INTERFERENCE COMPETITION AMONG FORAGING WADERS

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The research presented in this thesis was carried out at the Theoretical Biology Group and the Animal Ecology Group, which are both part of the Centre for Ecological and Evolutionary Studies of the University of Groningen (RuG), and at the department of Marine Ecology and Evolution of the Royal Netherlands Institute for Sea Research (NIOZ). The research was supported by the 'Breedtestrategie' program of the University of Groningen. Production of this thesis was partly funded by the University of Groningen, the Centre for Ecological and Evolutionary Studies and the Royal Netherlands Institute for Sea Research.

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‘... please always remember that a scientist's achievement may lie in many different areas: As an innovator (new discoveries, new theories, new concepts), as a synthesiser (bringing together scattered information, sharing relationships and interactions, particularly between different disciplines, like genetics and taxonomy), as a disseminator (presenting specialized information and theory in such a way that it becomes accessible to non-specialists [popularizer is a misleading term]), as a compiler or cataloguer, as an analyst (dissecting complex issues, clarifying matters by suggesting new terminologies, etc.), and in other ways. [....] The philosophers of the physical sciences have given us a very wrong picture of science, by implying that a scientist does only do either of two things: (1) Discover new facts (for which he may get the Nobel Prize) or (2) Propose new theories. Actually, much, if not most, of science is neither!’

Ernst Mayr to Will Provine (1979), quoted in W. Provine. 2005. Trends in Ecology and Evolution 20:411-413.

l’art pour l’art

CONTENTS

ABSTRACT

Competition is among the most studied topics in ecology, both theoretically and empirically. Nevertheless, understanding of competition is still rudimentary; ecologists are not quite able to tell why or to predict how much competing animals suffer from mutual interactions. This thesis strives to contribute to understanding of competition by studying the mechanisms of interference competition among waders (Charadrii), foraging in intertidal areas. It attempts to extend previous work by applying an experimental approach to the empirical study of interference competition and an evolutionary approach to its theoretical study.

The experiments presented in this thesis yielded the following results:

1. Chapter 2 reveals that (1) interference effects on intake rate are different for red knots (*Calidris canutus*) and ruddy turnstones (*Arenaria interpres*), (2) that the mechanistic basis of interference effects differed between these two species, but (3) that in neither of the two species interference effects resulted from kleptoparasitism (i.e., the stealing of food items), which is the most widely discussed interference mechanism.
2. Chapter 3 shows that the extent to which captive turnstones suffer from interference competition depends on both the spatial distribution of food and the relative social dominance status of focal individuals. When food is spatially clumped, interference competition may arise from the monopolisation of food clumps, and interference effects may be unrelated to the amount of agonistic behaviour. Chapter 4 shows that the spatial distribution of food affects the amount of agonistic behaviour and the distribution of free-living turnstones, but it does not affect the time focal individuals spent digging for food, which is taken as an approximation of intake rate.
3. Chapter 5 shows that the extent to which captive turnstones suffer from interference competition depends on the distribution of food and on the foragers' social dominance status (as before), but also on the divisibility of food, which is one of the differences between food items (indivisible) and food clumps (divisible).

Thus, interference competition among foraging waders need not result from the stealing of food items, but may also result from interactions over food clumps, and these two mechanisms may differ in a way that is essential to the interference process.

The theoretical chapter of this thesis (chapter 6) reveals that models of interference competition have not yet reached consensus about the kinds of interference behaviour that can be expected to evolve. Although evolutionary models of interference competition appear to be similar, they yield strikingly different predictions regarding the evolutionary stability of various interference strategies. To unify previous approaches, a systematic event-based description of the foraging process is presented and the use of techniques from Adaptive Dynamics theory is promoted. Through a critical discussion of the setup, the assumptions and the way of analysis of some evolutionary models of interference competition, crucial assumptions and potential pitfalls in modelling the evolution of interference behaviour are identified.

Together, these experimental and theoretical results contribute to a mechanistic and evolutionary understanding of interference competition. At the same time, they make it clear that we cannot claim having reached such an understanding yet. This implies that it still is premature to base models of population dynamics on presumed knowledge of the interference process.

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 equations[1] (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 competition[2]; 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 competition[3]. For me a proper understanding of competition entails ideas on the mechanisms of competition[4] 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 animals[8]. 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 homogenously 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 intertidal areas[1]

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

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[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 areas[1]

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

Table 1.2. Continued

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

[1] The column 'prey species' indicate the observed prey: 'decapods': decapod spec.; 'pisces': pisces spec.; 'mealworms': *Tenebrio molitor*; 'beach fleas': California beach flea, *Megalorchestia californiana*; 'bloodworm': *Glycera dibranchiate*; 'cockle': edible cockle, *Cerastoderma edule*; 'mussel': blue mussel, *Mytilus edulis*; 'lugworm': *Arenicola marina*; 'ragworm': *Nereis diversicolor*; 'amphipods': 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 ($\log_{10}$), or not (u).

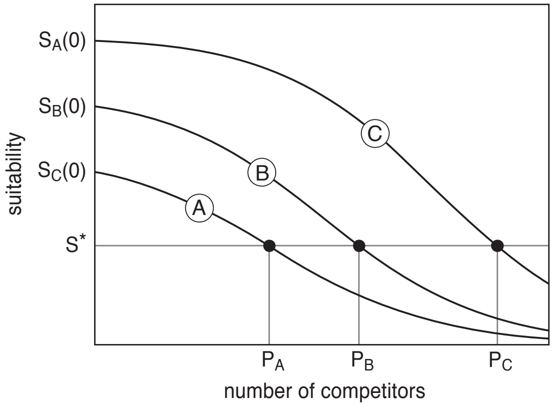

Figure 1.1. Illustration of the ideal-free-distribution model for a situation with three patches (*A,B* and *C*) that differ in their basic suitability, that is, in their suitability in the absence of competitors ($S_A(0)$, $S_B(0)$, $S_C(0)$). For each patch, suitability is assumed to decrease with 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 rate[11], 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 extent 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 Rodriquez 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 (chapter 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:

$$dN/dt = rN\,(K-N)/K \quad ,$$

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:

$$dN_1/dt = r_1N_1\,(K_1 - N_1 - \alpha_{1,2}N_2)/K_1 \quad ,$$
$$dN_2/dt = r_2N_2\,(K_2 - N_2 - \alpha_{2,1}N_1)/K_2 \quad ,$$

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		environment				subject of study	reference
			n_1	n_2	e_1	e_2	e_3	e_4		
Tringa totanus	redshank	mealworms	2	1	captive	in	aviary	art	fr	Goss-Custard, 1970b
Haematopus ostralegus	Eurasian oystercatcher	bivalves	10	1	captive	out	cages	art	fr	Hulscher, 1974
Haematopus ostralegus	Eurasian oystercatcher	cockle	1	1	captive	out	cages	nat	fr	Hulscher, 1976
Haematopus ostralegus	Eurasian oystercatcher	natural	u	u	free	-	-	nat	gfr	Koene, 1978
Calidris alba	sanderling	isopods, crabs	9	1	captive	in	aviary	art	fr	Myers et al., 1980
Haematopus ostralegus	Eurasian oystercatcher	mussel	4	1	captive	out	aviary	art	fr	Daan & Koene, 1981
Haematopus ostralegus	Eurasian oystercatcher	natural	u	u	free	-	-	nat	gfr	Zwarts & Drent, 1981
Haematopus ostralegus	Eurasian oystercatcher	tellin	1	1	captive	out	cages	nat	fr	Hulscher, 1982
Haematopus ostralegus	Eurasian oystercatcher	bivalves	1	1	captive	out	cages	art	fr	Wanink & Zwarts, 1985
Arenaria interpres	ruddy turnstone	mealworms	13	13	captive	in	aviary	art	mech	Whitfield, 1985
Arenaria interpres	ruddy turnstone	crab eggs	u	u	free	-	-	nat	mech	Sullivan, 1986
Arenaria interpres	ruddy turnstone	mealworms	13	10	captive	in	aviary	art	mech	Whitfield, 1988a
Haematopus ostralegus	Eurasian oystercatcher	cockle, mussel	7	1-3	captive	out	aviary	art	ar	Leopold et al., 1989
Haematopus ostralegus	Eurasian oystercatcher	cockle	7	2,3	captive	out	aviary	art	fr	Swennen et al., 1989
Calidris canutus	red knot	tellin, cockle	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
			n_1	n_2	e_1	e_2	e_3	e_4		
recent work										
Calidris canutus	red knot	cockle	5	5	captive	in	aviary	art	fr	Piersma et al., 2003
Calidris canutus	red knot	tellin, cockle	6	1	captive	in,out	aviary, cages	art	fr	van Gils et al., 2003a
Calidris canutus	red knot	mussel	4	1	captive	out	aviary	art	fr	van Gils et al., 2003b
Calidris canutus	red knot	mussel	5	1-5	captive	in	aviary	art	gfr	van Gils & Piersma, 2004
Calidris canutus	red knot	mussel	5	1-5	captive	in	aviary	art	fr	van Gils et al., 2005
Calidris canutus	red knot	mussel	10	1,2,4,8,16	captive	in	aviary	art	gfr, mech	Vahl et al., chapter 2
Arenaria interpres	ruddy turnstone	mealworms	15	1,3,5,9,13	captive	in	aviary	art	gfr, mech	Vahl et al., chapter 2
Arenaria interpres	ruddy turnstone	maggots	12	1,2	captive	in	aviary	art	mech	Vahl et al., chapter 3
Arenaria interpres	ruddy turnstone	crab eggs	u	u	free	-	-	art	mech	Vahl et al., chapter 4
Arenaria interpres	ruddy turnstone	mealworms	16	1,2	captive	in	aviary	art	mech	Vahl et al., chapter 5
Haematopus ostralegus	Eurasian oystercatcher	cockle	8	1,2	captive	out	aviary	art	mech	Rutten et al. in prep.a
Haematopus ostralegus	Eurasian oystercatcher	cockle	u	u	free	-	-	nat	ar	Rutten et al. in prep.b
Calidris canutus	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’: isopods spec.; ‘crabs’: sand crab spec.; ‘mussel’: blue mussel, *Mytilus edulis*; ‘tellin’: Balthic 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 (‘n_1’) and the number of foragers (‘n_2’); 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 ‘e_1’ indicates whether the experiment used captive or free-living (‘free’) foragers, column e_2 indicates whether, if captive foragers were used, the experiment was done indoors (‘in’) or outdoors (‘out’), column ‘e_3’ indicates whether cages, an aviary, or neigther (-) was used, and column ‘e_4’ 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 (Metcalfe, 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 (Metcalfe & Furness, 1985; Whitfield, 1985; Metcalfe, 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 peal 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 (Metcalfe, 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).

CHAPTER 2

THE MECHANISMS OF INTERFERENCE COMPETITION: TWO EXPERIMENTS ON FORAGING WADERS

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ABSTRACT

Models of population dynamics that include interference competition have often been applied to foraging waders and less so to other foragers, even though these models are, in principle, generally applicable. At present, however, it is still unclear whether interference competition is of importance for foraging waders. To support this idea experimental evidence and knowledge of the mechanisms underlying interference effects are required. We experimentally determined the relationship between forager density and foraging success in two wader species: the red knot (*Calidris canutus*) and the ruddy turnstone (*Arenaria interpres*). With each of the two species, we conducted an experiment consisting of 300 one-minute trials. In these trials we scored the behavior and the foraging success of focal individuals at specific combinations of bird and prey density. Irrespective of prey density, individuals of both species discovered fewer prey items at higher bird densities. Despite this, only in turnstones did intake rates decline with increasing bird density. Knots compensated for a lower prey-discovery rate by rejecting fewer prey items at higher bird densities. In knots, bird density had a complex, nonmonotonic effect on the time spent vigilant and searching. In turnstones the main effect of increased bird density was a reduction in the prey-encounter rate, that is, the reward per unit search time. Effects on the time spent vigilant and the time spent searching were less pronounced than in knots. Thus, the mechanistic basis of the effects of bird density was complex for each of the two species and differed between them.

INTRODUCTION

Competition among foraging animals is generally divided into two types (Keddy, 2001). *Exploitative competition* is the negative effect of others through the removal of resources (Grover, 1997; Park, 1954). *Interference competition* is the negative effect of others through behavioral interactions (Miller, 1967; Park, 1954). Because the presence of competing individuals may lower the survival and reproduction of foragers, competition can be important for the dynamics of animal populations (Christian, 1970; Gauthreaux, 1978). Most models of population dynamics consider only the effects of exploitative competition (Grover, 1997; Huisman and Weissing, 2001; Keddy, 2001). Interference competition, however, can be just as relevant (Goss-Custard, 1980) because behavioral interactions can be very costly (either directly, through injury or loss of energy or time, or indirectly, through a reduction in intake rate).

Models of population dynamics that include interference competition have often been applied to foraging waders (also known as shorebirds), and less so to other foragers, even though these models are, in principle, generally applicable (e.g., Stillman et al., 1997; Sutherland, 1983). Foraging success in these models is assumed to decrease with increasing forager density. This reduction in foraging success is generally assumed to result from agonistic interactions between the foragers, whereby interactions are thought to be over individual food items (e.g., kleptoparasitism). When more time is spent interacting, less time can be spent on searching for food, and therefore foraging success should decrease (e.g., Ruxton et al., 1992; Sirot, 2000; Stillman et al., 1997). At present, however, it is an open question whether interference competition is especially prevalent among foraging waders. The importance of interference competition among foraging waders may differ from that among other birds because of characteristics typical to the habitats used by foraging waders; the openness of their habitat, for example, may affect predator detection, and the distribution of their prey may also be unlike the distribution of prey of other species. Knowledge of the relationship between the density and the success of foragers and of the mechanisms responsible for this relationship, however, is still surprisingly rudimentary (van der Meer and Ens, 1997).

One reason why our knowledge is still limited is that experimental control of forager density is essential; natural changes in the distribution of foragers over resource patches may result in any relationship between forager density and foraging success between patches (van der Meer and Ens, 1997). Ideal-free-distribution theory (Fretwell and Lucas, 1970), for instance, assumes a direct negative effect of forager density on foraging success, but predicts no relationship between forager density and foraging success when measured between patches. However, it is no trivial task to manipulate the density of foraging birds. In his review on the relationship between density and success of birds, Beauchamp

(1998) reported only 12 studies where the researchers had been able to manipulate forager density while studying foraging success. None of these studies was on waders. The relationship between the density and the success of foragers was negative in only three of these studies. In contrast, the sole study in which the density of a foraging wader was varied experimentally (van Gils and Piersma, 2004), reported the expected decline in foraging success with forager density. This study did not address the behavioral mechanisms causing the decline in intake rate. Clearly, more manipulative studies are required for a satisfactory comparison between the effect of forager density on foraging success of waders and that of other birds. To understand potential differences between groups of birds, special attention should additionally be paid to the mechanisms underlying any effects of forager density on foraging success, as it is only through understanding such mechanisms that we can link effects of forager density with characteristics of the environment.

We conducted two experiments on the effect of forager density on foraging behavior and foraging success, using either red knots (*Calidris canutus*; henceforth called knots) or ruddy turnstones (*Arenaria interpres*; henceforth called turnstones). Knots and turnstones are both medium-sized waders that inhabit intertidal coastal areas outside the breeding season (Branson et al., 1978; Piersma and Davidson, 1992). Yet, the two species differ strongly in their feeding styles and dominance structure. It has been suggested that interference competition is of limited importance for knots (Stinson, 1980; van Gils and Piersma, 2004) but of major importance for turnstones (Metcalfe and Furness, 1986). Knots generally forage in large flocks of apparently varying individual membership in which no dominance structure is apparent (Metcalfe and Furness, 1986; Vahl and Piersma, personal observation). They eat mainly bivalves buried in soft sediments (Piersma et al., 1993a; Piersma et al., 1994), detecting their prey by probing the mud with their bill (Piersma et al., 1995; Zwarts and Blomert, 1992). Bivalves are swallowed whole and digested internally (Piersma et al., 1993b; van Gils et al., 2003). In contrast, turnstones forage in relatively small flocks of stable composition (Metcalfe, 1986; Metcalfe and Furness, 1985; Whitfield, 1988) in which a stable dominance hierarchy is generally formed (Metcalfe, 1986). They feed mainly on barnacles, mollusks and small crustaceans (Harris, 1979; Whitfield, 1990), for which they search by rooting through a layer of seaweed that usually covers these prey items (Fuller, 2003; Whitfield, 1990; Vahl and Piersma, personal observation). In each of these two waders, we experimentally determined the effect of forager density on foraging success by quantifying time allocation and prey-encounter rate under controlled conditions. The use of an indoor experimental shorebird facility enabled us to keep most factors of potential importance either constant (environmental conditions, energy expenditure and level of satiation) or fixed at different levels (prey density). In particular, it allowed us to vary forager density experimentally and unambiguously.

Thus, through an experimental manipulation of forager density, we hoped to determine the presence, nature and strength of interference effects. The use of two contrasting species of waders and two different prey densities should shed some light on the generality of interference effects and the behavioral mechanisms involved.

METHODS

The two experiments each consisted of 300 trials of 60 s. Both experiments had a multifactorial design and their general setup was comparable: in all trials, the foraging behavior of one bird was studied under a specific combination of bird and prey density. The experiment with turnstones included two additional factors: (1) the dominance position of the birds and (2) a refuge site that was either present or absent.

SUBJECTS

In the first experiment, from 13 to 28 May 2001, we used 25 knots (Table 2.1). In the second experiment, from 11 September to 8 October 2001, we used 27 turnstones. All birds were caught with mistnets at night on intertidal flats in the Wadden Sea (under Dutch bird ringing center license numbers 851 and 351 for knots and turnstones, respectively). Data were collected on 10 “focal” knots and 15 “focal” turnstones; nonfocal birds were used only to manipulate bird density. Assignment of focal status was random (knots) or based on dominance position (turnstones). Assuming a linear dominance hierarchy, cardinal-scale dominance positions were determined by means of a logit regression analysis (Tufto et al., 1998; van der Meer, 1992). To account for variation in dominance position, we designated as focal individuals the five lowest-, the five middle- and the five highest-ranking turnstones (called, respectively, *subordinate, intermediate* and *dominant*). To allow us to recognize focal birds from all angles, they received a unique mark. Focal knots were marked with a section of bright yellow or orange rubberized cloth (kapron), glued (with cyano-acrylate) to the back or scapular feathers. Focal turnstones had a small area of their back feathers bleached, using commercial hair bleach.

HOUSING AND PRE- AND POST-EXPERIMENTAL TREATMENT

All subjects were housed in two roosting aviaries measuring 4.3 x 1.2 m and 3.0 m high, in the indoor experimental shorebird facility of NIOZ (according to protocol 2000.04 of the DEC, the Dutch committee for animal experiments). The floor of these aviaries was continuously covered with a thin film of running seawater to keep the feet of the birds salty and wet, and a tray of running freshwater for drinking and bathing was always present. The indoor environment had a

Table 2.1. Numbers and characteristics of the subjects used. Status indicates whether behavior was recorded (focal birds) or not (nonfocal birds). Dominance position could only be determined for turnstones. Juvenile indicates first-year individuals. Sex was determined from DNA using standard methodology verified for these wader species by Baker et al. (1999).

			Dominance	Juvenile		Adult	
Species	Catch date	Status	position	♂	♀	♂	♀
Red knot	09 February 1997	Nonfocal	—	—	—	—	1[a]
	31 August 2000	Nonfocal		—	—	1[a,b]	—
	26-30 March 2001	Nonfocal		—	2	1	—
		Focal		—	—	—	1
	24 April 2001	Focal		—	—	5[c]	4[c]
		Nonfocal		—	—	5[c]	5[c]
Ruddy turnstone	23-25 September 2001	Focal	Dominant	—	—	3	2
		Nonfocal	Dominant	2	—	2	2
		Focal	Intermediate	1	2	1	1
		Nonfocal	Subordinate	2	3	—	1
		Focal	Subordinate	—	5	—	—

[a] Individual had been used in previous experiments.

[b] Catching date, molt pattern and weight curves indicated this knot to be of the subspecies canutus, whereas all others were of the subspecies *islandica*.

[c] Prior to the current experiment, 14 of these individuals had participated in an experiment on prey choice for 5 to 10 days. Conditions in both experiments were comparable except for the prey species used (*Macoma balthica* in the earlier experiment and *Mytilus edulis* in the current experiment).

constant air temperature (18 °C) and photoperiodic regime (15:9 h light:dark). The aviaries were illuminated by moonlight-mimicking lights between 2200 and 0700 h.

Outside the experimental trials, knots were fed blue mussels (*Mytilus edulis*), a common prey species in their natural environment (Piersma et al., 1993a; Zwarts and Blomert, 1992). We collected these mussels from nearby dykes. The mussels were rinsed, spread out over wire trays, and stored in running, unfiltered seawater for up to 5 days. Before serving them to the knots, we put the mussels through a mesh to break the byssus threads that held them together and to sort them by size. Lengths used in the experiment ranged from 13 to 17 mm. Turnstones were fed *ad libitum* with trout food pellets on days without trials, as well as between the end of an experimental day and the beginning of the next fasting period. Knots were denied food from 0800 h on an experimental day and tested between 1000 and 1800 h; turnstones were denied food from 2200 h and tested between 0930 and 1430 h on the next day.

To familiarize them with the experimental environment and procedure, all knots and turnstones participated in pilot trials for 3 and 8 days, respectively, prior to the experiments. During the pilot trials, we observed agonistic interactions (n = 321) among the turnstones and recorded the outcome of each interaction: winners were those individuals that either chased their opponent away or held their ground after being attacked. To study their consistency, we recorded agonistic interactions once more, soon after the turnstone experiment was finished (n = 548). Both knots and turnstones were released on intertidal mudflats in the Wadden Sea shortly after each experiment had ended.

EXPERIMENTAL SET-UP

Both roosting aviaries were separated from an experimental room (7 x 7 m and 3.5 m high) by a sliding door. During the experiments, we flooded the experimental room with seawater to a depth of 20 cm. The only dry areas remaining were one (“refuge absent"; knots and turnstones) or two (“refuge present”; turnstones) platforms (1 x 1 m and 15 cm deep) filled with sand and positioned slightly above the water level. Because these platforms were the only available places for the birds to stand on, bird density remained effectively constant within a trial. In the knot experiment, we inserted mussels into the sediment of the foraging platform to resemble a situation with buried prey. The mussels were inserted to a fixed depth (1.5 cm) and at arbitrary positions (cf. Piersma et al., 1995). In the turnstone experiment, we spread out mealworms (*Tenebrio molitor*) arbitrarily over the foraging platform, and then covered them with a 5-cm layer of seaweed (bladder-wrack *Fucus vesiculosus*). The refuge platform differed from the foraging platform only in that it did not contain prey items and was not covered by bladder-wrack.

We recorded foraging behavior of the subjects using two digital video cameras (Sony dcr-trv900e). One was positioned next to the foraging platform at a distance of 1.5 m for a sideways view, while the other was mounted 3.5 m directly above the foraging platform.

EXPERIMENTAL PROCEDURE

At the start of each experimental day, all birds were placed in groups of four in boxes measuring 50 x 35 cm and 25 cm deep. To minimize stress, we captured and housed the birds in darkness, as they were very quiet in the dark. Before each trial, a specific focal bird and the required number of nonfocal birds were transferred to one of the roosting aviaries. After opening the sliding door, the birds were attracted into the experimental room by dimming the lights in the roosting aviary while lighting the experimental room. Subjects readily flew to the experimental platforms and started to forage within seconds of the sliding doors being opened. The trials started the moment the focal bird began to forage and lasted for 150 s (knots) or 120 s (turnstones).

After each trial, lights were used again to entice birds back to the roosting aviary. If birds had to participate in another trial, they were returned to the boxes. Otherwise, they were transferred to the second roosting aviary, where they stayed until the last trial of the day had been performed. Focal knots and turnstones took part in on average 2.9 and 1.1 trials per day, respectively. Necessarily, the number of trials that nonfocal birds took part in exceeded this (averages of 8.8 and 6.5 for knots and turnstones, respectively).

In the knot experiment, depletion was estimated from observations on the number of mussels consumed or rejected during the previous trial. Initial prey densities were restored before the next trial through the addition of fresh mussels. In addition, the sandy sediment on the foraging platform and all prey items were renewed after 5 (bird densities 4, 8 or 16) or 10 (bird density 1 or 2) trials. In the turnstone experiment, the mealworm supply was renewed and the seaweed cover was replaced after each trial.

EXPERIMENTAL DESIGN AND STATISTICAL ANALYSIS

In the knot experiment, we studied the effects of the fixed factors *bird density* (A: 1, 2, 4, 8 and 16 birds) and *prey density* (B: 50 and 200 mussels). Although we refer to factor A as *bird density* , it could also be interpreted as *group size* because we manipulated the number of birds on a 1 m^2 platform (see Arenz, 2003; Fernandez-Juricic et al., 2004; Lima, 1990). We controlled for variability among individual birds by using a random factor focal bird (γ: 10 different birds). In the turnstone experiment, we also studied the effects of the fixed factors *bird density* (A: 1, 3, 5, 9 and 13 birds) and *prey density* (B: 50 and 200 mealworms), but in addition we studied the effect of the fixed factors *refuge present* (C: yes or no) and *dominance position* (D: dominant, intermediate and subordinate). The random factor *focal bird* was nested within the dominance position (γ[D]: five different turnstones per dominance position). Both experiments followed a split-plot design (Appendix).

TREATMENT LEVELS

The range of bird densities we used in the experiments encompasses and exceeds densities usually seen in the field (which, for both species, will usually not exceed 1 m^{-2}; Fuller, 2003; Vahl and Piersma, personal observation). Still, the densities are well below the physical maximum and the maximum observed in systems where food is extremely abundant. For instance, in Delaware Bay, USA, where knots and turnstones feed on the eggs of horseshoe crabs (*Limulus polyphemus*; Tsipoura and Burger, 1999), bird densities can be about three times the maximum density used in this experiment (Vahl and Piersma, personal observation). Using bird densities that exceed the natural levels at comparable resource densities may help us to understand why natural bird densities are generally lower.

We used prey items that resembled the natural prey and that were easy to get. Mussels are among the favorite prey species of knots (Zwarts and Blomert, 1992), and although mealworms are not part of the natural diet of turnstones, they resemble other invertebrates included in the diet (especially the larvae of wrack flies [Coelopidae], Fuller, 2003) and are strongly favored by turnstones (Whitfield, 1990). The low (50) and high (200) experimental prey densities used lie within the range of densities observed in the field for bivalves (Piersma et al., 1993a) and other invertebrates (Fuller, 2003). We buried the mussels in the soft-sediment of the foraging tray (as sometimes occurs on intertidal flats; Piersma, personal observation) in order to impose some search time on the knots.

The presence of a refuge may well affect opportunities for resource monopolization and the outcome of competition experiments (Łomnicki, 1988). We therefore included this factor in the turnstone experiment.

Wintering turnstones are known to form dominance hierarchies (Metcalfe, 1986); the high familiarity among turnstones in our experimental facility probably enhanced this process. Because dominance status was assigned on basis of the position in the dominance hierarchy, dominance was treated as an absolute attribute rather than as a relative quality (Francis, 1988).

RECORDED BEHAVIOR AND RESPONSE VARIABLES

We analyzed trials using The Observer 3.0 Event Recorder (Noldus Information Technology, Wageningen, The Netherlands). To limit effects of resource depletion, digestive constraints and satiation, foraging behavior and success were measured during the first 60 s of each trial. Our omission of the remainder of each trial from the video analysis also served to avoid potential end-effects (e.g. birds anticipating the end of a trial). Each trial was analyzed by two observers together, and all trials were examined twice. The first analysis was performed at one-fifth of normal speed using the side-view recording. The second analysis, performed in real time using the top-view recording, was used to verify the observations from the side-view tape. In both experiments, five behavioral categories were distinguished, each consisting of several different behaviors (Figure 2.1).

