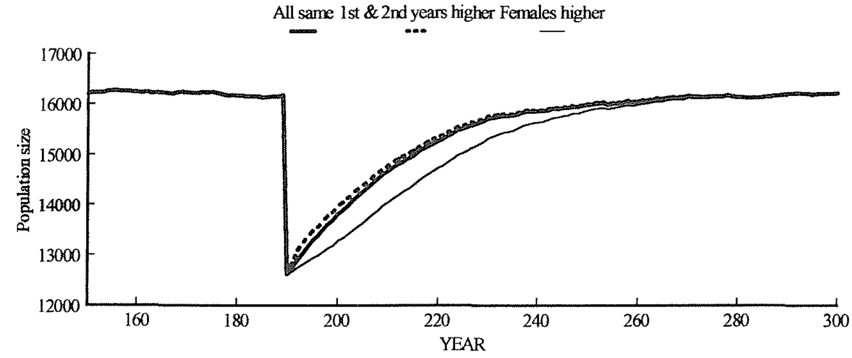


Fig. 5.6 Year plot showing the effect of one catastrophic event on equilibrium population size. All same = all groups have the same additional mortality, 1st & 2nd years higher = first and second year birds affected more by additional mortality, Females higher = females affected more by the additional mortality. Additional mortality for the whole population was 20% in all cases.

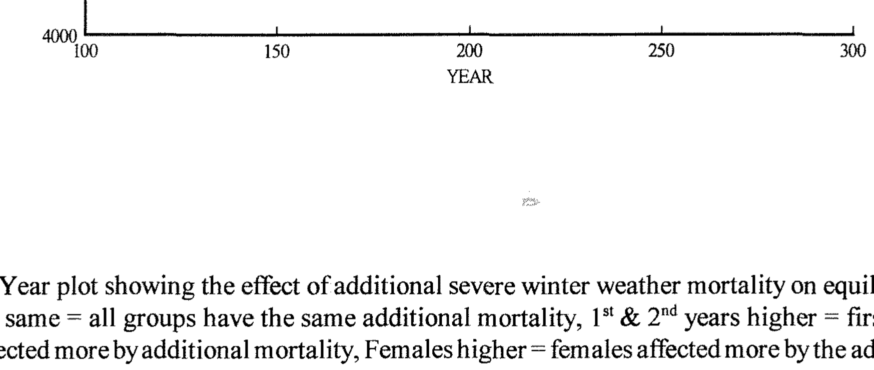


Fig. 5.7 Year plot showing the effect of additional severe winter weather mortality on equilibrium population size. All same = all groups have the same additional mortality, 1st & 2nd years higher = first and second year birds affected more by additional mortality, Females higher = females affected more by the additional mortality, Prob 0 = no severe winter weather. Mean additional mortality = 10%, probability of occurrence = 10%.

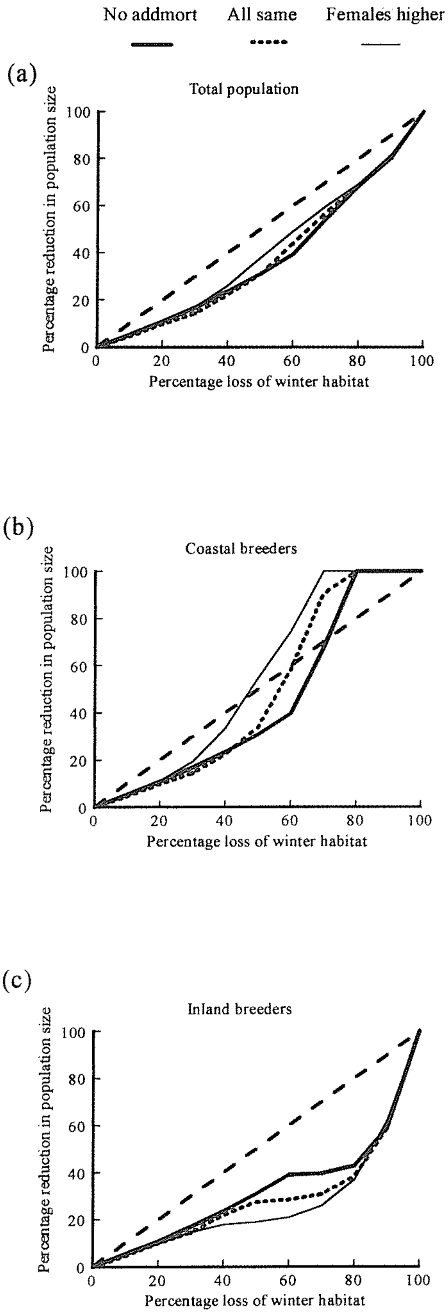


Fig. 5.8 The effect of severe winter weather on the population response to habitat loss. In all three scenarios there are sex differences in both density-independent and density-dependent winter mortality. No addmort = no additional winter mortality, All same = both sexes affected the same by additional winter mortality, Females higher = sex difference in additional mortality. Mean additional mortality = 10%, probability of occurrence = 10%. The diagonal line represents proportionality.

Additional severe winter weather mortality also affected the population response to habitat loss (Fig. 5.8). As winter mortality rates were higher, the coastal breeding subpopulation reached the point where all pairs were breeding at lower levels of winter habitat loss (Fig. 5.8b). Having a sex difference in additional mortality increased the sex bias in the population and so further reduced the rate of winter mortality at which there were no non-breeding adults were available to replace those that died (Table 5.1). Thus a sex difference in additional winter mortality further exaggerated the disproportional effect of winter habitat loss on the separate breeding subpopulations (Fig. 5.8b,c).

IV. CONCLUSIONS

These results suggest that any age- or sex-related differences in feeding specialisation that result in differential mortality rates and/or differential responses to habitat loss or change will have significant population consequences. Increasing the density-independent winter mortality of young birds or females significantly reduced population size. Increasing the strength of density-dependent winter mortality in young birds or females increased the reduction in population size resulting from habitat loss. Increasing female winter mortality also exaggerated the differential response to habitat loss of separate breeding subpopulations overwintering in the same place. Moreover, if additional severe winter weather killed more females than males, population size was reduced more than if there had been no sex bias in the birds that died.

It is generally accepted that the mortality of young birds is higher than that of adults (Boyd 1962; Evans & Pienkowski 1984). However, it is not always easy to monitor mortality rates in young migratory birds as, firstly, any scheme colour-ringing birds on the wintering grounds will not be able to catch all juveniles before some die and secondly, because young birds are more likely to emigrate to other overwintering areas. Thus any environmental change which increases the mortality of young birds only may not necessarily be noticed. We suggest that conservationists should pay attention to any age-related feeding specialisation which would mean that young birds may be affected more by environmental change that adults.

The size of shorebird populations is affected most by adult survivorship (Myers *et al.* 1987; Evans 1991; Hitchcock & Gratto-Trevor 1997). Much attention is paid, therefore, to adult winter mortality. This study has shown that if one sex has a higher mortality than another, total population size will be less than expected for a given mean rate of adult winter mortality. Increasing mortality in one sex in older birds had a marked influence not only on total population size, but also on the population sex ratio, the percent of pairs breeding and the population response to habitat loss or change. Any study of population dynamics should, therefore, be aware not only of age differences in mortality, but also of any differences in mortality between the sexes. Until now, population models designed to predict the effect of habitat loss or change on shorebirds have not considered sex differences in winter mortality (Goss-Custard & Durell 1990; Sutherland & Dolman 1994; Dolman & Sutherland 1995; Goss-Custard *et al.* 1995a,b; Goss-Custard *et al.* 1996; Goss-Custard & Sutherland 1997). Our results suggest that future models should consider including sex differences in mortality and sex differences in response to environmental change.

Chapter 6: INDIVIDUAL FEEDING SPECIALISATION: DISCUSSION

I.: MECHANISMS AND CONSTRAINTS

In Chapter 1, I described the different mechanisms that may be responsible for individual differences in feeding behaviour. These were (1) differences due to a patchy environment, (2) phenotypic differences and (3) frequency-dependent selection (Partridge & Green 1985). I chose to subdivided phenotypic differences into (a) morphological differences, (b) individually acquired skills and (c) differences in social status. I pointed out that these mechanisms were not mutually exclusive and that it is often difficult to establish their relative importance in any given situation. I also suggested that any specialisation can be seen as an individual strategy, and that the optimum strategy for any given individual will be conditional upon its specific priorities and constraints.

Research into Oystercatcher feeding specialisations has provided evidence for most of the above mechanisms, as follows:

Differences due to a patchy environment: age and sex differences have been found in Oystercatcher distribution in the non-breeding season (Swennen 1984; Durell & Goss-Custard 1996; Durell, Ormerod & Dare 1996a). However, it is difficult to establish whether these differences in distribution are the cause of differences in diet or whether feeding specialisations result in these differences in distribution. On countrywide scale, Oystercatchers overwintering in different estuaries will certainly be presented with different suites of available prey.

