

CHAPTER 1

GENERAL INTRODUCTION

In a world where natural resources are limited, competition is inevitable. This notion has been expressed comprehensively by Malthus in his *Essay on the principle of population* (first published in 1798). According to Malthus (1826) ‘all animated life has a constant tendency to increase beyond the nourishment prepared for it’, so that ‘the ultimate check to population appears to be the want of food’, a case that he has extensively and convincingly elaborated in the later editions of his essay. The inevitability of competition is also one of the building blocks of the theory of natural selection as presented by Darwin in his *On the origin of species* (1859). Like Malthus, Darwin reasoned that species have such a great potential fertility that their population size would increase exponentially (geometrically) if all individuals that are born would again reproduce successfully, so that the struggle for existence, part of which is competition, must be fierce (Mayr, 1982).

Its inevitability has put competition in the spotlights of ecology. In theoretical ecology, competition has featured prominently in the form of the Lotka-Volterra competition equations¹ (Kingsland, 1995). These equations capture both the idea that populations grow exponentially and the idea that competition puts a limit to population size. They form the starting point of much of the theoretical work that has been done on competition, including work on niches, limiting similarity, and community matrices (Grover, 1997; Keddy, 2001). Empirically, competition is also among the best studied topics of ecology. The number of field experiments on inter-specific competition, for instance, is unprecedented; Gurevitch et al. (1992) review 217 field experiments on competition in general, and several reviews exist for more restricted sub-sets of studies (Keddy, 2001).

The prominent position of competition in ecology notwithstanding, the process of competition is not well understood (Anholt, 1997; Keddy, 2001). Most theoretical work on competition has focussed on the effect of competition on populations and/or communities without considering the question how competition arises (Tilman, 1987). Similarly, too many empirical studies have put effort in detecting competition, and too few studies have focused on more useful questions, such as how organisms divide resources that are limited and how this depends on characteristics of organisms and their environment (Tilman, 1987; Peters, 1991; Keddy, 2001). The emphasis on describing competition may well be due to the dominant position of the Lotka-Volterra competition equations in ecology (Tilman, 1987). In these equations, both inter- and intra-specific competition are captured by a single parameter that merely describes the intensity of competition²; the mechanisms of competition remain unspecified.

In this thesis I strive for a better understanding of the conditions under which animals suffer from competition and of the intensity of this competition³. For me a proper understanding of competition entails ideas on the mechanisms of competition⁴ as well as ideas on the evolution of competition-related traits.

Knowledge of the mechanisms of competition is required to understand *how* animals compete at a snapshot of evolutionary time. Such knowledge is wanted to enable prediction of the prevalence and intensity of competition at novel conditions. While purely descriptive approaches do not allow for extrapolation beyond the range of conditions measured, it should in principle be possible to predict what happens under conditions that have not been studied previously if the mechanisms of competition are known (Tilman, 1987)⁵. Knowledge of the evolution of competition-related traits serves to understand *why* animals compete the way they do, that is, how they have come to do so. Such knowledge is wanted to put competition as it is currently occurring in its evolving context.

In studying competition, I deliberately focus on the behaviour of individuals. The dominating approach to studying competition in the twentieth century has been to treat competition as a population-level process, in the sense that variation between individuals has been neglected (Metz & Dieckmann, 1986). Between-individual variation, however, is essential to the mechanisms of competition (Lomnicki, 1988; DeAngelis & Gross, 1992)⁶ and to the evolution of competition-related characteristics (Darwin, 1859). Therefore, I think that any approach that neglects variation between individuals is unlikely to yield insight in the *how* and the *why* of competition (for a similar opinion, see Smith & Sibly, 1985; Lomnicki, 1988; Sutherland, 1996). Studying competition at the level of individuals has the extra advantage that properties of individual organisms and the mechanisms by which they interact with their environment are measured relatively easily, because of the temporal and spatial scale at which they operate (e.g., Huston et al., 1988). This advantage is huge. Population-level experiments on competition (for reviews, see McIntosh, 1970; Jackson, 1981; Connell, 1983; Schoener, 1983; Gurevitch et al., 1992) have attracted much criticism (Hurlbert, 1984; Underwood, 1986; Goldberg & Barton, 1992). Part of the criticism, such as the lack of replication, the absence of proper controls and the use of confounding designs, can be attributed to the difficulties associated with studying an organizational unit above the level of individuals.

THE GOAL

Striving for a better understanding of the conditions under which animals suffer from competition and of the intensity of this competition is a rather general goal for a thesis. Let me be more specific. Before I can do so, however, I have to define competition and to distinguish its basic forms. Competition is *the negative effect that one organism has upon another by consuming, or controlling access to, a common resource*⁷. As noted by Welden and Slauson (1986), a definition of competition like the one given above does not specify the ‘ends’ on which competition should be evaluated: to ascertain whether other organisms

have negative effects, a response variable on which negative effects are to be studied has to be specified. From an evolutionary perspective this response variable should be a measure of fitness. Classified on the basis of the mechanisms by which competition arises, two forms are generally distinguished (Keddy, 2001): *exploitative competition* occurs when one individual affects another indirectly, through the depletion of a resource, and *interference competition* occurs when one individual affects another directly, for instance, through outright physical attack, through threat behaviour, or through territoriality. A further distinction can be made between intra-specific and inter-specific competition.

With these definitions in hand I can specify my research goal. In studying competition, I will focus on intra-specific interference competition among foraging animals and I will evaluate competition in terms of a short-term response variable: intake rate, that is, the rate at which food is ingested. I restrict myself to *intra-specific* interference competition to simplify matters and because I think that intra-specific competition, at least from an evolutionary perspective, will generally be more important than inter-specific competition, given that requirements overlap most strongly among conspecifics. I focus on *interference* competition because I think understanding of this form of competition is most wanted. The exploitation of resources is a straightforward process, which is relatively easy to understand and to which much work has already been devoted (Grover, 1997). Behaviours underlying interference competition, on the contrary, are various and complex (e.g., Huntingford & Turner, 1987; Ens & Cayford, 1996; Hassell, 2000) and, as I will argue below, only some of these behaviours have been touched upon; understanding of interference competition is still rudimentary (van der Meer & Ens 1997). I focus on *foraging animals* because foraging is such an essential activity for animals and because I suspect that food is among the prime resources that animals are competing for. I evaluate competition in terms of negative effects on *intake rate*, because I think this to be a short-term measure of performance that is of relevance to foraging animals, because it is relatively easy to determine, and because it connects best to literature on foraging animals⁸. To these, I add two further refinements. First, I want to understand how foraging animals compete when they are foraging *under natural and unmanipulated conditions*. Second, I will focus on animals foraging in *standing stock systems* (van der Meer & Ens, 1997) rather than on animals foraging in *continuous input systems* (Sutherland & Parker, 1985, 1992)⁹ because standing stock systems are thought to be prevailing in nature (e.g., Tregenza, 1994; van der Meer & Ens, 1997).