In both species we studied the effect of treatment on *intake rate*, defined as the number of prey items swallowed per unit of total time ($\#s^{-1}$). Because not all prey items found were consumed, we also studied the effect on *prey-discovery rate*, defined as the number of prey items found per unit of total time ($\#s^{-1}$). To investigate the causes of interference effects, we calculated *time allocation*, defined as the total number of seconds allocated to each of the five behavioral categories (s), and *prey-encounter rate*, defined as the number of prey items found per unit of search time ($\#s^{-1}$). As differences in prey-encounter rate may reflect both differences in prey density and changes in foraging behavior, we also calculated the *searching efficiency*, defined as the proportion of available prey found per unit search time (m^2s^{-1}; i.e., we divided the prey-encounter rate by the initial prey density [either 50 or 200 m^{-2}]; this measure approximates

Behavioral category	Description
Search 	Focal bird searches for food using either vision or touch. Tactile search refers to probing the mud with the tip of the bill (knots) or rooting through seaweed (turnstones).
Handle 	Focal bird is in physical contact with a prey item. A distinction is made between prey previously undiscovered, prey previously rejected (knots) and prey stolen from others.
Interact 	Focal bird either initiates an interaction by taking up a threatening position or by moving quickly towards the opponent, or responds to a threatening or attacking non-focal bird by moving away from this opponent.
Vigilant 	Focal bird is looking around (head up): vigilance encompasses alertness directed at other birds (actually a form of interaction) and that towards some other aspect of the environment, as no distinction could reliably be made.
Other 	Focal bird is preening its feathers or pecking its identification mark.

Figure 2.1. Ethogram of foraging and interacting turnstones, with sketches of the behavioral categories recorded in the video analysis. The same ethogram was used for the knots.

the instantaneous area of discovery [see Holling, 1959; Piersma et al., 1995] but deviates from it as prey density was not constant throughout a trial). In the calculation of these response variables we excluded prey items that had been rejected before the focal bird found them.

MISSING VALUES AND THEIR TREATMENT

Not all trials were successful. In the knot experiment, the focal bird failed to forage normally in a number of trials. Instead, it spent its time pecking at the plumage mark, preening, or being highly inactive. Some of these trials were successfully repeated in the 2 days after the initial experimental period. However, as foraging was again not normal in nine of these repeated trials, a second repeat was performed on the third day after the experimental period. In total, this resulted in 283 successful trials and hence 17 missing data points. In the turnstone experiment, foraging behavior was interrupted in 11 trials, either due to disturbance by a bird that landed in the water or because the focal bird was preening. Each of these trials was repeated at the end of the same experimental day. This resulted in 300 successful trials.

DATA TRANSFORMATION

For the statistical analysis we assumed that the various treatments had a multiplicative effect on the response variables. We therefore log-transformed all mea-surements, as general linear models assume that effects interact in an additive way. Data on time allocation is compositional (Aitchinson, 1986); the sum of the time allocated to the various behavioral categories is constrained at 100 %. We therefore used ratios of time allocation for analysis.

For all response variables based on the number of prey items swallowed or discovered, we added the value one to avoid taking logarithms of zero. For data on time allocation, zero replacement was achieved by using the procedure for non-essential zeros in compositional data (Aitchinson, 1986). As the time spent interacting necessarily took a value of zero when there was only one forager, the analysis of interacting time (univariate, excluding bird density 1) was performed separately from the analysis of time allocation involving other behavioral categories (multivariate, including bird density 1). We do not present any information on the behavioral category “other”, as very little time was allocated to this category (for knots and turnstones, the average per trial was 1.1 and 0.8 s, respectively) and as it was not affected by any of the experimental factors. We judged assumptions of normality and homoscedasticity by visually inspecting probability plots (Miller, 1997).

HYPOTHESIS TESTING

Data were analyzed using the GLM procedure in SYSTAT 10 (SPSS Inc., Chicago, IL). The knot experiment was analyzed in accordance with the standard split-plot design. We grouped interaction terms between the block factor and the whole plot factors in the whole plot error term and those between the block factor and the subplot factor in the subplot error term. Replacement of the 17 missing values using the harmonic mean method (Miller, 1997) hardly affected test outcomes. Therefore, tests based on the 283 successful trials are presented.

The design of the turnstone experiment was not perfectly balanced with respect to the distribution of bird density over plots. Although this causes no problems for the GLM procedure, the estimated sums-of-squares are no longer independent, and some caution must be exercised with their interpretation. In the GLM model, we grouped four-way interactions in the error term, against which we tested all terms that included the random factor focal bird. Effects of the factor refuge present were tested against the plots; all other terms were tested against their interaction with the random factor focal bird.

RESULTS

INTAKE RATE AND PREY-DISCOVERY RATE

Individuals of both species discovered fewer prey items at higher bird densities and low prey density (Figure 2.2; Table 2.2A). From the lowest to the highest bird density studied, prey-discovery rate more than halved (Figure 2.2). The four-fold increase in prey density resulted in approximately a doubling of prey-discovery rate. Turnstones consumed almost all prey they discovered, and therefore their intake rate was affected by bird density ($F_{4,48} = 104.6$, $p < 0.01$) and

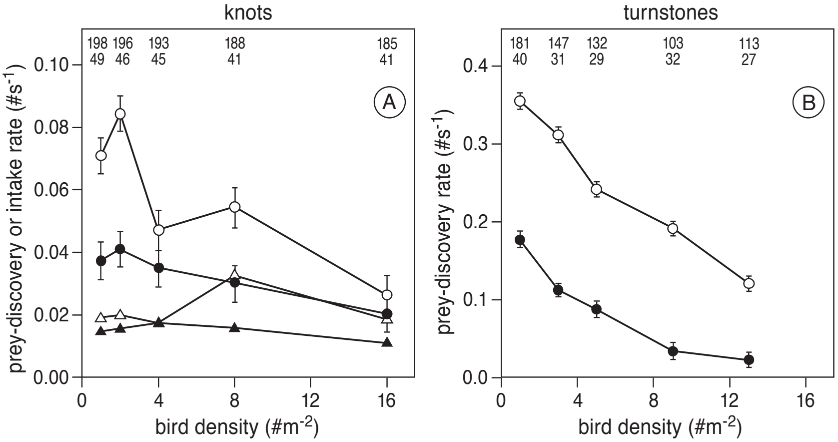

Figure 2.2. Foraging success of knots (A) and turnstones (B) at initial prey densities 50 (black) and 200 (white). For both species, foraging success is given as prey-discovery rate (circles). Intake rate was identical to prey-discovery rate in turnstones but not in knots, as only knots did not consume all prey items discovered. Therefore intake rate (squares) is given only for knots. Values above the graph indicate the estimated average number of prey items remaining after 60 s at prey density 50 (bottom row) and prey density 200 (top row). Symbols represent the means in accordance with the ANOVA model, that is, the least square means, and error bars represent one standard deviation of these means.

Table 2.2. GLM test results for knots and turnstones on prey-discovery rate (A), time allocation (B and C) and prey-encounter rate (D). Time could be allocated either to searching (T_S), handling (T_H), vigilance (T_V) or interacting agonistically with other birds (T_I). Treatment effects on time allocation were tested separately for effects on interacting time at bird densities higher than 1 (B) and time spent on other behaviors at all bird densities (multivariate; C). All tests were performed on log-transformed data after zero values had been treated as described in the text. To simplify representation, non-significant higher-order interaction terms in the turnstone experiment are grouped ("interaction terms"). Effects significant at the .05 level are indicated by bold p values.

	A				B				C				D			
Knots	Prey-discovery rate				$T_I / (T_S+T_H+T_V)$				T_V / T_S , T_H / T_S				Prey-encounter rate			
Factor	df	SS	F	p	df	SS	F	p	df	λ^a	F	Prob	df	SS	F	p
Between plots																
Block 'τ'	2	2.5			2	3.0			4, 324	0.9			2	0.6		
Bird density 'A'	4	14.9	9.6	<**0.01**	3	244.1	18.3	<**0.01**	8, 14	0.1	10.3	<**0.01**	4	9.5	7.4	<**0.01**
Prey density 'B'	1	8.7	22.4	<**0.01**	1	2.2	0.5	0.49	2, 1	0.5	10.4	<**0.01**	1	10.4	32.5	<**0.01**
A*B	4	1.6	1.1	0.41	3	6.7	0.5	0.69	8, 14	0.8	0.5	0.86	4	1.8	1.7	0.24
Whole plot error	18	7.0			14	62.2			36, 324	0.7			18	5.8		
Within plots																
Focal bird 'γ'	9	29.5	13.0	<**0.01**	9	70.4	2.4	**0.01**	18, 324	0.4	9.5	<**0.01**	9	12.4	5.2	<**0.01**
A*γ	36	8.8	1.0	0.53	27	118.5	1.3	0.14	72, 324	0.6	1.4	**0.03**	36	10.2	1.1	0.36
B*γ	9	3.3	1.5	0.17	9	37.3	1.3	0.26	18, 324	0.9	1.2	0.24	9	2.2	0.9	0.49
A*B*γ	36	6.6	0.7	0.87	27	76.9	0.9	0.64	72, 324	0.7	0.9	0.64	36	8.8	0.9	0.58
Subplot error	163	41.1			129	419.7							163	42.8		
Total	283				225								283			

Table 2.2. Continued

Turnstones	A				B				C				D			
	Prey-discovery rate				$T_I / (T_S+T_H+T_V)$				T_V / T_S , T_H / T_S				Prey-encounter rate			
Factor	df	SS	F	p	df	SS	F	p	df	λ^a	F	Prob	df	SS	F	p
Between plots																
Refuge 'C'	1	1.0	4.1	0.08	1	30.3	14.5	0.01	2, 7	0.3	7.0	0.02	1	0.7	2.4	0.16
Plot 'η(C)'	8	1.9			8	16.8			16, 74	0.8			8	2.5		
Within plots																
Subplot 'ξ(η[C])'	10	3.2			10	9.2			20, 74	0.7			10	3.8		
Bird density 'A'	4	46.1	100.9	<**0.01**	3	134.9	31.5	<**0.01**	8, 94	0.2	18.6	<**0.01**	4	50.8	59.8	<**0.01**
Prey density 'B'	1	48.3	212.6	<**0.01**	1	1.1	0.7	0.43	2, 11	0.1	81.0	<**0.01**	1	68.3	215.1	<**0.01**
Dominance 'D'	2	1.4	0.9	0.42	2	25.9	1.9	0.20	4, 22	0.6	1.3	0.29	2	2.2	1.7	0.22
Focal bird 'γ(D)'	12	9.0	4.7	<**0.01**	12	83.7	5.8	<**0.01**	24, 74	0.1	6.8	<**0.01**	12	7.6	3.2	<**0.01**
A* B	4	2.6	4.6	<**0.01**	3	6.2	1.7	0.18	8, 94	0.6	3.1	<**0.01**	4	0.6	0.8	0.50
A*C	4	0.8	1.1	0.38	3	12.5	3.0	**0.04**	8, 94	0.8	1.0	0.44	4	0.4	0.4	0.78
Interaction terms	215	31.6			172	230.6							215	42.9		
Error	38	6.1			24	28.7							38	7.5		
Total	300				240								300			

[a] Multivariate test statistic used is Wilks' λ.

prey density ($F_{1,12} = 204.2$, $p < 0.01$) in the same way as their prey-discovery rate. Knots, however, rejected some of the prey items they had found. Because fewer prey items were rejected at higher bird densities and at the low prey density, there was no straightforward effect of bird density ($F_{4,18} = 3.5$, $p = 0.03$) and prey density ($F_{1,18} = 17.1$, $p < 0.01$) on intake rate (Figure 2.2a), despite changes in prey-discovery rate. Apparently, knots compensated for a reduced prey-discovery rate by becoming less critical in their acceptance of prey items.

Turnstones occupying different dominance positions discovered (Table 2.2A) and consumed ($F_{2,12} = 1.0$, $p = 0.39$) an equal number of prey items. In addition, an equal number was discovered (Table 2.2A) and consumed ($F_{1,8} = 3.7$, $p = 0.09$) in the absence and presence of a refuge. In fact, the main effect of the presence of a refuge was a small increase in the number of times a bird flew off the foraging platform during an experimental trial (average 0.12 versus 0.05). As movement caused disturbance, this resulted in a small increase in the number of interactions. As intake rate and prey-discovery rate of turnstones did not depend on either dominance position or the absence or presence of a refuge, we do not further discuss the effects of these factors on time allocation and prey-encounter rate.

TIME ALLOCATION AND PREY-ENCOUNTER RATE

The reduction in prey-discovery rate with increasing bird density is generally assumed to be caused by an increase in time spent interacting, which, in turn, results in a reduction in time spent searching. Indeed, time spent on interactions increased monotonically with bird density in both species (Figure 2.3; Table 2.2B). However, interacting time seemed to have a marginal effect on searching time because both species spent less than 10% of their time on interactions. Other aspects of the birds' time allocation appeared to be at least as important.

Bird density had a strong effect on the time allocation of knots (Figure 2.3A,B; Table 2.2C), most obviously in the nonlinear effect on the time spent vigilant and searching. Vigilance time in knots was highest at a very low or very high bird density and searching time neatly mirrored this pattern (Figure 2.3A,B). Bird density also reduced prey-encounter rate, that is, the number of prey items encountered per second spent searching (Figure 2.4A; Table 2.2D). However, although knots found fewer prey items, total handling time did not decrease markedly with increasing bird density (Figure 2.3A,B), as the percentage of prey items rejected was lower at the higher bird densities. Time allocation of knots depended slightly on prey density (Fig 2.3A,B. Table 2.2C), probably because they encountered more prey per second spent searching when prey density was high (Figure 2.4A; Table 2.2D). The searching efficiency, that is, the proportion of available prey found per unit search time, was also different at the two prey densities ($F_{1,18} = 202.5$, $p < .01$; Figure 2.4B).

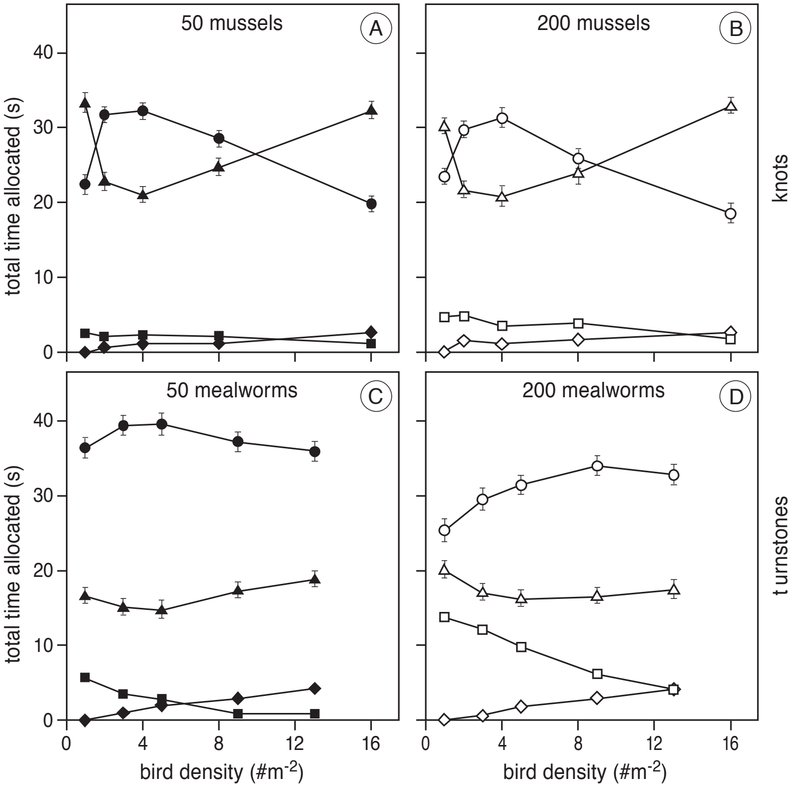

Figure 2.3. Total amount of time allocated to searching (circles), being vigilant (triangles), handling (squares) and interacting with other birds (diamonds) by knots (A and B) and turnstones (C and D) at prey densities 50 (A and C; filled symbols) and 200 (B and D; open symbols). Symbols represent least square means, and error bars represent one standard deviation of these means.

For turnstones, the main effect of bird density was a strong reduction in prey-encounter rate (Figure 2.4C; Table 2.2D). As a consequence, the birds spent less time handling at higher densities (Figure 2.3C,D). Although patterns in vigilance and searching time qualitatively resembled those observed in knots, the effects in turnstones were less pronounced (Figure 2.3C,D). Turnstones encountered about three times more prey when prey density was high than when it was low (Figure 2.4C; Table 2.2D), and therefore, they also spent more time handling and less time searching (Figure 2.3C,D). Prey density did not, however, affect vigilance or interacting time (Figure 2.3C,D; Table 2.2B). The searching efficiency did not depend on prey density ($F_{1,12}$ = 1.3, p = 0.27; Figure 2.4D).

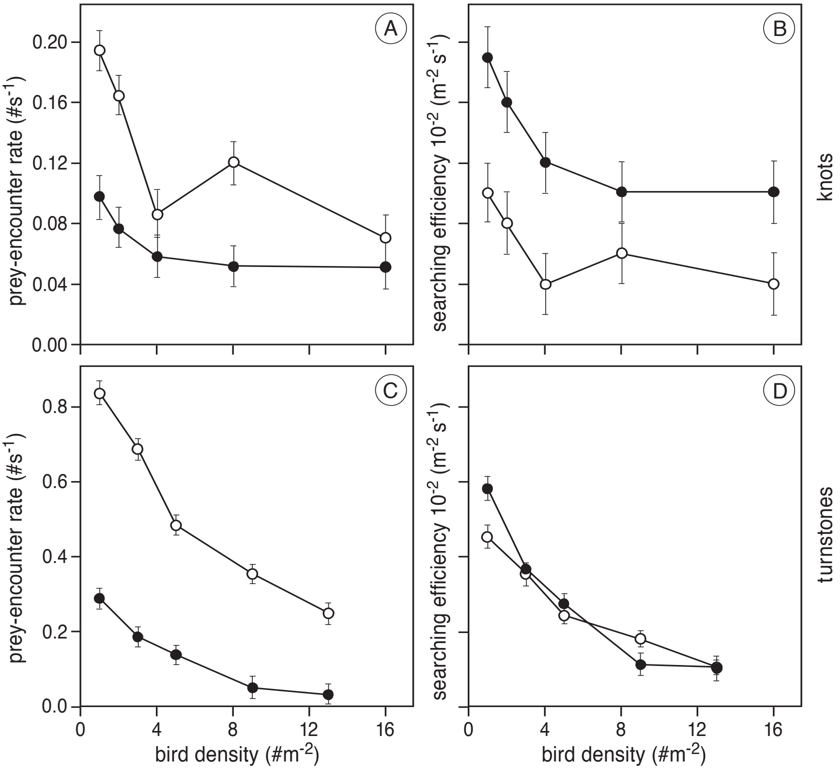

Figure 2.4. Prey-encounter rate (A and C) and searching efficiency (B and D) of knots (A and B) and turnstones (C and D) at prey densities 50 (black) and 200 (white). Symbols represent least square means, and error bars represent one standard deviation of these means.

Thus, bird density induced a lower prey-discovery rate in knots through effects on both vigilance and searching time and through changes in prey-encounter rate, whereas the prey-discovery rate in turnstones was lowered mainly through a reduced prey-encounter rate.

DISCUSSION

EXPLOITATIVE AND INTERFERENCE COMPETITION

In both knots and turnstones, prey-discovery rate decreased with increasing bird density (Figure 2.2). This indicates that for both species the main effect of the presence of conspecifics was negative. The decrease in prey-discovery rate was brought about by both forms of competition (exploitation and interference), as both resource depletion (Figure 2.2) and time spent interacting (Figure 2.3) were positively related to bird density. Although it is not possible to quantify the relative importance of exploitation and interference in these experiments, a closer look at the prey-discovery rates shows that resource depletion alone cannot account for the observed negative effect. After the 60-s observation period, the amount of remaining food (185 [knots] or 113 [turnstones]; Figure 2.2) at the highest bird density and the high initial prey density was still at least twice as high as the initial amount of food for solitary foragers at the low prey density. However, despite this difference in food density, prey-discovery rate in the latter condition was slightly higher than that in the former condition. This suggests that part of the observed effect was also due to interference, without ruling out other explanations, such as removal of the most detectable prey (Wanink and Zwarts, 1985). Clearly, a proper distinction of the two forms of competition requires an experiment in which food is not depleted.

MECHANISMS OF INTERFERENCE COMPETITION

Most mechanistic models of interference competition assume that animals interact over individual food items (e.g., Giraldeau and Caraco, 2000; Sirot, 2000; Stillman, et al., 1997). In our experiments, kleptoparasitic events were absent and prey density had no significant effect on interacting time. Therefore, it is very unlikely that interactions took place over individual food items. Many of the aggressive interactions we observed were directed to searching animals, suggesting that interactions concerned small food patches rather than individual food items. It seems that our current understanding of the adaptive value of the behavioral mechanisms of interference competition is still rudimentary, despite its central importance to all mechanistic approaches to the study of interference competition.

Increases in bird density reduced the prey-discovery rate through changes in both prey-encounter rate (Figure 2.4) and time allocation (Figure 2.3). Effects on time allocation were more complex than the monotonic effects on interacting and searching time assumed by models of interference competition. Several distinct processes may jointly account for this complex effect.

At low bird densities, searching time increased with bird density, while vigilance time decreased. Vigilance was especially reduced in knots, where the presence of a second bird resulted in the reduction of vigilance time by approximately one third. Such a reduction has often been observed (Beauchamp, 1998) and may have been a response to an increase in vigilance at the group level (e.g., Lima, 1995) or other beneficial effects of foraging in the presence of others, such as the dilution of predation risk (e.g., Lima, 1990). Assuming that this "group-size effect" increases with the extent to which species naturally form groups, the observed difference between the two species in the reduction in vigilance time is in line with the observation that knots generally occur in bigger groups in the field than turnstones (Myers, 1984).

At high bird densities searching time decreased with bird density, while interacting time and vigilance time increased. Such effects on searching and interacting time have been assumed in models of interference competition, but we found the size of the increase in interacting time to be very small. However, it is well known that vigilance behavior can serve several functions (Beauchamp, 2001; Desportes et al., 1991; Robinette and Ha, 2001), some of which could be interpreted as interacting. Vigilance may, for instance, serve to prevent others from mounting sudden attacks or serve to spot opportunities for kleptoparasitism on resources discovered by others (Smith et al., 2001). Therefore, acknowledging that some interactions may well have been subtle (scored as vigilance) rather than obviously agonistic (scored as interactions), part of the expected increase in interactions may have been reflected by the increase in vigilance time.

The increase from the lowest to the highest bird density led to a decrease in prey-encounter rate. This was especially apparent in turnstones, where handling time also decreased with increasing bird density. The decline in prey-encounter rate will partly have resulted from increased resource depletion at higher bird densities. Most likely, interference additionally lowered prey-encounter rate, especially so in knots where resource depletion was low. High bird density may, for instance, have resulted in a loss of concentration due to multiple tasking (Dukas, 1998) or a loss of control over the search path (Cresswell, 1997).

For both species more prey items were encountered when the initial prey density was high than when it was low (Figure 2.4A,C). For turnstones, the searching efficiency, that is, the proportion of available prey found per unit search time was the same at both prey densities, indicating that changes in prey-encounter rate were only due to the higher number of prey items. For knots, on the contrary, the searching efficiency was lower when the food density was high. This indicates that changes in the prey-encounter rate of knots were due not only to the higher number of prey items but also to differences in the birds' behavior at the two prey densities. Such behavioral differences could be caused by a reduction in the efficiency of the prey-detection system (Piersma et al., 1998) or in motivation or by a difference in the frequency with which buried prey items were rejected.

GENERALITY OF INTERFERENCE EFFECTS

Interference effects were similar in knots and turnstones in terms of interacting time, but may have differed in terms of vigilance time. Effects of forager density, however, were certainly not general because forager density affected other aspects of the foraging behavior of the two species differently. The reduction in vigilance time at low bird densities, for instance, was more pronounced in knots, whereas turnstones suffered most from a reduction in prey-encounter rate. This may have been due to intrinsic differences between the two species (e.g., search mode or performance of digestive organs; see Battley and Piersma, 2005) or to differences in the environment because prey species and substrate type differed as well. In view of this complex interplay of interference, depletion and vigilance effects, we think it is wrong to assume a general effect of forager density when modeling interference competition. Future research should attempt to understand how each of the behavioral mechanisms involved is affected by forager density, in order to predict how their combined effect depends on characteristics of the species and its environment.

RELEVANCE TO FIELD SITUATIONS

Conditions in the experimental facility obviously differed from those encountered in the field and birds in our study may well have altered their behavior accordingly. In particular, three aspects of our experiments may hamper direct interpretation of the conclusions for a natural setting.

The high rate of prey rejection by knots in the present experiment is uncommon in free-living individuals (Vahl and Piersma, personal observation). This change in behavior may be explained by various artificial aspects of our experimental setup, such as the relaxed climatic conditions, the abundance of food on offer, the high predictability of food, and the relatively short fasting period. As a consequence, the relevance of the observed effects of forager density on intake rate (but not prey-discovery rate) is probably quite limited. Instead, the conditional rejection of prey items hints at flexibility of behavior and shows that social interactions may affect foraging success even in the absence of noticeable effects on intake rate. Similar behavioral flexibility has been observed in oystercatchers (*Haematopus ostralegus*) in response to experimental variation in tide length (Swennen et al., 1989).

Contrary to our expectations, dominance position, included as a factor in the turnstone experiment, did not affect any of the response variables. It is unlikely that we assigned dominance positions incorrectly, as our assessments of dominance before and after the experiment were strongly correlated (Spearman rank correlation coefficient $r_{s,25} = 0.88$, $p < 0.001$). An alternative explanation is that in the experimental setup, birds could not actually benefit from their social dominance because they were not able to monopolize resources (Myers, 1984). Interestingly, the presence or absence of a refuge did not interact statistically with dominance position to explain foraging parameters. This indicates that this refuge was not enough to allow for monopolization of resources. Apparently, the turnstones preferred to endure social harassment on the foraging platform over staying on a platform with no food at all.

In this study we investigated the effects of treatments on instantaneous intake rate to allow a direct comparison with model assumptions. When interpreting these results for field situations, it should be realized that what foragers are striving to maximize is fitness rather than instantaneous intake rate and that processes minimized or excluded from our experiments may also play a role. Resource depletion and digestive constraints, for instance, have been shown to be of importance for the long-term intake rate of knots, together with social interference (van Gils and Piersma, 2004).

IMPLICATIONS

In our experiments, increased forager density led to reductions in the foraging success of the two species through both resource depletion and social interference. Thus, our results support the idea that interference competition is an important factor in determining the foraging success of waders, as is assumed when population dynamic models that include interference competition are applied to waders. However, interference competition may well occur for reasons other than those considered in these models, and the mechanistic basis of effects of bird density may be more complex than assumed. In our experiments, forager density affected foraging success through an increase in time spent interacting, a decrease in vigilance time, and a decrease in prey-encounter rate. Although similar mechanisms appeared to be at work, their importance differed. This implies that our current knowledge of the behavioral mechanisms causing interference competition is not sufficient to build robust models for the population dynamic of waders.

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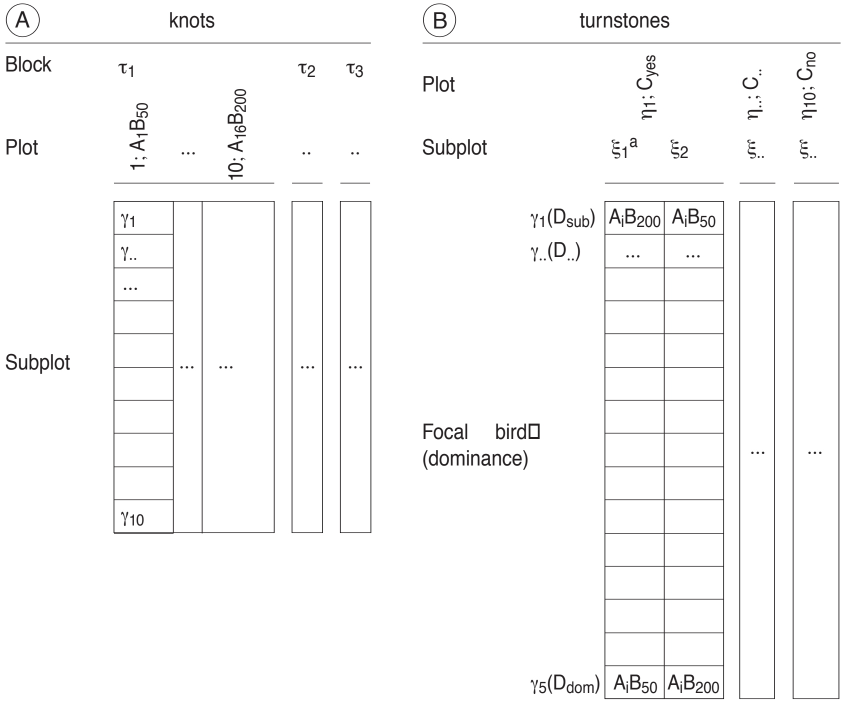
APPENDIX: DESIGN OF THE EXPERIMENTS

The multifactorial knot experiment (fixed factors *bird density* A with five levels: 1, 2, 4, 8 and 16 birds; and *prey density* B with two levels: 50 and 200 mussels: random factor *focal bird* γ with 10 levels; i.e., 10 different knots) followed a split-plot design (see Table 2.A1a), in which the two fixed factors A and B were among-plot factors. Each of the resulting 10 plots (factor A * factor B combinations) contained 10 subplots, one for each focal bird (factor γ). These 10 plots (i.e., 100 subplots) were replicated in three successive blocks, where block was treated as a random factor (τ with three levels). Both the order of subplots within plots and of plots within blocks was completely randomized in time. Plots took half a day, blocks took five consecutive days, and the whole experiment took 15 days.

