The implications for conservation of age- and sex-related feeding specialisations in shorebirds

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Age- and sex-related feeding specialisations have been found in several shorebird species. The phenotypic constraints to age- and sex-related feeding specialisations mean that birds may not be able to change diets or feeding methods when faced with any deterioration in their feeding conditions. Furthermore, should any increase in mortality affect a particular age group, or one sex, more than another, the resulting reduction in population size may be greater than if all birds were affected to the same extent. For this reason, it is important that conservation managers are aware of any age- or sex-related feeding specialisations in their study species.

INTRODUCTION

There has long been considerable interest in the conservation of migratory shorebirds, not least because of the international nature of their lifestyles (e.g. Piersma & Baker 2000). Shorebirds are relatively long-lived animals, so variation in annual survival usually has more influence on population size than variation in breeding success (Myers *et al.* 1987; Evans 1991; Hitchcock & Gratto-Trevor 1997). As most birds die during the non-breeding season (Evans 1991), conservation interests have been focused 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, coastal development, shellfishing, pollution and disturbance.

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 variation in individual behaviour can be critical in explaining demographic processes such as density-dependence (e.g. Sutherland 1996). For example, because individuals vary in their competitive ability and in their foraging ability, they will differ in their response to any increase in population density resulting from habitat loss. Such variation will determine how many individuals will fail to breed or starve at different population levels and is the underlying principle of behaviour-based models developed for shorebird populations (Sutherland & Dolman 1994; Goss-Custard & Sutherland 1997; Stillman *et al.* 2000; Stillman *et al.* 2001). Thus, understanding individual variation is of fundamental importance not only to population ecology, but also to practical conservation.

As well as varying in their foraging efficiency, individual birds can vary in their foraging strategy. Different individuals within a species may specialise on a particular habitat, a particular prey item and even on a particular way of handling that prey item (Durell 2000). Different strategies will not necessarily have equal payoffs and the optimum foraging strategy for any individual will be conditional upon its specific priorities and constraints. For example, most adult shorebirds in late winter will have the priority of accumulating reserves before migration. However, some of these adults may be prevented from feeding on the most profitable food resources because, for example, they are of low social status.

Individual feeding specialisations are found in many shorebird groups (Durell 2000). In this paper, I would like to stress the importance of those shorebird feeding specialisations which are related to a bird's age or to a bird's sex. I shall describe the mechanisms responsible for age- and sex-related feeding specialisations and explain how phenotypic constraints can restrict the foraging options available to certain groups of birds. I shall then consider the conservation implications of certain age groups and different sexes being more vulnerable than others to environmental change.

AGE-RELATED FEEDING SPECIALISATIONS

There are three mechanisms that can be responsible for age-related feeding specialisations: (i) morphological differences (ii) individually acquired skills and (iii) social status (Durell 2000). Juvenile birds tend to be smaller overall and have smaller bills than adults which means that they tend to specialise in smaller prey. In shorebirds, both juvenile curlew sandpipers *Calidris ferruginea* (Puttick 1978) and juvenile crab plovers *Dromas ardeola* (Fasola *et al.* 1996) have been shown to take smaller prey types than adults, whilst juvenile Eurasian oystercatchers *Haematopus ostralegus* take smaller size classes of the same prey types (Goss-Custard & Durell 1987; Triplet 1989; Durell *et al.* 1996a).

Juvenile birds also tend to be less efficient foragers than adults. Moreover, there is 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). Several shorebird studies have shown juveniles to be less efficient than adults when feeding on the same prey (Groves 1978; Burger 1980; Espin *et al.* 1983; Burger & Gochfield 1986; Goss-Custard

& Durell 1987). This difference in foraging ability may cause juveniles to specialise on different prey types or different feeding methods from adults. For example, juvenile black-winged stilts *Himantopus himantopus*, 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). Similarly, although hammering mussels *Mytilus edulis* open was the most profitable feeding method on the Exe estuary, UK, no juvenile oystercatchers were seen to use this technique (Goss-Custard & Durell 1987). Mussel-hammering appears to be a skill which takes some individuals several years to acquire.

