Wader disturbance: a theoretical overview

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This paper briefly reviews some work on foraging efficiency, competition and dispersion, which may help predict the effects of disturbance to wintering waders.

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INTRODUCTION

Each year hundreds of thousands of waterfowl overwinter on, or migrate through, the estuaries of north-west Europe (Prater 1981). These estuaries are dynamic habitats subject to intense anthropogenic pressures which pose increasing threats to overwintering populations of waders. Barrages (to generate electricity, control tidal surges or provide leisure facilities) and marina developments are proposed for a number of estuaries and represent one type of potential threat to many wader species through habitat loss and reduced feeding opportunities. Other threats include pollution, climatic change and rising sea levels which erode or inundate estuarine habitat (e.g. Burd 1992). Disturbance, particularly that caused by recreational activities, is increasingly perceived as a threat, especially since many recreational activities appear to be increasing in intensity, coverage or period of the year in which they take place. Direct evidence linking disturbance with population changes in waders is, however, generally lacking.

Recent research has predicted the effects of developments and associated loss of feeding habitat on wader populations (Goss-Custard & Moser 1988; Goss-Custard *et al.* 1991). This work has provided a theoretical framework for interpreting the consequences of loss of feeding habitat on individuals and populations. Brief disturbance can result in birds being temporarily deprived of feeding habitat (see Smit & Visser 1993). Sustained disturbance can also result in long-term loss of feeding habitat and a reduction in feeding opportunity. In theory, the only difference between disturbance and development is that its effects are usually more localised, temporary and reversible.

In this paper I discuss and briefly review some of the work on wader dispersion, competition, feeding efficiency and prey depletion that is relevant to research on disturbance, with the aim of encouraging researchers to consider disturbance in the context of some current theory.

This paper deals with disturbance to waders on their winter feeding grounds. It should be borne in mind that disturbance can also affect waders during their breeding season and during their migrations, and that the overall impact on population dynamics of breeding season disturbance and/or disturbance on migration staging areas could greatly compound that during the non-breeding season.

DEFINING DISTURBANCE

In any field of inquiry there is need for unambiguous definitions. Disturbance is, however, a rather nebulous concept which loosely describes causal relationships between a wide range of (usually) anthropogenic stimuli and the responses they elicit in animals. Disturbance can be defined operationally as any relatively discrete event in time that disrupts ecosystems, communities or populations, where disruption refers to a change in behaviour, physiology, numbers or survival. Disturbance varies in its magnitude, frequency, predictability, spatial distribution and duration. Moreover, species (and individuals within species) vary greatly in their susceptibility to disturbance and this susceptibility is likely to vary with age, season, weather and the degree of previous exposure (habituation).

As a general rule, disturbance to waders is highly localised in time and space. For example, recreational disturbance is concentrated usually in the upper shore zones of estuaries and is restricted mainly to daylight hours, especially weekends in summer. It has been suggested that birds, being highly mobile, are less susceptible to the effects of disturbance than many other groups of organisms.

EFFECTS OF DISTURBANCE ON THE INDIVIDUAL

One of the consequences of sustained, localised disturbance is that waders shift to alternative feeding sites. A wading bird must feed to meet its immediate energy requirements and if disturbance reduces intake rate below a critical threshold, it must emigrate or starve. Dispersion of the population is simply the sum of the foraging decisions of all individuals where natural selection has shaped individuals to maximise the rate at which they gather energy from food. Understanding the factors that determine dispersion and limit feeding densities is key to an understanding of the possible consequences of disturbance at the level of the individual.

Optimal foraging theory (OFT) is the theoretical framework, which has proved extremely valuable in generating testable hypotheses about prey selection and dispersion in relation to food supply in waders. Waders must choose what prey species to feed on, which size-classes to select and which food patches to exploit.

Numerous studies have shown that waders forage efficiently by feeding in the best areas and selecting the most profitable size-classes of prey (e.g. Cayford & Goss-Custard 1990). The result is that waders generally concentrate where prey density, prey availability and intake rates are relatively high and where energy expenditure is relatively low (Goss-Custard & Charman 1976). As overall numbers increase, densities tend to reach a maximum on the most preferred feeding areas (Goss-Custard *et al.* 1982). This pattern of dispersion approximates to the 'ideal-free distribution' (Fretwell & Lucas 1970) where differences in prey density are cancelled out by differential interference (the immediate and reversible reduction in intake rate as bird density increases) and feeding rates are similar for all sites.