The multifactorial turnstone experiment (fixed factors *bird density* A with five levels: 1, 3, 5, 9 and 13 birds; *prey density* B with two levels: 50 and 200 mealworms; *refuge present* C with two levels: yes and no; *dominance position* D with three levels: dominant, intermediate and subordinate; random factor *focal bird nested within dominance* (γ[D] with 5 different turnstones per dominance position) also followed a split-plot design (see Table 2.A1b), but the fixed factor C was the only among-plot factor. For each of the two levels of C, five replicate plots (random factor η) were laid out. Each plot contained 2 *subplots* (random factor ξ). Within each subplot 15 trials were performed, one for each of the 15 focal birds (γ[D]). Moreover, within each plot, each of the 30 combinations of the factors prey density (B) and focal bird (γ), was used once. Both the order of trials within subplots and the order of plots were completely randomized in time. Regardless of the plot – subplot structure, the five levels of the fixed factor bird density (A) were attributed at random over the 300 trials. Each subplot took 1 day, and each plot took 2 days, and the whole experiment lasted 20 days.

Table 2.A1. Schematic representation of the statistical designs used in the experiment with knots (A) and turnstones (B)



[a] The index 'i' represents one of the five levels of the factor bird density (A)

AFTERTHOUGHT ON CHAPTER 2

THE RANGE OF EXPERIMENTAL FACTORS

In both experiments described in chapter 2, bird densities are used that ‘encompassed and exceeded’ densities usually seen in the field: we used red knots at densities up to and including 16 individuals m^{-2} and turnstones at densities up to and including 13 individuals m^{-2}, whereas natural densities in the Dutch Wadden Sea will, for both species, usually not exceed 1 m^{-2} (Fuller, 2003; WKV, TP, personal observation; but see van Gils & Piersma, 2004). This evoked much (informal) criticism, for what can possibly be the relevance of studying the effect of densities that are rarely, if ever, encountered in the field? Ideas similar to this criticism feature regularly in texts on experimental treatment levels (e.g., Bernando, 1998; Petraitis, 1998). The opinion expressed in these texts is that treatment levels that are not encountered in the field cannot be informative about what happens in the field. I do not support this view. First, referring to what does and what does not happen in ‘the’ field can be misleading itself. To give an example, densities of knots foraging in the Dutch Wadden Sea may generally not exceed 1 knot m^{-2} (van Gils & Piersma, 2004). Elsewhere, however, much higher densities can be found; Gillings et al. [in prep.], for instance, report knot densities up to 36 individuals knots m^{-2} in their study in Delaware bay (USA). More importantly, however, I think that it can be very informative to determine what happens at extreme densities, even if those densities are not encountered in the field at all, or only rarely. Studying what happens at densities outside the natural range may be the best way to find out why such densities generally *do not* occur in the field and, thus, they may help to understand why natural densities are generally lower. For some questions, and I think that questions regarding competition are among them, the limit to treatment levels may be closer to what is physically possible than to what is naturally observed.

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CHAPTER 3

SPATIAL CLUMPING OF FOOD AND SOCIAL DOMINANCE AFFECT INTERFERENCE COMPETITION AMONG RUDDY TURNSTONES

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ABSTRACT

In studying the success of foraging animals, studies of interference competition have put emphasis on effects of competitor density, whereas studies of resource defense have focused on the effects of the spatial distribution of food within patches. Very few studies have looked at both factors simultaneously, that is, determined whether the effects of competitor density on foraging success depend on the spatial distribution of food. We studied the behavior and the foraging success of ruddy turnstones (*Arenaria interpres*) using an experiment in which we varied both the presence of a competitor and the food distribution. Because turnstones may differ strongly in their relative dominance status, we also experimentally varied the foragers' relative dominance status. We found that the presence of a competitor only reduced the foraging success of subordinate birds foraging at the clumped food distribution. At this condition, dominant and subordinate birds differed markedly in their foraging success. Contrary to our expectations, we did not observe more agonistic behavior at the clumped food distribution. This indicates that the amount of agonistic behavior observed may be a bad indicator of interference effects. These findings have specific implications for models of interference competition. Most notably they show that the effects of competitor density on agonistic behavior and foraging success may well depend on the spatial distribution of food and the foragers' relative dominance status. Additionally, our results suggest that social dominance will not be fully understood without considering long-term processes such as the formation and maintenance of social dominance hierarchies.

INTRODUCTION

Foraging animals often compete with one another for resources (Keddy, 2001). Because the presence of competing individuals may lower the success of foragers, competition may affect the survival and reproduction of foragers. Hence, competition can be important for the dynamics of animal populations (Christian, 1970; Gauthreaux, 1978). Negative effects of other foragers arise through resources, which can either be depressed (*prey depression*: Charnov et al., 1976; Goss-Custard, 1970) or depleted (*exploitative competition*: Grover, 1997; Park, 1954). Negative effects can also arise through behavioral interactions between competitors (*interference competition*: Miller, 1967; Park, 1954), including avoidance behavior (e.g., Baker et al., 1981), the stealing of resources (e.g., Brockmann and Barnard, 1979; Dolman, 1995; Ens et al., 1990), the monitoring of other foragers (Cresswell, 1997), the loss of control over search paths (e.g., Cresswell, 1997), and the loss of concentration (e.g., Dukas, 1998). Both resource competition and interference competition have been of central interest in behavioral ecology (e.g., Huntingford and Turner, 1987) and population dynamics (e.g., Grover, 1997; Keddy, 2001). Nevertheless, our understanding of interference competition in particular is still rudimentary (van der Meer and Ens, 1997).

Mechanistic models of interference competition originally assumed that interference competition results from the loss of time spent on agonistic interactions (e.g., Beddington, 1975; Ruxton et al., 1992). However, these models did not address the question as to why foragers should interact agonistically with each other (van der Meer and Ens, 1997). This question is of central importance for all mechanistic studies of interference competition (Huntingford and Turner, 1987). Agonistic interactions may be very costly in terms of time and energy, and risk of injury or death (Huntingford and Turner, 1987). Moreover, agonistic interactions may result in a reduced intake rate and in a redistribution of foragers over space, forcing some individuals into suboptimal habitats with, for instance, a high risk of predation and parasitism (Goss-Custard, 1980). From an adaptive point of view, agonistic behavior can only be understood if benefits outweigh the costs for at least some of the participants. More recent models of interference competition, addressing why foragers interact with each other (e.g., Broom and Ruxton, 1998; Giraldeau and Caraco, 2000; Sirot, 2000; Stillman et al., 1997), stipulate that the benefits of agonistic behavior arise from kleptoparasitism (food stealing) and the associated reduction in search time and handling time (Brockmann and Barnard, 1979; Giraldeau and Caraco, 2000). These models assume that individuals fight over single food items.

Interactions over individual food items are only possible when prey-handling time is sufficiently long (Ens et al., 1990). In many systems, such as geese feeding on grass (e.g., Black and Owen, 1989) and sparrows feeding on seeds (e.g., Barnard and Sibly, 1981), prey-handling time is short. Models of interference competition, therefore, do not provide a satisfying answer to the question why foragers interact agonistically in such systems. Alternatively, several studies have suggested that interactions may also concern small food clumps within a foraging patch (e.g., Amat and Obeso, 1991; Bautista et al., 1998; Myers et al., 1979; Stillman et al., 2002). If competition is mainly about access to profitable food clumps, then, obviously, the spatial distribution of food items should strongly influence interference effects (Grant, 1993). Models of interference competition do not account for effects of heterogeneous food distributions, as they assume that food is distributed homogeneously. This assumption is ubiquitous among foraging models, even though it is not often made explicitly. Most models based on Holling's disc equation, for instance, implicitly assume a homogeneous food distribution (Jeschke et al., 2002). If agonistic interactions concern within-patch food clumps, it may be crucial for our understanding of interference competition to study how the effects of competitor density on foraging success depend on the spatial distribution of food.

Although not often acknowledged in the literature on interference competition, the effect of the spatial distribution of food on the foraging process has received ample attention in the resource defense literature (e.g., Brown, 1964; Davies and Houston, 1984; Grant, 1993; Warner, 1980). Several studies of resource defense have experimentally varied the effect of the spatial clumping of food and studied the effects on agonistic behavior and foraging success (Table 3.1). These studies show that the spatial distribution of food often affects both foraging success and the level of agonistic behavior. Few of such resource defense experiments, however, have studied how the spatial clumping of food may interact with competitor density to affect foraging success (Table 3.1). Most of the resource defense experiments could not determine the combined effects of spatial clumping and competitor density either because they did not vary competitor density, that is, they measured at a single competitor density, or because they did not control competitor density. Competitor density should be controlled experimentally to exclude feedback loops between competitor density, agonistic behavior, and foraging success, which may well counteract the direct effects of competitor density. The potential importance of this can for instance be seen in the ideal-free-distribution theory (Fretwell and Lucas, 1970), which assumes a direct negative effect of competitor density on foraging success but predicts no such relationship between competitor density and foraging success when measured between patches. Only three studies (Benkman, 1988; Rubenstein, 1981; Theimer, 1987) measured the effects of spatial clumping at more than one experimentally controlled competitor density. Together these three studies indicate that interference effects may indeed depend on the spatial distribution of food, even though the conclusions of Benkman (1988) and Rubenstein (1981) should be treated with caution (see footnotes to Table 3.1).

Table 3.1. Experiments on the effect of spatial clumping on aggression and/or foraging success

Species	English name	Sample size[a] n1	n2	n3	Group size[b]	Additional experimental factors	Dominance[c]	Agonistic behavior[d]	Foraging success[e]	Factor[f]	Reference[g]
Mammals											
Equus burchelli	Plains zebra	1	2	3	9		No	0	No		1
Equus hemionus kulan	Asiatic wild ass	1	2	3	9		No	0	Yes		1
Lepus europaeus	Brown hare	u[b]	2	28	(1-11)		Yes	+	Yes	Dominance	2
Macaca mulatta	Rhesus monkey	1	2	3	17		Yes	+	Yes	Dominance	3
Macaca mulatta	Rhesus monkey	1	2	10	15	Food type	Yes	+,0,-	Yes	Food type, dominance	4
Macaca mulatta	Rhesus monkey	1	5	254	74	Food size	Yes	+,0	Yes	Type of aggression	5
Macaca radiata	Bonnet macaque	1	2	4	15		Yes	+		Dominance	6
Sciurus niger	Fox squirrel	u	3	104	u		No		Yes		7
Birds											
Junco hyemalis	Dark-eyed junco	u	2	u	(1-25)		No	+			8
Junco hyemalis	Dark-eyed junco	17	2	118	2, 3	Group size	Yes	-, 0	Yes	Group size, dominance	9
Lonchura punctulata	Spice finch	3	3	90	5		Yes		Yes		10
Loxia curvirostra	Red crossbill	5	3	300	1, 4	Group size	Yes	+	Yes, no	Group size	11[h]
Motacilla alba alba	White wagtail	u	2	4	(1-30)		No	+			12
Passer domesticus	House sparrow	u	7	35	(1-23)	Sex	No	+	No	Sex	13
Spizella arborea	American tree sparrow	2	3	30	8		No	+		Habitat	14
Spizella pusilla	Field sparrow	1	3	18	(2-4)		No	0			15
Sturnus vulgaris	European starling	1	4	12	11		No	+	No		16
Zenaida aurita	Zenaida dove	u	2	24	(1-15)	Temporal predictability	No	+		Temporal predictability	17
Zonotrichia albicollis	White-throated sparrow	1	3	18	(2-4)		No	+		Group size	15
Zonotrichia querula	Harris's sparrow	u	2	25	(1-10)		Yes	+		Group size, dominance	18

Fish											
Cichlasoma nigrofasciatum	Convict cichlid	7	3	21	3	Body size	Yes	+	Yes	Size	19
Elassoma evergladei	Everglades pygmy sunfish	12	2	72	1, 4, 8, 16	Group size, food type, sex	Yes		Yes	Dominance	20[i]
Oncorhynchus keta	Chum salmon	14	2	14	21		No	+			21
Oncorhynchus kisutch	Coho salmon	20	2	20	25	Food ration	No	0			22[j]
Oryzias latipes	Japanese medaka	18	6	18	8		No	+,-			23
Oryzias latipes	Japanese medaka	40	2	40	10	Temporal clumping	No	+,-		Temporal clumping	24
Salmo salar	Atlantic salmon	6	2	24	>850		No		Yes	Age	25
Tilapia rendalli	Redbreast tilapia	4	2	8	8		Yes		Yes		26[j]
Crustaceans											
Cherax quadricarinatus	Red-claw crayfish	16	2	54	60	Food ration	No	+			27
Insects											
Coccinella septempunctata	Seven-spotted lady beetle	20	2	20	9	Food density	No		Yes, no	Food density	28

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[a] Three aspects of sample size are given: the number of independent units (n1), the number of levels of spatial clumping (n2), and the total number of trials performed (n3).

[b] When group size was uncontrolled (all field experiments), the number of independent units was unknown (u). For these studies, we give (in brackets) the observed range of group sizes.

[c] The column "dominance" indicates whether differences in dominance positions are taken into account in the analysis.

[d] The column "agonistic behavior" indicates whether more (+), less (-), or the same amount (0) of agonistic behavior was shown when the level of spatial clumping of food increased. When more than one sign is given, multiple effects were reported.

[e] The column "foraging success" indicates whether spatial clumping affected some measure of foraging success. Note that this means that effects on growth rate are not included. When both "yes" and "no" are given, multiple effects were reported.

[f] The column "factor" indicates which factors interacted with spatial clumping in their effects on agonistic behavior, foraging success, or both. Note that these factors were not necessarily included in the experimental design.

[g] (1) Ganslosser and Dellert (1997), (2) Monaghan and Metcalfe (1985), (3) Southwick (1967), (4) Belzung and Anderson (1986), (5) Mathy and Isbell (2001), (6) Boccia et al. (1988), (7) Schmidt and Brown (1996), (8), Balph (1977), (9) Theimer (1987), (10) Giraldeau et al. (1990), (11) Benkman (1988), (12) Zahavi (1971), (13) Johnson et al. (2004), (14) Prescott (1987), (15) Pearson (1989), (16) Feare and Inglis (1979), (17) Goldberg et al. (2001), (18) Rohwer and Ewald (1981), (19) Grant and Guha (1993), (20) Rubenstein (1981), (21) Ryer and Olla (1995), (22) Ryer and Olla (1996), (23) Magnuson (1962) (exp IV), (24) Robb and Grant (1998), (25) Jørgensen et al. (1996), (26) McCarthy et al. (1999), (27) Barki et al. (1997), (28) Yasuda and Ishiwaka (1999).

[h] Benkman (1988) blocked treatment combinations within experimental days. The resulting unbalanced design is problematic, especially because the subjects appeared to be learning throughout the experiment. Moreover, results on aggression are only given for two of the three levels of spatial clumping.

[i] Rubenstein (1981) does not present the full results of his experiment. Instead, he consistently presents examples of the densities 4, 8, and 16.

[j] McCarthy et al. (1999) and Ryer and Olla (1996) simultaneously varied spatial and temporal clumping and therefore could not separate effects of spatial and temporal clumping.

Thus, studies of interference competition have focused on the effect of competitor density on foraging success, and studies of resource defense have concentrated on effects of spatial clumping, but very few studies have determined whether the effect of competitor density on foraging success depends on the spatial distribution of food.

In view of this lack of experimental studies, we examined the behavior and the foraging success of ruddy turnstones (*Arenaria interpres*; henceforth called turnstones) in an experiment in which we varied the spatial food distribution and the density of competitors. Unlike previous studies (Table 3.1), we studied effects of competitor density by systematically comparing the behavior and success of individuals foraging alone with that of the same individuals foraging in the presence of one competitor. This approach leaves out potential complicating effects of larger group sizes, which we studied in another experiment (Vahl et al., 2005). The use of an indoor experimental facility enabled us to keep most factors of potential importance constant (environmental conditions, energy expenditure and level of satiation). We chose to study turnstones because they generally forage in systems where prey-handling time is short and, hence, kleptoparasitism absent (Fuller, 2003; Harris, 1979; Whitfield, 1990). Wintering turnstones forage in relatively small flocks of stable composition (Metcalfe, 1986; Metcalfe and Furness, 1985) in which stable dominance hierarchies are generally formed (Metcalfe, 1986; Whitfield, 1988). Correspondingly, the turnstones in this experiment differed strongly in their relative dominance status. Similar differences in dominance status among foragers were present in many of the previous studies on the effect of spatial clumping, even though many of these studies did not consider them (Table 3.1). When present, it may be crucial to consider such differences in the study of foraging behavior (Baker et al., 1981; Daily and Ehrlich, 1984; Piper, 1997; Smith et al., 2001). Therefore, we additionally included the relative dominance status of the subjects as an experimental factor in our design. Previous studies that did take differences in dominance status into account, did so a posteriori, when analyzing their data (Table 3.1). We think this approach is potentially misleading, as dominance in these studies may be the result rather than the cause of observed foraging behavior. Therefore, we determined dominance status independently of our actual experiment.

In summary, we studied whether the effect of the presence of a competitor on the behavior and success of foraging turnstones depended on the spatial clumping of food, while taking into account differences in the foragers' relative dominance status. Based on the assumptions that agonistic interactions are only over food clumps, that interactions reduce intake rate because they cost time, that foragers behave as to maximize their intake rate, and that resources are not notably depleted in the course of our measurements, we expected the following results, in line with resource defense theory (Grant, 1993; Warner, 1980). When food is clumped, it might be beneficial to fight for and defend a profitable food clump. Hence, one should expect high levels of agonistic interactions, resulting in a lower intake rate in the presence of a competitor than in the absence of a competitor. Moreover, intake rates should be skewed, with dominant foragers having a higher intake rate than subordinate ones. When food is dispersed, it may not be economically defendable, and hence domination of food clumps should not be possible. Accordingly, we expected no agonistic interactions and intake rates that are not affected by the presence of a competitor. Because the absolute intake rates at both food distributions depended on experimentally determined characteristics, such as the ease with which individual food items and food clumps were found, we had no a priori expectations on which of both food distributions would yield the highest intake rate.

METHODS

SUBJECTS AND HOUSING

We used 17 turnstones (6 females, 11 males; sexed with a standard molecular assay verified for waders by Baker et al., 1999), caught with mistnets on an intertidal mudflat in the eastern Dutch Wadden Sea (53°29′ N, 6°15′ E) on 8 October 2002. We housed the turnstones in the indoor experimental shorebird facility of NIOZ, Texel. We caught and housed the turnstones according to Dutch legislation (Dutch bird-ringing center license number 351 and DEC protocol 2000.04, respectively). In the experimental facility they had two roosting aviaries (measuring 4.3 x 1.2 m and 3.0 m high) and an experimental room (7 x 7 m and 3.5 m high) at their disposal. A thin film of running seawater continuously covered the floors of the roosting aviaries to keep the feet of the birds salty and wet, and a tray of running freshwater for drinking and bathing was always present. The floor of the experimental room was covered by a 30-cm layer of sand to mimic one of the natural habitats of turnstones. The indoor environment was constant with respect to air temperature (18°C), water temperature (10°C) and light regime (12:12 h light:dark). Moonlight-mimicking lights illuminated the aviaries between 1900 and 0700 h.

PRE-EXPERIMENTAL TREATMENT

The experiment took place from 20 November to 5 December 2002. By then, the birds had been accustomed to the aviaries and the experimental procedure for several weeks. To familiarize them with the experimental environment and procedure, the birds participated in pilot trials for 26 days, prior to the experiment.

In the first three pilot days, we determined the social dominance hierarchy. In 24 trials, we observed agonistic interactions among six randomly chosen birds. We recorded the outcome of each interaction (n = 760): winners were those individuals that either chased their opponent away or that held ground after being attacked. Assuming a linear dominance hierarchy, we determined cardinal scale rank positions by means of a logit regression analysis (Tufto et al., 1998; van der Meer, 1992). Previously, we used the same technique to study the stability of the dominance hierarchy among a group of 27 captive turnstones (Vahl and van Dullemen, unpublished data). Their dominance hierarchy was rather stable during the 6 months measured. Similarly, dominance hierarchies among turnstones in the field are known to be stable (Metcalfe, 1986; Whitfield, 1988), and the results from the current experiment also confirm a stable hierarchy. During winter, no differentiation is apparent among male and female turnstones, and, correspondingly, the position in the dominance hierarchy was independent of sex in this experiment. We designated the three highest-ranking and the two lowest-ranking birds as “nonfocal” individuals and the 12 other birds as “focal individuals”. We collected data on the focal individuals; we only used the nonfocal birds as experimental competitors and to vary the relative dominance status of the focal individuals. To recognize the birds from all angles, we bleached a small area of the back feathers of the focal birds, using commercial hair bleach.

In the remaining 23 pilot days, we trained the birds to recognize food distribution on a foraging platform instantaneously (i.e., prior to landing on the platform; see Appendix). This minimized behavioral changes associated with information gain in the course of a trial, and it excluded the possibility that food distribution had no effect simply because the birds did not know it.

EXPERIMENTAL SETUP

During the experiments, we flooded the experimental room with seawater to a depth of 20 cm. The only dry area remaining was a foraging platform (1 m^2) consisting of four gravel tiles positioned 20 cm above the water level. We recorded the foraging behavior of the subjects using two digital video cameras (Sony dcr-trv900e). One camera was positioned next to the foraging platform at a distance of 1.5 m for a sideways view; the other was mounted directly above the foraging platform at a height of 3.5 m.

In all trials we placed 80 maggots (Diptera larvae) on the foraging platform. To ensure that the birds had to search for their food, we then covered the foraging platform with a 5-cm layer of seaweed (bladder-wrack, *Fucus vesiculosus*). This layer of *Fucus* resembled the natural foraging substrate of turnstones (Fuller, 2003; Whitfield, 1990). Although maggots are not part of the natural diet of turnstones (Fuller, 2003; Harris, 1979; Whitfield, 1990), they resemble other invertebrates included in the diet (especially the larvae of wrack flies, Coelopidae; Fuller, 2003), and the turnstones were keen to eat them. We used 80 maggots per trial to minimize the effects of depletion and because both the density of 80 maggots m-2 and the local density of 1280 maggots m^{-2} (clumped condition) lie within the range of invertebrate densities encountered by foraging turnstones in the field (Fuller, 2003). We placed maggots on the foraging platform in either a dispersed or a clumped way. Turnstones are likely to encounter various levels of clumping of food in the field, though the relative frequency of each level will be hard to assess. To make the food distribution dispersed, we divided the foraging platform into 16 squares of 25 x 25 cm, and we spread out five maggots arbitrarily over each square. We made the food distribution clumped by putting all 80 maggots on one randomly chosen square. We attached white or black plates (1.0 x 0.30 m and 5.0 mm thick) to the sides of the foraging platform to signal a dispersed and a clumped food distribution, respectively (see Appendix).

We varied the relative dominance status of focal birds, defined as the consistent ability of one bird to cause its specific opponent to yield in agonistic encounters (Piper, 1997), through choice of the nonfocal competitor. We assigned focal birds to either be a dominant or a subordinate by the addition of one of the two lowest-ranking or one of the three highest-ranking nonfocal birds, respectively. Hence, dominance was a relative quality rather than an individual attribute (Francis, 1988; Piper, 1997). Thus, rather than studying the determinants of relative dominance status, we chose to study the consequences of a given dominance status.

EXPERIMENTAL PROCEDURE

We deprived the birds of food from 1800 h and tested them between 0930 and 1200 h on the next day. At the start of each experimental day, we placed all birds in fixed groups of two or three in boxes measuring 50 x 35 cm and 25 cm deep, keeping focal and nonfocal birds separated. The birds were very quiet in the dark, and we thus captured and housed them in darkness to minimize stress. Before each trial, we transferred a specific focal bird to one of the roosting aviaries, either on its own or together with a nonfocal bird. After opening the sliding door, we attracted the birds into the experimental room by dimming the lights in the roosting aviary while lighting the experimental room. Subjects readily flew to the experimental platform and started to forage within seconds of the sliding doors being opened. The trials started at the moment the focal bird began to forage and then lasted for 120 s.

After each trial we used lights again to entice birds back to the roosting aviary. We transferred the birds to the second roosting aviary and we counted the number of unconsumed maggots left on the foraging platform. We then repeated the procedure. After the trials, we kept all birds together in the experimental room and the two roosting aviaries, with sliding doors open and water level low, and we provided trout food pellets *ad libitum* till the next food-deprivation period.

EXPERIMENTAL DESIGN AND STATISTICAL ANALYSIS

We studied the effects of the fixed factors *food distribution* (clumped or dispersed), *competitor present* (yes or no), and *dominance status* (dominant or subordinate), while accounting for effects of the random block factors *focal bird, replicate*, and *experimental day within replicate*. The experiment consisted of six, instead of eight, different treatment combinations, as dominance status was a relative measure and required the presence of a competitor. We used a 6 x 6 Latin square design (Fisher and Yates, 1963) to distribute the six treatment combinations over six focal individuals and six experimental days. We replicated the experiment both within and between focal individuals by using two times six experimental days and two times six focal individuals. Thus, the experiment consisted of 12 experimental days on each of which 12 focal birds foraged at one of six different treatment combinations.

In principle, each bird took part in one trial per day. However, because three treatment combinations required the participation of a subordinate nonfocal forager, and as we had only two such birds, each day one focal bird had to participate twice, once as a nonfocal. In two of the trials, the focal individual's relative dominance status was not as intended, and in one trial the focal individual was highly inactive. We repeated these three trials at the end of the same experimental day. We thus accumulated 144 successful trials.

RECORDED BEHAVIOR AND RESPONSE VARIABLES

We analyzed trials using The Observer 3.0 Event Recorder (Noldus Information Technology, Wageningen, The Netherlands). To limit effects of resource depletion, digestive constraints, and satiation, we measured foraging behavior and success during the first 60 s of each trial. Our omission of the remainder of each trial from the video analysis also served to avoid potential end effects (e.g., birds anticipating the end of a trial). The same two observer examined all trials together. In a first analysis of each trial, we used the side-view recording, which we analyzed at one-fifth of normal speed. In a second analysis, we used the top-view recording to verify the observations from the side-view tape. We distinguished five behavioral categories (*search, handle, interact, vigilant*, and *other*), each consisting of several different behaviors (for a description see Vahl et al., 2005).

We studied the effect of treatment on *intake rate*, defined as the number of maggots swallowed per total time (number per min). We additionally scored the time spent on the food clump (%), we determined their *time allocation* (defined as the total number of seconds allocated to each of the five behavioral categories), and we scored the rate of agonistic interactions (number per min-1). In doing so we distinguished between offensive (*attack* and *threat*) and submissive (*escape* and *avoid*) interactions, and additionally we distinguished between high-intensity (*attack* and *escape*) and low-intensity (*threat* and *avoid*) interactions. We defined high-intensity interactions as those in which the bird that initiated the interaction was actively moving towards its opponent.

DATA TRANSFORMATION AND HYPOTHESIS TESTING

Data on time allocation is compositional (Aitchinson, 1986): the sum of the time allocated to the various behavioral categories is constrained at 100 %. We therefore analyzed the ratio of time spent on interactions over time spent on searching, handling, and vigilance behavior. Furthermore, we assumed that the various treatments had a multiplicative effect on all response variables. Because general linear models (GLMs) assume that effects interact in an additive way, we log-transformed all measurements. To avoid taking logarithms of zero, we added the value one to all observations on intake and on the number of interactions. For data on interaction time, zero replacement was achieved by using the procedure for nonessential zeros in compositional data (Aitchinson, 1986).

We analyzed the experiment in accordance with the standard Latin square design, using the GLM procedure in SYSTAT 10 (SPSS Inc., Chicago, IL). We judged assumptions of normality and homoscedasticity by visually inspecting probability plots (Miller, 1997).