Morphological differences: Oystercatchers with shorter, stouter bills, the majority of which are males, specialise in hard-shelled prey whilst those with longer, thinner bills, the majority of which are females, specialise on worm feeding (Hockey & Underhill 1984; Durell *et al.*1993; Ens *et al.* 1996). Also, when feeding on hard-shelled prey, males specialise in 'hammering' the prey open whilst females specialise in 'stabbing', or taking the prey *in situ* (Durell *et al.*1993; Hulscher *et al.*1996a).

Individually acquired skills: when feeding on mussels, no juvenile Oystercatchers were seen to use the hammering technique (Goss-Custard & Durell 1987). Mussel-hammerers only adopted the hammering technique in their second or third winter, suggesting that mussel hammering is a skill which takes some individuals some time to acquire (Goss-Custard & Durell 1987). Differences in experience or skill may also be the reason why individual Oystercatchers specialise in hammering mussels open on either the ventral side or the dorsal side (Durell & Goss-Custard 1984; Sutherland & Ens 1987) and in hammering *Macoma* open on either the right or left valve (Hulscher1982).

Differences in social status: young Oystercatchers tend to be subdominant to adults and immature birds, which fed on preferred mussel beds throughout the summer, were displaced when the adults returned in the autumn (Goss-Custard *et al.* 1982b). These displaced birds either moved to less preferred mussel beds or changed diet altogether, feeding on mudflats and in fields (Goss-Custard & Durell 1983).

Frequency-dependent selection: this is the one mechanism for which there is no empirical evidence. However, frequency-dependence must play some role in an individual's choice of feeding specialisation. It is possible, for example, that an Oystercatcher's initial choice of hammering mussels on the dorsal or ventral side is frequency-dependent.

Whatever the mechanisms involved, the main constraints to Oystercatcher feeding specialisation are phenotypic: certain individuals appear to be restricted in their choice of habitat, diet or feeding method because of their bill structure, their social status or their individual skill. In my review of shorebird feeding specialisations, I concluded that most shorebird specialisations were phenotypically constrained. In particular, individual feeding strategies were determined to a large extent by morphological differences, particularly differences in bill size.

Individual specialisation in other animals also appears to be primarily determined by differences in morphology or social status. Sex differences in diet or habitat use have been found in many size dimorphic species, including raptors, owls, skuas and gulls (Andersson & Norberg 1981; Temeles 1985; Greig, Coulson & Monaghan 1985), snakes (Forsman 1991; Shine *et al.* 1998), kangaroos (Newsome 1980), primates (Gautier-Hion 1980) and ungulates (Bowyer 1984; Clutton-Brock, Iason & Guinness 1987; Perez-Barbara & Gordon 1999). Sex differences in bill size have also been associated with differences in diet or habitat use in a wide variety of bird species (Selander 1966; Hogstad 1976; Aulen & Lunberg 1991; Williams 1991; Gosler & Carruthers 1994). Age- and sex-related feeding specialisations in several bird species other than shorebirds have also been explained by differences in social status (Davies & Green 1976; Peters & Grubb 1983; Ekman & Askenmo 1984; Gustafsson 1988).

There are many different reasons, and many different hypotheses, for individual differences in morphology, but they can be divided into those which are and those which are not ultimately determined by the food supply. Trophic polymorphisms which are not related to age or sex have been shown to be adaptations to prey or habitat variability. Bill size polymorphism in the Hook-billed kite was related to the available size ranges of its prey, terrestrial snails (Smith & Temple 1982). In both African finches (Smith 1987) and Darwin's finches (Gibbs & Grant 1987) bill size polymorphism was seen to be a genetic adaptation to an oscillating environment, where a particular bill size was the optimum in different years. In lake dwelling fish, the evolution of different morphs has been attributed to the lack of interspecific competition and the availability of vacant niches (Skulason & Smith 1995). Such polymorphisms can thus be seen as adaptations for a varied and changing environment.

On the other hand, although the degree of sexual dimorphism can be related to the nature of the prey taken (Andersson & Norberg 1981; von Schantz & Nilsson 1981; Temeles 1985), sex differences in body size are usually considered to be a function of a species' breeding system and the role played by each sex in egg formation, territory acquisition and defence, competition for mates and/or parental care. Sex differences in bill length, although enabling monogamous pairings to exploit a wider range of food resources, may also primarily be a secondary sex characteristic promoting rapid pair formation. Less attention has been paid to age differences in morphology, but they can be assumed to be developmental. Age and sex-related polymorphisms, therefore, are less likely to be ultimately caused by variations in the food supply.

There is also no reason to suppose that differences in social status are primarily adaptations designed to cope with variations in the food supply. Thus feeding specialisations which are age- and sex-related are constrained by phenotypic differences which are not primarily dietary adaptations. In this thesis, I concentrated on the three main feeding specialisations found amongst Oystercatchers on the Exe estuary: mussel-hammering, mussel-stabbing and worm/clam feeding. These three specialisations were related to age (Goss-Custard & Durell 1983) and to sex (Durell *et al.* 1993). I suggest that not only are the phenotypic constraints underlying these specialisations unlikely to be adaptations designed to cope with a variable food supply, but also that they will result in the different age and sex groups being restricted in their choice of diet or feeding method.

II. FITNESS IMPLICATIONS

Different feeding specialisations will be associated with different benefits and different risks. The implications of this are that individuals which specialise on less profitable prey will be at greater risk of having poor body condition, of failing to breed or of dying. The research presented in this thesis showed that there were significant differences in body condition and mortality of Oystercatchers with different feeding specialisations. Mussel-hammerers had higher body condition indices and lower rates of mortality than mussel-stabbers and all mussel feeders had higher body condition indices and lower rates of mortality than worm/clam feeders. One would expect, therefore, mussel-hammering to be the preferred feeding strategy. However, not all individuals are capable of employing this technique. As shown above, mussel-hammerers need to have shorter, stouter bills and have a certain degree of skill or experience. It is also likely that, as mussel-hammerers are more prone to interference than birds with other feeding specialisations (Stillman *et al.* 1996), they need to have higher competitive abilities. On the other hand, worm feeders have much lower levels of interference than mussel feeders

(Durell *et al.* 1996b). Worms are also intrinsically easier to manipulate than mussels and there is no risk of bill damage. For these reasons, one would expect worm feeders to be those birds with less robust bills, less skill or of lower social status.

As the majority of mussel-hammerers were adult males and the majority of worm/clam feeders were young birds and females one would predict that young birds and females would have higher rates of winter mortality than adult males. Young Oystercatchers on the Exe are known to have higher mortality rates than adults (Goss-Custard *et al.* 1982a). In this study, there were insufficient data to compare mortality rates between the sexes, but Durell & Goss-Custard (1996) demonstrate how the male bias amongst adult Oystercatchers on the Exe estuary must be due, in part, to higher female mortality. I suggest that these age- and sex-related differences in mortality are due, at least in part, to the fitness consequences of individual feeding specialisations.

I am not aware of any studies on other species that have compared the fitness of individuals specialising in particular diets or feeding methods. However, it is generally assumed that when particular individuals are excluded from a feeding area, diet or feeding method by more dominant animals the preferred diet or feeding method will be the most profitable. There is also every reason to suppose that, as with the Oystercatcher, there will be significant fitness differences between certain diets or feeding methods. More research is needed to investigate the fitness implications of feeding specialisation in other animals.

III. POPULATION CONSEQUENCES

Understanding variation in individual behaviour can be critical in explaining demographic processes such as density-dependence (eg. Sutherland 1996b). Because individuals will vary in, for example, their competitive ability or their foraging efficiency, they will differ in their response to increases in population density. Such variation will determine how many individuals will fail to breed or to starve at different population levels and is the underlying principle of the individuals-based models developed for shorebird populations (Sutherland & Dolman 1994; Goss-Custard *et al.* 1996a; Goss-Custard & Sutherland 1997; Stillman *et al.* 2000).

The fact that individual Oystercatchers specialise on particular diets and feeding methods adds complexity to the way in which individuals vary in their foraging ability. As there are fitness consequences associated with Oystercatcher feeding specialisations, whole sections of the population may have a higher chance of survival than others. Moreover, as feeding specialisations are age- and sex-related, there will be differential mortality between age groups and between the sexes. This age- and sex-related differential mortality can have a marked effect on population structure and population size. Using a modelling approach, I showed that increasing the mortality of young Oystercatchers had little effect on population structure, but substantially reduced population size. Increasing female mortality had a marked effect on population structure, population size and the population response to habitat loss. By producing a male bias in the breeding population, increasing female mortality reduced the number of potential breeding pairs and thus decreased breeding output. Moreover, any increase in mortality which affected one sex more than the other resulted in a greater reduction in population size than if the increase affected both sexes the same.