However, probably the most important mechanism for age-related feeding specialisation in shorebirds is social status. Many studies have shown that subdominant individuals are excluded from preferred feeding areas (Wunderle 1991). With young shorebirds, therefore, it is difficult to establish whether their exclusion from certain feeding areas, or from more profitable feeding methods, is due to their poorer foraging ability or their lower social status. For whichever reason, it is generally accepted that feeding areas with higher proportions of young birds are less preferred. Goss-Custard *et al.* (1982) showed how immature oystercatchers, which had fed on the preferred mussel beds on the Exe estuary throughout the summer, were displaced when the adults returned in the autumn. These displaced birds either moved to less preferred mussel beds or changed diet altogether, feeding on mudflats and in fields (Goss-Custard & Durell 1983). Similarly, on the Tyninghame estuary in Scotland, juvenile redshank *Tringa totanus* were excluded by adults from an area with a lower risk of predation and fed on the adjacent saltmarsh instead (Cresswell 1994). Age differences in distribution have been found in purple sandpipers *Calidris maritima* (Summers *et al.* 1990b), dunlin *Calidris alpina* (Clark 1983; van der Have *et al.* 1984), turnstone *Arenaria interpres* (Whitfield 1985) and oystercatchers (Swennen 1984; Durell *et al.* 1996b).

Age differences in distribution amongst overwintering shorebirds are thus usually the result of young birds being excluded from preferred feeding areas and/or from more profitable diets. This means that many young birds are forced to feed in suboptimal habitats, or in areas more at risk from, for example, parasites or predation. Moreover, should the habitats utilised by young birds be removed, there is a very low chance of the affected birds being able to move into areas already occupied by older birds, so they would be forced to feed in even less suitable habitats, or starve.

SEX-RELATED FEEDING SPECIALISATIONS

Sex-related feeding specialisations can also be related to social status, with the more dominant sex, usually males, excluding the other from preferred feeding areas. This has been shown to be the case in several bird species (Davies & Green 1976; Peters & Grubb 1983; Ekman & Askenmo 1984; Gustafsson 1988) and may well be one of the reasons for sex differences in distribution found in shorebirds (Greenhalgh 1968; Page *et al.* 1972; Page 1974; Baker 1975; Atkinson *et al.* 1981; Buchanan *et al.* 1986; Nicoll *et al.* 1988; Summers *et al.* 1990b; Durell & Goss-Custard 1996). However, there is little direct evidence of this in shorebirds to date.

The most frequently cited mechanism of sex-related feeding specialisation in shorebirds is morphological differences. Many shorebird species are sexually dimorphic in body size and/or bill size (Durell 2000). If the sexes differ in size, it is very likely that they will differ in their energetic requirements and in the way that 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 and feeding method have been found in at least 13 species of shorebird, all of which have size differences between the sexes. These include four species of oystercatcher (Hockey & Underhill 1984; Durell *et al.* 1993; Lauro & Nol 1995; Ens *et al.* 1996), bar-tailed godwits *Limosa lapponica* (Smith & Evans 1973; Zwarts 1985), Eurasian curlews *Numenius arquata* (Zwarts 1979; Townshend 1981), ruddy turnstones (Whitfield 1990), grey phalaropes *Phalaropus fulicaria* (Ridley 1980), Eurasian woodcocks *Scolopax rusticola* (Fadat *et al.* 1979), curlew sandpipers (Puttick 1978, 1981), pectoral sandpipers *Calidris melanotos* (Holmes & Pitelka 1968), dunlin (Holmes & Pitelka 1968; Clark 1983) and purple sandpipers (Summers *et al.* 1990a). Many other shorebirds 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. However, 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.