RESULTS

FORAGING SUCCESS

The presence of a competitor had a strong effect on intake rate, but this effect depended both on the food distribution and on the relative dominance status of the focal bird (Figure 3.1A; Table 3.2). The intake rate of birds foraging alone was more than two times higher when food was clumped than when it was dispersed, probably because all birds were able to find the food clump within 60 s and the subsequent discovery of individual maggots was rather easy. When food was dispersed, birds achieved the same intake rate in the presence of a competitor as when foraging alone, regardless of their dominance status. When food was clumped, the presence of a competitor did not affect the intake rate of dominant birds. However, the presence of a competitor reduced the intake rate of subordinate birds more than threefold (Figure 3.1A). Still, the intake of subordinate birds was not zero because they sometimes found the food clump first and because dominant birds sometimes temporarily left the food clump to search elsewhere on the foraging platform. Intake rates varied considerably between individuals (Table 3.2).

Table 3.2. Treatment effects on intake rate, time spent on the food clump, interacting time, and on the number of offensive (*attack, threat*) and submissive (*escape, avoid*) interactions Interacting time is analyzed as the ratio of time spent on interactions (T_I) over time allocated to searching (T_S), handling (T_H) or vigilance (T_V) behavior. GLM test results on log-transformed data are given. Effects significant at the 0.05 level are indicated by bold p values.

	Intake rate			Time spent on the food clump			Interaction time ($T_I/(T_S+T_H+T_V)$)			Offensive behavior			Submissive behavior		
	df	*F*	*p*	df	*F*	*p*	df	*F*	*p*	df	*F*	*p*	df	F	p
Replication	1	3.2	0.08	1	0.0	0.84	1	1.2	0.28	1	0.4	0.53	1	0.0	1.00
Day(replication)	10	0.7	0.74	10	0.8	0.64	10	0.2	0.99	10	1.0	0.49	10	1.3	0.25
Focal individual	11	3.4	<**0.01**	11	1.5	0.17	11	1.1	0.37	11	2.0	**0.05**	11	1.2	0.28
Treatment	5	26.7	<**0.01**	2	28.9	<**0.01**	3	5.9	<**0.01**	3	77.3	<**0.01**	3	898.9	<**0.01**
Food distribution 'A'	1	30.7	<**0.01**	—	—	—	1	4.5	**0.04**	1	1.7	0.19	1	0.7	0.42
Presence of competitor 'B'	1	21.3	<**0.01**	1	13.1	<**0.01**	—	—	—	—	—	—	—	—	—
Dominance status 'C'	1	29.9	<**0.01**	1	44.8	<**0.01**	1	2.3	0.13	1	206.4	<**0.01**	1	2695.3	<**0.01**
A * B	1	4.3	**0.04**	—	—	—	—	—	—	—	—	—	—	—	—
A * C	1	47.4	<**0.01**	—	—	—	1	10.8	<**0.01**	1	23.9	<**0.01**	1	0.7	0.42
Error	116			47			70			70			70		
Total	143			71			95			95			95		

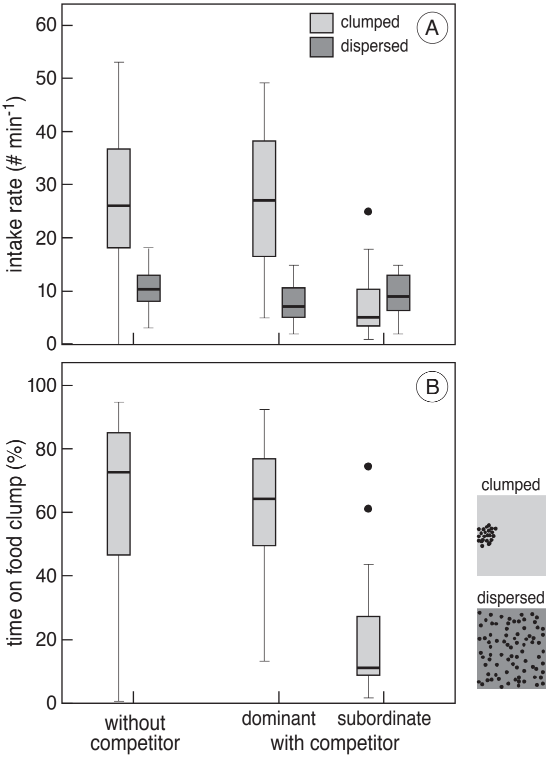

Figure 3.1. Box plots of foraging success (A) at the clumped and dispersed food condition and, for the clumped food distribution only, the time birds spent on the food clump (B). Horizontal lines mark median values, boxes encompass the central 50 % of the data, and whiskers show the range, apart from outliers that are marked as dots.

TIME SPENT ON THE FOOD CLUMP

Dominant birds spent the same amount of time on the food clump in the absence and the presence of a competitor, whereas subordinate birds spent less than a third of their time on the food clump when a competitor was present rather than absent (Figure 3.1B; Table 3.2).

TIME ALLOCATION

At all conditions, the birds spent most of their time on searching and, to a lesser extent, on vigilance, while only a small amount of time was spent on interactions (Table 3.3). The amount of time spent vigilant was constant over all treatment combinations, whereas the time allocated to searching, handling, and interacting differed per treatment combination (Table 3.2 and 3.3). Solitary foragers handled more and searched less when food was clumped than when food

Table 3.3. Total amount of time (s) allocated to the behavioral categories searching (T_S), handling (T_H), vigilance (T_V), and interacting (T_I) per treatment combination Because data on the behavioral category 'other' is not presented, the sum of the time allocated to these four behaviors is only approximately equal to the total trial duration (60 s). Numbers in parentheses represent 1 SD.

Food distribution	Competitor present	Dominance status	T_S	T_H	T_V	T_I
Clumped	No	—	34.6 (3.6)	11.2 (5.0)	14.0 (6.5)	—
	Yes	Dominant	33.8 (5.9)	11.1 (5.3)	12.1 (6.6)	2.7 (1.9)
	Yes	Subordinate	38.9 (4.9)	3.3 (1.6)	13.3 (4.6)	4.1 (1.0)
Dispersed	No	—	43.6 (4.9)	4.0 (0.8)	12.1 (5.1)	—
	Yes	Dominant	38.6 (5.8)	3.0 (1.0)	12.8 (4.4)	5.3 (3.1)
	Yes	Subordinate	39.6 (4.2)	3.7 (1.3)	12.9 (4.1)	3.3 (0.8)

was dispersed (Table 3.3). When food was dispersed, the birds spent as much time handling and searching in the presence of a competitor as when foraging alone, regardless of dominance status. When food was clumped, the same was true for dominant birds, but subordinate birds handled less and searched more when a competitor was present. The amount of time spent on interactions depended on both food distribution and relative dominance status (Table 3.2), as only dominant birds spent more time interacting when food was dispersed than when food was clumped.

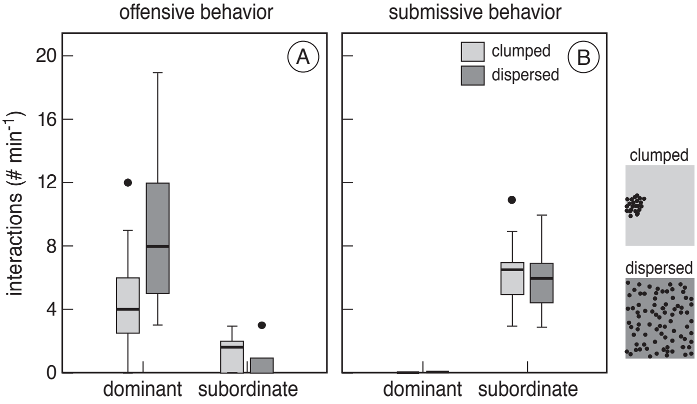

Figure 3.2. Box plots of the rate of agonistic interactions for dominant and subordinate birds, at a clumped or dispersed food distribution. We distinguished between offensive interaction behavior directed by focal birds to subordinate competitors (attacks and threats; A) and submissive interaction behavior in response to offensive behavior directed by the nonfocal bird (escapes and avoidances; B). See Figure 3.1 for an explanation of the composition of box

OFFENSIVE VERSUS SUBMISSIVE BEHAVIOR

Dominant birds directed more offensive interactions to their competitors than did subordinate birds and especially so when food was dispersed (Figure 3.2A; Table 3.2). Dominant birds did not perform submissive behaviors in response to offensive behavior directed to them by subordinate competitors. Instead, they responded aggressively when attacked by a subordinate competitor (Figure 3.2B). These results did not change when we took the intensity of agonistic behavior into account (not shown).

DO ABSOLUTE DOMINANCE POSITIONS MATTER?

The behavior and success of the turnstones depended strongly on their relative dominance status (Figure 3.1 and 3.2; Table 3.2). When tested on the residuals of the full model (which included relative dominance status), the difference in rank number (i.e., position in the dominance hierarchy) between focal birds and their nonfocal competitor did not explain any extra variation in intake rate (GLM, $F_1 = 0.08$, $p > 0.5$) or in the number of agonistic interactions (GLM, $F_1 = 0.01$, $p > 0.5$). Apparently, knowledge on the relative dominance status of competing individuals sufficed to explain variation in the behavior and success of the turnstones.

DISCUSSION

Treatment effects on foraging success were as expected. Nevertheless, the effects on agonistic behavior deviated from our expectations. To our surprise, dominant and subordinate birds differed strongly in their intake rates when food was clumped, even though they spent the same amount of time on agonistic interactions. This suggests that the amount of agonistic behavior shown by an individual and its intake rate are not directly related. When food is clumped, dominant foragers can apparently monopolize food with few interactions. The most important lesson to be drawn from this is that it may be difficult to predict interference effects from the amount of agonistic behavior observed.

The treatment factors affected agonistic behavior in such a way that two of our expectations were not met. First, the experimental birds did not interact more when food was clumped than when food was dispersed. Instead, dominant birds even spent slightly more time on offensive behavior when food was dispersed. Thus, subordinate birds did not increase their level of agonistic behavior when food was clumped, even though their intake rate was reduced severely at this condition. A similar result was found by some of the other experimental studies (e.g., Belzung and Anderson, 1986; Theimer, 1987). The most extreme example is probably given by Southwick (1967), who found that subordinate rhesus macaques (*Macaca mulatta*) would, in response to diminished food supplies, rather die from starvation than increase their level of agonistic behavior towards dominant individuals. Our results are most likely a consequence of the turnstones being highly familiar with each other. When familiarity is high, relative dominance status of foragers may be so well established that little agonistic behavior is required to maintain ownership of resources (e.g., Balph, 1977). This would imply that aspects related to the formation and maintenance of dominance hierarchies, such as familiarity among the foragers, may well be crucial for a full understanding of interference behavior. Regardless of the proximate explanation, the lack of a behavioral response by subordinate birds to altered food conditions poses the interesting question as to why foragers acquiesce in a subordinate position. Individual differences in physical characteristics could explain this, but the answer to this question is far from obvious given that dominance hierarchies may also arise from arbitrary conventions alone (Hammerstein, 1981; Maynard-Smith and Parker, 1976). Evolutionary biologists have studied this question for a long time (e.g., Landau, 1951), but this problem has certainly not been resolved (e.g., Mesterton-Gibbons and Dugatkin, 1995; van Doorn et al., 2003a,b). Second, contrary to our predictions, turnstones did not cease to interact agonistically when food was dispersed. This can be explained in various ways. Even when the birds were familiar with each other, some agonistic interactions may, for instance, have been needed to serve long-term goals, such as the formation and maintenance of dominance hierarchies (Piper, 1997). Alternatively, the observed agonistic behavior at the dispersed food distribution might reflect the inability of turnstones to adapt to such a distribution. The latter seems a reasonable option because food in the field is often aggregated (Taylor, 1961), and the chance to obtain access to a food clump by displacing another individual may therefore in general be high.

In comparing these results with previous experiments, it is interesting to note that our results correspond well with those of the only other study on spatial clumping that studied competition among two foragers (Theimer, 1987). Dominant dark-eyed juncos (*Junco hyemalis*) also obtained more food than subordinate juncos when food was clumped and the same amount of food when food was dispersed. Moreover, the number of agonistic interactions among the juncos was also less when food was clumped. This suggests that effects of spatial clumping on agonistic behavior and foraging success may be general among species. However, it should be realized that the possibility to generalize over other experimental conditions may be restricted. This is clearly illustrated by the study of Theimer (1987), who found different effects of spatial food distribution for groups of two and groups of three birds. This might well be the reason that previous experiments (Table 3.1), which all strongly differed from each other in their design, gave the impression that general effects were absent.

IMPLICATIONS

We found that the strength of interference effects depended strongly on both the spatial food distribution and on the foragers' relative dominance status. The presence of a competitor only strongly reduced intake rate when food was clumped and when the focal bird was subordinate. Together with the fact that interactions over individual food items were absent in our experiment, this result suggests that interference competition in our experiment arose through agonistic interactions over food clumps. The quantitative relevance of these findings will depend on the relative frequency with which foragers encounter heterogeneously distributed food in the field. Unfortunately, little is known about the frequency with which food distributions occur at specific levels of heterogeneity (Theimer, 1987). Our understanding of the importance of agonistic interactions over food clumps as an interference mechanism would, therefore, clearly benefit from a systematic investigation of food distributions in the field.

Furthermore, we found that knowledge on the foragers' relative dominance status sufficed to explain variation in the behavior and success of the turnstones. One important consequence of this is that for species with a strong dominance structuring any group will consist of dominant and subordinate individuals, even groups composed of the highest or lowest ranked individuals only. In addition, we found that dominant birds cannot always take advantage of their dominance status. Instead, the extent to which they can do so may depend on external conditions, such as the food distribution. Thus, we could have interpreted the effects of the presence of a competitor without acknowledging the foragers' dominance status when food was dispersed, but certainly not so when food was clumped. This finding can probably be generalized to all conditions that affect the extent to which resources or space can be monopolized. Another challenge for future research on interference competition may therefore lie in the prediction of such conditions (Grant, 1993; e.g., Cresswell, 2001).

Most models of interference competition cannot explain the strong interference effect that we observed because they assume interference competition to arise solely from kleptoparasitism (i.e., interactions over individual food items: e.g., Broom and Ruxton, 1998; Giraldeau and Caraco, 2000; Sirot, 2000). Acknowledging interactions over food clumps as a potential interference mechanism would provide us with an explanation for the fact that many species interact agonistically with each other in systems where prey-handling time is short, that is, in the absence of kleptoparasitism. Incorporating these interference mechanisms in models of interference competition may therefore strongly improve our ability to predict interference effects.

To this end, it is an interesting question whether food clumps are different from food items in an essential way. When such differences are absent, food clumps could simply be redefined as the new food items, and the existing models of interference competition could be used to model agonistic interactions over food clumps. This would only require the replacement of model parameters that are characteristics to food items with those that capture clump characteristics, such as clump-handling time. Stillman et al. (2002) took this approach when modeling interference in common cranes (*Grus grus*) foraging on clumps of cereal seeds, thus assuming that agonistic interactions over food clumps are “similar” to those concerning food items. If, on the contrary, agonistic interactions over food clumps and food items are different from each other, the simple redefinition of food items cannot be used to model interactions over food clumps, and models of interference competition should actually be extended to incorporate interactions over food clumps. This may, for instance, be done by relaxing the basic modeling assumption that food is distributed homogeneously. Several studies have already shown how heterogeneous food distributions can be modeled (e.g. Arditi and Dacorogna, 1988; Cosner et al., 1999; Ruxton and Gurney, 1994).

At first glance, it may seem reasonable to assume that interactions over food clumps and interactions over food items are not essentially different, especially because many of the behaviors constituting both types of interactions are similar. For instance, regardless of what is at stake, foraging animals may try to steal or defend a resource and avoid or monitor other foragers. However, despite this similarity in the underlying behaviors, interactions over individual food items and small food clumps have distinguishing features that may well affect the composition of costs and benefits and hence the strategic choices of individuals. For instance, unlike most food items, food clumps generally can be divided among multiple foragers because they consist of multiple food items. Thus, although foragers that supplant other foragers from food clumps can be considered to “kleptoparasitize” these food clumps (e.g., Smith et al., 2002), this process may differ from kleptoparasitism over food items in that the supplanted foragers may have exploited their food clumps at least partly before being supplanted. Another potential difference is that winning interactions over individual food items provides foragers with concrete resources, whereas winning interactions over food clumps merely results in an increased chance of finding food in the near future. Because uncertainty about rewards is known to affect decision processes (e.g., Kühberger and Perner, 2003), the fact that foragers have less information on the rewards of an interaction over food clumps may also cause kleptoparasitism over food clumps to deviate from that over food items. Future experimental and theoretical investment should be directed at the differences between the various types of interactions and the consequences of these differences for our predictions on interference behavior.

However, regardless of the relation between interactions over food clumps and interactions over food items, there may be more fundamental problems in the way we currently model interference competition. Models of interference competition all assume that interference effects arise through the loss of time to agonistic interactions. We found that there was no such straightforward relationship between the amount of agonistic behavior of an individual and its intake rate and attributed this to the strong establishment of the relative dominance status of the birds. The prime importance of social dominance in this and many other foraging experiments (e.g., Baker et al., 1981; Piper, 1997; Smith et al., 2001) suggests that long-term processes such as acquiring and maintaining dominance status may be connected to the foraging process in such an intimate way that we cannot fully understand the foraging process without them. In the presence of such long-term processes even basic assumptions like the maximization of intake rate may no longer hold.

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APPENDIX: PILOT TRIALS

In the first 14 training pilot days we attempted to teach the birds to associate food distribution with a sign of a specific color and shape. Because these attempts were not successful, we trained the birds in the next nine pilot days to recognize the food distribution on the foraging platform instantaneously (i.e., prior to landing on the platform) on the basis of the same black and white plates that we also attached to the sides of the foraging platform in the actual experiment. During these 9 days each bird performed, on its own, 21 trials of about 60 s. The setup in these trials differed from the experimental setup in that two foraging platforms were present. We positioned the additional platform 3 m from the first platform, and this second platform only differed from the first platform in its food distribution, and hence the color of the plates attached to its sides. We studied the birds' preferences for each food distribution/plate color by recording on which platform each bird landed first in the last four pilot trials. After the experiment, each bird performed another four trials to study potential changes in preference. We tested preference, using a goodness of fit test for binomial distributions with $p = q = 0.5$.

The frequency distribution of preference for a specific food distribution deviated significantly from binomial, both before ($\chi^2 = 34.45$, df = 4, $p < 0.001$) and after ($\chi^2 = 28.33$, df = 4, $p < 0.001$) the experiment, indicating that most birds were able to distinguish between the two platforms on the basis of the color of the plates attached to the platforms. Before the experiment, an equal number of birds preferred both food distributions, whereas after the experiment the birds only preferred the clumped food distribution. The difference in preference before and after the experiment indicates that learning to instantaneously recognize platform color and/or food distribution continued throughout the experiment and that, at least after the experiment, the birds based their choice on the food distribution rather than on platform color.

CHAPTER 4

INTERFERENCE COMPETITION, THE SPATIAL DISTRIBUTION OF FOOD AND FREE-LIVING FORAGERS

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SUBMITTED TO ANIMAL BEHAVIOUR

ABSTRACT

Studies of interference competition among foraging animals generally assume that variation in the spatial distribution of food can be neglected. This assumption may be problematic as resource defence experiments suggest that such variation is of the essence in some interference mechanisms. Interpretation of the results of field experiments on this topic, however, is hard because of the way these experiments have been analysed: variation in the abundance of foraging animals has consistently been treated as nuisance or as a predictor variable, whereas it usually is one of the prime responses. We performed a field experiment in which we provided wild ruddy turnstones (*Arenaria interpres*) with experimental plots that varied in the distance between a fixed number of so-called food pits, and, using multivariate statistics, we studied effects on the combination of the turnstones' behaviour and abundance. We found that when food pits were more spaced out, turnstones were present in higher numbers, while interacting less with each other, but that they spent about the same time digging for food, our measure of intake rate, at each inter-pit distance. These findings imply that to reliably predict the combination of the number, intake rate and amount of aggression of turnstones, the spatial distribution of food has to be known. We would not have reached this conclusion if we had used univariate statistics or if we had treated variation in forager abundance as mere nuisance. Moreover, treating forager abundance as a response variable led to the insight that while experiments on captive foragers usually exclude patch choice decisions, experiments on free-living foragers necessarily involve patch choice decisions.

INTRODUCTION

The intake rate of foraging animals is often negatively related to the density of foragers because of competition. Competition is generally thought to arise in either of two ways (Keddy 2001). *Exploitative competition* is the negative effect of others through the removal of resources. As the exploitation of resources is a straightforward process, this type of competition is (presumably) relatively easy to understand. Interference competition is the negative effect of others through direct interactions between individuals. Behaviours underlying *interference competition* are various and complex (e.g., Huntingford & Turner 1987; Ens & Cayford 1996; Hassell 2000) and our understanding of this type of competition is still rudimentary (van der Meer & Ens 1997; Vahl et al. 2005a, b).

Students of interference competition among foraging animals usually study the effects of forager density concurrently with effects of food density (van der Meer & Ens 1997). In this approach it is implicitly assumed that variation in the spatial abundance of resources ('spatial clumping') does not affect the interference process. This may well be problematic. According to literature on resource defence, the 'economically defendability' (Brown 1964) of a given amount of food should decrease with the surface area over which the food is spread (Warner 1980; Grant 1993), as both the movement costs involved with defending a food clump and the number of intruding competitors are expected to be higher when the food is spread over a larger area (Davies & Houston 1984). With defendability decreasing, the use of aggressive behaviour to acquire resources and the extent to which resources will be monopolized should also be reduced when food is more spread out (Grant 1993). Numerous empirical studies have determined the effects of spatial clumping on the amount of aggression and resource monopolization; generally (though not unanimously) these studies confirm the resource defence expectations (for a review, see Vahl et al. 2005a).

The effect of spatial clumping on resource defence suggests that the spatial distribution of food has to be considered explicitly in order to arrive at a better understanding of interference competition; variation in the spatial distribution of food may well be of the essence in at least one mechanism underlying interference competition – resource monopolisation. Acknowledging variation in the spatial distribution of food may therefore be crucial, especially since natural food distributions generally are not homogeneous (Taylor 1961; Wiens 1976). Unfortunately, neither the literature on interference competition, nor the literature on resource defence provides clear-cut expectations on how the spatial clumping of food should affect the relationship between forager density and intake rate. Some empirical studies, however, shed light on this question. At least four studies (Rubenstein 1981; Theimer 1987; Benkman 1988; Vahl et al. 2005a) have manipulated both the spatial distribution of food and the abundance (i.e., either the number or the density) of foragers to determine effects on the amount of aggression and intake rate. These studies found that the spatial clumping of food strongly affected the interference process, but that effects could not be understood without considering variation in the relative social dominance status of the foragers. Theimer (1987) and Vahl et al. (2005a), for instance, found that dominant foragers can better monopolize food that is spatially clumped than food that is dispersed, and that as a consequence, subordinate foragers suffer more from interference competition when food is clumped than when food is dispersed.

The extent to which these findings are important to understand the behaviour of free-living animals foraging under natural conditions is still an open question, because the four studies mentioned above were all conducted in the laboratory, using captive foragers. The most direct approach to study whether interference effects among free-living foragers depend on the spatial distribution of food would involve manipulation of both the spatial distribution of food and the density of wild foragers (Vahl et al. 2005b). Manipulating the density of free-living foragers, however, is very difficult and we are not aware of any study that has attempted to do so. Therefore, the most relevant data to date comes from studies that have manipulated the spatial distribution of food in the field, but not the density of foraging animals. Several such experiments have been performed (Table 4.1). Quite consistently, these studies found that with increasing plot size (1) the number of foragers increased, whereas forager density decreased and (2) the amount of aggression decreased (see Table 4.1). With regard to the correlations between forager abundance and intake rate or the amount of aggression, and with regard to effects of plot size on intake rate and the amount of aggression after correction for variation in forager abundance, the studies were less consistent (Table 4.1).

Unfortunately, interpretation of these results is not straightforward. The way these field experiments have been analysed complicates their interpretation in two ways. The first complication regards the way these studies dealt with variation in forager abundance. As mentioned above, forager abundance was an uncontrolled response variable in all field experiments, and, indeed, most of the studies reported a change in forager abundance in response to variation in the spatial distribution of food (Table 4.1). Nevertheless, when analysing the correlations between forager abundance, intake rate and the amount of aggression, some of the studies treated forager abundance as a predictor variable, either by including forager abundance as a covariate in an ANCOVA (Johnson et al. 2004) or by defining abundance categories (Balph 1977). Similarly, when studying treatments effects on intake rate and the amount of aggression, several of the studies treated variation in forager abundance as nuisance which had to be corrected for statistically, either by treating forager abundance as a covariate in ANCOVAs (Elgar 1987; Johnson et al. 2004, 2006), by treating forager abundance as a predictor variable in regression analyses (Goldberg et al. 2001), or

Table 4.1. Field experiments on the effect of the plot size (X) on the abundance (Y_1), the foraging success (Y_2) and the frequency of (per-capita) agonistic behaviour (Y_3) of free-living foragers†

species	English name	size of experiment		food	surface area	main effects					correlations					corrected effects			ref.
						XY_1			XY_2	XY_3	Y_1Y_2		Y_1Y_3			$XY_2\|Y_1$	$XY_3\|Y_1$		
		n_1	n_2			$Y_{1,n}$	$Y_{1,d}$	Y_1			$Y_{1,n}$	$Y_{1,d}$	$Y_{1,n}$	$Y_{1,d}$	Y_1	$Y_{1,n}$	$Y_{1,n}$	$Y_{1,d}$	
birds																			
Junco hyemalis	dark-eyed junco	2	u	amount	variable	(+)	(-)			(-)			+,0				-		1
Passer domesticus	house sparrow	2	u	neither	variable				(+)	-	0,-		+						2
Passer domesticus	house sparrow	7	35	density	variable	+	-			-	+		+,0	+		0		-	3
Passer domesticus	house sparrow	2	26	density	variable	(+)		0	0	-	+,0,-		(-)						4
Turdus merula	European blackbird	2	498	density	variable						-					(0)	(-)		5
Zenaida aurita	Zenaida dove	2	24	amount	constant			+		0,-					+,0,d,c				6
-	several passerines‡	2	24	amount	constant			+											7
mammals																			
Lepus europaeus	European hare	2	28	amount	constant					(-)		+,0,-		+,0					8

† The column 'size of experiment' indicates the number of levels of plot size (n_1), and the total number of trials performed (n_2). For some studies the latter aspect is unknown (u). The column 'food' indicates whether the amount or the density of food was kept constant, or neither of them. The column surface area indicates whether the surface area over which forager abundance was expressed was constant or not; in the former case, effects on the number and the density cannot be distinguished (Y_1), whereas in the latter case, the number ($Y_{1,n}$) and the density ($Y_{1,d}$) of foragers are uncoupled. In the 'main effects' column, the 'correlations' column and in the 'corrected effects' column, it is indicated whether the relationship or the correlation between two variables was negative (-), positive (+), absent (0), dome-shaped (d) or cubic (c). Signs within brackets are not given by the original author(s), but are deduced by us. The correlation between forager abundance and amount of aggression in the study of Goldberg et al. (2001) depended on the temporal predictability of food patches; the correlations between forager abundance and intake rate and amount of aggression in the study of Monaghan & Metcalfe (1985) depended strongly on the dominance status of foragers. All other multiple effects depended on plot size.

‡ Included in the analyses were northern red cardinals (*Cardinalis cardinalis*), field sparrows (*Spizella pusilla*) & white-throated sparrows (*Zonotrichia albicollis*).

references: (1) Balph 1977, (2) Elgar 1987, (3) Johnson et al. 2004, (4) Johnson et al. 2006, (5) Cresswell 1997, (6) Goldberg et al. 2001, (7) Pearson 1989, (8) Monaghan & Metcalfe 1985 by excluding observations on higher abundances from the analyses (Cresswell 1997). Several of these approaches violate statistical assumptions (e.g., the independence of predictor variables, the absence of measurement error on predictor variables, and the absence of feedback effects of response variables on predictor variables). All of them are unwanted, because they distract attention from what may be the most important effect of the spatial distribution of food – a change in the abundance of foragers. The second complication lies in the fact that none of the studies acknowledged the multivariate nature of their data; to study treatment effect on forager abundance, intake rate and the amount of aggression, all investigators used univariate statistics. Such an approach precludes the detection of effects on combinations of response variables, and it invokes the risk of an inflated type I error (Harris, 1975).