Population models developed in order to understand better the effect of habitat loss or change on shorebird population size included age differences in mortality but did not considered sex differences (Goss-Custard & Durell 1990; Goss-Custard *et al.* 1995b,c). These models also assumed that all individuals were affected in the same way and to the same extent by habitat loss. Later game-theoretic, individuals-based models included age classes, but did not consider any sex difference in individual foraging success (Sutherland & Dolman 1994; Goss-Custard *et al.* 1996a; Goss-Custard & Sutherland 1997; Stillman *et al.* 2000). Although it is often desirable to maintain simplicity in modelling, my work on Oystercatchers has highlighted the importance of considering sex differences in mortality and sex ratios amongst individuals of breeding age. Failure to do so may lead to erroneous assumptions being made about, for example, the balance required between rates of reproduction and mortality in order to maintain any given animal population.

IV. CONSERVATION IMPLICATIONS

There has long been considerable interest in the conservation of migratory shorebirds, not least because of the international nature of their lifestyles (eg. Piersma & Baker 2000). Shorebirds are relatively long-lived animals, so variation in adult survival matters more to population size than variation in breeding success (Myers *et al.* 1987; Evans 1991; Hitchcock & Gratto-Trevor 1997). As most adults die during the non-breeding season (Evans 1991), conservation interests have been focussed on protecting those habitats used by shorebirds on migration and during the winter months. These habitats are also concentrated in temperate latitudes, where there is often considerable pressure from, for example, improved agricultural techniques, land reclamation, shellfishing, pollution and disturbance. One of the main concerns of conservationists, therefore, is predicting the effect on shorebird populations of any reduction in the area or the quality of these habitats.

The use of behavioural studies to inform conservation strategies has proved to be extremely valuable (see examples in Gosling & Sutherland 2000). Understanding the way in which animals behave can provide valuable insights into population ecology and population response to environmental change. In particular, understanding the way in which individuals vary in their behaviour is of fundamental importance not only to population ecology, but also to practical conservation. Individual feeding specialisation is one way in which individuals may vary in their behaviour and, as I have shown in Chapter 1, feeding specialisation is not uncommon in many shorebird groups.

The main implication for conservation of individual variation in feeding strategy is that, if individuals specialise on a particular habitat or a particular diet they will be affected to a greater or lesser degree by any environmental change. Any habitat loss or change will affect a particular geographical area, a particular habitat or a particular suite of prey species. Thus removal of certain feeding areas will affect only particular groups of birds. Habitat loss will also result in increased competition for the remaining resources. Some individuals may be more susceptible to increased competition, particularly if they specialise on a diet or feeding method associated with already high levels of interference. Individuals will be particularly vulnerable if they are unable to move to another area or to switch to a different diet.

The phenotypic constraints to Oystercatcher feeding specialisations have particular relevance for conservationists. Phenotypic constraints mean that individuals will be restricted in their choice of feeding strategy and may not be able to change diets when faced with any deterioration in their feeding conditions. Phenotypic constraints are also largely related to a bird's age or a bird's sex, so that vulnerable individuals will often represent a significant proportion of a certain section of the population, for example juveniles or females. If one age or sex group is affected more than another by any deterioration in conditions, the effect on population size can be greater than would be predicted if all groups were affected equally. Age- and sex-related feeding specialisations should, therefore, be of particular concern to conservationists.

It is not always easy to identify different ages and sexes in overwintering shorebirds and studies aimed at predicting the effect of habitat change or loss will not always know the age and sex composition of a particular population, or how the ages and sexes are distributed over the habitats available. Yet understanding the distribution of the different age and sex groups may be critical in understanding the effect of any change. For this reason, it is important that conservationists are aware of any age- or sex-related feeding specialisations in their study species that may result in particular age or sex groups feeding in different habitats, or being more vulnerable to loss of feeding sites. Also, population models built to predict the effect of habitat loss or change should be able to incorporate age and sex differences in mortality and age and sex differences in response to change. Failure to take into account age or sex differences could lead to erroneous conclusions and policy decisions based on flawed predictions.

V. FUTURE WORK

Although it would appear that research into Oystercatchers has been particularly exhaustive, there are still questions that remain. In particular, it needs to be confirmed that adult females do have higher mortality than males. It would also be interesting to discover if the male bias found on the Exe is a local phenomenon or whether, as may be the case, there is a male bias amongst the whole north-west Europe population. Less easy to achieve, but most interesting, would be to monitor the effect of actual habitat loss on an Oystercatcher population to see whether one sex or age group is particularly affected and to see how flexible the birds are in their behavioural response to change.

Population models developed for Oystercatchers are now being applied to other groups of shorebirds (unpublished information). More research is needed into individual variation in feeding strategy in other shorebirds: for example, investigating the mechanisms involved in any feeding specialisations and determining whether they are phenotypically constrained. In particular, more needs to be known about the different benefits and risks associated with different habitats or diets and how these will affect mortality rates in different groups of birds. Should any habitat loss or change occur, any monitoring exercise should pay particular attention to the age and sex distribution of those birds that are adversely affected.

REFERENCES

Andersson, M & Norberg, R.A. (1981) Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. *Biological Journal of the Linnean Society* **15**, 105-130.

Atkinson, N.K., Summers, R.W., Nicoll, M. & Greenwood, J.J.D. (1981) Population, movements and biometrics of the Purple Sandpiper *Calidris maritima* in eastern Scotland. *Ornis Scandinavica* **12**, 18-27.

Aulen, G., & Lundberg, A. (1991) Sexual dimorphism and patterns of territory use by the White-backed Woodpecker *Dendrocopus leucotos. Ornis Scandinavica* **22**, 60-64.

Baillie, S. (1980) The effect of the hard winter of 1978/79 on the wader populations of the Ythan estuary. *Wader Study Group Bulletin* **28**, 16-17.

Baker, A.J. (1974) Criteria for ageing and sexing New Zealand Oystercatchers. *New Zealand Journal of Marine and Freshwater Research* **8**, 211-221.

Baker, A.J. (1975) Age structure and sex ratio of live-trapped samples of South Island Pied Oystercatchers (*Haematopus ostralegus finschi). Notornis* **22**, 189-194.

Barbosa, A. & Moreno, E. (1999) Evolution of foraging strategies in shorebirds: an ecomorphological approach. *The Auk* **116**, 712-725.

Berg, A. (1993) Food resources and foraging success of Curlews *Numenius arquata* in different farmland habitats. *Ornis Fennica* **70**, 22-31.

Beukema, J.J., Essink, K., Michaelis, H., & Zwarts, Z. (1993) Year-to-year variability in the biomass of macrozoobenthic species living at different places on the tidal flats in the Wadden Sea. *Hydrobiologica* **142**, 199-207.

Blem, C.R. (1976) Patterns of lipid storage and utilisation in birds. *Amateur Zoologist* **16**, 671 -684.

Blem, C.R. (1990) Avian energy storage. *Current Ornithology, Vol. 7* (ed. D.M. Power), pp. 59-113. Academic Press, New York.

Blomqvist, D., Johansson, O.C., Unger, U., Larsson, M. & Flodin, L-A. (1997) Male aerial display and reversed sexual size dimorphism in the dunlin. *Animal Behaviour* **54**, 1291-1299.

Boates, J.S. & Goss-Custard, J.D. (1989) Foraging behaviour of Oystercatchers *Haematopus ostralegus* during a diet switch from worms *Nereis diversicolor* to clams *Scrobicularia plana. Canadian Journal of Zoology* **67**, 2225-2231.

Boates, J.S. & Goss-Custard, J.D. (1992) Foraging behaviour of Oystercatchers *Haematopus ostralegus* specialising on different species of prey. Canadian Journal of Zoology **70**, 2398-2404.

Bowyer, R.T. (1984) Sexual segregation in Southern Mule Deer. *Journal of Mammology* **65**, 410-417.

Boyd, H. (1962) Mortality and fertility of European Charadrii. *Ibis* **104**, 368-387.

Brunton, D.H. (1988a) Sexual differences in reproductive effort: time-activity budgets of monogamous Killdeer, *Charadrius vociferus. Animal Behaviour* **36**, 705-717.

Brunton, D.H. (1988b) Energy expenditure in reproductive effort of male and female Killdeer (*Charadrius vociferus). Auk* **105**, 553-564.

Buchanan, J.B., Brennan, L.A., Schick, C.T., Herman, S.G. & Johnson, T.M. (1986) Age and sex composition of wintering Dunlin populations in western Washington. *Wader Study Group Bulletin* **46**, 37-41.

Burger, J. (1980) Age differences in foraging Black-necked stilts in Texas. *Auk* 97, 633-636.

Burger, J. & Gochfield, M. (1985) Age-related differences in foraging in the Masked Lapwing *Vanellus miles* in Australia. *Emu* **85**, 47-48.

Burger, J. & Gochfield, M. (1986) Age differences in foraging efficiency of American Avocets *Recurvirostra americana. Bird Behaviour* **6**, 66-71.

Caldow, R.W.G., Goss-Custard, J.D., Stillman, R.A., Durell, S.E.A. Le V. dit, Swinfen, R. & Bregnballe, T. (1999) Individual variation in the competitive ability of interference-prone foragers: the relative importance of foraging efficiency and susceptibility to interference. *Journal of Animal Ecology* **68**: 869-878.