It is probable that bill morphology is one of the most important determinants of sex-related feeding specialisation in shorebirds. In the majority of cases, females have longer bills than males (Durell 2000). This means that females are at an advantage when feeding on more deeply buried, and usually larger, prey. On the other hand, males are probably better adapted to feeding on surface prey, including insects during the breeding season. In the best known example, the oystercatcher, the shorter, sturdier bills of the males are more suited to breaking open hard-shelled, and very profitable, prey such as mussels (Hulscher & Ens 1992; Durell *et al.* 1993). Whatever the advantages of different bill sizes, it is also true that bill morphology will restrict an individual's choice of feeding strategy. In oystercatchers, for example, very few males specialise on worm feeding and very few females specialise on mussel-hammering (Durell *et al.* 1993).

PHENOTYPIC CONSTRAINTS

I have identified differences in morphology, individual skill and social status as being the most important mechanisms responsible for age- and sex-related feeding specialisations in shorebirds. I have also suggested how these differences in phenotype can restrict an individual's choice of feeding strategy. In this section, I would like to consider the implications of these phenotypic constraints in greater detail.

Sex differences in diet and habitat use have been found in many size dimorphic birds, particularly raptors, owls, skuas and gulls (Andersson & Norberg 1981; Greig *et al.* 1985; Temeles 1985). 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 & Lundberg 1991; Williams 1991; Gosler & Carruthers 1994). There are many different reasons, and many different hypotheses, for individual differences in morphology, but they can be divided into those that are and those that are not ultimately determined by the food supply. Some trophic polymorphisms have been shown to be adaptations to prey

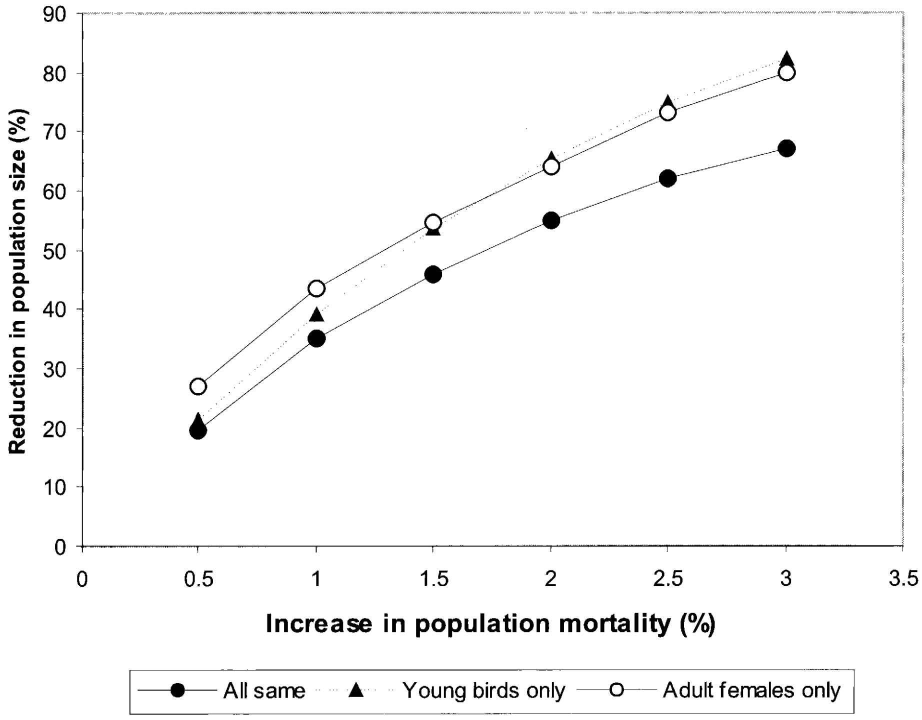

Fig. 1. The reduction in population size resulting from an increase in the proportion of a population dying each year affecting (i) all birds the same (ii) first and second year birds only and (iii) adult females only.

or habitat variability. For example, bill size polymorphism in the hook-billed kite *Chondrohierax uncinatus* was related to the available size ranges of its prey, terrestrial snails (Smith & Temple 1982). Similarly, in both African finches (Smith 1987) and Darwin's finches *Geospiza* (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. These polymorphisms, which can be seen as adaptations for a varied and changing environment, were not related to age or sex.