THE SYSTEM

What is an appropriate study system given my goal? I focus on waders (Charadrii: Hayman et al., 1986) foraging in intertidal areas. Using foraging waders to study competition and resulting spatial distributions has several advantages:

- 1) Many wader species use intertidal areas for the larger part of the year, either as a migratory stop-over site, that is, to refuel during migration towards or from other wintering grounds, or as a wintering ground itself (van de Kam et al., 2004). While in the intertidal areas, foraging is by far the main activity of waders: for some of the species, foraging can take up as much as 95% of the available daylight hours (Baker, 1981; Goss-Custard et al., 1977b) as well as a substantial part of the night (e.g., Dugan, 1981; Dodd & Colwell, 1998).
- 2) The tidal nature of their foraging grounds forces waders to redistribute themselves repeatedly, almost on an hourly basis (Recher, 1966; Burger et al. 1977; Zwarts & Drent, 1981). This has the advantage that there are numerous more or less independent situations in which the interplay between interference competition and distribution can be studied. Moreover, exploitation will most probably not have a major effect on the distribution of waders, as exploitation of intertidal food stocks operates on a time scale exceeding a single tide (e.g., Zwarts et al., 1996; Dolman & Sutherland, 1997).
- 3) Waders in intertidal areas can be studied while foraging both under manipulated and under unmanipulated conditions. Especially the latter is a major advantage, as for several other groups of organisms, such as passerines, seabirds, insects, fish or mammals, it is often difficult to study the natural, that is, unmanipulated, foraging behaviour. Due to their size waders are quite conspicuous animals and in intertidal areas both their number and their behaviour can be observed rather easily, as there is nothing to obstruct the eye (Drinnan, 1957; Ens & Cayford, 1996) and as waders also forage during day-time. The advantage of studying conspicuous organisms with easily visible behaviour may especially be apparent when studying the mechanisms of competition (Keddy, 2001).
- 4) The diet of waders has several convenient characteristics. In intertidal areas, waders feed almost exclusively on marine invertebrates, so that their diet (or at least the digestible part) is rather homogeneously made up of flesh. This has the advantage that different prey species can be compared in a single currency – biomass, or ash-free dry-weight. Were waders omnivorous, such would be much more complicated because of the large biochemical differences in the composition of animals and plants. Moreover, densities of marine invertebrates are relatively easy to quantify (e.g., Zwarts & Wanink, 1993), marine invertebrates are often sessile (at least on the scale at which waders operate), and there is no recruitment during the period that waders

forage on them (O'Connors & Brown, 1977), and only little growth. These characteristics make intertidal areas, at least in the period that waders use them, a 'model' standing stock system.

- 5) The behaviour of waders foraging in intertidal areas has been studied in detail (e.g., Blomert et al., 1996; Goss-Custard, 1996; van de Kam et al., 2004), and interference competition and the mechanisms underlying it have also achieved quite some attention (see the Background section below).

Of course, there are also disadvantages to studying interference competition among non-breeding waders foraging in intertidal areas. Waders are, for instance, labour-intensive to do experiments with, and it is difficult to follow the foraging behaviour and patch choice of free-living, individual waders because of the difficulty to recognize them individually or to catch and mark them, and because the spatial scale of their daily foraging behaviour can be considerable. Other disadvantages become especially apparent when inference is to be made at a spatial and/or temporal scale exceeding that of their daily foraging behaviour. The migratory nature of most waders, for instance, makes quantification of their year-round behaviour difficult. The fact that waders generally are long-lived does not facilitate the determination of their life-time performance. Acknowledging that no system will be free of disadvantages, studying interference competition among foraging waders seems worth a go.

BACKGROUND

The study of interference competition among foraging waders has a rich history. It started from an interest in the instantaneous distribution of foragers over food patches (e.g., van der Baan et al., 1958; Wolff, 1969; Goss-Custard, 1970a; Zwarts, 1974; Bryant, 1979). Intertidal foraging grounds are far from homogeneous, and the choice of where to forage was thought to be of prime importance, especially so because the tidal nature of the foraging grounds forces the waders to continuously redistribute themselves (Recher, 1966; Burger et al., 1977; Zwarts & Drent, 1981). Two biotic factors were thought to determine the distribution of foraging waders: the density of available prey, and the density of the foragers themselves (Goss-Custard, 1980; Zwarts, 1980). That most waders would choose the patches with highest food densities just seemed logical but it was also realized that if all foragers would select the best patch, forager density would be so high that some negative effects could be expected. Such negative effects could potentially nullify the advantage of the high food density, making it more advantageous for some to leave for a food patch with a somewhat lower food density (Goss-Custard, 1977b, 1980; Zwarts, 1974, 1980, 1981; Zwarts &

Drent, 1981; Sutherland, 1983). As exploitation was thought to take time, interference was considered the most likely cause of such negative effects of high forager densities (Goss-Custard, 1980).

EMPIRICAL DEVELOPMENTS

Empirical contributions on interference competition can be organized along three lines. First, many studies have determined the *aggregative response*, that is, the relationship between food density and forager density (Hassell, 1966). Second, many studies have determined whether foraging waders actually suffer from interference competition and the conditions under which they do so. Third, several studies have identified potential interference mechanisms.

The relationship between food density and forager density has been studied for a variety of species (Table 1.1). Often, but not always, a positive correlation could be found between the density of foragers and the density of at least one of their prey species. Additionally, several studies found that the proportion of foragers in a less preferred area was higher when more foragers were present in a system (Zwarts, 1974, 1976, 1980; Goss-Custard, 1977a, 1977b, 1981; Zwarts & Drent, 1981; Goss-Custard et al., 1981, 1982; Meire & Kuyken, 1984). This observation is generally interpreted as support for the idea that foraging waders preferentially use good food patches, but that interference competition forces some into lower quality food patches when the number of foragers is high (the 'buffer effect'; Kluyver & Tinbergen, 1953). Only a single study has considered the distribution of foraging waders experimentally. Leopold et al. (1989) studied prey selection by captive Eurasian oystercatchers (*Haematopus ostralegus*; henceforth called oystercatchers) in a two-patch situation. Their experiment involved three oystercatchers among which a clear dominance hierarchy existed. In line with ideas about interference competition, they found that the patch choice of the individual with intermediate dominance status strongly depended on the presence of a more dominant competitor. Surprisingly, however, the patch choice of the subordinate oystercatcher was unaffected by the absence or presence of its higher-ranked competitors.