Camphuysen, C.J., Ens, B.J., Heg, D., Hulscher, J.B., Van der Meer, J. & Smit, C.J. (1996) Oystercatcher *Haematopus ostralegus* winter mortality in The Netherlands: the effect of severe weather and food supply. *Ardea* **84A**, 469-492.

Castro, G., Myers, J.P. & Ricklefs, R.E. (1992) Ecology and energetics of Sanderlings migrating to four latitudes. *Ecology* **73**, 833-844.

Clark, N.A. (1982) The effects of the severe winter weather in December 1981 and January 1982 on waders in Britain. *Wader Study Group Bulletin* **34**, 5-7.

Clark, N. A. (1983) The ecology of Dunlin (*Calidris alpina L.*) wintering on the Severn Estuary. PhD Thesis, University of Edinburgh.

Clark, N.A. (1993) Wash Oystercatchers starving. *BTO News* **185**, 1,24.

Clutton-Brock, T.H., Guinness, F.E. & Albon, S.D. (1982) *Red Deer: Behaviour and Ecology of Two Sexes.* Edinburgh University Press, Edinburgh.

Clutton-Brock, T.H., Iason, G.R. & Guinness, F.E. (1987) Sexual segregation and density-related changes in habitat use in male and female Red deer (*Cervus elaphus*). *Journal of Zoology, London* **211**, 275-289.

Cramp, S. & Simmons, K.E.L. (1983) *The Birds of the Western Palearctic, Vol. 3*. Oxford University Press, Oxford.

Cranswick, P.A., Kirby, J.S. & Waters, R.J. (1992) *Wildfowl and wader counts 1991-1992: the results of the National Waterfowl Counts and Birds of Estuaries Enquiry in the United Kingdom.* Wildfowl and Wetlands Trust, Gloucester.

Cresswell, W. (1994) Age-dependent choice of redshank (*Tringa totanus*) feeding location: profitability or risk? *Journal of Animal Ecology* **63**, 589-600.

Cresswell, W. & Whitfield, D.P. (1994) The effects of raptor predation on wintering wader populations at the Tyninghame estuary, southeast Scotland. *Ibis* **136**, 223-232.

Dare, P.J. (1970) The movements of Oystercatchers Haematopus ostralegus L. visiting or breeding in the British Isles. *Fishery Investigations, Series II* **25**, 1-137.

Dare, P.J. (1977) Seasonal changes in body-weight of Oystercatchers *Haematopus ostralegus. Ibis* **119**, 494-506.

Dare, P. J. & Mercer A.J. (1973) Foods of the Oystercatcher in Morecambe Bay, Lancashire. *Bird Study* **20**, 173-184.

Davidson, N.C. (1981) Survival of shorebirds (Charadrii) during severe weather: the role of nutritional reserves. *Feeding and survival strategies of estuarine organisms,*(eds N.V. Jones & W.J. Wolff), pp. 231-249. Plenum Press, New York.

Davidson, N.C. (1982) Changes in the body-condition of redshanks during mild winters: an inability to regulate reserves? *Ringing and Migration* **4**, 51-62.

Davidson, N.C. (1983) Formulae for estimating the lean weights and fat reserves of live shorebirds. *Ringing and migration* **5**, 49-64.

Davidson, N.C. & Clark, N.A. (1985) The effects of severe weather in January and February 1985 on waders in Britain. *Wader Study Group Bulletin* **44**, 10-16.

Davidson, N.C. & Evans, P.R. (1982) Mortality of Redshanks and Oystercatchers from starvation during severe weather. *Bird Study* **29**, 183-188.

Davidson, N.C., Townshend, D.J., Pienkowski, M.W. & Speakman, J.R. (1986a) Why do curlews *Numenius* have decurved bills? *Bird Study* **33**, 61-69.

Davidson, N.C., Evans, P.R. & Uttley, J.D. (1986b) Geographical variation of protein reserves in birds: the pectoral muscle mass of Dunlins *Calidris alpina* in winter. *Journal of Zoology* **208**, 125-133.

Davies, N.B. (1982) Behaviour and competition for scarce resources. *Current Problems in Sociobiology* (ed. King's College Sociobiology Group), pp.363-380. Cambridge University Press, Cambridge.

Davies, N.B. & Green, R.E. (1976) The development and ecological significance of feeding techniques in the Reed Warbler (*Acrocephalus scirpaceus*). *Animal Behaviour* **24**, 213-229.

Desprez, M., Rybarczyk, H., Wilson, J.G., Ducrotoy, J.P., Sueur, F., Olivesi, R. & Elkaim, B. (1992) Biological impact of eutrophication in the bay of Somme and the induction and impact of anoxia. *Netherlands Journal of Sea Research* **30**, 149-159.

Dugan, P.J., Evans, P.R., Goodyer, L.R. & Davidson, N.C. (1981) Winter fat reserves: disturbance of regulated levels by severe weather conditions. *Ibis* **123**, 359 - 363.

Durell, S.E.A. Le V. dit & Goss-Custard, J.D. (1984) Prey selection within a size class of mussels, *Mytilus edulis*, by Oystercatchers, *Haematopus ostralegus*. *Animal Behaviour* **32**, 1197-1203.

Durell, S.E.A. Le V. dit & Goss-Custard, J.D. (1996) Oystercatcher *Haematopus ostralegus* sex ratios on the wintering grounds: the case of the Exe estuary. *Ardea* **84A**, 373-381.

Durell, S.E.A. Le V. dit, Goss-Custard, J.D. & Caldow, R.W.G. (1993) Sex-related differences in diet and feeding method in the Oystercatcher *Haematopus ostralegus*. *Journal of Animal Ecology* **62**, 205-215.

Durell, S.E.A. Le V. dit, Ormerod, S.J. & Dare, P.J. (1996a) Differences in the population structure between two Oystercatcher roosts on the Burry Inlet, South Wales. *Ardea* **84A**, 383-388.

Durell, S.E.A. Le V. dit, Goss-Custard, J.D. & Perez-Hurtado, A. (1996b) The efficiency of juvenile Oystercatchers *Haematopus ostralegus* feeding on Ragworms *Nereis diversicolor*. *Ardea* **84A**, 153-157.

Durell, S.E.A. Le V. dit, Goss-Custard, J.D. & Clarke, R.T. (1997) Differential response of migratory subpopulations to winter habitat loss. *Journal of Applied Ecology* **34**, 1155-1164.

Durell, S.E.A. Le V. dit, Goss-Custard, J.D., Clarke, R.T. & McGrorty, S. (2000) Density-dependent mortality in Oystercatchers *Haematopus ostralegus*. *Ibis* **142**: 132-138.

Durell, S.E.A. Le V. dit, Goss-Custard, J.D., Caldow, R.W.G., Malcolm, H.M. & Osborn, D. (2001) Sex, diet and feeding-method related differences in body condition in the Oystercatcher *Haematopus ostralegus*. *Ibis* **143**: 107-119.

Edwards, C.A. & Lofty, J.R. (1977) *Biology of Earthworms.* Chapman & Hall, London.

Ekman, J.B. & Askenmo, C.E.H. (1984) Social rank and habitat use in Willow tit groups. *Animal Behaviour* **32**, 508-514.

Ekman, J.B. & Hake, M.K. (1990) Monitoring starvation risk: adjustments of body reserves in greenfinches (*Cardueis chloris* L.) during periods of unpredictable foraging success. *Behavioural Ecology* **1**, 62-67.

Ekman, J.B. & Lilliendahl, K. (1993) Using priority to food: fattening strategies in dominance structured willow tit *Parus montanus* flocks. *Behavioural Ecology* **4**, 232-238.

Ens, B.J. (1992) *The Social Prisoner: causes of natural variation in reproductive success of the Oystercatcher.* PhD thesis. University of Groningen.

Ens, B.J. & Goss-Custard, J.D. (1984) Interference among Oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*, on the Exe estuary. *Journal of Animal Ecology* **53**, 217-231.

Ens, B.J., Kersten, M., Brenninkmijer, A. & Hulscher, J.B. (1992) Territory quality, parental effort and reproductive success of Oystercatchers (*Haematopus ostralegus*). *Journal of Animal Ecology* **61**, 703-715.

Ens, B.J., Bunskoeke, A.J., Hoekstra, R., Hulscher, J.B., Kersten, M. & De Vlas, S.J. (1996a) Prey choice and search speed: why simple optimality fails to explain the prey choice of Oystercatchers *Haematopus ostralegus* feeding on *Nereis diversicolor* and *Macoma balthica. Ardea* **84A**, 73-89.

Ens, B.J., Briggs, K.B., Safriel, U.N. & Smit, C.J. (1996b) Life history decisions during the breeding season. *The Oystercatcher: from individuals to populations,* (ed. J.D. Goss-Custard), pp. 186-218. Oxford University Press, Oxford.

Espin, P.M.J., Mather, R.M. & Adams, J. (1983) Age and foraging success in Black-winged Stilts. *Ardea* **71**, 225-228.