To solve these interpretational problems, the field experiments could be reanalyzed. Rather than doing so, we performed a new field experiment to describe effects of the spatial distribution of food on free-living foragers, and we took care to avoid the above-mentioned shortcomings in the statistical analyses. In this experiment, we provided wild birds with experimental plots in their usual foraging area, and we manipulated the distribution of food by varying the distance between a fixed number of regularly distributed food pits. We recorded the responses of visiting ruddy turnstones (*Arenaria interpres*; henceforth called turnstones), a species that we previously used to address the same question in laboratory experiments on captive foragers (Vahl et al. 2005a,b). In analysing our experiment, we used multivariate statistics and we tried to be consistent in acknowledging forager abundance as a response variable; rather than treating variation in forager abundance as nuisance, we treated it as one of the prime response variables. In the discussion, we examine whether the use of univariate statistics and the use of ANCOVAs (which treat forager abundance as nuisance) would have affected our results, and we reflect on the way in which multivariate analysis helps to clarify the research question.

METHODS

We designed our experiment according to a randomized block design: we studied the effect of one treatment factor – the distance between food pits – with three levels (10, 20 and 30 cm) and we blocked our observations in groups of three trials (we refer to these blocks as 'triplets') to minimize variation due to measurements at different moments in time. The experiment consisted of 10 triplets, each containing all three inter-pit distances once (in random order). There was one missing value and hence we had 29 data points.

We studied treatment effects on three response variables: the number, intake rate and the amount of aggressive behaviour of turnstones. As plot size varied between treatments, the density of turnstones did not have a one-to-one relationship with the number of turnstones. Moreover, the experimental plots did not only attract turnstones, but also sanderlings (*Calidris alba*), red knots (*Calidris canutus*), laughing gulls (*Larus atricilla*), herring gulls (*Larus argentatus*), ring-billed gulls (*Larus delawarensis*) and starlings (*Sturnus vulgaris*). To see whether conclusions would be different if measures of abundance other than the number of turnstones were used, we repeated all analyses using (1) the density of turnstones ($\#m^{-2}$), (2) the biomass (kg), or (3) the biomass density (kgm^{-2}) of all species present on the experimental plot as the measure of abundance.

STUDY SYSTEM AND SUBJECTS

The experiment was conducted at one of the beaches of Delaware Bay, U.S.A., on five days between 24 and 30 May 2003. Delaware Bay is one of the most important spring stopover sites for shorebirds along the east coast of North America (Clark et al. 1993). Turnstones are among the most abundant species in the bay, with peak counts of over 100.000 individuals (Clark et al. 1993). The main food source for turnstones foraging in this bay are the eggs of horseshoe crabs (*Limulus polyphemus*; Tsipoura & Burger 1999). Turnstones forage on loose eggs that are brought to the beach surface by the re-working of waves, tides, and bioturbation of horseshoe crabs and other fauna (Kraeuter & Fegley 1994; Sherman et al. 1994) but they are also able to dig up clusters of eggs buried in the sand (Sullivan 1986; Tsipoura & Burger 1999). In doing so, they attract individuals of several other species (Myers et al. 1979) that cannot reach buried eggs themselves. In 2003 the amount of food on the beaches was relatively low (Smith & Bennett 2004) and turnstones got crab eggs mainly by digging for them in the sediment.

STUDY SITE AND EXPERIMENTAL SET-UP

The experiment was performed at one beach in the village Reed's Beach, Cape May County, New Jersey. This beach is quite small (depth x width: 10 x 90 m). It is unique in that it is enclosed by 2 m high walls on all but the bay-side. Hence, the beach has a basin-like appearance. Since this beach was completely flooded at high tide, and since at low tide the birds would be far out on the mudflats, we conducted all trials at incoming or outgoing tides (X ± SD = 2.32 ± 0.33 h before and 1.34 ± 0.46 h after high tide). Triplets took 45 min at most (X ± SD = 34.6 ± 5.3 min).

In each trial we created one experimental plot at approximately 3 m from the water line. To mark experimental plots for the observers, we placed black stones, which were abundant on the beach, on their corners. Each plot contained 25 food pits, positioned in a regular 5 x 5 grid. Food pits were holes of approximately fixed size and cylindrical shape; we created them by pressing a film canister in the sand (diameter: 31 mm; depth: 51 mm). In each pit, we placed a spoonful of crab eggs (X ± SD = 4.2 ± 0.7 g, N = 50), corresponding to approximately 750 eggs (1 gram of eggs = 183.1 ± 16.3 eggs [based on 9 egg counts]), and a thin layer of sand (5.7 ± 0.2 ml, N = 10) to cover the eggs. The upper 4 cm of each pit was left empty so that foragers could easily see the food pits. Eggs used in the experimental trials were isolated from sediment samples by elutriation, and had been stored at 4 °C for at most one day. The experimental food pits resembled the pits turnstones dug themselves to reach buried egg clusters, both in size (depth: 51.3 ± 7.4 mm, N = 16) and shape, and turnstones were eager to forage in them. Importantly, food at the experimental plot was abundant and easy to gather relative to food in the direct neighbourhood of the experimental plot (as was also clear from the strong preference of foragers for the experimental plots).

Between trials we experimentally varied the distance between food pits. The smaller two experimental inter-pit distances (10 cm and 20 cm) fell below the size range of turnstones (length: 210 – 255 mm; Hayman et al., 1986). Nevertheless, monopolization of multiple food pits required the turnstones to move actively between food pits at each of the three inter-pit distances. While varying the distance between food pits, we kept constant the number of food pits per plot and the number of eggs per food pit. Consequently, the size of the experimental plot (0.25, 1.00 or 2.25 m^2) and the density of food pits (100, 25 or 11 $\#m^{-2}$) varied concurrently with inter-pit distance. We think that the simultaneous variation of several aspects of the distribution of food is inevitable in experiments on the effect of the spatial distribution of food.

During each trial we recorded the behaviour of birds on the experimental plot with a video-camera (Sony dcr-trv 900e), positioned on the veranda of one of the elevated houses bordering the beach. Experimental plots were only 20-30 m away from the camera. Although birds that foraged on the experimental plot could see the observer and the camera, this did not seem to affect them, probably because they were used to people, and because the observers were not actually on the beach.

EXPERIMENTAL PROCEDURE

The same two observers (WKV & KM) conducted all trials together. To create an experimental plot, one observer set foot on the beach from the site opposite to that of the camera. In doing so, he necessarily disturbed the birds foraging on the beach, which readily took off for another beach. However, new birds would arrive even before the observer had left the beach, and the first birds generally started to feed on the experimental plot within the first minute after preparation. Video-recording started when the first turnstone entered the experimental plot and lasted for five minutes. Trials in which (at any moment) more than three laughing gulls, and/or more than one herring gull or ring-billed gull were present were excluded from the experiment.

VIDEO ANALYSIS AND RECORDED BEHAVIOUR

We analysed our video-recordings at one-fifth of normal speed, using The Observer 4.1 Event Recorder (Noldus Information Technology 2002). To minimize start-effects, such as a gradual rise in the number of foragers, we discarded the first 60 s of each record. To limit effects of resource depletion, digestive constraints and satiation, we additionally discarded the last 60 s of each record. Thus, we restricted all analyses to a 180 s time span. Because of an external disturbance one trial only lasted for about 220 s. After exclusion of the first 60 s, we therefore had only a 160 s interval for analysis. We extrapolated response variables for this trial by multiplying all events with a factor 180 / 160.

We calculated the abundance (either the number or the density) of foragers as the average of 5 s interval counts of the number of individuals per species on the experimental plot. Collective biomass was estimated by summing for all species the product of the average number of individuals (Table 4.2) and the median body mass of an individual (sanderling: 71.5 g; turnstone: 137.0 g; red knot: 152.5 g; laughing gull: 320.0 g; big gull: 802.5 g; mass values from del Hoyo et al. 1996, and starling: 82.5 g; Feare 1984). Note that, we grouped herring gulls and ring-billed gulls in the category 'big gulls', because our subjective observations suggest that the two species had the same effect on turnstones.

To determine intake rate and the amount of aggression, we recorded the behaviour of focal turnstones. As focal individual we chose the turnstone closest to the centre of the experimental plot. When a focal turnstone left the experimental plot, we continued the analysis by recording the behaviour of a new focal bird. We approximated intake rate by measuring the time spent digging in the food pits (%); when 'digging', turnstones were actively routing with their bill through the sand. We could not measure intake rate directly, because plot size restricted the extent to which we could zoom in on the turnstones. However, digging time and intake rate (the number of swallowing movements)

Table 4.2. The number of individuals per species observed on the experimental plot. Given are the averages per treatment with the associated standard deviations and maxima in brackets

	inter-pit distance (cm)		
species	10	20	30
turnstone	2.9 (1.3; 4.9)	9.4 (1.6; 11.5)	12.1 (4.5; 20.9)
sanderling	2.0 (1.9; 4.9)	3.8 (2.8; 7.6)	8.3 (8.2; 21.1)
red knot	0.1 (0.1; 0.3)	0.1 (0.4; 1.2)	0.2 (0.4; 1.4)
laughing gull	0.4 (0.4; 0.9)	0.5 (0.5; 1.4)	0.6 (0.9; 2.2)
'big gulls'	0.1 (0.1; 0.3)	0.0 (0.1; 0.2)	0.0 (0.1; 0.3)
starling	0.1 (0.1; 0.3)	0.1 (0.1; 0.4)	0.2 (0.3; 0.7)

were strongly correlated ($R^2 = 0.91$, $F_{1,67} = 641.7$, $P < 0.01$) in an observational dataset gathered on nearby beaches by systematically recording the behaviour of foraging turnstones for 60 s ($N = 68$). We measured the amount of aggression as the number of intra-specific agonistic interactions that focal turnstones performed per trial (#/180 s). Interactions comprised 'fighting', 'attacking', 'threatening', 'avoiding' or 'escaping' (for a detailed description of the latter four interaction behaviours: see Vahl et al. 2005b). In analyses based on all species, the amount of aggression was measured as the rate of all (intra- and inter-specific) interactions performed by focal turnstones.

DATA TRANSFORMATION AND HYPOTHESIS TESTING

We analyzed our data using the GLM procedure in SYSTAT 10 (SPSS Inc. 2000), treating both 'triplet' and 'inter-pit distance' as categorical factors. This procedure is able to handle missing values. In all graphs that include information on triplets, we replaced the missing value with the associated treatment average. We log-transformed all response variables (Vahl et al. 2005a, b). In the analyses, we did not replace the missing value; to study the effects of our treatment factor, we ran a MANOVA on the combination of the three response variables – the number of turnstones, the time spent digging and the rate of intra-specific interactions. We repeated this analysis trice, using either the density of turnstones, the biomass of all species or the biomass density of all species as measure of abundance. In each of the four MANOVAs, we used a 0.01 significance level. This implies that the overall experimentwise error rate did not exceed 0.04. We judged assumptions of normality and homoscedasticity by visually inspecting probability plots (Miller 1997).

RESULTS

The distance between food pits had a significant effect on the combination of the number of turnstones on the experimental plots, their intake rate, and the amount of their aggression (Table 4.3). There was almost no overlap between the combination of the three response variables at the three inter-pit distances, as is clear from both the multivariate representation – the three clouds of points were clearly separated (Figure 4.1A) – and from the strong correlation between the inter-pit distance and the first canonical variate (Table 4.3). The most pronounced effect was on the combination of the number of turnstones and the of amount of their aggression (Figure 4.1D), and on the combination of the number of turnstones and their intake rate (Figure 4.1B); the combination of the amount of aggression and intake rate was not so much affected (Figure 4.1C). The combination of response variables at the smallest inter-pit distance differed mainly from that at the two larger inter-pit distances in that fewer turn-

Table 4.3. The effect of inter-pit distance (X) on the number of foragers (Y_1), the percentage of time turnstones spent digging (Y_2) and the rate of agonistic interactions (Y_3). Given are MANOVA results, the canonical correlations regarding inter-pit distance (X), and the associated canonical loadings. on log-transformed data Effects significant at the 0.01 level are indicated by bold P-values†

	multivariate ANOVA Y_1 Y_2 Y_3			
	df	value†	F	P
triplet	27, 44	0.19	1.2	0.25
inter-pit distance (X)	6, 30	0.05	18.0	<0.01

X	canonical correlation analysis						
	correlations				loadings		
	r	χ^2	df	P	Y_1	Y_2	Y_3
variate 1	0.97	76.3	6	<0.01	-0.70	-0.17	0.08
variate 2	0.46	5.9	2	>0.05			

† The MANOVA results indicate that the combination of the three (log-transformed) response variables differs significantly between the three inter-pit distances, but not between the ten triplets. The canonical correlation analysis gives the correlation (r) between inter-pit distance (X) and two canonical variates, which are compound variables formed by the linear combination of response variables that results in the greatest amount of among-group to within-group variation. Inter-pit distance is strongly and significantly correlated with the first canonical variate, but not with the second. The canonical loadings indicate the correlation between the first canonical variate and each of the three response variables; as it turns out, it is the number of turnstones (Y_1) that is most closely aligned with the first canonical variate.

‡ Value given is Wilks' lambda; other multivariate statistics led to identical conclusions.

stones were present at the smallest inter-pit distance (Figs 1A, D and G). The combination of response variables, however, also differed between the two larger inter-pit distances; when food pits were 20 cm apart, the turnstones, which were present in slightly lower numbers than when food pits were 30 cm apart, interacted more with each other (Figs 1A, D and F).

The effect of inter-pit distance on the combination of response variables is furthermore apparent from the correlations among the responses variables (Table 4.4); inter-pit distance affects the correlation between the number of turnstones and both the time spent digging (Figure 4.1B) and the rate of agonistic interactions (Figure 4.1D). Especially the latter correlation depends much on whether or not variation in inter-pit distance is acknowledged. Overall, that is , when variation in inter-pit distance is neglected, the number of turnstones is uncorrelated with the rate of agonistic interactions, while when variation in inter-pit distance is acknowledged, the number of turnstones and the amount of aggression are clearly positively correlated (Figure 4.1D).

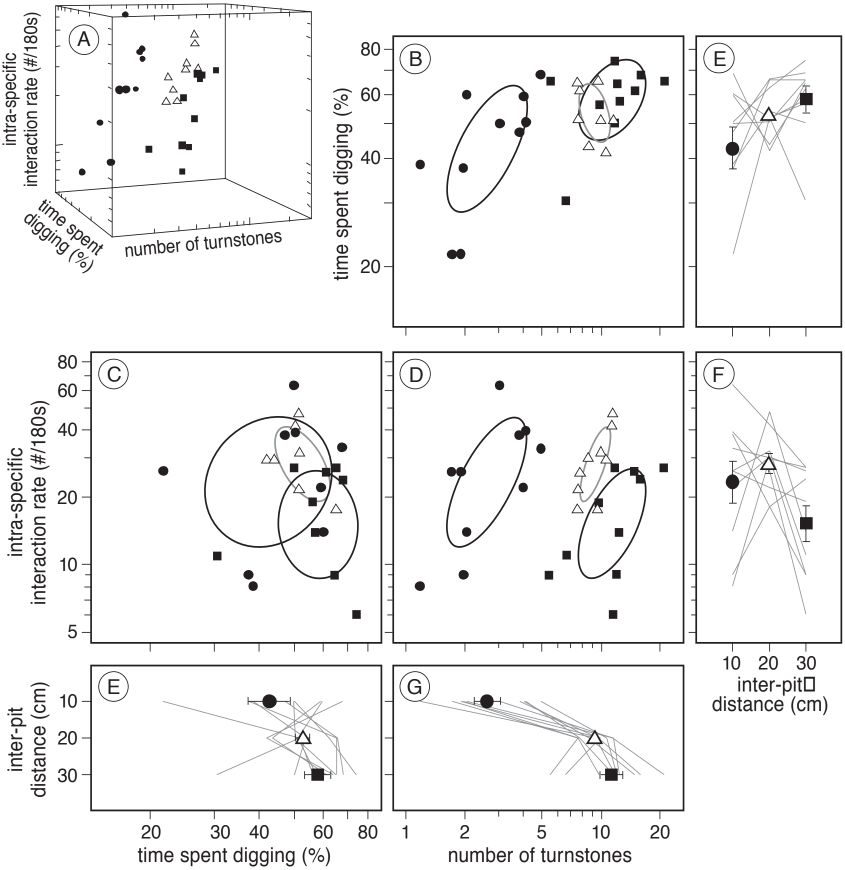

Figure 4.1. Effects of the distance between food pits on the three response variables – the number of turnstones, the time spent digging (our measure of intake rate) and aggression. In all panels, symbols (circles, triangles and squares) indicate inter-pit distance (10, 20 and 30 cm, respectively). Panel A gives the three-dimensional relationship between the three response variables. The panels B–D and the panels E–G give the two- and one-dimensional projections of this three-dimensional relationship, respectively. Note that panel E features twice. In panels A–D symbols represent averages per trial. In panels B–D ellipses indicate the 95% confidence intervals of the mean for each inter-pit distance (confidence intervals for the intermediate treatment level are dashed). In panels E–G symbols represent averages per treatment level, and error bars indicate one standard error of the treatment averages. The thin grey lines connect observations within triplets; they represent the ten blocks of our randomized block design.

Table 4.4. Correlations among the three (log-transformed) response variables – the number of turnstones (Y_1), the time spent digging (Y_2), and the intra-specific interaction rate (Y_3). For each pair of response variables, the simple (unconditioned) correlation coefficients are given, as well as the 1st, and 2nd order correlation coefficients conditioned on either the block factor triplet, the distance between food pits (X), or both (as indicated by the set of variables given within braces)†

N = 29	(partial) correlation coefficients							
	simple		1st order				2nd order	
pair	set	r_s	set	r_s	set	r_s	set	r_s
Y1Y2	{-}	0.59	{X}	0.50	{triplet}	0.61	{triplet, X}	0.36
Y1Y3	{-}	0.13	{X}	0.65	{triplet}	-0.04	{triplet, X}	0.61
Y2Y3	{-}	-0.09	{X}	0.01	{triplet}	-0.19	{triplet, X}	-0.03

† The effect of the distance between food pits on the correlations between the response variables can be studied in two ways: (1) simple correlations can be compared with first order partial correlations conditioned on the distance between food pits, and (2) first order partial correlations conditioned on the block factor triplet can be compared with the second order partial correlations conditioned on both the block factor triplet and the distance between food pits.

TURNSTONE DENSITY

Even though turnstones were present in higher numbers when the distance between food pits was larger, their density was lower at this condition. Effects on the number and the density of turnstones could be different because the distance between food pits also affected the size of experimental plots; the surface area of experimental plots was nine times larger when food pits were far apart than when food pits were close together. Analyses based on the density of turnstones yielded qualitatively the same results as analyses based on the number of turnstones: inter-pit distance had a strong ($r = 0.89$) and significant effect on the combination of the three response variables (Wilks' lambda = 0.17, $F_{6,30} = 7.1$, $P < 0.01$). The main difference between the three inter-pit distances was in the combination of turnstone density and intake rate and in the combination of turnstone density and the amount of aggression: when food pits were 30 cm apart, turnstone density was about half of that at the two smaller inter-pit distances (Figure 4.2B), whereas intake rate was somewhat higher and the amount of aggression lower than at the two smaller inter-pit distances. That turnstone density did not differ significantly between the 10 cm and the 20 cm treatment suggests that the increase in the number of turnstones between these two treatment levels was proportional to the corresponding increase in plot size.

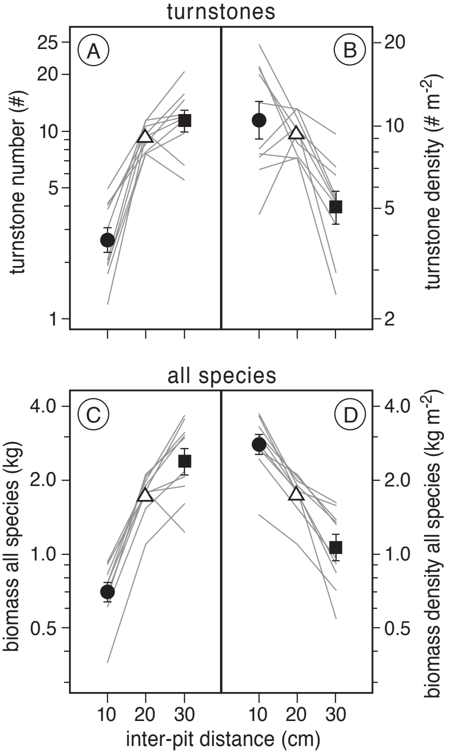

Figure 4.2. The effect of the distance between food pits on (A) the number and (B) the density of turnstones, and on (C) the biomass and (D) the biomass density of individuals of all species on the experimental plot. Symbols represent averages per inter-pit distance, error bars represent one standard error of these averages, and thin grey lines connect observations within triplets and represent the ten blocks. Note that panel A corresponds to Fig. 2.1G.

ALL SPECIES

Effects of inter-pit distance on the biomass and the biomass density of the individuals of all species together were similar to effects on the number and density of turnstones (Figure 4.2). With increasing distance between the food pits, the biomass of all species together increased (Figure 4.2C), but not so much as to be proportional to the increase in plot size; therefore, the biomass density of all species together decreased with inter-pit distance (Figure 4.2D). Effects on the rate of intra- and inter-specific interactions together were also similar to those on the rate of intra-specific interactions alone (Figure 4.3). Even though the number of individuals of species other than turnstones was substantial, most interactions of focal turnstones were directed at conspecifics; at all three inter-pit distances, the rate of inter-specific interactions (Figure 4.3B) was much

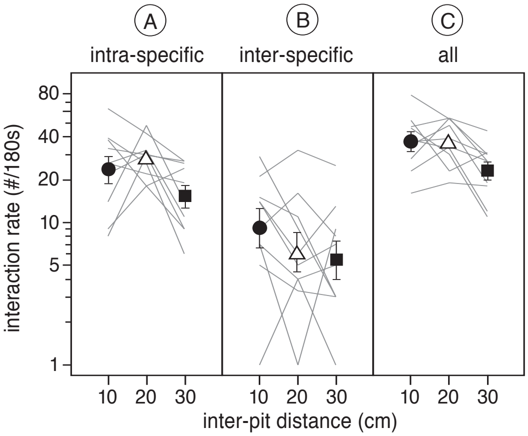

Figure 4.3. The effect of the distance between food pits on (A) the rate of intra-specific interactions, (B) the rate of inter-specific interactions, and (C) the rate of all (intra- and inter-specific) interactions. Symbols represent averages per inter-pit distance, error bars represent one standard error of these averages, and thin grey lines connect observations within triplets and represent the ten blocks. Note that panel A corresponds to Figure 4.1F, but that the ordinate has a different range.

lower than the rate of intra-specific interactions (Figure 4.3A). Most inter-specific interactions comprised of attacks and threats towards the many sanderlings that tried to share the food pit owned by the focal forager, and escapes and avoidances from the occasional gull that was attracted by the experimental plot. Statistically, treatments effects on biomass and biomass density were also highly comparable to those on the number and the density of turnstones, respectively.

DISCUSSION

The spatial distribution of food strongly affected the behaviour and success of the free-living foragers participating in our experiment. Multivariate analysis showed that it was the combination of, especially, the number of turnstones and the amount of their aggressive behaviour that depended on the spatial distribution of food. Inspection of the correlation coefficients also revealed that the correlation between the number of turnstones and both their intake rate and their aggressive behaviour depended on the distance between food pits. The immediate lesson that can be drawn from this finding is that there was not a one-to-one relationship between the amount of food and the combination of the three response variables; the same amount of food yielded a different combination of the three response variables, depending on the spatial distribution of the food.

This implies that to reliably predict the number, intake rate and amount of aggressive behaviour of turnstones, the spatial distribution of food has to be known. Additionally, these findings imply that the pressure exerted by turnstones on their prey varied with the distance between food pits; when food was spaced out, the product of intake rate and the number of foragers (the 'foraging pressure') was higher (Figure 4.4). This illustrates the idea that reduced predation pressure as a result of increased predator interference may be an important advantage of clumping to prey, as was pointed out by Taylor (1977). Although clearly outside the scope of this study, this suggests that the small-scale distribution of food may ultimately affect the dynamics of both predators and their prey.

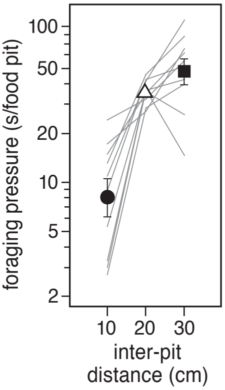

Figure 4.4. The estimated foraging pressure per inter-pit distance. Foraging pressure was calculated as the product of the average number of turnstones and the time spent digging per trial. Symbols represent averages per inter-pit distance, error bars represent one standard error of these averages, and thin grey lines connect observations within triplets and represent the ten blocks.

While the number of turnstones increased with inter-pit distance, the density of turnstones decreased. This shows that the relationship between the number of foragers and surface area is not one-to-one; just as the relationship between the number of foragers and the amount of food, this relationship depends on the spatial distribution of food. Effects on the biomass and the biomass density of all species on the experimental plot strongly resembled these effects on the number and the density of turnstones, suggesting that effects of the spatial distribution of food are general over species, conform the findings of Pearson (1989). The general conclusion that can be drawn from tests that use either turnstone density, all species biomass or all species biomass density as measure of abundance, is the same as that from tests that use the number of turnstones:

the spatial distribution of food affects the combination of the abundance, intake rate and amount of aggression of free-living foragers.

As plot size, food density and inter-pit distance varied concurrently, we cannot determine to which of these three aspects of the food distribution the foragers responded. Although this may seem as a flaw to the experimental design, we think that simultaneous variation of various aspects of the distribution of food is inevitable. Indeed, in all field experiments on the effect of the spatial distribution of food, several aspects of the distribution of food varied concurrently. We think that effects of the various aspects of food distribution can only be disentangled by performing a sequence of experiments that vary in the aspects of food distribution that are simultaneously manipulated. Meanwhile, we need to be careful in attribution treatment effects to specific aspects of the food distribution, and we need to take in account the subtle differences between experiments when comparing experiments.

COMPARISON WITH PREVIOUS WORK

Our results deviated from those of previous field experiments in that none of the previous experiments detected effects on the combination of response variables. To see whether we would have reported different main effects of the spatial distribution of food on each of the three response variables if we had not analysed our data using multivariate statistics, we performed ANOVAs on each of the three response variables (see APPENDIX A). Similarly, to study whether we would have drawn different conclusions regarding the correlations of the number of foragers with intake rate and amount of aggression and regarding the treatment effects after correction for variation in the number of foragers, we performed ANCOVAs on intake rate and amount of aggression, with the number of turnstones as a covariate (see APPENDIX B).

Based on the ANOVA test results we would have concluded that the distance between food pits had a significant main effect only on the number of turnstones on the experimental plot, and not on their intake rate, nor on the amount of their aggression. These findings would have corresponded to the results of Balph (1977) and Johnson et al. (2004, 2006), who also found the number of foragers to increase with plot size, and to the results of Johnson et al. (2006), who also reported plot size not to affect intake rate (Table 4.1). However, these results would have contradicted the general finding that amount of aggression decreases when food is spaced out. Based on the ANCOVA test results, we would have concluded that neither the distance between food pits nor the number of turnstones affected the intake rate of turnstones, and that both the distance between food pits and the number of turnstones affected the rate of intra-specific interactions. These results would have corresponded to those of Balph (1977), Johnson et al. (2004) and Cresswell (1997) in the treatment effects found after correction for variation in the number of foragers, but they would have differed from the results found by most other field experiments with regard to the correlations between the number of foragers with intake rate and amount of aggression (Table 4.1).

ADDED VALUE OF THE MULTIVARIATE ANALYSIS

The most obvious virtue of our multivariate analysis is that we were able to detect an effect of the distance between food clumps on the combination of the number of foragers and the amount of their aggression. This would not have been possible if we would have use univariate statistics, whether we had corrected for variation in the number of turnstones (ANCOVA) or not (ANOVA). The use of statistical tests, however, should not be made dependent on the experimental results only. Rather, tests should be selected on the basis of their match with the experimental design. The use of ANCOVAs to detect treatment effects in experiments in which forager abundance is a response variable, for instance, can not be justified because it violates several statistical assumptions (Sokal & Rohlf 1995). For instance, analysis of covariance assumes independence of the covariate and the response variable. That forager abundance would be independent of either intake rate or amount of aggression is not at all obvious. Feedback effects of the rate of intra-specific interactions on the number of turnstones, are, for instance, quite likely, given that the prime reason of aggression may be to lower the number of competitors. Similarly, analysis of covariance assumes that the covariate itself is not affected by the treatment. In most field experiments, the number of foragers was affected by the spatial distribution of food. In our experiment, the number of turnstones was even the response variable that was affected most strongly by the distance between food pits. Also, analysis of covariance assumes that the covariate is measured without error and that it is under control of the investigators. Such was clearly not the case for the number of turnstones and therefore the ANCOVA results may be biased.