In about half of the studies on interference effects, intake rate was found to be negatively correlated with forager density (Table 1.2). The other half did either not find a significant correlation between intake rate and forager density, or they found intake rate to increase with forager density. Interference effect seemed to prevail among some species, and to depend upon the prey species. Furthermore, interference effects have been shown to depend on variation in the feeding method, the age, and the dominance position of interfering individuals, as well as on several environmental characteristics, including the size and the density of prey, and the type of habitats (Table 1.2). In determining the relationship between forager density and intake rate, the general approach has been correlational. Very few studies have determined this relationship experi-

Table 1.1. Observational studies on the aggregative response among waders foraging in inter-tidal areas¹

species	English name	prey species	results	reference
<i>Calidris alpine</i>	dunlin	ragworm	+	Bryant, 1979
<i>Calidris alpine</i>	dunlin	polychaete	+	Goss-Custard et al., 1977a
<i>Calidris alpine</i>	dunlin	all	+	Rands & Barkham, 1981
<i>Calidris canutus</i>	red knot	mudsnail	+,0	Bryant, 1979
<i>Calidris canutus</i>	red knot	tellin	+	Prater, 1972
<i>Calidris canutus</i>	red knot	tellin	0	Zwarts et al., 1992
<i>Calidris canutus</i>	red knot	tellin, cockle	+	Piersma et al., 1993
<i>Calidris canutus</i>	red knot	various	0	Goss-Custard et al., 1977a
<i>Calidris ferruginea</i>	curlew sandpiper	various	±	Puttick, 1984
<i>Calidris mauri</i>	western sandpiper	corophium.	+	Colwell & Landrum, 1993
<i>Calidris minutilla</i>	least sandpiper	corophium	+	Colwell & Landrum, 1993
<i>Calidris pusilla</i>	semi-palmated sandpiper	mudshrimp	+	Hicklin & Smith, 1984
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	cockle	+	Goss-Custard, 1977b
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	cockle	0	Horwood & Goss-Custard, 1977
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	cockle	0	Triplet et al., 1999
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	cockle	+	Meire, 1996
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	cockle	+	O'Conner & Brown, 1977
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	cockle	+	Rands & Barkham, 1981
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	cockle	±	Sutherland, 1982
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	mussel	+	Goss-Custard et al., 1977a
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	mussel	+,0	Meire & Kuyken, 1984
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	mussel, tellin	+	Bryant, 1979
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	various	0	Ens et al., 1996
<i>Limosa lapponica</i>	bar-tailed godwit	various	0	Bryant, 1979
<i>Numenius arquata</i>	Eurasian curlew	ragworm	+	Goss-Custard et al., 1977a
<i>Numenius arquata</i>	Eurasian curlew	ragworm	+	Bryant, 1979
<i>Numenius arquata</i>	Eurasian curlew	ragworm	0	Zwarts, 1979
<i>Numenius arquata</i>	Eurasian curlew	various	0	Rands & Barkham, 1981
<i>Tringa totanus</i>	redshank	mudshrimp	+,0	Goss-Custard, 1970a
<i>Tringa totanus</i>	redshank	ragworm	+	Goss-Custard et al., 1977a
<i>Tringa totanus</i>	redshank	ragworm, mudsnail	+	Bryant, 1979

¹ The column 'prey species' indicates the prey species used to determine the aggregative response; 'ragworm': *Nereis diversicolor*; 'polychaete': Polychaete spec.; 'all': total prey biomass; 'mudsnail': *Hydrobia ulvae*; 'tellin': Balthic tellin, *Macoma balthica*; 'cockle': edible cockle, *Cerastoderma edule*; 'corophium': Corophium spec.; 'mudshrimp': *Corophium volutator*; 'mussel': blue mussel, *Mytilus edulis*. The column 'results' indicates whether food density and forager density were related positively (+), negatively (-) or not related (0); ± indicates that forager density increased with increasing food density at the lower food densities, but decreased with food density at the higher food densities.

mentally, that is, by manipulating forager density. The perhaps earliest attempt in this direction has not been published: Koene and Drent tried to manipulate the density of foraging oystercatchers by introducing captive individuals to an intertidal area in The Netherlands, and by placing model oystercatchers on that area (Koene, 1978; Zwarts & Drent, 1981; RH Drent, personal communication).

Several interference mechanisms have been identified (for reviews, see Goss-Custard, 1970a, 1980; Ens & Cayford, 1996). In mentioning the most prominent ones, I will divide these mechanisms in two groups, based on their effect. First, foragers may lose time and energy in behavioural interactions with their competitors. Potential interactions include avoidance behaviour, threat display, overt aggression or conspecific vigilance (Ens & Cayford, 1996). Second, the efficiency of foragers may be reduced, either because foragers lose control over their search paths (e.g., Cresswell, 1997; Prop & Quinn, 2004), because they lose access to preferred feeding spots (e.g., Dolman, 1995; chapter 3), or because they have to divide their attention over multiple tasks (e.g., Mackworth, 1970; Dukas, 1998)¹⁰. Most of these mechanisms have been deduced from unmanipulated observations. Sullivan (1986), however, manipulated the distribution of food on a beach in New Jersey, USA, to study interference mechanisms among foraging ruddy turnstones (*Arenaria interpres*; henceforth called turnstones). She found more agonistic interactions when food was clumped than when food was distributed evenly, and interpreted this as support for the idea that interference competition among turnstones results from interactions over preferred feeding spots. Whitfield (1985) performed a similar experiment on captive turnstones. He also found that patchily distributed prey evoked more aggression than evenly distributed prey.