Esselink, P. & Zwarts, L. (1989) Seasonal trend in burrow depth and tidal variation in feeding activity of *Nereis diversicolor. Marine Ecology Progress Series* **56**, 243-254.

Evans, P.R. (1979) Adaptations shown by foraging shorebirds to cyclical variations in the activity and availability of their intertidal invertebrate prey. *Cyclic phenomena in marine plants and animals* (eds E. Naylor & R.G. Hartnoll), pp. 357-366. Pergamon Press, Oxford.

Evans, P.R. (1980) Movements of wader populations between estuaries: some questions raised by studies at Teesmouth. *Wader Study Group Bulletin* **29**, 6.

Evans, P.R. (1991) Seasonal and annual patterns of mortality in migratory shorebirds: some conservation implications. *Bird Population Studies: Relevance to Conservation and Management* (eds C.M. Perrins, J.-D. Lebreton & G.J.M. Hirons), pp. 346-359. Oxford University Press, Oxford.

Evans, P.R. & Pienkowski, M.W. (1984) Population dynamics of shorebirds. *Shorebirds: Breeding Behaviour and Populations* (eds. J. Burger & B.L. Olla), pp. 83-123. Plenum Press, New York and London.

Evans, P.R., Goss-Custard, J.D. & Hale, W.G. (1984) *Coastal Waders and Wildfowl in Winter.* Cambridge University Press, Cambridge.

Fadat, C., Ferrand, Y. & Martinel, J. (1979) *Bull. Mens. Office Natn. Chasse* **27**, 26-33.

Fasola, M., Canova, L. & Biddau, L. (1996) Foraging habits of Crab Plovers *Dromas ardeola* overwintering on the Kenya coast. *Colonial Waterbirds* **19**, 207-213.

Fogden, M.P.L. & Fogden, P.M. (1979) The role of fat and protein reserves in the annual cycle of the Grey-backed camaroptera in Uganda (Aves: Sylvidae). *Journal of Zoology* **189**, 233-258.

Forsman, A. (1991) Variation in sexual size dimorphism and maximum body size among adder populations: effects of prey size. *Journal of Animal Ecology* **60**, 253-267.

Gauthreaux, S. (1982) The ecology and evolution of avian migration systems. *Avian Biology*, Vol. 6 (eds D.S. Farner & J. R. King), pp. 93-167. Academic Press, New York and London.

Gautier-Hion, A. (1980) Seasonal variations of diet related to species and sex ins community of *Cercopithecus* monkeys. *Journal of Animal Ecology* **49**, 237-269.

Gerard, B.M. (1967) Factors affecting earthworms in pastures. *Journal of Animal Ecology* **36**, 235-252.

Gibbs, H.L. & Grant, P.R. (1987) Oscillating selection on Darwin's finches. *Nature* **327**, 511-513.

Goater, C.P. (1988) Patterns of helminth parasitism in the Oystercatcher *Haematopus ostralegus*, from the Exe estuary, England. PhD thesis, University of Exeter.

Goater, C.P.(1993) Population biology of *Meiogymnophallus minutus* (*Trematoda: Gymnophallidae*) in cockles *Cerastoderma edule* from the Exe estuary, England. *Journal of the Marine Biological Association* **73**, 163-177.

Gosler, A.G. (1996) Environmental and social determinants of winter fat storage in the great tit *Parus major*. *Journal of Animal Ecology* **65**, 1-17.

Gosler, A.G. & Carruthers, T.D. (1994) Bill size and niche breadth in the Irish Coal tit *Parus ater hibernicus*. *Journal of Avian Biology* **25**, 171-177.

Gosler, A.G., Greenwood, J.J.D. & Perrins, C. (1995) Predation risk and the cost of being fat. *Nature* **378**: 644-644.

Gosler, A.G., Greenwood, J.J.D., Baker, J.K. & Davidson, N.C. (1998) The field determination of body size and condition in passerines: a report to the British Ringing Committee. *Bird Study* **45**, 92-103.

Gosling, L.M. & Sutherland, W.J. (2000) *Behaviour and Conservation* (eds) Cambridge University Press, Cambridge.

Goss-Custard, J.D. (1969) The winter feeding ecology of the redshank *Tringa totanus*. *Ibis* **111**, 338-356.

Goss-Custard, J.D. (1981) Oystercatcher counts at roosts and at feeding grounds. *British Birds* 74, 197-199.

Goss-Custard, J.D. (1984) Intake rates and food supply in migrating and wintering shorebirds. *Shorebirds: Migration and Foraging behaviour* (eds J. Burger & B.L. Olla), pp. 233-270. Plenum Press, London and New York.

Goss-Custard, J.D. (1993) The effect of migration and scale on the study of bird populations: 1991 Witherby Lecture. *Bird Study* **40**, 81-96.

Goss-Custard, J.D. (1996) *The Oystercatcher: from individuals to populations* (ed.). Oxford University Press, Oxford.

Goss-Custard, J.D. & Durell, S.E.A. Le V. dit (1983) Individual and age differences in the feeding ecology of Oystercatchers, *Haematopus ostralegus*, wintering on the Exe. *Ibis* **125**, 155-171.

Goss-Custard, J.D. & Durell, S.E.A. Le V. dit (1984a) Feeding ecology, winter mortality and the population dynamics of Oystercatchers, *Haematopus ostralegus*, on the Exe estuary. *Coastal waders and wildfowl in winter* (eds P.R. Evans, J.D. Goss-Custard & W.G.Hale), pp. 190-208. Cambridge University Press, Cambridge.

Goss-Custard, J.D. & Durell, S.E.A. Le V. dit (1984b) Winter mortality of adult oystercatchers on the Exe estuary. *Wader Study Group Bulletin* **40**, 37-38.

Goss-Custard, J.D. & Durell, S.E.A. Le V. dit (1987a) Age-related differences in Oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*. I. Foraging efficiency and interference. *Journal of Animal Ecology* **56**, 521-536.

Goss-Custard, J.D. & Durell, S.E.A. Le V. dit (1987b) Age-related differences in Oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*. II. Aggression. *Journal of Animal Ecology* **56**, 537-548.

Goss-Custard, J.D. & Durell, S.E.A. Le V. dit (1987c) Age-related differences in Oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*. III. The effect of interference on overall intake rate. *Journal of Animal Ecology* **56**, 549-558.

Goss-Custard, J.D. & Durell, S.E.A. Le V. dit (1988) The effect of dominance and feeding method on the intake rate of Oystercatchers, *Haematopus ostralegus*, feeding on mussels. *Journal of Animal Ecology* **57**, 827-844.

Goss-Custard, J.D. & Durell, S.E.A. Le V. dit (1990) Bird behaviour and environmental planning: approaches in the study of wader populations. *Ibis* **132**, 273-289.

Goss-Custard, J.D. & Sutherland, W.J. (1997) Individual behaviour, populations and conservation. *Behavioural Ecology: an evolutionary approach (4th edition)* (eds. J.R.Krebs & N.B. Davies), pp. 373-395. Blackwell Science, Oxford.

Goss-Custard, J.D. & West, A.D. (1997) The concept of carrying capacity and shorebirds. In *Effect of habitat loss and change on waterbirds* (Eds J.D. Goss-Custard, R. Rufino & A. Luis). ITE Symposium no. 30. HMSO, London.

Goss-Custard, J.D., Jenyon, R.A., Jones, R.E., Newbury, P.E. & Williams, R. le B. (1977) The ecology of the Wash. II. Seasonal variation in the feeding condition of wading birds (*Charadrii). Journal of Applied Ecology* **14**, 681-700.

Goss-Custard, J.D., McGrorty, S., Reading, C.J. & Durell, S.E.A. le V. dit (1980) Oystercatchers and Mussels on the Exe estuary. *Essays on the Exe Estuary*. Devon Association, Special Volume **2**, 161-185.

Goss-Custard, J.D., Durell, S.E.A. le V. dit, Sitters, H.P. & Swinfen, R. (1982a) Age-structure and survival of a wintering population of Oystercatchers. *Bird Study* **29**, 83-98.

Goss-Custard, J.D., Durell, S.E.A. le V. dit, McGrorty, S. & Reading, C.J. (1982b) Use of mussel *Mytilus edulis* beds by oystercatchers *Haematopus ostralegus* according to age and population size. *Journal of Animal Ecology* **51**, 543-554.

Goss-Custard, J.D., Durell, S.E.A. le V. dit & Ens, B.J. (1982c) Individual differences in aggressiveness and food stealing among wintering Oystercatchers *Haematopus ostralegus* L. *Animal Behaviour* **30**, 917-928.

Goss-Custard, J.D., Clarke, R.T. & Durell, S.E.A. le V. dit (1984) Rates of food intake and aggression of oystercatchers, *Haematopus ostralegus*, on the most and least preferred mussel, *Mytilus edulis*, beds of the Exe estuary. *Journal of Animal Ecology* **53**, 233-245.