A more useful construct for interpreting wader dispersion is the 'ideal despotic model' (Fretwell & Lucas 1970) which recognises individual differences in competitive ability and assumes that individuals compete for the best sites in an attempt to maximise intake rates. If disturbance forces birds to move (temporarily or permanently) the question arises as to whether alternative feeding areas can accommodate displaced individuals and what effect increased bird density will have on intake rates, body condition and, ultimately, the fitness of those individuals which move. Evidence suggests that as bird density increases, average intake rates decline in some species as a result of increased competition, increased prey depletion and a greater proportion of the population feeding in sub-optimal areas (Goss-Custard 1980). However, not all individuals are affected to the same degree. Juveniles and sub-dominant adults are most susceptible to the effects of interference and this probably contributes to the disproportionately high mortality of young birds, especially during cold weather.

Sustained levels of disturbance can force birds to change feeding sites and may reduce intake rates. However, waders have a phenomenal capacity to vary their intake rate in response to changing environmental and physiological demands. For example, Swennen *et al.* (1989) have shown experimentally that captive Oystercatchers *Haematopus ostralegus* increase their feeding rates as the time available for feeding is reduced. Many wader species are known to increase their daily food intake by feeding in fields adjacent to estuaries during high water and feeding at night (Dugan 1981). Such behaviour might buffer the worst effects of disturbance.

EFFECTS OF DISTURBANCE ON THE POPULATION

The maximum number of birds an area can support (carrying capacity) will be determined by the density and availability of preferred prey, rates of prey depletion and the level of competition between individuals (interference). Only where populations are limited, or are close to limitation, by the quality and availability of wintering habitat can disturbance impact negatively in such places on wader populations by increasing mortality or decreasing recruitment. A key question is whether wader populations are limited by the availability of prey, but this is a difficult question to answer. It is relatively easy to measure the behavioural responses of birds to disturbance, but it is much more difficult to quantify the effect that these changes in behaviour have on population dynamics. Goss-Custard & Moser (1988) have shown for Dunlin *Calidris alpina* at least, that the decline in the overall wintering population in Britain between 1983-1986 was a function of habitat loss resulting from spread of cord-grass *Spartina,* supporting the view that feeding habitat is a major limiting factor for this species and that carrying capacity had been reached. Clearly, more research is needed on the carrying capacity of estuaries and the extent to which waders are limited by food supply before we can predict the effects of disturbance on populations.

MEASURING DISTURBANCE

Most studies have attempted to establish causality between disturbance and dispersion by measuring the behavioural responses of waders to disturbing stimuli. This approach provides data on relative levels of disturbance at different sites and comparative data on the susceptibility of species to different stimuli. The rate, predictability and severity of disturbing stimuli are, however, highly variable and the effects of disturbance are likely to be additive, so frequency data are limited in their usefulness.

As we have seen, quantifying the effects of disturbance on populations is problematic because of the difficulty in isolating key variables. One way round this is to take a behavioural measure such as feeding rate (which is highly correlated with the dependent measure being sought), and make the assumption that a reduction in feeding opportunity might reduce feeding rates. This would affect body condition and, consequently, survival or productivity (Owen 1993).

An alternative approach is to correlate observed distributions of waders with characteristics of individual sites, produce a multivariate model which predicts wader densities from significant environmental variables, and then attempt to explain deviations in the site-specific predictions of the model from actual densities in terms of disturbance (Bell & Fox 1991). As Owen (1993) states, this approach quantifies the potential of a site for waders and then calculates the degree to which this potential is reduced by disturbance. A similar approach has been adopted by Goss-Custard *et al.* (1991) to develop a model for predicting wader densities in a post-barrage Severn estuary based on prey densities, sediment parameters, exposure times and shore-line topography. One of the difficulties is that the models on which predicted wader use is based must explain a large fraction of the variation in the dependent variable (bird density). This level of precision is rarely achieved with ecological data, especially where many environmental and social factors combine to determine the variable in question (i.e. feeding density). Second, measurements must cover the full range of bird densities, and be completely independent of disturbance. Finally, there is always the problem that even the closest association may not indicate causality.

One suggestion is that experimental field manipulations may offer an alternative method for establishing links between disturbance, dispersion and population dynamics in waders. This approach has the advantage that species can be targeted and confounding variables such as habituation, season, time, temperature and even individual variation can be experimentally or statistically controlled. More importantly, data collection is not constrained by the infrequency or unpredictability of natural disturbing activities and the data is relatively free from bias.

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