THEORETICAL DEVELOPMENTS

In their study of foraging oystercatchers, Zwarts and Drent (1981) had pointed out the possibility that the opposing effects of food density and forager density (interference) might be accounted for by the ideal-free-distribution model of Fretwell and Lucas (1970). This idea was elaborated by Sutherland (1983), who showed, mathematically, how the model could be used to predict the distribution of foraging waders. The ideal-free-distribution model was originally developed to predict the distribution of breeding birds over different habitats. To make the model applicable to foraging waders, Sutherland (1983) assumed that the intake rate achieved by a foraging animal in a certain food patch approximated the suitability of that patch. After this modification, the model uses the assumption that forager density negatively affects intake rate to predict the distribution and intake rate of foraging animals. In specific, the model predicts that the density of foragers will be positively related with the density of food in the various patches, but that the intake rate will be the same in all patches (Figure 1.1).

Table 1.2. Observational studies on the relationship between forager density and intake rate of waders foraging in intertidal areas¹

species	English name	prey species	results	individual differences	factors	transformation forager intake density rate	reference
<i>Arenaria interpres</i>	ruddy turnstone	decapods, pisces	+			u	Fleischer, 1983
<i>Arenaria interpres</i>	ruddy turnstone	decapods, pisces	0		tide	u	Fleischer, 1983
<i>Arenaria interpres</i>	ruddy turnstone	mealworms	0,-	dominance		log ₁₀	Whitfield, 1985
<i>Calidris alba</i>	sanderling	unknown	+,±		habitat	u	Silliman et al., 1977
<i>Calidris minutilla</i>	least sandpiper	beach fleas	-		prey density, humans	u	Yasue, 2005
<i>Charadrius semipalmatus</i>	semipalmated plover	bloodworm	0		prey density, humans	u	Yasue, 2005
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	cockle	-	age	date, tide, prey density, prey size	log ₁₀	Triplet et al., 1999
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	cockle	0			log ₁₀	Sutherland & Koene, 1982
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	cockle, mussel	0		prey density, prey size	log ₁₀	Ens et al., 1996
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	mussel	-	feeding method		log ₁₀	Stillman et al., 1996
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	mussel	0,-	dominance		log ₁₀	Ens & Goss-Custard, 1984
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	mussel	-			log ₁₀	Koene, 1978
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	mussel	-			log ₁₀	Zwarts & Drent, 1981
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	mussel	+,0,-	age	month	u	Goss-Custard & Durell, 1987a
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	mussel	0,-	dominance, feeding method		u	Goss-Custard & Durell, 1988
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	mussel	-	age		u	Goss-Custard & Durell, 1987b
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	mussel	-	feeding method		u	Stillman et al., 1996
<i>Limosa lapponica</i>	bar-tailed godwit	lugworm	0			u	Yates et al., 2000
<i>Numenius arquata</i>	Eurasian curlew	ragworm	-			u	Zwarts, 1981

Table 1.2. Continued

species	English name	prey species	results	individual differences	factors	transformation forager intake density rate	reference
<i>Tringa totanus</i>	redshank	amphipods	0		prey density, date, daytime, temp	u	Cresswell, 1994
<i>Tringa totanus</i>	redshank	various	0,-	feeding method		u	Goss-Custard, 1976
<i>Tringa totanus</i>	redshank	mudshrimp	0			u	Goss-Custard, 1970a
<i>Tringa totanus</i>	redshank	mudshrimp	-			log ₁₀ u	Selman & Goss-Custard, 1988
<i>Tringa totanus</i>	redshank	mudshrimp	-			log ₁₀ u	Selman & Goss-Custard, 1988
<i>Tringa totanus</i>	redshank	mudshrimp	-			u	Yates et al., 2000

1. The column 'prey species' indicate the observed prey: 'decapods': decapod spec.; 'piscies': piscies spec.; 'nealworms': *Tenebrio molitor*; 'beach fleas': California beach flea, *Megalorhystia californiana*; 'bloodworm': *Glycera dibranchiata*; 'cockle': edible cockle, *Cerastoderma edule*; 'mussel': blue mussel, *Mytilus edulis*; 'lugworm': *Arenicola marina*; 'ragworm': *Nereis diversicolor*; 'amphipod spec.': mudshrimp: *Corophium volutator*. The column 'results' indicates whether forager density and intake rate were related positively (+), negatively (-) or not related (0); ± indicates that intake rate increased with increasing forager density at the lower densities, but decreased with forager density at the higher forager densities. The column 'individual difference' indicates which between-individual variation was accounted for. The column 'factors' indicates which factors were controlled for in the statistical analysis: 'tide': time in tide; 'humans': human density; 'temp': temperature. The column 'transformation' indicates whether in the statistical analyses forager density and/or intake rate were log10-transformed (log₁₀), or not (u).

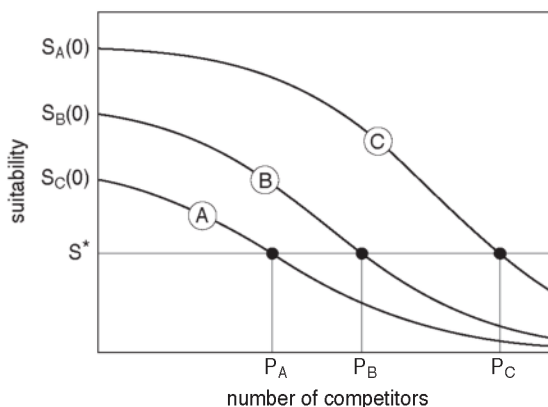


Figure 1.1. Illustration of the ideal-free-distribution model for a situation with three patches (A, B and C) that differ in their basic suitability, that is, in their suitability in the absence of competitors ($S_A(0)$, $S_B(0)$, $S_C(0)$). For each patch, suitability is assumed to decrease with the number of competitors present in that patch. The ideal-free-distribution model assumes that animals will distribute themselves over patches so as to experience maximal patch suitability. At any point in time, the model predicts that the number of animals is higher in habitats with higher basic suitability (i.e., $P_A > P_B > P_C$), and that the suitability achieved in all patches is the same: $S_A(P_A) = S_B(P_B) = S_C(P_C) = S^*$

A subsequent important theoretical contribution was provided by van der Meer and Ens (1997), who recognized that the work on interference competition can be structured around two building blocks: 1) the *generalized functional response*, that is, the relationship between food density, forager density and intake rate¹¹, and 2) the *aggregative response*, that is, the relationship between food density and forager density. Van der Meer and Ens (1997) identified six different models of the generalized functional response, and they used the ideal-free-distribution model to derive predictions of the aggregative response from each of them. They found that the six models generated strongly different predictions on the aggregative response. This result is striking, especially because the six models yielded overlapping generalized functional response curves and because predictions on the aggregative response were all generated in the same way – by means of the ideal-free-distribution model. Apparently, subtle differences among the generalized functional response models strongly affected predictions on the aggregative response.