Goss-Custard, J.D., Cayford, J.T., Boates, J.S. & Durell, S.E.A. le V. dit (1987) Field tests of the accuracy of estimating prey size from bill length in oystercatchers *Haematopus ostralegus*, eating mussels *Mytilus edulis*. *Animal Behaviour* **35**, 1078-1083.

Goss-Custard, J.D., Warwick, J.M., Kirby, R., McGrorty, S., Clarke, R.T., Pearson, B., Rispin, W.E., Durell, S.E.A. Le V. dit & Rose, R.J. (1991) Towards predicting wading bird densities from predicted prey densities in a post-barrage Severn Estuary. *Journal of Applied Ecology* **28**, 1004-1026.

Goss-Custard, J.D., Caldow, R.W.G., Clarke, R.T., Durell, S.E.A. Le V. dit & Sutherland, W.J. (1995a) Consequences of habitat loss and change in wintering migratory birds: predicting the local and global effects from studies of individuals. *Ibis* **137**, Suppl. 1, 56-66.

Goss-Custard, J.D., Clarke, R.T., Briggs, K.B., Ens, B.J., Exo, K.-M., Smit, C., Beintema, A.J., Caldow, R.W.G., Catt, D.C., Clark, N., Durell, S.E.A. Le V. dit, Harris, M.P., Hulscher, J.B., Meininger, P.L., Picozzi, N., Prŷs-Jones, R., Safriel, U.N. & West, A.D. (1995b) Population consequences of winter habitat loss in a migratory shorebird. I. Estimating population parameters. *Journal of Applied Ecology* **32**, 320-336.

Goss-Custard, J.D., Clarke, R.T., Durell, S.E.A. Le V. dit, Caldow, R.W.G. & Ens, B.J. (1995c) Population consequences of winter habitat loss in a migratory shorebird. II. Model predictions. *Journal of Applied Ecology* **32**, 337-351.

Goss-Custard, J.D., Durell, S.E.A. le V. dit, Goater, C.P., Hulscher, J.B., Lambeck, R.H.D., Meininger, P.L. & Urfi, J. (1996a) How Oystercatchers survive the winter. *The Oystercatcher: from individuals to populations,* (ed. J.D. Goss-Custard), pp. 133-154. Oxford University Press, Oxford.

Goss-Custard, J.D., McGrorty, S. & Durell, S.E.A. Le V. dit (1996b) The effect of Oystercatchers *Haematopus ostralegus* on shellfish populations. *Ardea* **84A**, 453-468.

Goss-Custard, J.D., Durell, S.E.A. Le V. dit, Clarke, R.T., Beintema, A.J., Caldow, R.W.G., Meininger, P.L. & Smit, C.J. (1996c) Population dynamics: predicting the consequences of habitat change at the continental scale. *The Oystercatcher: from individuals to populations,* (ed. J.D. Goss-Custard), pp. 352-383. Oxford University Press, Oxford.

Goss-Custard, J.D., West, A.D., Clarke, R.T., Caldow, R.W.G. & Durell, S.E.A. Le V. dit (1996d) The carrying capacity of coastal habitats for Oystercatchers. *The Oystercatcher: from individuals to populations,* (ed. J.D. Goss-Custard), pp. 327-351. Oxford University Press, Oxford.

Goss-Custard, J.D., Ross, J. McGrorty, S., Durell, S.E.A. Le V. dit, Caldow, R.W.G.& West, A.D. (1998) Locally stable wintering numbers in the Oystercatcher *Haematopus ostralegus* where carrying capacity has not been reached. *Ibis* **139**, 104-112.

Greenhalgh, M.E. (1968) The sex ratio of migrant ruffs. *Bird Study* **15**, 210-212.

Greig, S.A., Coulson, J.C. & Monaghan, P. (1985) Feeding strategies of male and female adult Herring gulls (Larus argentatus). *Behaviour* **94**, 41-59.

Gross, M.R. (1996) Alternative reproductive strategies and tactics: diversity within sexes. *Trends in Ecological Evolution* **11**, 92-98.

Groves, S. (1978) Age-related differences in Ruddy Turnstone foraging and aggressive behaviour. *Auk* **95**, 95-103.

Gustafsson, L. (1988) Foraging behaviour of individual coal tits, *Parus ater*, in relation to their age, sex and morphology. *Animal Behaviour* **36**, 696-704.

Harris, M.P. (1967) The biology of Oystercatchers *Haematopus ostralegus* on Skokholm Island, S. Wales. *Ibis* **109**, 180-193.

Hayman, P., Marchant, J. & Prater, A.J. (1986) *Shorebirds: an identification guide to the waders of the world.* Christopher Helm, London.

Heppleston, P.B. (1972) The comparative breeding ecology of Oystercatchers (*Haematopus ostralegus*) in inland and coastal habitats. *Journal of Animal Eco*logy **41**, 23-51.

Heppleston, P.B. & Kerridge, D.F. (1970) Sexing Oystercatchers from bill measurements. *Bird Study* 17, 48-49.

Hitchcock, C.L. & Gratto-Trevor, C. (1997) Diagnosing a shorebird local population decline with a stage-structured population model. *Ecology*, **78**, 522-534.

Hockey, P.A.R. & Underhill, L.G. (1984) Diet of the African Black Oystercatcher *Haematopus moquini* on rocky shores: spatial, temporal and sex-related variation. *South African Journal of Zoology* **19**, 1-11.

Hogstad, O. (1976) Sexual dimorphism and divergence in winter foraging behaviour of Three-toed Woodpeckers *Picoides tridactylus. Ibis* **118**, 41-50.

Holmes, R.T. & Pitelka, F.A. (1968) Food overlap among coexisting Sandpipers on northern Alaskan tundra. *Systematic Zoology* **17**, 305-318.

Hori, M (1993) Frequency-dependent natural selection in the handedness of scale eating cichlid fish. *Science* **260**, 216-219.

Horwitz, W. (1965) *Official methods of analysis of the association of official agricultural chemists.* 10th edition. Association of Official Agricultural Chemists, Washington.

Hulscher, J.B. (1982) The Oystercatcher *Haematopus ostralegus* as a predator of the bivalve *Macoma balthica* in the Dutch Wadden Sea. *Ardea* **70**, 89-152.

Hulscher, J.B. (1990) Survival of Oystercatchers during hard winter weather. *Ring* **13**, 167-172.

Hulscher, J.B. (1996) Food and feeding behaviour. *The Oystercatcher: from individuals to populations,* (ed. J.D. Goss-Custard), pp. 7-29. Oxford University Press, Oxford.

Hulscher, J.B. & Ens, B.J. (1992) Is the bill of a male Oystercatcher a better tool for attacking mussels than the bill of the female? *Netherlands Journal of Zoology* **42**, 85-100.

Hulscher, J.B. (1996) Food and feeding behaviour. *The Oystercatcher: from individuals to populations* (ed. J.D. Goss-Custard), pp. 7 - 29. Oxford University Press, Oxford.

Hulscher, J.B., Alting, D., Bunskoeke, A.J., Ens, B.J. & Heg, D. (1996a) Subtle differences between male and female Oystercatchers *Haematopus ostralegus* in feeding on the bivalve *Macoma balthica. Ardea* **84A**, 117-130.

Hulscher, J.B., Exo, K-M. & Clark, N.A. (1996b) Why do Oystercatchers migrate? *The Oystercatcher: from individuals to populations,* (ed. J.D. Goss-Custard), pp. 155-185. Oxford University Press, Oxford.

Ito, Y. (1972) On the methods for determining density-dependence by means of regression. *Oecologia* **10**, 347-372.

Jehl, J.R. & Murray, B.G. (1986). The evolution of normal and reverse sexual size dimorphism in shorebirds and other birds. *Current Ornithology, Volume 3,* (Ed. R.F. Johnston), pp. 1-86. Plenum Press, New York.

Jones, P.J. & Ward, P. (1976) The level of reserve protein as the proximate factor controlling the timing of breeding and clutch-size in the red-billed Quelea *Quelea quelea. Ibis* **118**, 547-574.

Jönsson, P.E. (1991) Reproduction and survival in a declining population of the Southern Dunlin *Calidris alpina schinzii. Wader Study Group Bulletin* **61 Suppl**, 56-68.

Jönsson, P.E. & Alerstam, T. (1990) The adaptive significance of parental role division and sexual size dimorphism in breeding shorebirds. *Biological Journal of the Linnean Society* **41**, 301-314.

Kersten, M. & Piersma, T. (1987) High levels of energy expenditure in shorebirds: metabolic adaptions to an energetically expensive way of life. *Ardea* **75**, 175-187.

Ketterson, E.D. & Nolan, V. Jr. (1983) The evolution of differential migration. *Current Ornithology Vol. 1* (ed. R.F. Johnston), pp. 357-402. Plenum Press, New York.

King, J.R. (1972) Adaptive periodic fat storage by birds. *Proceedings of the International Ornithological Congress (The Hague)* **XV**, 200 - 217.