Perhaps more importantly, however, the correct identification of the relationship between the various variables involved in the experiment helps to clarify the way in which the experimental results are to be interpreted. In experiments in which the number of foragers is an uncontrolled response variable, feedback effects of aggression and intake rate on the number of foragers are possible; in response to changes in amount of aggression and intake rate, foragers may adjust their distribution over food patches. Interpretation of the results of such experiments therefore requires considerations on patch choice decisions of the foragers. In experiments in which the number of foragers is experimentally controlled and thus a predictor variable, on the contrary, feedback effects of aggression and intake rate on the number of foragers are deliberately excluded and experimental results can be interpreted without considerations on patch choice. This implies that whether or not the number of foragers is experimentally controlled actually changes the research question that can be addressed. If the number of foragers is experimentally controlled, the effects the spatial distribution of food on intake rate and amount of aggression can be studied *per se*; if the number of foragers is not experimentally controlled it is the consequences of these effects on the distribution of foraging animals over patches of food and the resulting relationships between the number of foragers, intake rate and amount of aggression that can be studied. These are different things; even when the same effects of the spatial distribution of food on intake rate and amount of aggression *per se* operate in experiments in which the number of foragers is experimentally controlled as in experiments in which the number of foragers is not experimentally controlled, these two kinds of experiments can yield different results. One implication of this insight is that it can not easily be determined whether captivity affects the relationship between spatial clumping, aggression and intake rate. To just compare results of experiments on free-living foragers with results of experiments on captive foragers does not suffice, because these experiments differ in whether they used captive or free-living foragers *and* in whether or not they excluded patch choice decisions.

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APPENDIX 4A: UNIVARIATE ANALYSES

To study whether univariate analysis of each of the three response variables would have led to different conclusions than the multivariate analysis, we reanalyzed our data using ANOVAs on intake rate, on the rate of intra-specific interactions and on the number of turnstones, after log-transforming each of these three response variables. In these ANOVAs, inter-pit distance (X) was included as a (categorical) treatment factor, and triplet as a (categorical) block factor. To facilitate comparison of conclusions with conclusions drawn in the main text, we used a 0.01 significance level in all tests in both appendices.

We found that the distance between food pits had a significant effect on the number of turnstones on the experimental plots ($F_{2,17} = 66.5$, $P < 0.01$), but not on the intake rate of these turnstones ($F_{2,17} = 3.8$, $P = 0.04$), nor on the amount of their aggressive behaviour ($F_{2,17} = 3.2$, $P = 0.07$). The largest main effect on the number of turnstones was between the two smallest inter-pit distances; when food pits were 20 cm apart, more than three times as many turnstones were attracted by the same number of food pits and the same amount of food than when food pits were 10 cm apart (Figure 4.1G). The intake rate of turnstones, measured as the percentage of time that focal turnstones spent digging, increased with the distances between food pits, but treatment averages did not differ significantly (Figure 4.1E). Similarly, the rate of intra-specific interactions was lower when food pits were 30 cm apart than when they were 10 or 20 cm apart, but the overlap between treatments was substantial, and this effect was not statistically significant (Figure 4.1F). The block factor triplet did not explain variation in any of these three responses (statistics not shown; Figs 1E, F and G).

APPENDIX 4B: ANALYSES OF COVARIANCE

To study whether a univariate analysis that treats the number of foragers as a predictor variable would have led to different conclusions than the multivariate analysis presented in this paper, we reanalyzed our data using ANCOVAs on log-transformed intake rate and log-transformed rate of intra-specific interactions. In these ANCOVAs, inter-pit distance (X) was included as a (categorical) treatment factor, triplet as a (categorical) block factor, and the number of turnstones as a covariate (C). Additionally, the interaction between the treatment factor and the covariate (X·C) was included.

With regard to intake rate, we found the slope of the regression line of intake rate on the number of turnstones to be the same for all three inter-pit distances (as indicated by the non-significance of the interaction term (X·C): $F_{2,14} = 1.7$, $P = 0.22$). After removing the interaction term from the model, we found that intake rate actually did not depend on the number of turnstones (as indicated by the non-significance of the covariate (C): $F_{1,16} = 2.3$, $P = 0.15$). After removing the covariate from the model (which reduced the model to a simple ANOVA) we found that the distance between food pits did not significantly affect intake rate either (X: $F_{2,17} = 3.8$, $P = 0.04$). Based on this analysis, we would conclude that intake rate was about the same at each inter-pit distance and that variation in intake rate was independent of variation in the number of turnstones.

Performing the same analysis on the rate of intra-specific interactions, we found the slope of the regression line of amount of aggression on the number of turnstones to be the same for all three inter-pit distances (X·C: $F_{2,14} = 0.8$, $P = 0.48$). After removing the interaction term from the model, we found that the rate of intra-specific interactions was significantly affected by both the distance between food pits (X: $F_{2,16} = 9.3$, $P < 0.01$) and the number of turnstones (C: $F_{1,16} = 9.3$, $P < 0.01$). Post hoc comparisons (Bonferroni method) revealed that it was the largest inter-pit distance that differed significantly from the two smaller ones (1 vs 2: -0.49, $P = 0.08$; 1 vs 3: -0.85, $P < 0.01$; 2 vs 3: -0.36, $P < 0.01$). Based on this analysis we would conclude that inter-pit distance significantly affected the turnstones' amount of aggressive behaviour, as did the number of turnstones.

AFTERTHOUGHTS ON CHAPTER 4

When forager density is not under experimental control, foragers may adjust their distribution over food patches. We argued therefore that in such studies the density of foragers should be treated as an uncontrolled response variable, just as intake rate and the amount of aggression are. Only in experiments in which forager density is experimentally controlled, effects of forager density on intake rate can be studied *per se*. Here, I present three ideas that follow on this insight. First, I discuss how the experiment presented in chapter 4 can be interpreted as a patch choice experiment. Second, I discuss the relationship between the generalized functional response and the aggregative response. Third, I discuss the extent to which the generalized functional response can be determined through observations on foraging animals that are free to choice among food patches.

A SEQUENTIAL PATCH CHOICE EXPERIMENT

The general approach to study patch choice decisions is to provided several patches to one or more foraging animals simultaneously (for a review: see Tregenza, 1995). Our experiment was not set up in such a way. Instead, in each trial, we provided free-living birds with a single experimental food patch. This set-up can be interpreted as a 'simultaneous' patch choice experiment in which foragers could choose between the experimental patch and 'the environment'. Interpreted in this way, our experiment would make a rather weak patch choice experiment, because we have little quantitative information about the quality of the environment. However, there may be another, more fruitful way of looking at our experiment.

To minimize variation due to measurements at different moments in time, we performed trials in groups of three ('triplets'), whereby each treatment level of the factor inter-pit distance featured once in each triplet. Under the assumption that the environment was constant throughout triplets, the within-triplet response of the free-living birds to the three treatment levels can be interpreted in terms of patch choice. Such an interpretation would render our experiment as a *sequential* patch choice experiment. Let me make this clear by comparing predictions of the ideal-free-distribution model with our experimental results.

In its original form (Fretwell and Lucas 1970), the ideal-free-distribution model predicts patch quality to affect the number of foragers, but not their intake rate; more foragers should gather in the better patches, but as a consequence the intake rate of all foragers should be the same (no predictions are made regarding the amount of aggression). If the intrinsic quality of patches is assumed to increase with the extent to which food is spaced out, these predictions of the ideal-free-distribution model would imply that the number of turnstones on the experimental plots should be higher when food is more spaced out, whereas the time spent digging (our measure of intake rate) should be the same at each of the three inter-pit distances. Thus, interpreted as a sequential patch choice experiment, our data would actually match the predictions of the ideal-free-distribution model. Although this match should be treated with caution[1], I think the example nicely shows how our experiment can be interpreted as a sequential patch choice experiment.

Although we never designed our experiment for this reason, our design may have one advantage over simultaneous patch choice experiments. For foragers it may be easier to distinguish between one experimental patch and the environment than between two (or more) experimental patches, because foragers are presumably more familiar with their environment than with experimental patches, and because experimental food patches usually differ less from each other than from the environment. The downside of this is that a difference in knowledge of the environment and of experimental patches introduces the question of how animals cope with risk.

RELATING RESPONSES

The notion that the interpretation of experiments as studying the direct causal effects of forager density or as studying the consequences of such effects depends on whether or not forager density is experimentally controlled, made me reconsider the relationship between the generalized functional response and the aggregative response. First, I thought about these two responses as quite distinct. Now I have come to think of them as intimately related. In the absence of patch choice, that is, when animals are forced to forage on a specific patch, there is but one relationship; the generalized functional response. As I said in the General introduction, this response describes the relationship between food density, forager density and intake rate. To emphasis the fact that it captures the functional response and what has been referred to as the interference response, I think it may be illuminating to visualize this relationship in three dimensions, together with its two-dimensional projections (Figure 4.5): the functional response and the interference response can be found by projecting the 3-d relationship (Figure 4.5A) on the food density – intake rate plane (Figure 4.5B) and the forager density – intake rate plane (Figure 4.5C), respectively.

The aggregative response cannot be derived from the generalized functional response directly. To do so requires the use of a model that specifies how animals distribute themselves over food patches (a ‘distribution model’). What this model does, is to specify what combinations of food density, forager density and intake rate will be realized. The ideal-free-distribution model, for instance, predicts that at any moment in time, animals will achieve the same intake rate at different combinations of food density and forager density, that is, all observations will lie on lines of equal intake rate (‘isoclines’; Figure 4.6A-C). Once the way foraging animals distribute themselves over food patches has been speci-

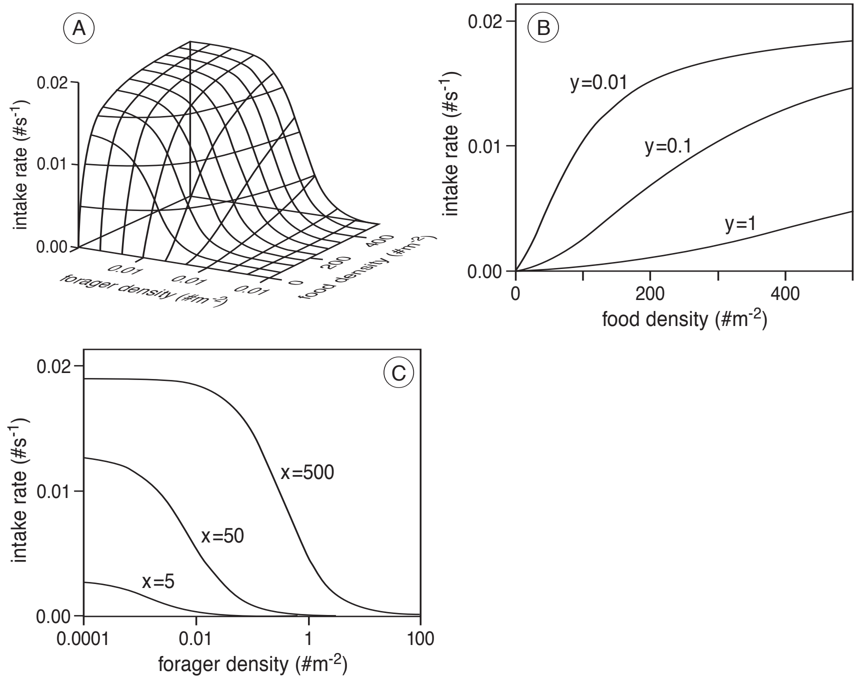

Figure 4.5. Example of a generalized functional response curve, that is, the relationship between food density, forager density and intake rate (A). This response extends the well-known relationship between food density and intake rate – the functional response (B) – by accounting for a negative effect of forager density on intake rate (C). The latter two relationships can visually be derived from the generalized functional response by projecting lines of constant forager density *y* and food density *x* on the food density - intake rate and the forager density – intake rate plane, respectively. Note that forager density is plotted on a logarithmic scale.

fied, the aggregative response can be found visually by projecting the generalized functional response on the food density – forager density plane (Figure 4.6D). How the aggregative response can be derived from the generalized functional response analytically was explained by van der Meer and Ens (1997).

DETERMINING THE GENERALIZED FUNCTIONAL RESPONSE

One implication of the above line of thinking is that the generalized functional response can be determined both in the absence and in the presence of patch choice. To see that this is the case, it should be realized that all observations on food density, forager density and intake rate in multi-patch situations (i.e., in the presence of patch choice) lie on the generalized functional response (Figure 4.6). This implies that by collecting enough data of animals foraging in multi-patch situations, it should be possible to determine the generalized functional

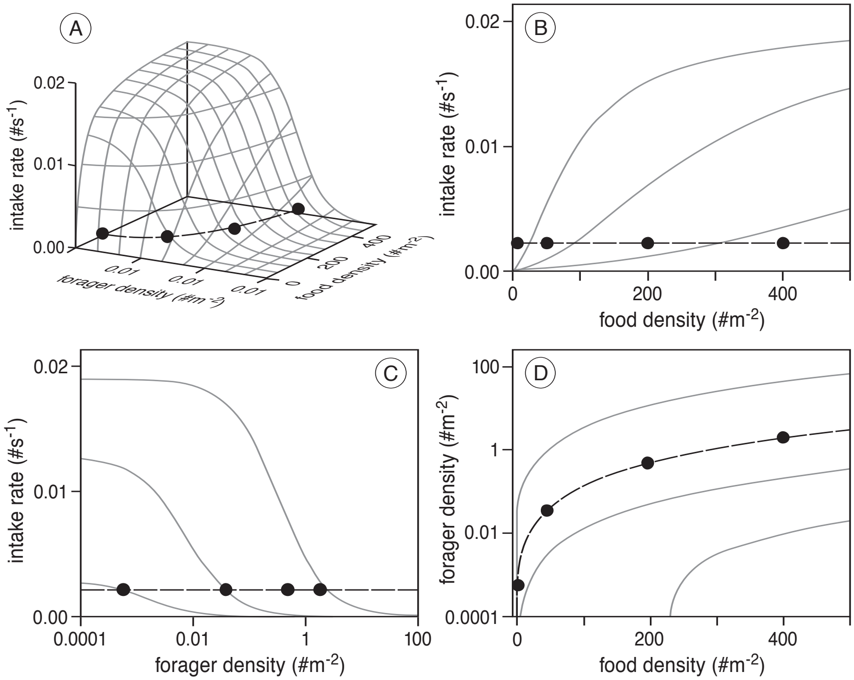

Figure 4.6. Predictions (black dots) of the realized combinations of food density, forager density and intake rate in a four-patch system. These predictions are generated from the combination of a generalized functional response (thin grey lines) and the ideal-free-distribution model. At any moment in time, only a very limited part of the underlying generalized functional response is realized; all observations on intake rate lie on a straight line. Panels A-C as in Figure 4.6. Panel D give the aggregative response, i.e. the realized combinations of food density and forager density. The aggregative response can be derived from the realized generalized functional response (A) by projecting isoclines of intake rate on the food density - forager density plane (D). Note that forager density is plotted on a logarithmic scale.

response. Hence, whether observations are gathered in the absence or presence of patch choice does not determine whether or not the generalized functional response can be determined; that can be done either way. What differs between the two types of observations is the ease with which they allow for determination of this relationship.

Observations on foraging animals that cannot choose between food patches provide the most straightforward way to determine the generalized functional response, because such observations are not affected by feedback effects of aggression and/or intake rate on forager density. This implies that intake rate can be measured at any experimentally determined combination of food density and forager density, and thus that the generalized functional response can easily be determined for the whole range of relevant food densities and forager densities. In a multi-patch situation, on the contrary, foraging animals can choose between food patches, and hence feedback effects may come into play; foragers may adjust their distribution in response to, or even in anticipation of, interference effects. As a consequence, combinations of food density and forager density realized in a multi-patch system will not be random; instead, they will be inter-correlated (i.e., there will be collinearity). Certain combinations of food density and foragers density will feature less often than other combinations, and some combinations may not be encountered at all. For instance, of high forager densities on patches with a low food density, or observations of low forager densities on patches with high food density will not often be realized. This implies that observations gathered from a multi-patch system may not easily reveal the entire generalized functional response. In fact, the may reveal only a very small part of it. Figure 4.6 illustrates the potential severity of this idea: according to the ideal-free-distribution model, at any moment in time, all observations on food density, forager density and intake rate will lie on an isocline of intake rate. This isocline lies on the generalized functional response, but it reveals only a very limited part of it. Of course, a larger part of the generalized functional response may be revealed by collecting observations over a longer period of time. However, doing so may increase the risk of confounding effects of uncontrolled factors. Thus, the generalized functional response can be determined from observation of animals foraging in a multi-patch situation, but this involves two risks. Observations may reveal only a small part of the generalized functional response, so that interference effects are likely to be underestimated, and they may be confounded by effects of uncontrolled factors.

NOTE

[1] We never designed the experiment to study patch choice decisions, and therefore too much emphasis on a match between experimental results and the predictions of the ideal-free-distribution model would be opportunistic. Moreover, the assumption that patch quality increases with inter-pit distance is not obvious. As is clear from chapters 3 and 5, the relationship between the distribution of food and the intrinsic quality of patches may well differ for birds of different dominance status. Also, the failure to detect an effect on the time spent digging (our measure of intake rate) may indeed be actual (as predicted by the ideal-free-distribution model), but it may also have been due to a lack of statistical power.

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CHAPTER 5

FOOD DIVISIBILITY AND INTERFERENCE COMPETITION AMONG CAPTIVE RUDDY TURNSTONES (*ARENARIA INTERPRES*)

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SUBMITTED TO ANIMAL BEHAVIOUR

ABSTRACT

Interference competition among foraging animals arises from agonistic interactions between foragers. Interactions can concern single food items but also clumps of food. Food clumps consist of multiple food items, and are therefore easier to divide between foragers than food items. Theoretical studies indicate that differences in divisibility can be essential to the interference process. Empirically, however, little is known about effects of resource divisibility on interference competition. Therefore, we performed an experiment with captive ruddy turnstones (*Arenaria interpres*). Turnstones foraged either alone or together with a competitor. We offered food at two so-called food pits and varied the divisibility of food in these pits by burying a fixed number of food items either in several layers (divisible) or in a single layer (indivisible). Additionally, we varied the distance between the food pits. We accounted for differences in the social dominance status of foragers by using pairs of foragers as our experimental unit; each pair had both a dominant and a subordinate member. We found a strong asymmetry in the intake of birds of different dominance status. The strength of this asymmetry depended on both the divisibility of food and on the distance between food pits. Only when food was divisible did subordinate foragers get a finder's advantage; only when food pits were close to each other could dominant foragers monopolize food pits. These findings imply that to understand and predict interference competition we need to consider both the detailed characteristics of resources, and the determinants of dominance status.

INTRODUCTION

Interference competition among foraging animals is the negative effect of forager density on intake rate that results from interactions between foragers (Miller 1967). There is a variety of ways in which foraging animals can interact, but most attention has been paid to agonistic interactions over food, probably because such interactions are the most obvious. Mechanistic studies of interference competition have concentrated on agonistic interactions that concern single food items ('kleptoparasitism': Sutherland 1996; Krause & Ruxton 2002). In some predator-prey systems, however, interactions over food items are not possible, because the handling time of food items is so short that a food item is ingested before it can be stolen. This may, for instance, be the case for geese foraging on grass (e.g., Black & Owen 1989) and for passerines foraging on seeds (e.g., Barnard & Sibly 1981). To explain interference competition in such systems, it has repeatedly been suggested that interference competition may also arise from agonistic interactions over clumps of food (for references: see Vahl et al. 2005a).

We are interested in the question as to whether it matters what is at stake in agonistic interactions, that is, whether food items and food clumps differ in a way essential to how we think about interference competition. By definition, food clumps differ from food items in that they are composed of multiple items. This difference may be essential to the interference process, because it affects the extent to which food can be divided over multiple foragers, that is, the 'divisibility' of food.

Few theoretical studies have invested the extent to which the divisibility of resources affects the interference process. Most models assume that resources are either all indivisible (e.g., Hawk-Dove games) or all divisible (e.g., Producer -Scrounger models), but whether or not resource divisibility affects the interference process is generally not studied. Recently, Broom & Ruxton (2003) used a Hawk-Dove game to address the effect of resource divisibility; they compared a model in which resources were consumed throughout the handling process (the 'apple model') with a model in which resources were consumed at the end of the handling process (the 'orange model'). The extent to which resources can be divided differs between these two models; in the apple model each handler gets a proportional part of the resource, whereas in the orange model the whole reward goes to a single (the last) handler. This difference in resource divisibility profoundly affected the extent to which foragers were found to suffer from interference competition: while the relationship between aggressiveness and forager density was positive in the apple model, this relationship was negative in the orange model.

Empirically, little is known of the effects of resource divisibility on interference competition. Several studies have shown that the spatial clumping of food (i.e., the distribution of resources) can affect agonistic behaviour and intake rate (for a review: see Vahl et al. 2005a); when resources are more clumped in space they can be monopolized more easily, so that there is less division of the resources. Only Elgar (1986) was able to show directly that the divisibility of a resource (and not its distribution) affected the social behaviour of foraging animals: when bread was offered to house sparrows (*Passer domesticus*), the same amount of bread brought about more chirrup calls (and thus more joiners) when it was offered as (divisible) crumbs rather than as (indivisible) slices.

To empirically study how resource divisibility affects the interference process, we performed two runs of the same experiment with captive ruddy turnstones (*Arenaria interpres*). We varied the divisibility of food in two so-called food pits by burying a fixed number of food items either in several layers (divisible) or in a single layer (indivisible). We composed food pits in such a way that the handling time and the reward was the same for divisible and indivisible food pits; we only varied the relationship between handling time and reward. To study the effect of forager density, we systematically compared the behaviour and the food intake of focal turnstones that foraged alone or with a competitor. We accounted for variation in the social dominance status of foragers by using pairs of birds as the basic unit of our experiment; each pair had both a dominant and a subordinate member. Additionally, we varied the distance between the two food pits, because a previous experiment indicated that inter-pit distance can be of prime importance; it may determine the extent to which resources can be monopolized, as we found in a field experiment on free-living turnstones (Vahl et al. submitted).

METHODS

SUBJECTS

Thirty turnstones were caught with mist nets on an intertidal mudflat in the eastern Dutch Wadden Sea (53°29′N, 6°15′E) on 15 October 2003. We housed these birds in the indoor experimental shorebird facility of NIOZ, Texel. Twenty-two individuals were selected to participate in pilot trials in which we determined the dominance hierarchy among the turnstones (8 to 12 March). Anticipating the experimental design, we selected sixteen of these birds and grouped them in eight pairs of two. To make these sixteen birds individually recognizable, we bleached a small (approximately 25 x 25 mm) area of their back feathers, using commercial hair bleach. After an extensive series of pilot trials (15 March to 19 April), we conducted the experiment from 20 to 29 April, using all eight pairs. As one of the birds died during this experiment, we decided to perform the experiment a second time (3 to 6 May), using a selection of four of the seven remaining pairs. All selections were done with the use of a random number generator. Non-experimental and experimental turnstones were released on an intertidal mudflat in the Wadden Sea on 22 April and 12 May, respectively. At this time of the year, weather conditions are mild, food is ample, and there are plenty of turnstones around to join in migration to the breeding areas. Catching, housing and releasing occurred according to Dutch legislation (Dutch bird ringing centre license number 351 and Dutch animal ethics committee protocol 2004.01, respectively).

HOUSING

In the experimental facility the turnstones had two roosting aviaries (measuring 4.3 x 1.2 m and 3.0 m high) and an experimental room (7 x 7 m and 3.5 m high) at their disposal. A thin film of running seawater continuously covered the floors of the roosting aviaries to keep the feet of the birds salty and wet, and a tray of running freshwater for drinking and bathing was always present. On days on which no trials were performed trout feeding pellets were present *ad libitum*. The floor of the experimental room was covered by a 30-cm layer of sand, to mimic one of the natural habitats of turnstones. The indoor environment was approximately constant with respect to air temperature (range: 12.3 – 19.0 °C). Moonlight-mimicking lights illuminated the aviaries between 1900 and 0700 h. A compact disc containing sea sounds (‘Ocean Surf’; Solitudes Ltd., Toronto, Canada) was played continuously to buffer sudden noises from outside the aviaries.

PRE-EXPERIMENTAL TREATMENT

On the first five pilot days, we determined the dominance hierarchy among the turnstones (for methods: see Vahl et al. 2005a) on the basis of 930 agonistic interactions, which we collected in 36 trials. Interactions generally encompassed threat or attack behaviour of one individual and avoid or escape behaviour of another individual. Only occasionally these interactions would involve physical contact (one bird pecking the other); in no instance did such contact lead to visual physical harm. Although we would have been prepared to intervene when either a bird was physically harmed, or when it was being exhausted by its opponent, such intervention was not required in any of the trials.

Knowledge of the dominancy hierarchy enabled us to determine the relative rank of pair members independently of the experimental trials. As we paired the birds at random, the difference in absolute dominance position of pair members varied between pairs. Regardless of the difference in absolute dominance position, however, all pairs contained one (dominant) individual that consistently dominated its (subordinate) pair member. We used this relative dominance status of the pair members to account for variation in dominance, treating dominance status as a relative quality rather than as an (absolute) individual attribute (Francis 1988; Piper 1997).

In 24 other pilot days, we familiarized the birds with the experimental set-up. On each of these pilot days, all birds performed one trial, either alone, or together with its pair member.

EXPERIMENTAL SET-UP

On experimental days, we flooded the experimental room with seawater, such that the only places remaining dry were two elevated platforms (1 x 1 m each, located at constant positions, 3 m apart from each other). One of these platforms served as foraging patch; here we placed a tray (1 x 1 m and 10 cm deep) filled with sand. The other platform served as refuge; on this platform we only placed two layers of gravel tiles, to give both platforms the same height. Behaviour on the foraging patch was recorded using two digital video cameras (Sony dcr-trv900e). One camera, positioned 1.75 m from the foraging patch, was set fixed to record the whole patch; the other camera, positioned 6 m from the foraging patch, was used to zoom in the on the forager(s) as much as possible.

The foraging patch always contained two identical food pits, which were positioned either 5 cm ('close') or 63 cm ('far') from each other. To manipulate the divisibility of the food in the pits while keeping all other aspects constant, the food pits had a very specific, standardized composition (Figure 5.1). Food pits contained five defrosted mealworms (Tenebrio molitor) of approximately constant length (mean ± SD: 23.5 ± 1.7 mm [estimated on the basis of 50 measurements]). Between trials, we varied the distribution of these mealworms within the two food pits; mealworms were positioned either in a clump, just below the deepest ring ('clustered'), or apart from each other, one below each ring ('layered'). We used rings to make the handling time for mealworm in the layered condition approximately constant; for the same reason we varied the amount of sand between rings (Figure 5.1). This specific set-up ensured that both the number of mealworms (the total reward), and the time to find all mealworms (the total handling time) was the same for clustered food pits as for layered food pits. What varied was the relationship between handling time and reward (the reward function); when the within-pit food distribution was layered, reward cumulated throughout the handling process, whereas when it was clustered, all reward was received at the end of the handling process.