Two of the models reviewed by van der Meer and Ens (1997) were derived mechanistically, from conceptual considerations of the foraging process. Both models are based on concepts from reaction kinetics; they assume that foraging animals can be in three mutually exclusive behavioural states (searching, handling and fighting), and that intake rate can be inferred from the transitions

rates between these three mutual states. These two models do not account for variation between individuals. Recently, other mechanistic models have been developed that do account for between-individual variation (e.g., Holmgren, 1995; Stillman et al., 1997).

As was noted by van der Meer and Ens (1997), the original mechanistic models do not consider the adaptive value of interference behaviour; they treat foraging animals as 'aimless billiard balls' with no choice but to act aggressively when encountering each other. Recent mechanistic models of the generalized functional response have started to extend the original models by considering the adaptive value of interference behaviour (e.g., Broom & Ruxton, 1998; Ruxton & Broom, 1999; Sirot 2000). The central question in these evolutionary models is how interference behaviour is shaped by natural selection. In addressing this question, these models specify that interference competition arise from *kleptoparasitism*, that is, aggressive interaction over food items; they account for variation between individuals by allowing individuals to vary in their interference strategy.

MATCHING THEORY WITH DATA

Goss-Custard et al (1995a,b) and Stillman et al. (2000b) have compared model predictions with observations on free-living oystercatchers foraging on mussels. They based their models on a phenomenological description of the generalized functional response and on the basic idea of the ideal-free-distribution model (that foragers choose patches so as to maximize their intake rate). With regard to the distribution of oystercatchers over mussel beds, Goss-Custard et al. (1995b) found the predicted pattern to resemble the observed pattern, though on the most preferred beds, predicted densities were higher than observed densities. Stillman et al. (2000b) found a positive correlation between observed and predicted densities at each of the mussel beds; the relationship between these two variables, however, did deviate significantly from unity.

RECAPITULATION

From the short review above it may be clear that much progress has been made in studying interference competition among foraging waders. Empirical studies have identified several interference mechanisms, and they have shown that interference competition affects the distribution and the intake rate of several species. Furthermore, it has become clear that interference effects may vary between individuals, and that several environmental factors may influence the prevalence of interference competition. Theoretical studies have provided tools to study interference effects on intake rate and to link such effects to the distribution of foragers over patches of food. Some of the theoretical contributions have been mechanistic and the most recent models have started to address the evolution of interference behaviour.

However, it is also clear that a proper understanding of interference competition has not been reached yet. Much variation in the prevalence and intensity of interference competition was found both between and within species. Some factors that may explain this variation have been identified, but this has not yet led to much explanatory power. Few mechanistic models of the generalized functional response have been derived, but these models have not yet led to a coherent view on the mechanistic details of interference competition. The evolution of interference behaviour has recently also been addressed, but there is not yet consensus on what interference strategies will be evolutionarily stable. Few attempts have been made to predict the extent to which foraging waders will suffer from interference competition, but these attempts were all based on a phenomenological description of interference competition.

THE APPROACH OF THIS THESIS

In this thesis, I try to improve understanding of interference competition by focusing on the generalized functional response. I use two approaches. First, I develop an experimental approach in which I study the mechanisms by which foraging waders suffer from interference competition. Previous studies of interference competition among foraging waders have almost exclusively used a correlational approach, with the inevitable risk of confounding effects of uncontrolled factors (Ens & Cayford, 1996; van der Meer & Ens, 1997). The experimental approach should be added to the toolbox of students of interference competition to raise the level of quantitative detail and to determine the causal processes that underlie interference competition (van der Meer & Ens, 1997). Performing experiments on waders may not be easy, but several pioneers have already showed that it is possible (see Box I). Second, I develop a unifying, systematic approach to modelling the generalized functional response both mechanistically and evolutionarily. The approach of previous models of the generalized functional response has largely been phenomenological. Some models had a conceptual basis, but only few of them also specified a mechanism of interference competition and accounted for variation between individuals. I believe that future models should not only have a conceptual basis, but should specify the mechanisms of interference competition, should account for between-individual variation and should consider the evolution of interference behaviour. The recent evolutionary approach to modelling interference competition already provides a promising improvement.

THE EXPERIMENTAL APPROACH

I started by studying the generalized functional response experimentally, measuring intake rate of waders at experimentally determined food densities and

forager densities (chapter 2). With the help of several students, I have performed the same experiment twice, first using red knots (*Calidris canutus*; henceforth called knots), then using turnstones (Box II). In both experiments we have focused on the behaviour of captive individuals foraging in the experimental mudflat facility of the Royal NIOZ on Texel. The use of captive foragers enabled us to compare the performance of the same individuals at different environmental conditions, thereby excluding confounding effects of individual differences in dominance status, age, sex, foraging ability and the like. The experimental mudflat facility allowed for control over most abiotic conditions (e.g., weather, light regime and sediment composition) as well as over most biotic conditions (e.g., predation risk, disease risk, prey composition). For both knots and turnstones it had proven feasible to perform experiments under laboratory conditions (e.g., Piersma et al., 1995; Whitfield, 1985, 1988a).

The one aspect of the experiments described in chapter 2 that surprised me most was that kleptoparasitism, that is, the stealing of food items, was absent. This finding left me puzzled with the question why foraging waders would interfere with each other, if not to steal food items. One possibility is that agonistic interactions concern food clumps rather than single food items. If interactions are over food clumps, interference effects should depend on the distribution of food. To see whether they do, Tamar Lok and I performed an experiment on captive turnstones, examining how the presence of a competitor affects the intake rate of a focal turnstone when food is clumped and when food is dispersed (chapter 3). The results of this experiment support the idea that interference may be over clumps of food rather than over food items. The real insight from this experiment, however, regards the overriding effect of the dominance status of the foragers.

Motivated by these findings on the effect of food distribution on the behaviour and intake rate of captive turnstones, Kim Meijer and I performed a similar experiment with free-living foragers on the beaches of Delaware Bay, New Jersey, USA (chapter 4). During spring migration, the number of turnstones in this bay is so high that it is possible to attract wild foragers to experimental plots. We manipulated the spatial distribution of food by varying the distance between food clumps. In general terms the results of this experiment are in line with those of the experiment performed in chapter 3. However, the two experiments differ from each other in quite a fundamental way.