Klomp, H. (1980) Fluctuations and stability in Great Tit populations. *Ardea* **68**, 205-224.

Lambeck, R.H.D. & Wessel, E.G.J. (1991) Seasonal variation in mortality of the oystercatcher (*Haematopus ostralegus*). *Progress Report: Delta Institute for Hydrobiological Research,* (eds C.H.R. Heip & E.S. de Bruijn, E.S.), pp. 22-24. Koninklijke Nederlands Akademie van Wetenschappen, Amsterdam.

Lauro, B. & Nol, E. (1995) Feeding behaviour, prey selection and bill size of Pied and Sooty Oystercatchers in Australia. *Wilson Bulletin* **107**, 629-640.

Lima, S.L. (1986) Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology* **67**, 377-385.

Manly, B.F.J. (1997) *Randomisation, bootstrap and Monte-Carlo methods in biology.* Second edition. Chapman and Hall, London.

Marcström, V. & Mascher, J.W. (1979) Weights and fat in Lapwings *Vanellus vanellus* and Oystercatchers *Haematopus ostralegus* starved to death during a cold spell in spring. *Ornis Scandinavica* **10**, 235-240.

Mascher, J.W. & Marcström, V. (1976) Measures, weights and lipid levels in migrating Dunlin *Calidris a. alpina L.* at the Ottenby Bird Observatory, south Sweden. *Ornis Scandinavica* 7, 49-59.

Maynard-Smith, J. (1982) *Evolution and the Theory of Games.* Cambridge University Press, Cambridge.

McGrorty, S., Clarke, R.T., Reading, C.J. & Goss-Custard, J.D. (1990) Population dynamics of the mussel *Mytilus edulis*: density changes and regulation of the population in the Exe estuary, Devon. *Marine Ecology Progess Series* **67**, 157-169.

McNamara, J.M. & Houston, A.I. 1987. Starvation and predation as factors limiting population size. *Ecology* **68**, 1515-1519.

McNamara, J.M. & Houston, A.I. (1990) The value of fat reserves and the tradeoff between starvation and predation. *Acta Biotheoretica* **38**, 37-61.

Miller, E.H. (1983) Habitat and breeding cycle of the Least Sandpiper (*Calidris minutilla*) on Sable Island, Nova Scotia. *Canadian Journal of Zoology* **61**, 2880-2898.

Mueller, H.C. (1989) Aerial agility and the evolution of reversed sexual size dimorphism (RSD) in shorebirds. *Auk* **106**, 154-155.

Myers, J.P. (1981) A test of three hypotheses for latitudinal segregation of the sexes in wintering birds. *Canadian Journal of Zoology* **59**, 1527-1534.

Myers, J.P., Morrison, R.I.G., Antas, P.Z., Harrington, B.A., Lovejoy, T.E., Sallaberry, M., Senner, S.E. & Tarak, A. (1987) Conservation Strategy for migratory species. *American Scientist*, **75**, 19-26.

Newell, R.C. (1962) Behavioural aspects of the ecology of *Peringia* (= *Hydrobia*) *ulvae. Estuarine Coastal Marine Science* **138**, 49.

Newsome, A.E. (1980) Differences in the diets of male and female red kangaroos in central Australia. *African Journal of Ecology* **18**, 27-31.

Newton, I. (1969) Winter fattening in the Bullfinch. *Physiological Zoology* **42**, 290 -301.

Nicoll, M., Summers, R.W., Underhill, L.G., Brockie, K. & Rae, R. (1988) Regional, seasonal and annual variations in the structure of Purple Sandpiper *Calidris maritima* populations in Britain. *Ibis* **130**, 221-233.

Owen, M. & Cook, W.A. (1977) Variations in body weight, wing length and condition of Mallard *Anas platyrhynchos platyrhynchos* and their relationship to environmental changes. *Journal of Zoology* **183**, 377-395.

Page, G. (1974) Age, sex moult and migration of Dunlins at Bolinas Lagoon. *Western Birds* **5**, 1-12.

Page, G., Fearis, B. & Jurek, R.M. (1972) Age and sex composition of western sandpipers on Bolinas Lagoon. *Californian Birds* **3**, 79-86.

Partridge, L. (1976) Individual differences infeeding efficiencies and feeding preferences of captive great tits. *Animal Behaviour* **24**, 230-240.

Partridge, L. & Green, P. (1985) Intraspecific feeding specialisations and population dynamics. In *Behavioural Ecology* (Eds R.M. Sibley & R.H. Smith), pp. 207-226. Blackwell Scientific Publications, Oxford.

Perez-Barberia, F.J. & Gordon, I.J. (1999) Body size dimorphism and sexual segregation in polygynous ungulates: an experimental test with Soay sheep. *Oecologia* **120**, 258-267.

Perrins, C.M. (1970) The timing of birds' breeding seasons. *Ibis* **112**, 242-255.

Peters, W.D. & Grubb, T.C. (1983) An experimental analysis of sex-specific foraging in the Downy Woodpecker, *Picoides pubescens*. *Ecology* **64**, 1437-1443.

Pienkowski, M.W. & Evans, P.R. (1984) Migratory Behavior of Shorebirds in the Western Palearctic. *Shorebirds: Migration and Foraging behaviour* (eds J. Burger & B.L. Olla), pp. 74-123. Plenum Press, London and New York.

Pienkowski, M.W., Lloyd, C.S. & Minton, C.D.T. (1979) Seasonal and migrational weight changes in Dunlins. *Bird Study* **26**, 134-148.

Piersma, T & Baker, A.J. (2000) Life history characteristics and the conservation of migratory shorebirds. *Behaviour and Conservation* (eds L.M. Gosling & W.J. Sutherland), pp. 105 -124. Cambridge University Press, Cambridge.

Pierce, R.J. (1986) Observations on behaviour and foraging of the Ibisbill *Ibidorhyncha struthersii* in Nepal. *Ibis* **128**, 37-47.

Prater, A.J., Marchant, J.H. & Vuorinen, J. (1977) *Guide to the identification and ageing of Holarctic waders.* BTO Guide 17, Tring.

Puttick, G.M. (1978) The diet of the Curlew Sandpiper at Langebaan Lagoon, South Africa. *Ostrich* **49**, 158-167.

Puttick, G.M. (1981) Sex-related differences in foraging behaviour of Curlew Sandpipers. *Ornis Scandinavica* **12**, 13-17.

Pyke, G.H., Pulliam, H.R. & Charnov, E.L. (1977) Optimal foraging: a selective review of theory and tests. *Q. Rev. Biol.* **52**, 137-154.

Ricklefs, R.E. (1974) Energetics of reproduction in birds. *Avian Energetics* (ed. R.A. Paynter), pp. 152-292. Nuttall Ornithologists' Club, Cambridge, Massachusetts.

Ridley, M.W. (1980) The breeding behaviour and feeding ecology of Grey Phalaropes *Phalaropus fulicarius* in Svalbard. *Ibis* **122**, 210-216.

Rogers, C.M. (1987) Predation risk and fasting capacity: do winter birds maintain optimal body mass? *Ecology* **68**, 1051-1061.

Rubega, M.A. (1996) Sexual size dimorphism in Red-necked phalaropes and functional significance of non-sexual bill structure variation for feeding performance. *Journal of Morphology* **228**, 45-60.

Rybarczyk, H., Elkaim, B., Wilson, J.G. & Loquet, N. (1996) Eutrophication in the Baie de Somme: Consequences and impacts on the benthic population. *Oceanologica Acta* **19**, 131-140.

Safriel, U.N., Harris, M.P., Brooke, M. de L. & Britton, C.K. (1984) Survival of breeding oystercatchers *Haematopus ostralegus*. *Journal of Animal Ecology* **53**, 867-877.

Sandercock, B.K. & Gratto-Trevor, C.L. (1997) Local survival in Semipalmated Sandpipers *Calidris pusilla* breeding at La Pérouse Bay, Canada. *Ibis* **139**, 305-312.

Sears, J. (1988) Assessment of body condition in live birds: measurement of protein and fat reserves in the Mute Swan, *Cygnus olor*. *Journal of Zoology* **216**, 295-308.

Selander, R.K. (1966) Sexual dimorphism and differential niche utilisation in birds. *Condor* **68**, 113-151.

Selander, R.K. (1972) Sexual selection and dimorphism in birds. *Sexual selection and the Descent of Man 1871-1971* (ed. B. Campbell), pp. 180-230. Aldine, Chicago.

Shine, R. (1991) Intersexual dietary divergence and the evolution of sexual dimorphism in snakes. *American Naturalist* **138**, 103-122.

Shine, R., Harlow, P.S., Keogh, J.S. & Boeadi (1998) The influence of sex and body size on food habits of a giant tropical snake, *Python reticulatus*. *Functional Ecology* **12**, 248-258.

Skulason, S. & Smith, T.B. (1995) Resource polymorphism in vertebrates. *Trends Ecol. Evol.* **10**, 366-370.