In composing the food pits, we were inspired by the foraging situation of turnstones foraging in Delaware Bay, U.S.A., where turnstones regularly have to dig for their main food source (Sullivan 1986; Vahl et al. submitted). Although we are not aware of any comparable foraging situation along the East Atlantic flyway, the experimental birds learned to dig for their food within days. In doing so, they did not seem to be bothered by the glass cups. Moreover, it took only few days before most of the experimental birds could skilfully remove the metal rings out of the cups by putting their bill in the hole of the metal rings

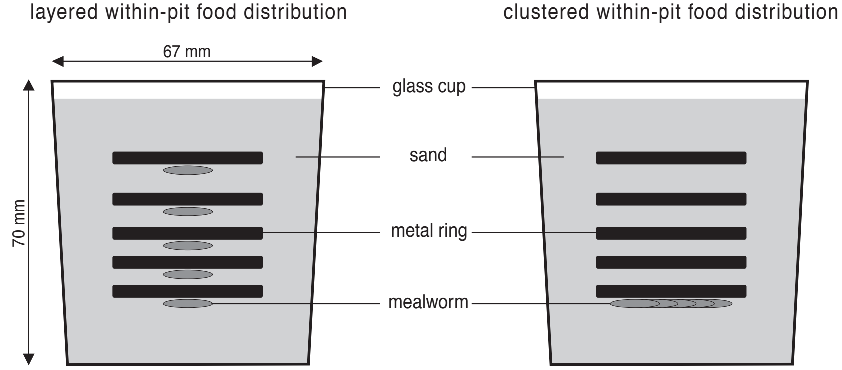

Figure 5.1. Schematic representation of two food pits. Each food pit consisted of a glass cup, buried in the sediment and filled with a constant amount of sand (12 spoons of 12 cm3); the upper 4 mm of each glass cup remained empty. Each cup contained five metal rings (inner and outer diameter: 13 and 36 mm, respectively), which were positioned at fixed depths, separated from each other by a fixed amount of sand (4,1,1,1,2,3, spoons from the bottom upwards; this distribution kept the amount of sand that had to be removed per metal ring effectively constant, given that some sand covering the higher rings fell on the lower rings). Each cup contained five mealworms, which were either positioned apart from each other, one below each ring (layered; left drawing), or in a cluster, just below the deepest ring (clustered; right drawing).

and then tossing them up. The turnstones were keen to eat the mealworms, even though mealworms are not part of their natural diet (e.g., Fuller 2003).

EXPERIMENTAL PROCEDURE

In the first run of the experiment, we deprived the birds of food from 1500 h and tested them between 0900 and 1300 h on the following day. After all trials had been performed, we weighed all birds and we visually checked their condition. Between 1300 and 1500 h, we provided trout feeding pellets *ad libitum* as well as some extra mealworms. The length of the deprivation period and the amount of extra mealworms were chosen such that the birds were maximally motivated to forage in the experimental trials, maintained good condition and stayed within their natural weight range (84 – 190 g; del Hoyo et al. 1996).

On experimental days, members of the same pair together awaited trials in boxes (measuring 50 x 35 cm and 25 cm high) that were placed in a dark room to minimize stress. At the start of each trial, we transferred either one ('competitor absent') or two ('competitor present') specific birds to one of the roosting aviaries. After opening a sliding door, we attracted the birds into the experimental room by dimming the lights in the roosting aviary whilst lighting the experimental room. Subjects readily flew to the experimental platform and started to dig in the food pits within seconds of the sliding doors being opened.

The trials started at the moment the first bird began to forage, and then lasted till 30 s after the tenth mealworm had been consumed, or after 600 s had passed, whichever came first. After each of the birds had performed its trial, we put all birds together in the experimental room and the two roosting aviaries, with sliding doors open and water level low (so that birds could also use the sandy spaces between the raised platforms).

In the second run of the experiment the same procedure was followed, but now there were two experimental sessions per day: one between 0900 and 1200 h and the other between 1300 and 1500 h. In this run of the experiment birds were deprived of food from 1700 h on the day preceding an experimental day.

VIDEO ANALYSIS AND RECORDED BEHAVIOUR

The same two observers (WKV & SAK) examined all trials together, using The Observer 4.1 Event Recorder (Noldus Information Technology, Wageningen, The Netherlands). Per trial, we recorded all prey captures within 600 s, noting both food pit and finder. For the first 120 s, we additionally recorded in detail the whereabouts of the foragers (i.e., whether they were on the one food pit, on the other, on the foraging platform or elsewhere), as well as their behaviour. Most importantly, we determined the amount of time the turnstones were ‘interacting’, that is, either ‘fighting’ (both foragers behave aggressively), ‘threatening’ (the aggressor does not approach its opponent), ‘attacking’ (the aggressor does move towards its opponent), ‘avoiding’ (in response to a threat) or ‘escaping’ (in response to being attacked).

EXPERIMENTAL DESIGN AND STATISTICAL ANALYSIS

We studied the effect of four fixed factors: Competitor presence (absent [0] or present [1]), Within-pit food distribution (both food pits clustered or both food pits layered), Inter-pit distance (close or far) and Dominance status (dominant or subordinate). As it is difficult to assign both levels of the factor Dominance status to an individual bird, we decided to use pairs of birds, rather than individual birds, as the basic unit of our experiment. We estimated treatment effects that were independent of the factor Dominance status by running a test on the sum of the response of pair members (which yields identical results as using the average response), and we estimated treatment effects that were dependent of the factor Dominance status by running the same test on the difference in response of pair members. This approach is identical to that used in a split-plot design with Dominance status as a within-plot factor.

In both runs of the experiment, we accounted for effects of the random block factors Bird pair, and Experimental day by using a Latin square design (Fisher & Yates 1963) to distribute the treatment combinations (of Competitor presence, Within-pit food distribution, and Inter-pit distance) over trials. At the ‘competitor absent' treatments, the two members of a pair performed a trial separately, one directly after the other. In the first run of the experiment, we had eight bird pairs and eight treatment combinations (2 x 2 x 2), so that we could use an 8 x 8 Latin square design. In the second run of the experiment, we could no longer use eight bird pairs (one of the birds had died). Therefore, we decided to use a 4 x 4 Latin square design to distribute the four treatment combinations of Competitor presence and Within-pit food distribution over four bird pairs and four experimental days. To additionally estimate the effect of Inter-pit distance, we introduced morning and afternoon sessions. Each bird pair performed the same trial twice on a single day, once at each inter-pit distance; the two levels of Inter-pit distance were assigned randomly to either the morning or the afternoon session. Thus, to study effects of Inter-pit distance in the second run of the experiment, we used a split-plot design with Experimental day and Inter-pit distance as whole-plot factors.

We studied treatment effects on trial duration (s), intake (#) and intake rate (#s^{-1}), whereby we defined intake as the number of mealworms swallowed in a trial, and intake rate as the ratio of intake to trial duration. To detect the mechanisms underlying any effects on trial duration, intake and intake rate, we additionally studied effects on the time spent on food pits (%), and the time spent interacting (%). These latter two responses are expressed as a percentage of the trial duration (censored at 120 s), whereby time spent on empty food pits is excluded.

MISSING VALUES AND THEIR TREATMENT

As one of the experimental birds died in the middle of the first run of the experiment, we had four missing values: three at the 'competitor absent' treatment and one at the 'competitor present' treatment. Therefore, we had in total 60 rather than 64 paired observations on the 8 bird pairs. Following Yates (1933), we replaced these missing values and we adjusted the degrees of freedom in all tests correspondingly. All 32 paired observations of the second run of the experiment were successful.

Foragers were not able to find all ten mealworms within 600 s in 11 trials. In presenting treatment effects on trial duration, we first verbally report on the 11 censored trials, and we then present the data and statistics on the uncensored trials. In calculating intake rate we did not make this distinction.

DATA TRANSFORMATION AND HYPOTHESIS TESTING

We analysed both runs of the experiment using the GLM procedure in SYSTAT 10 (SPSS Inc., Chicago, IL). We analysed the first run of the experiment according to the standard Latin square design. The second run of the experiment was analysed according to the standard split-plot design, with Experimental days and Inter-pit distance as whole plot factors.

We assumed that the treatment factors had a multiplicative effect on trial duration, intake and intake rate. Because general linear models assume treatment effects to interact in an additive way, we log-transformed all observations on these three response variables. To avoid taking logarithms of zero, we added the values of 0.12 and 0.25 to observations on the number of mealworms swallowed in the first and second run of the experiment, respectively; these specific values were chosen because they minimized the effect of unusual observations (Berry 1987). As time spent on food pits and time spent interacting both comprise percentages, we applied a Freeman and Tukey's arcsine transformation to all observations on these two responses; more specifically, we applied the slightly modified version given by Zar (1996). For all five response variables, we first performed the transformation, and we then calculated the sum and the difference of observations on dominant and subordinate foragers. Visually inspection of probability plots (Miller 1997) indicated that model residuals of intake, time spent on food pits and time spent interacting were not normally distributed, not even after transformation. Therefore, we repeated the analyses on these three response variables using a randomisation test to study the likelihood of our data (Manly 1997). As randomisation results were almost identical to the GLM results, only the latter are presented.

RESULTS

TRIAL DURATION

Foragers were not able to find all ten mealworms within 600 s in ten trials (16.7 %) of the first run of the experiment and in one trial (3.1 %) of the second run of the experiment. The foragers that did not find ten prey items were all foraging alone; most of them were subordinate individuals (10 out of the 11 cases), foraging at food pits that were far apart (7 out of 11 cases) and in which food items were clustered (8 out of 11 cases).

Trials in which all ten food items were found generally lasted longer for birds in the first run of the experiment than for birds in the second run of the experiment (X ± SD: 151.5 ± 152.3 s, N = 118 versus 109.9 ± 119.3 s, N = 63; Figure 5.2). In both runs of the experiment, birds foraging alone needed more time to find all ten mealworms than birds foraging together with a competitor, and when foraging alone, subordinate birds needed more time than dominant birds. Statistically, this result is indicated by the interaction between Competitor presence and Dominance status (A x D), which was significant in both runs of the experiment (Table 5.1 & 5.2). These observations suggest that the birds became more skilful throughout the experiment, and that subordinate birds were less skilled in finding the food than dominant individuals, even when foraging alone.

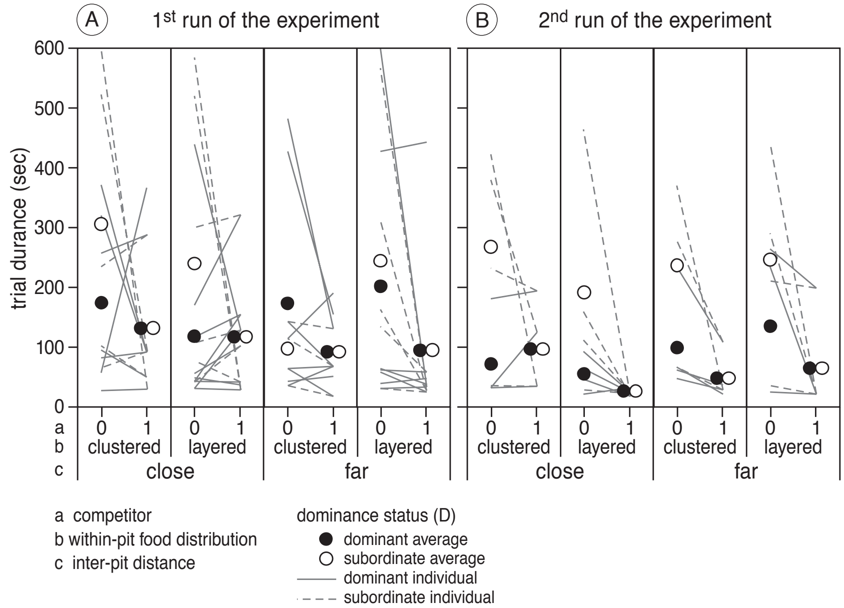

Figure 5.2. The duration of trials in which all ten food items were found in the first (a) and the second (b) run of the experiment. Each graph contains four compartments, one for each combination of the factors Within-pit food distribution and Inter-pit distance, as indicated by the labels on the x-axis. Each compartment shows the effect of the absence (0) or presence (1) of a competitor on the duration of trials; dots represent averages per treatment combination. Thin grey lines connect observations on the same individual, but only within compartments. Note that by definition, trials last as long for subordinate birds as for dominant birds when they forage together (i.e., at the 'Competitor presence 1' condition).

INTAKE

In both runs of the experiment, birds foraging together with a competitor achieved a lower intake than birds that foraged alone (Figure 5.3). The strength of this competition effect differed markedly between dominant and subordinate individuals; under most conditions dominant foragers got almost as many of the food items when foraging in the presence of a competitor as when foraging alone, whereas subordinate birds found only few of the food items when foraging together with a competitor. This effect was especially apparent in the second run of the experiment. How much subordinate birds suffered from competition depended on the distribution of food within food pits and on the distance between food pits. In the first run of the experiment subordinate foragers got more mealworms when the within-pit food distribution was layered than when it was clustered, and also when food pits were placed far apart rather than close to each other. In the second run of the experiment, subordinate birds foraging

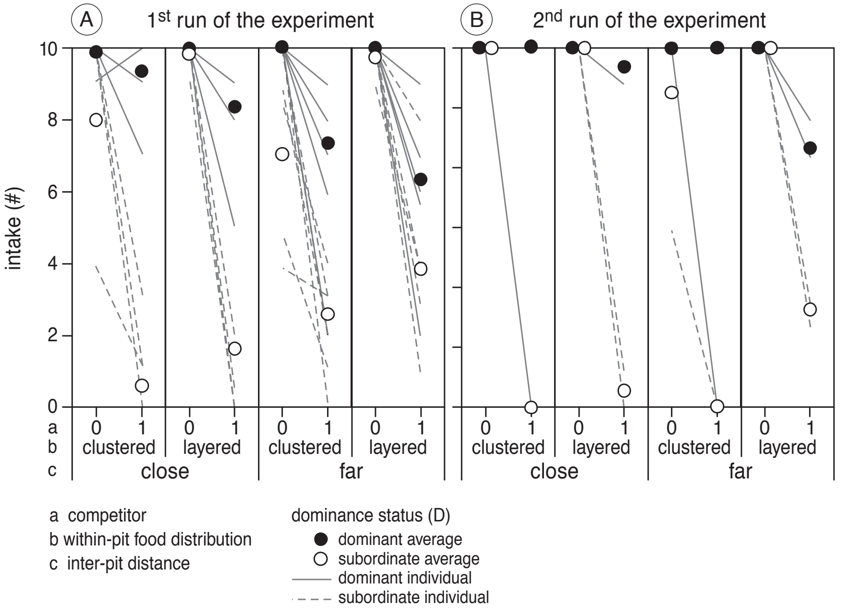

Figure 5.3. The intake of the turnstones in the first (a) and the second (b) run of the experiment. Like in Figure 5.2, each graph contains four compartments, as indicated by the labels on the x-axis. Each compartment shows the effect of the absence (0) or presence (1) of a competitor on intake; dots represent averages per treatment combination. Thin grey lines connect observations on the same individual within each compartment.

in the presence of a competitor only got some mealworms when food pits were far apart and when the within-pit food distribution was layered. In line with these observations, there was a significant interaction between the Within-pit food distribution and Dominance status (B x D), and between Competitor presence, Inter-pit distance and Dominance status (A x C x D) in the first run of the experiment, and between all four factors (A x B x C x D) in the second run of the experiment (Table 5.1 & 5.2).

INTAKE RATE

Effects on intake rate, the ratio of intake to trial duration, were less straightforward than effects on either intake or trial duration separately (Figure 5.4); treatment effects on intake rate different between the two runs of the experiment and effects varied much between bird pairs. In the first run of the experiment, dominant foragers on average achieved the same intake rate when forag-

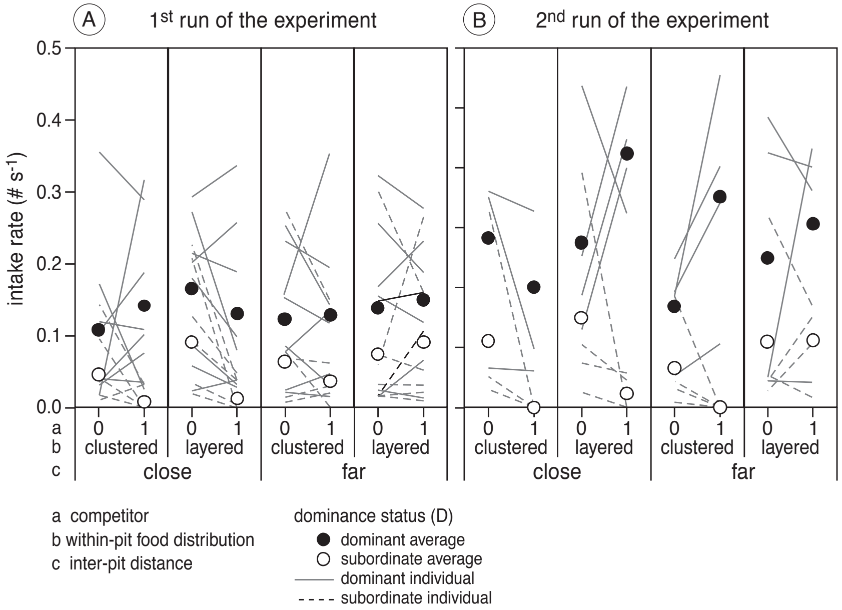

Figure 5.4. The intake rate of the turnstones in the first (a) and the second (b) run of the experiment. Like in Figure 5.2, each graph contains four compartments, as indicated by the labels on the x-axis. Each compartment shows the effect of the absence (0) or presence (1) of a competitor on intake rate; dots represent averages per treatment combination. Thin grey lines connect observations on the same individual within each compartment.

ing alone as when foraging together with a competitor, whereas subordinate birds the presence achieved a lower intake rate when foraging with a competitor, especially when food pits were close to each other. In the second run of the experiment, effects on the intake rate of subordinate birds were comparable to those found in the first run of the experiment, but effects on the intake rate of dominant foragers were quite different: dominant birds generally achieved a higher intake rate when foraging together with a competitor than when foraging alone, but this effect depended much on the inter-pit distance and the within-pit food distribution, and it varied strongly between birds. Statistically, these findings are reflected in a significant interaction between Competitor presence, Inter-pit distance and Dominance status (A x C x D) in the first run of the experiment, and in significant interactions between Competitor presence and Inter-pit distance (A x C), and between Competitor presence, Within-pit food distribution and Dominance status (A x B x D) in the second run of the experiment (Table 5.1 & 5.2).

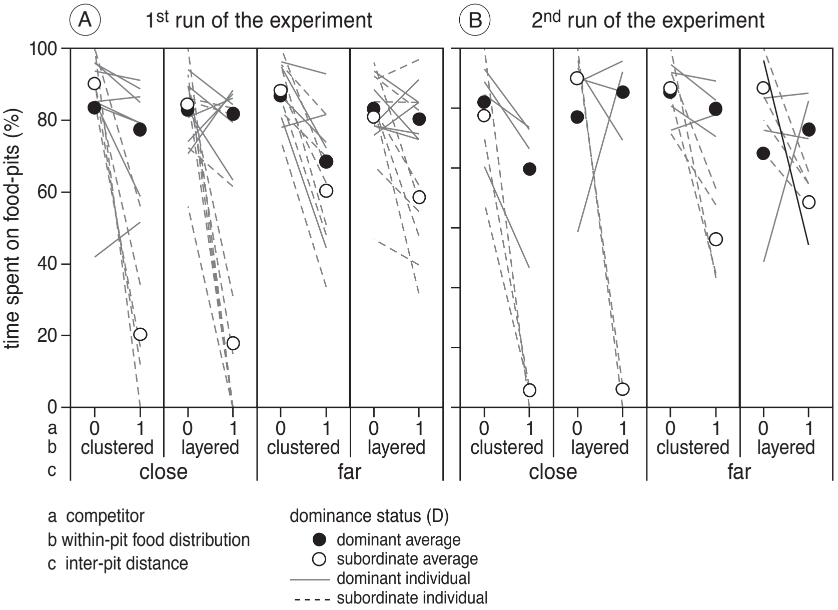

Figure 5.5. The time spent on food pits in the first (a) and the second (b) run of the experiment. Like in Figure 5.2, each graph contains four compartments, as indicated by the labels on the x-axis. Each compartment shows the effect of the absence (0) or presence (1) of a competitor on the time spent on food pits. Dots represent averages per treatment combination, and thin grey lines connect observations on the same individual within each compartment.

TIME ALLOCATION

Foragers differed markedly in the time they spent on the food pits (Figure 5.5). Dominant individuals spent about the same amount of time on food pits under all conditions. Subordinate birds also spent about the same amount of time on food pits under all conditions, but only so when they were foraging alone. When subordinate birds were foraging in the presence of their dominant pair member, they spent much less time on food pits when these were far from each other than when these were close to each other, regardless of the within-pit food distribution. This effect was especially apparent in the second run of the experiment, in which subordinate individuals hardly spent any time on the food pits at all. Statistically, this effect is reflected in the interaction term between Competitor presence, Dominance status and Inter-pit distance (A x C x D), which was significant in both runs of the experiment (Table 5.1 & 5.2). As time spent on food pits was highly correlated with the time spent digging for food (Pearson correlation coefficient: $r = 0.98$, $t_{192} = 68.2$, $P < 0.001$), variation in the time spent on food pits explains at least partly why dominant foragers

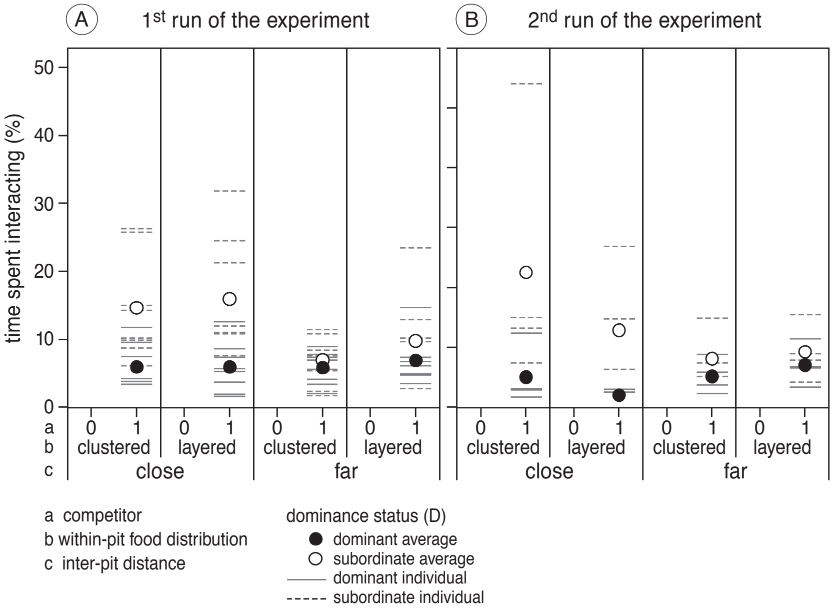

Figure 5.6. The time turnstones spent interacting in the first (a) and the second (b) run of the experiment. Like in figure 5.2, each graph is composed of four compartments as indicated by the labels on the x-axis. Within each compartment, a distinction is made between the absence (0) or presence (1) of a competitor (for conformity with other graphs). Note that interactions occur only when a competitor is present. Dots represent averages per treatment combination, whereas thin grey lines indicate observations on individuals.

found so much more food items than subordinate foragers when food pits were close to each other; apparently, dominant birds were able to monopolize the food pits under this condition.

Depending on the distance between the food pits, foragers also differed in the time they spent interacting (Figure 5.6). When food pits were far apart, dominant and subordinate spent about the same amount of time on interactions, regardless of the within-pit food distribution; what generally happened under this condition was that both foragers occupied a food pit until the dominant forager decided to supplant its subordinate competitor from the food pit; sometimes this happened because the dominant forager had emptied its own food pit, but this was not always the case. Such supplant-interactions took about the same time for dominant and subordinate foragers. Sometimes, however, the subordinate forager was the first to leave its food pit (even though this food pit was not empty yet) in an attempt to join its dominant competitor. Joining, however, was never tolerated so that the subordinate bird could but resume foraging at the food pit that it had left. When the food pits were close to

Table 5.1. Treatment effects on the response variables of the first run of the experiment[a]

	Trial duration (s)			Intake (#)			Intake rate ($\#s^{-1}$)			Time spent on food pits (%)			Time spent interacting (%)		
(dom + sub)	df	SS	F	df	SS	F	df	SS	F	df	SS	F	df	SS · 10^{-2}	F
Constant	1	674.3		1	116.7		1	428.0		1	263.0		1	1159.7	
Bird pair	7	12.6		7	5.2		7	13.7		7	1.3		7	28.0	
Day	7	5.0		7	1.1		7	10.4		7	0.3		7	12.7	
A	1	3.4	**30.0**	1	15.8	**90.1**	1	1.7	**5.6**	1	7.3	**148.8**		–	–
B	1	0.1	1.3	1	1.3	**7.6**	1	4.1	**13.5**	1	0.0	0.2	1	1.6	1.0
C	1	0.0	0.2	1	1.1	**6.4**	1	2.5	**8.1**	1	0.8	**17.0**	1	6.7	4.1
A x B	1	0.0	0.4	1	0.0	0.0	1	0.1	0.3	1	0.2	**4.7**		–	–
A x C	1	0.8	**7.1**	1	1.4	**7.7**	1	3.6	**11.7**	1	1.0	**20.3**			
B x C	1	0.0	0.0	1	0.0	0.2	1	0.0	0.0	1	0.0	0.0	1	0.8	0.5
A x B x C	1	0.3	2.3	1	0.0	0.0	1	0.8	2.6	1	0.0	0.2			
Error	28	3.6		38	7.4		38	12.8		38	2.1		13	22.7	
Total	50	25.0		60	33.3		60	49.6		60	13.0		31	67.0	
(dom - sub)															
D	1	0.8	**5.5**	1	17.9	**68.4**	1	30.4	**107.6**	1	2.7	**47.2**	1	25.6	**43.3**
Bird pair x D	7	2.8		7	9.6		7	24.8		7	0.7		7	7.8	
Day x D	7	1.1		7	0.9		7	1.5		7	0.3		7	6.2	
A x D	1	1.2	**7.8**	1	8.7	**33.2**	1	2.1	**7.6**	1	3.8	**68.2**		–	–
B x D	1	0.0	0.1	1	1.9	**7.3**	1	2.2	**7.7**	1	0.1	1.5	1	0.5	0.8
C x D	1	0.0	0.1	1	2.5	**9.7**	1	2.8	**9.8**	1	1.2	**21.4**	1	10.9	**18.4**
A x B x D	1	0.0	0.0	1	0.0	0.1	1	0.1	0.3	1	0.0	0.0		–	–
A x C x D	1	0.0	0.0	1	3.0	**11.3**	1	3.5	**12.4**	1	1.7	**30.1**		–	–
B x C x D	1	0.0	0.0	1	0.0	0.1	1	0.1	0.4	1	0.0	0.3	1	0.0	0.0
A x B x C x D	1	0.0	0.1	1	0.0	0.0	1	0.0	0.0	1	0.0	0.2		–	–
Error	28	4.7		38	11.0		38	11.9		38	2.4		13	8.3	
Total	50	9.2		60	37.7		60	48.9							

[a] Given are GLM results of the treatment factors Competitor presence (A), Within-pit food distribution (B), and Inter-pit distance (C) on the responses of dominant and subordinate pair members, after these were the log-transformed (trial duration, intake and intake rate) or arcsine-transformed (time spent on food pits and time spent interacting). Treatment effects independent of the foragers' Dominance status (D) were found by using the sum of the response of both pair members ('dom + sub'; upper half), whereas treatment effects that depended on this factor were found by using the difference in the response of dominant and subordinate pair members ('dom – sub'; lower half). Effects significant at the 0.05 level are indicated by bold F values.