The results so far supported the idea that it is clumps of food, rather than individual food items, that turnstones are fighting for. But does it matter what they are fighting for, either food items or food clumps? Anticipating that this question may become a crucial factor in future models of interference competition and resource defence, Sjouke Kingma, Dolores Rodriguez and I performed an experiment in which we studied interference effects among captive turnstones that forage on so-called 'food pits' that are either divisible or not (chap-

ter 5). The extent to which food can be divided among foraging animals may be among the essential differences between food items and food clumps; food clumps are composed of multiple items and can therefore be split among multiple foragers more easily than can food items.

THE THEORETICAL APPROACH

In the course of my Ph.D. project, several models have been published that take into account the evolution of aggressive behaviour, while studying interference competition. Although these models appear to be very similar, they yield strikingly different predictions regarding the evolutionary stability of various interference strategies. In an attempt to unify previous models, my co-authors and I developed a framework that allows for a more systematic approach to studying the evolution of interference behaviour (chapter 6). We applied this framework to some previous models to identify the crucial assumptions and pitfalls in modelling the evolution of interference behaviour.

NOTES

- ¹ The Lotka-Volterra competition equations are based on the Pearl-Verhulst logistic equation of population growth (Kingsland, 1995). In its classic form the logistic equation can be written as:

$$\frac{dN}{dt} = rN \frac{(K - N)}{K} ,$$

where N is population size, r is the population growth rate and K is the carrying capacity, that is, the maximum population size that can be sustained in a system. The Lotka-Volterra competition equations extend this equation by accounting for competition between species:

$$\frac{dN_1}{dt} = r_1 N_1 \frac{(K_1 - N_1 - \alpha_{1,2} N_2)}{K_1} ,$$

$$\frac{dN_2}{dt} = r_2 N_2 \frac{(K_2 - N_2 - \alpha_{2,1} N_1)}{K_2} ,$$

where $\alpha_{1,2}$ is the inter-specific competition coefficient that represents the resource utilization of species 1 compared with the resource utilization by species 2 (Vandermeer & Goldberg, 2003).

- ² The Lotka-Volterra equations account for inter-specific competition explicitly, through the competition coefficient α ; intra-specific competition is accounted for only implicitly, through the carrying capacity K .
- ³ I agree with Peters (1991) that striving 'to understand' is among the more nebulous goals in science (together with 'to examine', 'to illuminate', 'to investigate' and 'to explain why'). Nevertheless, I also agree with Pickett et al. (1994) that understanding is the overarching goal of science. To avoid the pitfalls laid bare by Peters (1991), I spell out my research goal in considerable detail, and I develop an approach that is as quantitative as possible without giving in on my overall goal to understand how animals compete. To start: I define understanding as the match between confirmable natural phenomena and independent predictions generated *a priori* from conceptual considerations. This definition is a

modification of the definition given by Pickett et al. (1994), who define understanding as 'an objectively determined, empirical match between some set of confirmable, observable phenomena in the natural world and a conceptual construct'. Further considerations on the goal of science and the relative merit of predictions and understanding can be found in the first Reflection that follows on the General discussion.

- 4 Note that this implies that I consider a *phenomenological* approach to be insufficient to reach a proper understanding of competition because such an approach does not yield insight in the mechanisms of interference competition. I define mechanistic models as models that specify how the phenomenon of interest comes about, with the prerequisite that model parameters can be measured independently of the model in which they feature. Phenomenological models do not specify how the phenomenon of interest comes about. Further considerations on the term 'mechanistic' as opposed to 'phenomenological' can be found in the second Reflection that follows on the General discussion.
- 5 Of course, this rests on the premise that the mechanisms themselves are the same at the novel conditions as at the conditions under which they were determined. Although this will not necessarily be the case, I do think that the extrapolative ability of a mechanistic approach potentially exceeds that of a purely descriptive approach.
- 6 Numerous authors have emphasized that the assumption that variation between individuals can be negligible can lead to very unrealistic predictions (e.g., see the papers in DeAngelis & Gross, 1992). This case has been made very clear by Lomnicki (1988), who argued that, under the assumption of strict equality of individuals, the addition of a single individual can kill an entire population. His reasoning is as convincing as it is simple. If a certain population consists of n individuals, all requiring x resources to survive, and if there are nx resources available, each individual will get $nx/n = x$ resources and all will survive. If one individual would be added to this population, so that it would contain $n + 1$, instead of n individuals, each individual would get $nx/(n + 1)$ resources, which is less than the required amount x , so that all would die. Thus, the assumption that individuals are all alike, both in their requirements and in the share of the resources that they get, has the rather unrealistic consequence that mortality is an all-or-nothing step function of population size for all individuals.
- 7 This definition is a modification of the definition given by Keddy (2001); it deviates from it in two ways. First, according to Keddy the competed resource 'has to be limited in availability'. I find this extra requirement superfluous; even if negative effects would arise in the midst of plenty, I would speak of competition. Second, I add to the definition given by Keddy that the resource has to be common to both organisms involved; two organisms are not competing if the one organism is controlling access to a resource that only the other organism is after. Note that the definition does not specify resources. Keddy (2001) defines a resource as 'a substance that is consumed by an organism and that produces increased size or performance as availability increases'. Grover (1997) defines a resource as 'an entity that stimulates population growth, at least over some range of availability, and which are consumed'. I think both definitions are too narrow, because resources do not have to be consumable. To give an example: nest boxes are resources for passerines (e.g., de Heij, 2006). Furthermore, to be consistent with the definition of competition, the characteristic that is stimulated should not be specified. Thus, to me a resource is 'an entity that potentially has a positive effect to the organism that consumes it, or that controls access to it'.
- 8 For considerations on the evolution of interference competition, this approach requires the assumption that intake rate is a useful approximation of fitness. This is not at all obvious, and little is known about the actual relationship between intake rate and fitness. Nevertheless, I think it is the best I can do at the moment.
- 9 Various attempts have been made to distinguish these two basic types of systems (e.g., Sutherland & Parker, 1985; Lessells, 1995; van der Meer & Ens, 1997). I think that the

crucial difference between the two types lies in the rate at which food enters a system relative to the rate at which food is consumed; in standing stock systems, food enters the system at a time scale longer than that at which animals forage, so that it can safely be assumed that there is no replenishment of food while the animals are foraging, whereas in continuous input systems food is replenished at a time scale comparable to that at which animals forage.