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 (Jehl & Murray 1986). Sex differences in bill length, although enabling monogamous pairings to exploit a wider range of food resources, must primarily be a secondary sex characteristic. 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 unlikely to be ultimately caused by variations in the food supply.

There is also no reason to suppose that differences in individual skill and social status are primarily adaptations designed to cope with variations in the food supply. Thus, feeding specialisations that are age- and sex-related are constrained by phenotypic differences that are not primarily dietary adaptations. Moreover, because these phenotypic constraints apply to a particular age or a particular sex, whole groups of birds may be restricted in their choice of diet and feeding method, and thus more vulnerable to any changes in their food supply.

CONSERVATION IMPLICATIONS

There are two main conservation implications of individual feeding specialisations. First, different feeding strategies will involve different benefits and different risks. Some prey are more profitable than others, some more variable than others, and some prey or habitats are more risky to feed on or in than others because of, for example, higher risk of infection by parasites or higher risk of predation. Evidence that different strategies have different payoffs has been provided by work on oystercatchers overwintering on the Exe estuary (Durell *et al.* 2001a). Oystercatchers that specialised in mussel-hammering had higher body condition indices and lower rates of winter mortality than mussel-stabbers, and all mussel feeders had higher body condition indices and lower rates of winter mortality than birds that fed on the mudflats on worms *Nereis diversicolor* and clams *Scrobicularia plana*. Oystercatchers that fed in upshore areas and in fields were found to be more at risk from parasite infection (Goss-Custard *et al.* 1996), and those that fed in fields were more at risk from mammalian predation and from accidental death (Durell 2000). On the Exe estuary, therefore, it would appear that mussel feeding is more profitable and less risky than worm/clam feeding.

Secondly, any habitat loss or change may only affect one particular area, one particular habitat or one particular suite of prey species. For example, development on one estuary may affect different groups of birds more than development in another. More specifically, removal of cockle beds will primarily affect cockle-feeding birds, mussel-fishing will affect mussel-feeding birds, whilst bait-digging will affect worm feeders. Any upshore development, such as a port, will have a greater affect on birds that need to feed in upshore areas, and any development on adjacent land, or any agricultural change, will affect those birds that need to feed in fields at high water. Furthermore, environmental changes, such as global warming, sea-level rise or pollution may only affect particular prey types. All these factors will mean that some birds will be more vulnerable than others to any change that might occur.

In many circumstances, higher mortality amongst certain individuals will have little effect on population size, except, perhaps, on a local scale. However, the importance of age- and sex-related feeding specialisations is that a whole age group, or a particular sex, may suffer higher mortality than the rest of the population. I have used a population dynamics model, based on the oystercatcher, to show that any increase in mortality that affected young birds or females more than others substantially reduced population size (Durell *et al.* 2001b). I give another example here (Figure 1). In this case, I increased the winter mortality of a whole population by a certain proportion, but had the same percentage increase affecting (i) all ages and the sexes the same (ii) affecting only first and second year birds and (iii) affecting only adult females. When the increase in mortality affected only young birds, or only females, the reduction in population size was much greater than when all birds were affected to the same extent. Increasing the mortality of young birds did not have so much effect at low mortalities, but had a greater effect as the number of young birds dying increased (Figure 1). Increasing only female mortality, however, had an effect even at very low increases in mortality. Increasing female mortality has a marked effect on population structure, population size and the population response to habitat loss (Durell *et al.* 2001b). Most importantly, by producing a male bias in the breeding population, increasing female mortality reduces the number of potential breeding pairs for a given population size and thus reduces breeding output.

CONCLUSIONS

It is not always easy to identify different ages and sexes in overwintering shorebirds and studies aimed at predicting the effect of habitat loss or change 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, as I hope I have shown here, understanding the distribution of the different age and sex groups may be critical in understanding the effect of any change. For this reason, data collected by wader ringers can be invaluable in discovering and documenting age and sex biases at specific sites. Moreover, 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.

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