Smith, P.C. & Evans, P.R. (1973) Studies of shorebirds at Lindisfarne, Northumberland. 1. Feeding ecology and behaviour of the Bar-tailed Godwit. *Wildfowl* **24**, 135-139.

Smith, T.B. (1987) Bill size polymorphism and intraspecific niche utilisation in an African finch. *Nature* **329**, 717-719.

Smith, T.B. & Temple, S.A. (1982) Feeding habits and bill polymorphism in Hook-billed Kites. *Auk* **99**, 197-207.

Stillman, R.A., Goss-Custard, J.D., Clarke, R.T. & Durell, S.E.A. le V. dit (1996) Shape of the interference function in a foraging vertebrate. *Journal of Animal Eco*logy **65**, 813-824.

Stillman, R.A., Goss-Custard, J.D. & Caldow, R.W.G. (1997). Modelling interference from basic foraging behaviour. *Journal of Animal Ecology* **66**, 692-703.

Stillman, R. A., Goss-Custard, J. D., West, A. D., Durell, S. E. A. Le V. dit, Caldow, R. W. G., McGrorty, S. & Clarke, R. T. (2000) Predicting mortality in novel environments: tests and sensitivity of a behaviour-based model. *Journal of Applied Ecology* **37**, 564-588.

Summers, R.W., Smith, S., Nicoll, M. & Atkinson, N.K. (1990a) Tidal and sexual differences in the diet of Purple Sandpipers *Calidris maritima* in Scotland. *Bird Study* **37**, 187-194.

Summers, R.W., Strann, K-B., Rae, R. & Heggås, J. (1990b) Wintering Purple Sandpipers in Troms county, northern Norway. *Ornis Scandinavica* **21**, 248-254.

Sutherland, W.J. (1996a) Predicting the consequences of habitat loss for migratory populations. *Proceedings of the Royal Society of London* **263**, 1325-1327.

Sutherland, W.J. (1996b) *From individual behaviour to population ecology*. Oxford University Press, Oxford.

Sutherland, W.J. & Dolman, P.M. (1994) Combining behaviour and population dynamics with applications for predicting the consequences of habitat loss. *Proceedings of the Royal Society London Series B* **255**, 133-138.

Sutherland, W.J. & Ens, B.J. (1987) The criteria determining the selection of mussels *Mytilus edulis* by Oystercatchers *Haematopus ostralegus*. *Behaviour* **103**, 187-202.

Sutherland, W.J., Ens, B.J., Goss-Custard, J.D. & Hulscher, J.B. (1996) Specialisation. *The Oystercatcher: from Individuals to Populations* (ed. J.D. Goss-Custard), pp. 56-76. Oxford University Press, Oxford.

Swennen, C. (1984) Differences in the quality of roosting flocks of Oystercatchers. *Coastal waders and wildfowl in winter* (eds P.R. Evans, J.D. Goss-Custard & W.G.Hale), pp. 177- 189. Cambridge University Press, Cambridge.

Swennen, C., Bruijn, L.L.M. de, Duiven, P., Leopold, M.F. & Marteijn, E.C.L. (1983) Differences in bill form of the Oystercatcher *Haematopus ostralegus*; a dynamic adaptation to specific foraging techniques. *Netherlands Journal of Sea Research* **17**, 57-83.

Székely, T., Cuthill, I.C. & Kis, J. (1999) Brood desertion in Kentish plover: sex differences in remating opportunities. *Behavioural Ecology* **10**, 185-190.

Teather, K.L. & Nol, E. (1997) Mixed sexual dimorphism in Semipalmated plovers. *Condor* **99**, 803-806.

Temeles, E.J. (1985) Sexual size dimorphism of bird-eating hawks: the effect of prey vulnerability. *The American Naturalist* **125**, 485-499.

ter Braak, C.J.F. (1992) Permutation versus bootstrap significance tests in multiple regression and ANOVA. *Bootstrapping and Related Techniques*, (ed. K.H.Jockel), pp. 79-86. Springer-Verlag, Berlin.

Townshend, D. J. (1981) The importance of field feeding to the survival of wintering male and female Curlews *Numenius arquata* on the Tees estuary. *Feeding and survival strategies of estuarine organisms* (eds N.V. Jones & W.J. Wolff), pp. 261-273. Plenum Press, New York.

Triplet, P. (1989) Sélectivité alimentaire liée à l'age chez l'Huitriez-pie *Haematopus ostralegus* consummateur de *Nereis diversicolor* en Baie de Somme. *Gibier Faune Sauvage* **6**, 427-436.

Vader, W.J.M. (1964) A preliminary investigation into the reactions of the infauna of the tidal flats to tidal fluctuations in water level. *Netherlands Journal of Sea Research* **2**, 189.

van der Have, T.M., Nieboer, E. & Boere, G.C. (1984) Age-related distribution of Dunlin in the Dutch Wadden Sea. *Coastal waders and wildfowl in winter* (eds P.R. Evans, J.D. Goss-Custard & W.G.Hale), pp. 160-176.

Van Eerden, M.R. & Munsterman, M.J. (1995) Sex and age dependent distribution in wintering Cormorants *Phalacrocorax carbo sinensis* in Western Europe. *Ardea* **83**, 285-297.

Varley, G.C., Gradwell, G.R. & Hassell, M.P. (1973) *Insect population ecology*. Blackwell Scientific Publications, Oxford.

Von Schantz, T. & Nilsson, I.N. 1981) The reversed size dimorphism in birds of prey: a new hypothesis. Oikos **36**, 129-132.

Ward, P. (1969) The annual cycle of the Yellow-vented Bulbul *Pycnonotus goiavier* in a humid equatorial environment. *Journal of Zoo*logy **157**, 25-45.

Watson, A. (1980) Starving Oystercatchers in Deeside after severe snowstorm. *Scottish Birds* **11**, 55-56.

Whitfield, D.P. (1990) Individual feeding specialisations of wintering Turnstone *Arenaria interpres*. *Journal of Animal Ecology* **59**, 193-211.

Whitfield, D.P., Evans, A.D. & Whitfield, P.A. (1988) The impact of raptor predation on wintering waders. *Acta XIX Congressus Internationalis Ornithologici*, 674-687.

Wilson, J & Davidson, N.C. (1982) Weight-watchers of the world unite: you have nothing to lose but poor data. *Wader Study Group Bulletin* **35**, 23-25.

Williams, T.D. (1991) Foraging ecology and diet of Gentoo Penguins *Pygoscelis papua* at South Georgia during winter and an assessment of their winter prey consumption. *Ibis* **133**, 3-13.

Witter, M.S. & Cuthill, I.C. (1993) The ecological costs of avian fat storage. *Philosophical Transanctions of the Royal Society* **340**, 73-92.

Wunderle, J.M. Jr. (1991) Age-specific foraging proficiency in birds. *Current Ornithology Vol. 8* (ed. D.M.Power), pp. 273-324. Plenum Press, New York and London.

Zwarts, L. (1979) Feeding ecology of Curlew. *Wader Study Group Bulletin* **26**, 28.

Zwarts, L. (1985) The winter exploitation of Fiddler Crabs *Uca tangeri* by waders in Guinea-Bissau. *Ardea* **73**, 3-12.

Zwarts, L. & Wanink, J. (1989) Siphon size and burying depth in deposit and suspension-feeding benthic bivalves. *Marine Biology* **100**, 227-240.

Zwarts, L. & Wanink, J. (1991) The macrobenthos fractions accessible to waders may represent marginal prey. *Oecologia* **87**, 581-587.

Zwarts, L. & Wanink, J. (1993) How the food supply harvestable by waders in the Wadden Sea depends on the energy content, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. *Netherlands Journal of Sea Research* **31**, 441-476.

Zwarts, L., Cayford, J.T., Hulscher, J.B., Kersten, M., Meire, P.M. & Triplet, P. (1996a) Prey size selection and intake rate. In *The Oystercatcher: from individuals to populations,* (ed. J.D. Goss-Custard), pp. 30-55. Oxford University Press, Oxford.

Zwarts, L., Hulscher, J.B., Koopman, K., Piersma, T. & Zegers, P.M. (1996b) Seasonal and annual variation in body weight, nutrient stores and mortality of Oystercatchers *Haematopus ostralegus. Ardea* **84**A, 327-372.

Zwarts, L., Hulscher, J.B., Koopman, K. & Zegers, P.M. (1996c) Body weight in relation to variation in body size of Oystercatchers *Haematopus ostralegus. Ardea* **84**A, 21-28.

Zwarts, L., Hulscher, J.B., Koopman, K. & Zegers, P.M. (1996d) Discriminating the sex of Oystercatchers *Haematopus ostralegus. Ardea* **84**A, 1-12.

Zwarts, L., Hulscher, J.B. & Zegers, P.M. (1996e) Weight loss in Oystercatchers *Haematopus ostralegus* on the roost and after capture. *Ardea* **84**A, 13-20.

Zweers, G.A. & Gerritsen, A.F.C. (1997) Transitions from pecking to probing mechanisms in waders. *Netherlands Journal of Zoology* **47**, 161-208.