- ¹⁰ Prey depression, that is, the temporary decrease of the accessible fraction of prey that results from a behavioural response of the prey, is often seen as another mechanism underlying interference competition (e.g., Stillman et al., 2000a; Yates et al., 2000). According to the definitions given above, however, this mechanism underlies exploitative competition rather than interference competition. This view is supported by Charnov et al. (1976), who consider depletion ('exploitative depression') and prey depression ('behavioural depression') as two forms of prey depression.
- ¹¹ This response extends the well-known *functional response*, that is, the relationship between food density and intake rate (Solomon, 1949; Holling, 1959) by accounting for effects of forager density on intake rate. In principle, a model of the generalized functional response captures effects of both exploitative and interference competition. To isolate effects of interference competition, students of interference competition generally restrict their attention to the instantaneous effect of food and forager density on intake rate (van der Meer & Ens, 1997); *instantaneous* effects regard interference competition when the exploitation of resources is a relatively slow process (Goss-Custard, 1980).

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BOX 1.1 EXPERIMENTS ON FORAGING WADERS

Experimental work on the foraging behaviour of waders has been done on captive and on free-living foragers (see Table). Work on the foraging behaviour of captive waders was pioneered by Goss-Custard (1970b), Hulscher (1974, 1976, 1982), and Myers et al. (1980). Goss-Custard (1970b) studied how captive redshanks (*Tringa totanus*) selected among the size of their prey (mealworms), while foraging on a wooden platform in an indoor environment. His approach was later followed by Marshall (1981), and Whitfield (1985, 1988a), who studied feeding behaviour and the aggressive behaviour of foraging turnstones. Hulscher (1974) studied how environmental conditions, such as the tidal regime and the light conditions, and prey characteristics affected the intake rate of captive oystercatchers foraging on an artificial mudflat in an outdoor cage. This approach was later followed by Wanink and Zwarts (1985), who studied whether the intake rate of a captive oystercatcher could be predicted from a prey selection model. In later experiments, Hulscher brought out a captive oystercatcher to a cage that he constructed (each tide anew) on natural mudflats (Hulscher, 1976, 1982). Myers et al. (1980) studied the foraging behaviour of sanderling (*Calidris alba*) foraging on an artificial mudflat placed in an indoor aviary, an approach later followed by Piersma et al. (1995) and van Gils et al. (2003a) to study the foraging behaviour of knots.

In later years, several authors have used an outdoor aviary in which a tidal regime could automatically be imposed, to see how the foraging behaviour of captive oystercatchers depended on the length of the tide (Daan & Koene, 1981; Swennen et al., 1989; Leopold et al., 1989). The same cages were later used by Rutten et al. (in prep.a) and van Gils et al. (2003b, 2005) to study the foraging behaviour of captive oystercatchers and knots, respectively. Over the last ten years, several experiments have been performed on the behaviour of knots foraging in a large indoor aviary that contains an artificial mudflat upon which a tidal regime can automatically be imposed (Piersma et al., 2003; van Gils & Piersma, 2004; Folmer, unpublished; chapter 2, 3 and 5).

Experiments involving free-living waders were initiated by Koene and Drent (Koene, 1978; Zwarts & Drent, 1981), who tried to manipulate the density of oystercatchers by placing artificial oystercatchers on an intertidal area in The Netherlands, and by introducing captive birds to that area. Sullivan (1986) manipulated the distribution of food on a beach in New Jersey to study the aggressive behaviour of foraging turnstones, an approach that I followed (chapter 4). Rutten et al. (in prep.b) manipulated the density of free-living oystercatchers foraging in an estuary in The Netherlands, by chasing oystercatchers off specific beds of the edible cockle (*Cerastoderma edule*) in order to raise the density on near-by beds.

Table Box1.1. Experiments on the intake rate or interference behaviour of foraging waders (in chronological order)¹

species	English name	prey species	size	n ₁	n ₂	e ₁	e ₂	e ₃	e ₄	subject of study	reference
<i>Tringa totanus</i>	redshank	mealworms	2	2	1	captive	in	aviary	art	fr	Goss-Custard, 1970b
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	bivalves	10	10	1	captive	out	cages	art	fr	Hulscher, 1974
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	cockle	1	1	1	captive	out	cages	nat	fr	Hulscher, 1976
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	natural	u	u	u	free	-	-	nat	gfr	Koene, 1978
<i>Calidris alba</i>	sanderling	isopods, crabs	9	9	1	captive	in	aviary	art	fr	Myers et al., 1980
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	mussel	4	4	1	captive	out	aviary	art	fr	Daan & Koene, 1981
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	natural	u	u	u	free	-	-	nat	gfr	Zwarts & Drent, 1981
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	tellin	1	1	1	captive	out	cages	nat	fr	Hulscher, 1982
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	bivalves	1	1	1	captive	out	cages	art	fr	Wanink & Zwarts, 1985
<i>Arenaria interpres</i>	ruddy turnstone	mealworms	13	13	13	captive	in	aviary	art	mech	Whitfield, 1985
<i>Arenaria interpres</i>	ruddy turnstone	crab eggs	u	u	u	free	-	-	nat	mech	Sullivan, 1986
<i>Arenaria interpres</i>	ruddy turnstone	mealworms	13	13	10	captive	in	aviary	art	mech	Whitfield, 1988a
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	cockle, mussel	7	7	1-3	captive	out	aviary	art	ar	Leopold et al., 1989
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	cockle	7	7	2,3	captive	out	aviary	art	fr	Swennen et al., 1989
<i>Calidris canutus</i>	red knot	tellin, cockle	5	5	1	captive	in	aviary	art	fr	Piersma et al., 1995

Table Box1.1. Continued

species	English name	prey species	size		environment				subject of study	reference
			n1	n2	e1	e2	e3	e4		
recent work										
<i>Calidris canutus</i>	red knot	cockle	5	5	captive	in	aviary	art	fr	Piersma et al., 2003
<i>Calidris canutus</i>	red knot	tellin, cockle	6	1	captive	in, outaviary,	cages	art	fr	van Gils et al., 2003a
<i>Calidris canutus</i>	red knot	mussel	4	1	captive	out	aviary	art	fr	van Gils et al., 2003b
<i>Calidris canutus</i>	red knot	mussel	5	1-5	captive	in	aviary	art	gfr	van Gils & Piersma, 2004
<i>Calidris canutus</i>	red knot	mussel	5	1-5	captive	in	aviary	art	fr	van Gils et al., 2005
<i>Calidris canutus</i>	red knot	mussel	10	1,2,4,8,16	captive	in	aviary	art	gfr, mech	Vahl et al., chapter 2
<i>Arenaria interpres</i>	ruddy turnstone	mealworms	15	1,3,5,9,13	captive	in	aviary	art	gfr, mech	Vahl et al., chapter 2
<i>Arenaria interpres</i>	ruddy turnstone	maggots	12	1,2	captive	in	aviary	art	mech	Vahl et al., chapter 3
<i>Arenaria interpres</i>	ruddy turnstone	crab eggs	u	u	free	-	-	art	mech	Vahl et al., chapter 4
<i>Arenaria interpres</i>	ruddy turnstone	mealworms	16	1,2	captive	in	aviary	art	mech	Vahl et al., chapter 5
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	cockle	8	1,2	captive	out	aviary	art	mech	Rutten et al. in prep.a
<i>Haematopus ostralegus</i>	Eurasian oystercatcher	cockle	u	u	free	-	-	nat	ar	Rutten et al. in prep.b
<i>Calidris canutus</i>	red knot	mussel	5	1-8	captive	in	aviary	art	gfr, ar	Folmer et al. unpublished

1 The column 'prey species' indicates the prey species used in the experiment; 'mealworms': *Tenebrio molitor*; 'bivalves: unknown bivalves; 'cockle': edible cockle, *Cerastoderma edule*; 'natural': unmanipulated prey; 'isopods spec.': isopods larvae. The column 'sand crab spec.': 'mussel': blue mussel, *Mytilus edulis*; 'tellin': Bathic tellin, *Macoma balthica*; 'crab eggs': eggs of horseshoe crabs, *Limulus polyphemus*; 'maggots': Diptera larvae. The column 'size' indicates the number of different individuals that has been used in the experiment ('n1') and the number of foragers ('n2'); if the number of foragers was an experimental factor, all treatment levels are given. In experiments on free-living foragers the number of different individuals was unknown (u) and the number of competitors was uncontrolled (u). The column 'environment' captures various aspects of the experimental environment: column 'e1' indicates whether the experiment used captive or free-living ('free') foragers, column e2 indicates whether, if captive foragers were used, the experiment was done indoors ('in') or outdoors ('out'), column 'e3' indicates whether cages, an aviary, or neither (-) was used, and column 'e4' whether the birds foraged on a mudflat or not ('no'), and if they foraged on a mudflat whether this was an artificial ('art') or a natural ('nat') mudflat. The column 'subject' indicates whether the experiment focussed on the functional response (effect food density on intake rate; 'fr'), on the generalised functional response (effect of food density and forager density on intake rate; 'gfr'), on the aggregative response (the realized relationship between food density and forager density; 'ar'), or a mechanism of interference

BOX 1.2 THE RUDDY TURNSTONE (*ARENARIA INTERPRES*)

TAXONOMY AND OCCURRENCE

Ruddy turnstones (henceforth called turnstones) breed along the northern most fringes of the Holarctic; their breeding distribution is almost circumpolar (Whitfield, 2002; del Hoyo et al., 1996). Two subspecies are generally recognized: *A. i. morinella* and *A. i. interpres*. The *morinella* subspecies breeds in arctic North-America; the *interpres* subspecies breeds in the rest of the Holarctic region (from northeast Canada to west Alaska), except for west and south Alaska, where it is replaced by the black turnstone (*Arenaria melanocephala*), the only other member of the genus *Arenaria*. Of the nominate subspecies four populations can be distinguished on the basis of their breeding sites, migration routes and wintering grounds (but not their morphology: Engelmoer & Roselaar, 1998). Outside the breeding season, the distribution of turnstones is almost world-wide.

HABITAT TYPE AND HABITAT USE

Wintering turnstones can be found chiefly on rocky shores, weedy reefs and along the tide edge. The number of turnstones using the same wintering area is generally low, not exceeding a few hundreds (Metcalf, 1986; Fuller, 2003). Extensive ringing programs, and the use of unique colour bands have revealed that the site-fidelity of wintering turnstones is high, both within and between years (Metcalf & Furness, 1985; Whitfield, 1985; Metcalf, 1986; Summers et al., 1989; Burton & Evans, 1997).

FOOD AND FORAGING TECHNIQUES

With regard to their food, turnstones are extreme opportunists; they have among the most varied diets of all wader species (Gill, 1983). Stomach and regurgitate analysis has revealed that their main food source is generally formed by amphipods, barnacles, crabs, and small bivalve and gastropod molluscs (Davidson, 1971; Prater, 1972; Jones, 1975; Glutz von Blotzheim, 1977; Harris, 1979). Occasionally, however, they may also eat eggs, carrion (e.g., bivalve remains,

sheep, cat, wolf, and corpse), and supply from man (e.g., bread, meat, dog food, household scraps, soap, potato peel and oatmeal; Gill, 1983). Turnstones differ from most other waders in that the bill of a turnstone contains relatively few mechanoreceptors (Herbst's Corpuscles; Hoerschelmann, 1972), making it less suitable for tactile search. Indeed, turnstones predominantly search for their food visually. In doing so, they exhibit several specialized feeding techniques (Whitfield, 1990). Their ability to 'turn stones' is well-known: with quick jerking movements they can flip over objects such as stones, shells and seaweed, to quickly pecked at or chased the prey found underneath. Another techniques used include routing through piles of seaweed, digging substantial holes in sandy sediment, probing mudflats, hammer-probing barnacles, and pecking surfaces (Whitfield, 1990).

SOCIAL BEHAVIOUR

Turnstones have the reputation of being pugnacious and quarrelsome (Beven & England, 1975). On their wintering grounds, they mainly operate in small and often scattered parties, generally not exceeding 20 or 30 individuals (Metcalf, 1986). The familiarity among individuals in their wintering area is thought to be high – turnstones are individually recognizable by their plumage (Ferns, 1978; Whitfield, 1988a) -, and often a clear dominance structure exists, which is thought to be site-specific (Whitfield, 1985). While aggressive, turnstones assume a typical posture known as the 'tail-depressed' posture (Groves, 1978).

PREDATION AND SURVIVAL

Turnstones are predated upon by small raptors (e.g., sparrow hawks, merlins and peregrines; Whitfield, 1988b). Their annual survival, however, is high, and in line with this, the ruddy turnstone is among the long-lived wader species (with records up to 19 years).