Table 5.2. Treatment effects on the response variables of the second run of the experiment[a]

		Trial duration (s)			Intake (#)			Intake rate (#s^{-1})			Time spent on food pits (%)			Time spent interacting (%)		
	(dom + sub)	df	SS	F	df	SS	F	df	SS	F	df	SS	F	df	SS · 10^{-2}	F
wholeplot	Constant	1	405.9		1	59.5		1	168.3		1	126.0		1	513.7	
	Day	3	1.0		3	0.0		3	0.9		3	0.1		3	20.5	
	C	1	0.2	0.3	1	0.1	4.7	1	0.0	0.0	1	0.7	**330.2**	1	0.5	0.5
	Error	3	1.5		3	0.1		3	1.9		3	0.0		3	3.5	
subplot	Bird pair	3	6.1		3	0.1		3	5.4		3	0.1		3	19.8	
	A	1	5.5	**33.0**	1	13.1	**648.1**	1	1.7	**7.5**	1	4.6	**62.7**			
	B	1	1.0	**5.7**	1	0.9	**44.3**	1	3.4	**14.7**	1	0.0	0.3	$\overline{1}$	$\overline{0}.6$	$\overline{0}.5$
	A x B	1	0.1	0.5	1	0.7	**35.2**	1	1.6	**6.8**	1	0.1	1.1	–	–	–
	A x C	1	0.6	3.5	1	0.2	**11.6**	1	1.3	**5.8**	1	0.7	**9.6**	–	–	–
	B x C	1	0.3	1.5	1	0.2	**11.6**	1	0.0	0.1	1	0.1	1.6	1	3.8	3.1
	A x B x C	1	0.5	2.7	1	0.1	**7.2**	1	0.0	0.2	1	0.0	0.0	–	–	–
	Error	14	2.3		15	0.3		15	3.4		15	1.1		3	3.7	
	Total	31	17.4		32	15.9		32	19.7		32	7.4		16	38.2	
	(dom - sub)															
wholeplot	D	1	1.5	**229.5**	1	12.2	**294.1**	1	22.8	**638.6**	1	1.7	**49.3**	1	23.5	**15.7**
	Day x D	3	0.5		3	0.0		3	0.7		3	0.3		3	4.2	
	C x D	1	0.0	1.9	1	0.3	7.1	1	0.4	**11.4**	1	0.8	**23.3**	1	10.2	6.8
	Error	3	0.0		3	0.1		3	0.1		3	0.1		3	4.5	
subplot	Bird pair x D	3	1.5		3	0.1		3	2.2		3	0.1		3	9.1	
	A x D	1	1.5	**12.9**	1	11.5	**419.0**	1	4.5	**36.0**	1	3.6	**71.2**	–	–	–
	B x D	1	0.0	0.3	1	1.4	**49.9**	1	1.9	**15.7**	1	0.1	1.0	1	0.6	0.2
	A x B x D	1	0.0	0.3	1	1.1	**41.5**	1	0.7	**5.7**	1	0.1	2.1	–	–	–
	A x C x D	1	0.0	0.1	1	0.4	**15.1**	1	0.3	2.4	1	0.4	**8.1**	–	–	–
	B x C x D	1	0.0	0.0	1	0.4	**15.1**	1	0.4	3.2	1	0.1	2.3	1	0.1	0.0
	A x B x C x D	1	0.0	0.0	1	0.3	**10.7**	1	0.3	2.5	1	0.1	1.1	–	–	–
	Error	14	1.6		15	0.4		15	1.9		15	0.8		3	7.9	
	Total	31	5.1		32	16.1		32	13.3		32	6.5		16	33.9	

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[a] Interpretation as Table 5.1.

each other, subordinate individuals spent more time on interactions than did the dominant forager. As when food pits were far apart, this effect was independent of the within-pit food distribution. What generally happened under this condition was that the subordinate forager attempted to reach the food pits, evoking a threatening behaviour of the dominant forager, which occupied one of the food pits, but monopolized both. Such monopolization interactions were short for dominant foragers, which had but to lift their head and threat, but considerably long for subordinate birds, which had to run away from their dominant competitor. Although this pattern of time allocation to interactions was comparable between the two runs of the experiment, the interaction term between Dominance status and Inter-pit distance (C x D) was only significant in the first run of the experiment (Table 5.1 & 5.2). Albeit being non-significant in the second run of the experiment, this interaction term explained considerable variation in both runs of the experiment, as indicated by the sum of squares (SS) and the variance ratios (F).

DISCUSSION

Resource divisibility affected the way turnstones divided the food; subordinate birds foraging in the presence of a competitor were more likely to get some mealworms when these were offered in several layers than when these were placed in a single layer at the bottom of food pits. This effect was not due to subordinate birds spending more time on the food pits when food was offered in layers, nor to the loss of time spent interacting under the clustered condition. Instead, subordinate birds achieved a higher intake when food was divisible because they got a finder's advantage under this condition. Subordinate birds that were supplanted from food pits in which food was clustered got nothing, even though they sometimes spent a considerable amount of time digging. The most extreme illustration of this was found in the second run of the experiment, where subordinate birds, foraging at food pits that are far apart and at food that is clustered within food pits, spent about 50 % of their time on food pits but got none of the mealworms. A similar mismatch between time investment and intake was reported by Di Bitetti & Janson (2001), who observed that subordinate capuchin monkeys (*Cebus apella*) consumed only a small percentage of the experimentally offered resources, even though they discovered a high percentage of the feeding platforms.

That the divisibility of resources may affect the division of food over foragers because of a finder's advantage in the case of divisible resources was already assumed by several models of interference competition. What our results additionally show, however, is that the effect of resource divisibility may interact with the distribution of resources. Subordinate birds got more mealworms when food pits were divisible than when food pits were indivisible, but especially so when food pits were far apart. When food pits were close to each other, dominant foragers could monopolize them, so that subordinate foragers got even fewer food items. This effect was most pronounced in the second run of the experiment, in which the monopolization of food pits that were close to each other was so strong that subordinate foragers could not even get a finder's advantage when food pits were divisible.

The most striking result of our experiment, however, was the large and consistent difference in the intake of dominant and subordinate foragers. By no means was the effect of the presence of a competitor general for foragers of different dominance status; under some conditions the presence of a competitor had no effect on the intake of dominant foragers, but a very strong negative effect on the intake of subordinate foragers. This result is striking especially because we assigned the birds a social dominance status at random, so that subordinate members of some pairs had a higher dominance ranking (i.e., they were more dominant) than the dominant members of other pairs. Apparently, knowledge of the relative dominance status suffices to explain much of the variation in the behaviour and the intake of interacting birds. We reached the same conclusion in a previous experiment (Vahl et al. 2005a).

LEARNING

Throughout the experiment, the turnstones improved their foraging skills, as was apparent from the shorter duration of trials in the second run of the experiment. We tried to prevent the birds from changing their behaviour during the experiment by performing a considerable number of pilot trials, but apparently we did not succeed. In principle, a change in foraging skills is unwanted because it adds variation to the data, which may blur effects of the experimental factors. Within the two runs of our experiment, however, the change in foraging skills will probably not have affected our treatment estimates, because the block factor Experimental day in the Latin Square design controlled for any time-related confounding. Differences between birds at the start of our experiment and differences between the two runs of our experiment, on the contrary, may have been due to changes in the birds' foraging skills. In fact, we think that the change in foraging skills explains at least two of our findings.

First, subordinate birds were less successful in finding all ten mealworms and they needed more time to find the mealworms than dominant birds, even when foraging alone. This is surprising as we assigned birds a dominance status at random, so that there should be no intrinsic differences between the subordinate and the dominant individuals. The most likely explanation for this difference in foraging skills is that subordinate birds were already excluded from the food pits in pilot trials in which they foraged together with their dominant competitor. This would imply that although subordinate individuals and dominant individuals performed the same number of pilot trials, subordinate birds effectively got less experience in handling the food pits, because there were excluded from the food pits in half of the pilot trials. From this explanation it becomes apparent that dominance status and foraging skills may well be interrelated.

Second, subordinate birds foraging together with a competitor got no food at all from clustered food pits in the second run of the experiment, whereas they got some in the first run. This difference probably arose because dominant birds learned to first empty one food pit before supplanting their subordinate competitor from the other. As dominant birds were quicker to find food than subordinate birds, they could empty one food pit and supplant their subordinate competitor before this competitor had reached the food, so that the dominant bird managed to get all the resources. This explanation illustrates that the foraging skills of dominant birds *relative* to those of subordinate birds may be of prime importance to the interference process.

CONCLUSIONS

Interference competition was expressed mainly as an asymmetry in the distribution of food over foragers of different dominance status. The strength of this asymmetry depended on the distance between food pits, because dominant foragers could monopolize food pits only when these were close to each other, as we also found in a previous experiment (Vahl et al. 2005a). In addition, however, the skew in resource distribution between dominant and subordinate pair members depended on the divisibility of food, because subordinate foragers got a finder's advantage only when resources were divisible. As the second run of the experiment showed, the effect of the distance between food pits and of resource divisibility can sometimes interact. These results imply that for the interference process it matters whether foragers are interacting over food items or over food clumps, because food clumps can be split over multiple foragers more easily than can food items. The overriding effect of the social dominance status of foragers shows that when interference competition results from the monopolization of resources, differences in dominance status are of crucial importance to understand and predict the interference process.

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CHAPTER 6

WHY DO FORAGERS FIGHT FOR FOOD? A UNIFYING EVOLUTIONARY PERSPECTIVE

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UNPUBLISHED MANUSCRIPT

ABSTRACT

In many species, the intake rate of foraging individuals is negatively related to forager density due to agonistic interactions among foragers. Recently a variety of game theory models has been developed to address the question how such interference behaviour is shaped by natural selection. These modelling approaches have not yet led to a comprehensive understanding of interference competition; models that appear to be very similar yield strikingly different predictions regarding the evolutionary stability of various interference strategies. Here we attempt to unify approaches. To avoid model inconsistencies, we plead for a systematic, event-based description of the foraging process, the explicit account of feedback effects and the systematic derivation of a payoff function. To analyze the resulting evolutionary game, we use techniques from Adaptive Dynamics theory, since classical ESS techniques can be highly misleading when applied to the payoff functions resulting from interference competition. By means of this unified approach, we show that foraging animals can generally be expected to make their aggressive behaviour dependent on the role they play in interactions, that alternative evolutionarily stable interference strategies may evolve at the same ecological conditions, and that interference effects on intake rate cannot be taken for granted as the logical outcome of evolution. By critically discussing the setup, the assumptions and the way of analysis of some evolutionary models of interference competition, we identify crucial assumptions and potential pitfalls in modelling the evolution of interference behaviour, and we demonstrate that the discrepancies between earlier model predictions often reflect seemingly subtle differences in the assumptions on behavioural flexibility.

INTRODUCTION

The intake rate of foraging animals is often negatively related to the density of foragers because of competition. Such negative effects can have major implications for the spatial distribution and population growth rates of both predators and their prey (Christian 1970; Gauthreaux 1978; Goss-Custard 1980). Competition is generally thought to arise in either of two ways (Keddy 2001). *Exploitative competition* is the negative effect of others through the removal of resources. As the exploitation of resources is a straightforward process, this type of competition is (presumably) relatively easy to understand. Interference competition is the negative effect of others through direct interactions between individuals. Behaviours underlying *interference competition* are various and complex (e.g., Huntingford & Turner 1987; Ens & Cayford 1996; Hassell 2000), and our understanding of this type of competition is still rudimentary (van der Meer & Ens 1997; Vahl et al. 2005a, b).

Several models have been developed to account for interference effects of forager density on foraging success. The original attempts have been reviewed by van der Meer and Ens (1997), who identified two broad approaches. Some ('phenomenological') models used an empirical relationship between foraging success and forager density to model the effect of interference, without further specification of the way interference competition comes about. Although such descriptive models may be useful for practical purposes, they yield little understanding of the interference process. Other ('mechanistic') models borrowed concepts from reaction kinetics to relate foraging success and forager density, assuming that interference competition arises from the loss of time spent in aggressive interactions. Such conceptual models seem a more promising approach to gain an understanding of the mechanistic basis of interference competition. This, however, is only partially the case, because these conceptual models do not consider the evolutionary question why foraging animals would interact with each other in the first place. The models assume foraging animals to interfere in a specific way without considering the adaptive value of such behaviour; as such, foraging animals are treated as 'aimless billiard balls' with no choice but to act aggressively when encountering each other (van der Meer & Ens 1997).

Recently, a variety of models has been developed that do consider the adaptive value of interference behaviour (e.g., Broom & Ruxton 1998; Sirot 2000; Dubois et al. 2003). The central question in these evolutionary models is how interference behaviour is shaped by natural selection. In addressing this question, these evolutionary models embed basic ideas from evolutionary game theory in a context that is based explicitly on a mechanistic description of animal foraging behaviour, using the mechanistic concepts from the original, non-adaptive models of interference competition. These evolutionary models extend previous work on evolutionary game theory (for reviews: see e.g., Maynard Smith 1982; Parker 1984; Hines 1987; Giraldeau & Livoreil 1998) by combining the study of frequency-dependent effects of aggressive behaviour with that of density-dependent ('interference') effects.

Although the number of evolutionary models of interference competition is growing rapidly, a comprehensive understanding of interference competition has not yet been achieved. Models that appear to be very similar yield strikingly different predictions regarding the evolutionary stability of various interference strategies. This is, for instance, clear from a comparison of those models of interference competition that (1) study the evolution of aggressive behaviour, (2) use the Hawk-Dove game, and (3) explicitly account for density-density dependent effects of foraging (for a short description of the most prominent of these models, see Table 6.1). These models address the same questions in similar ways. For instance, all of these models assume that foraging animals can be in a small number of mutually exclusive behavioural states, such as searching or handling, and they all predict how much foraging animals should behave aggressively in each of their behavioural states. Nevertheless, the models lead to strikingly different predictions regarding possible evolutionarily stable interference strategies, and regarding the effect of ecological variables on these predictions (Table 6.2). They vary, for instance, in their predictions on the nature and the number of evolutionary stable interference strategies, and there is no consensus on the effects of some prime ecological parameters. Regarding the effect of forager density, for instance, some models predict the frequency of aggressive conflicts to be high when the encounter rate with competitors is high, whereas other models predict few such conflicts, and yet other models predict the frequency of aggressive conflicts to be independent of the rate of competitor encounter.

This paper has a double purpose. We start by developing a systematic approach for studying the evolution of interference behaviour. This approach is event-based and centres on a decision tree that visualises the foraging game. For the analysis of the evolutionarily stability of various interference behaviours, it relies on Adaptive Dynamics theory, which can be seen as a refinement of the methods of evolutionary game theory. With the help of this approach, we show that the degree to which a foraging animal behaves aggressively should reflect its behavioural state (i.e., whether it entered a conflict as a searcher or as a handler). We also demonstrate that at a substantial range of ecological conditions, interference strategies can be expected that do not result in a negative relationship between intake rate and forager density at all. The main purpose of the paper, however, is to discuss more critically the assumptions and pitfalls associated with modelling the evolution of interference behaviour. To this end, we discuss the models presented in Table 6.1 in the light of our systematic approach. We show that although these models have broadly the same struc-

Table 6.1. Description of models of interference behaviour that (1) study the evolution of aggressive behaviour, (2) use the Hawk-Dove game, and (3) explicitly account for density-dependent effects of foraging[†]

	special characteristics	sub-models
Broom & Ruxton 1998	use an event-based approach to evaluate different interference strategies; use a differential equation approach to study consequences of different strategies on the interference effect	1. foragers search for food and for handlers concurrently (yes) 2. trade-off between searching for food and searching for handlers (no)
Broom & Ruxton 2003	extend Broom & Ruxton (1998); decision to behave aggressively is made dependent on the handling time invested by handling opponent	1. 'apple model': food is consumed during handling (yes; model a) 2. 'orange model': food is consumed after all handling has been done (yes; model b)
Broom et al. 2004	upgrade Broom & Ruxton (1998) by allowing both searchers and handlers the choice to behave aggressively; use an approach that is mostly event-based	1. searchers and handlers same probability of winning fights (yes; model a) 2. searchers and handlers different probability of winning fights (yes; model b)
Sirot 2000	uses an entirely event-based approach; keeps track of three types of prey items – those that are, those that will be, and those that will not be object of a conflict	
Dubois et al. 2003	consider effects of group size; forager density is assumed to affect interference behaviour only through effects on finder's advantage; do not keep track of number of foragers in each behavioural state	1. only energy consequences considered (no) 2. energy and time consequences considered (no) 3. Hawk-Dove game with multiple challengers (yes)
Dubois & Giraldeau 2003	iterated Hawk-Dove game in which foragers become familiar with their competitors; Hawk strategy is compared with Tit-for-Tat strategy	1. payoff function evaluated is expected gain (yes) 2. evaluates variance in expected gain (no) 3. evaluates coefficient of variation of gain (no)
Dubois & Giraldeau 2005	unite Hawk-Dove game with Producer-Scrounger game; incorporate predation risk for interfering foragers; do not keep track of number of foragers in each behavioural state	

[†] All of these models are based on the idea that foraging animals can be in few, mutually exclusive, behavioural states; indicated are only the special characteristics of the models. When a paper contained more than one model, sub-models are described and it is indicated whether we do (yes) or do not (no) consider them in our discussion of interference models.

Table 6.2. Predictions of evolutionary models of interference competition. Note that the models differ considerably in their predictions on whether specific interference strategies are expected to be evolutionarily stable, and on the effect of two of the prime model parameters – the rate at which unhandled food is found (*ax*) and the rate at which competitors are encountered (*by*) – on the frequency with which foraging animals are expected to always behave aggressively (i.e., to play the Hawk strategy)

		ESS†						Alternative ESSs	Parameter effects§	
reference		Dove	mixed	semi-mixed	Bourgeois	anti-Bourgeois	Hawk	possible?‡	ax↑	by↑
Broom & Ruxton 1998		-	-	no	some	-	some	no	H↓	0
Broom & Ruxton 2003	a	-	-	0	some	-	some	H&B	H↓, H↓↑	H↑
	b	-	-	0	some	-	some	no	H↓	H↓
Broom et al. 2004	a	0	0	0	no	some	some	H&X	0,H↓	0,H↓
	b	0	0	0	some	some	some	H&X, B&X	0,H↓	0,H↓
Sirot 2000		no	some	-	-	-	some	no	H↓	H
Dubois et al. 2003		no	some	0	0	0	some	no	H↓	H↑↓
Dubois & Giraldeau 2003		no	-	-	-	-	some	no	H↓	H
Dubois & Giraldeau 2005		no	no	some	no	no	some	no	H↓	H

† Indicated is whether a strategy is excluded by explicit assumptions (-), ignored as a possible ESS (0), or predicted to occur under some conditions (some), or under no conditions (no).

‡ Indicated is whether no alternative ESSs are predicted to occur under the same ecological conditions (no), or else, which of the Hawk (H), Bourgeois (B) and anti-Bourgeois (X) ESSs are predicted to co-occur under the same ecological conditions.

§ Indicated is whether the frequency of the Hawk strategy is positively (↑), negatively (↓) or not (0) correlated to the rate at which unhandled food is found (*ax*) and the rate at which com petitors are encountered (*by*), or whether these relationships are concave (↓↑) or convex (↑↓). When alternative ESSs co-occur, multiple relationships are given.

ture, they differ substantially in the precise assumptions they make regarding, for instance, the structure of interactions, the presence of asymmetries and their payoff function. Such differences, although seemingly of minor importance, turn out to strongly affect predictions regarding the evolutionary stability of interference strategies.

A MODELLING FRAMEWORK

GENERAL OUTLINE

We consider a population of animals foraging in an environment that is determined by two main parameters: the density of food items x and the density of foragers y. We assume both food and foragers to be randomly distributed at constant density. This implies that food is not depleted and that the population of foragers is closed. Food items are assumed to be all alike, having a fixed energetic value to foragers, and requiring a fixed handling time. Foragers are assumed to be identical in all aspects other than their interference behaviour. At any moment in time, however, foragers may differ in the behavioural state they are in. Building on the approach of the original mechanistic models of interference competition (e.g., Beddington 1975; Ruxton et al. 1992), foraging animals are assumed to be in one of three, mutually exclusive, states: they can be *searching* for, *handling*, or *fighting* over, a food item.

To evaluate the behaviour of the foragers, we use an event-based approach; we consider a focal forager and keep track of the events that may happen to this forager, the actions that the forager can perform in response to these events, and the consequences of these actions to the behavioural state of the forager. In response to most events, a forager has no choice but to perform a specific action. Some events, however, create a choice situation; the action chosen in such a situation is determined by the forager's individual strategy. Each event and action has an expected consequence in terms of energy and time. For each sequence of events and actions, we can determine its probability of occurrence, as well as the energy and time consequences associated with it. Weighing consequences with probabilities, we get the payoff function associated with a strategy of the focal forager. This payoff function we use to evaluate the evolutionary stability of alternative strategies.

MODEL STRUCTURE

EVENTS, ACTIONS AND STRATEGIES

To visualize the possible events, actions and strategic decisions, we use a decision tree (Figure 6.1). This tree starts with a focal forager that has just entered the searching state. Each chain of branches ends with the event or action that brings the focal forager back to the searching state. Two events can happen to

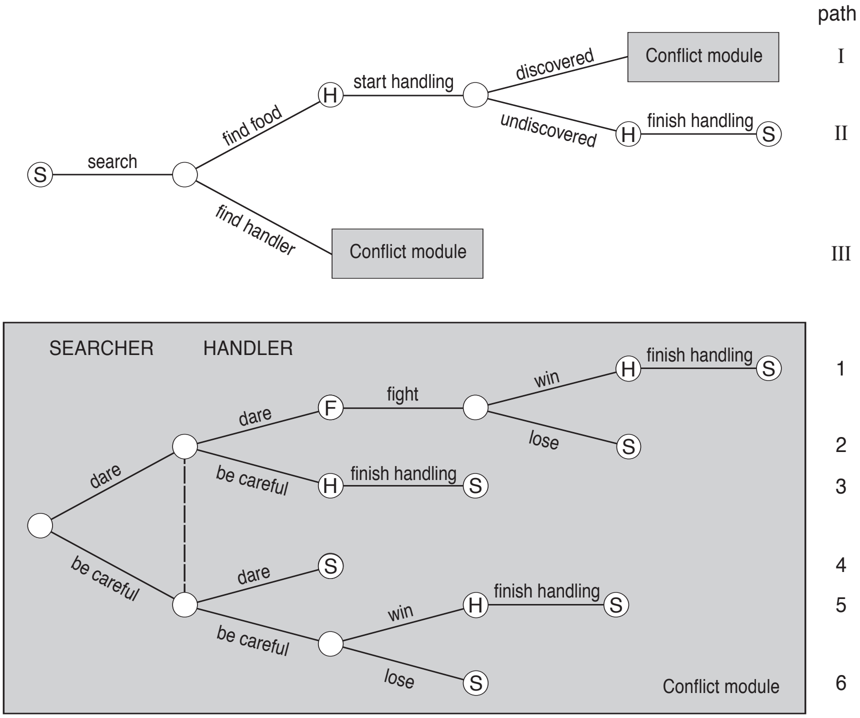

Figure 6.1. The foraging game visualized by a decision tree that keeps track of all possible events and actions that can occur to a focal forager. The decision tree starts with a forager in the searching state (S) and accordingly, each of the 13 paths through the decision tree end when the foragers re-enters the searching state. In the meantime, the forager may have been in the handling (H) and/or the fighting (F) state. The dotted line in the conflict module indicates that searchers and handlers choose an action simultaneously, without knowing the action of their opponent.

this searching forager. With probability γ it finds an unhandled food item, and with probability $1 - \gamma$ it finds a competitor that is handling a food item. In the latter case, a conflict arises. In the former case the forager starts handling the food item and its behavioural state changes from searching to handling. When handling, again two events can happen to the forager: with probability κ it is discovered by a searching competitor and a conflict arises; with probability $1 - \kappa$ the forager is not discovered. In the latter case the forager continues to handle its food item until it can be consumed; after consumption the forager re-enters the searching state. In the model discussed here, κ is implemented as a chance event. Alternatively, we could have treated it as a strategic decision; such would, for instance, have been appropriate in a producer-scrounger context.

When a conflict arises, the former searcher and the former handler both choose, simultaneously and independently, between two actions; they are either aggressive or not. In referring to these two behavioural options, we follow Crowley (2000); foragers either 'dare' or they 'are careful'. The choice of either action is specified by their personal strategies P. Strategies have two components: the tendency p_s to 'dare as a searcher' and the tendency p_h to 'dare as a handler'. If both opponents in a conflict choose to dare, they start a fight, with their state changing correspondingly. When fighting, two events can happen: with probability α the searcher wins the fight, and with probability $1 - \alpha$ the searcher loses the fight. If only one of the two opponents of a conflict dares, the daring forager wins the conflict and the careful forager loses it. If neither opponent dares, there is a peaceful contest, with both opponents having the same chance of winning. Winners take the food item and finish the handling of it, after which they re-enter the searching state. We assume that each food item is contested only once. This implies that handlers are certain not to be discovered while handling a food item that they have won in a contest. Losers re-enter the searching state. The conflict just described resembles the basic Hawk-Dove game with a role-asymmetry (Maynard-Smith & Parker 1976; Hammerstein 1981).

ENERGETIC CONSEQUENCES, TEMPORAL CONSEQUENCES AND PROBABILITIES

Only some actions have net energetic consequences (generically denoted by G for gain; for an overview of all symbols used: see Table 6.3). A handler that consumes a food item gains a constant amount of energy v; it is assumed that food items are always consumed as a whole and instantaneously. A forager that enters the fighting state loses a constant amount of energy c. In the model developed here, we assume that there is no finder's advantage, but such an advantage could easily be included in the model by assuming that a searcher that finds a food item gains a constant amount of energy d (in which case a handler that consumes a food item gains $v - d$ instead of d energy units).

All actions bear a time consequence (generically denoted by T for time). We assume that foragers search simultaneously for unhandled food items and for food items that are being handled by a competitor, and that the discovery process of either type of food items is random. Under these assumptions, the expected time to find either a food item, or a handler t_s equals the inverse of the prey encounter rate, which is the sum of the rate λ_a at which unhandled food items are encountered and the rate λ_b at which food items owned by handlers are encountered:

$$t_s = \frac{1}{\lambda_a + \lambda_b} \qquad [1]$$

The rate at which searchers encounter unhandled food items is a simple function of the constant rate a at which they search for unhandled food items and

Table 6.3. List of symbols used.

Symbol	Definition	Units
a	'Area of discovery of food': rate at which the environment is searched for food items	m^2s^{-1}
b	'Area of discovery of handlers': rate at which the environment is searched for handlers	m^2s^{-1}
c	Energy cost of each fight	J
d	Finder's advantage	J
$F_{P,\hat{P}}$	Invasion fitness of focal forager playing strategy P in a population playing strategy $\hat{P}$	-
G	Expected energy consequence	J
M	Mutational variance-covariance matrix	-
P	Strategy, combining a value for p_s and for p_h	-
p_s	Probability to dare as a searcher	-
p_h	Probability to dare as a handler	-
T	Expected time consequence	s
t_f	'Fighting time': expected time required to fight an opponent	s
t_h	'Handling time': expected time required to handle a food item before consumption	s
t_{h_1}	'Initial handling time': expected time spent handling before discovery by competitor	s
t_{h_2}	'Final handling time': expected time spent handling after discovery by competitor	s
t_s	'Searching time': expected time required to find either a food item or a handler	s
v	Energy value of each food item	J
$W_{P,\hat{P}}$	Payoff of focal forager playing strategy P in a population playing strategy $\hat{P}$	Js^{-1}
x	Food density	$\#m^{-2}$
y	Forager density	$\#m^{-2}$
α	Probability of winning when fighting	-
γ	Probability of finding a unhandled food item when searching	-
ε	Fraction of foragers with a mutant strategy	-
κ	Probability of being discovered when handling	-
λ_a	Rate at which searchers find unhandled food items	$\#s^{-1}$
λ_b	Rate at which searchers find food items owned by handlers	$\#s^{-1}$
λ_s	Rate at which a handler is discovered by searchers	$\#s^{-1}$
ζ_k	Probability that focal forager achieves consequence k (k = 'gain v', 'lose c', or 'spend t_{h_0}, t_{h_1}, t_{h_2} or t_f')	-
$\hat{\rho}_i$	Fraction of foragers in the population that are in state i (i = *searching, handling* or *fighting*)	-
τ	Evolutionary time	†
φ_j	Probability that focal forager passes the decision tree through path j (j = 1 .. n)	-

† The appropriate unit of evolutionary time depends on the rate at which mutations arise in the population. For instance, if mutation would create a single new mutant per generation, the unit of evolutionary time would correspond roughly to the generation time of the population under study.

the density of food items x:

$$\lambda_a = ax \qquad [2]$$

The rate at which a handler is discovered by searchers is somewhat more complicated and will be specified below. The probability γ of a searcher finding an unhandled food item equals the proportion of food items found unhandled:

$$\gamma = \frac{\lambda_a}{\lambda_a + \lambda_b} \qquad [3]$$

We assume that food items take a constant time t_h to handle. A forager that encountered an unhandled food item will thus spent t_h time handling when it is not discovered by a competitor. When it is discovered by a competitor, however, it will have spent part, but not all, of this time. Assuming that the discovery of handlers is a random process and that handler are discovered by searchers at a constant rate λ_s (which will be defined below), we take the probability κ of a handler being discovered by a searcher as one minus the null-term of the Poisson distribution:

$$\kappa = 1 - e^{-\lambda_s t_h} \qquad [4]$$

Under the same assumptions, the expectation for the handling time invested before being discovered t_{h_1} given that a handler is discovered equals the average waiting time of an exponential distribution divided by the probability κ of being discovered:

$$t_{h_1} = \frac{1}{\kappa} \int_0^{t_h} t\lambda_s e^{-\lambda_s t}\, dt = \frac{1}{\kappa}\left[\left(1 - e^{-\lambda_s t_h}\right)\lambda_s - e^{-\lambda_s t_h} t_h\right] = \lambda_s - \frac{1-\kappa}{\kappa} t_h \qquad [5]$$

The expected handling time left for the winner of a conflict t_{h_2} is simply the difference between the total handling time t_h and the handling time invested prior to being discovered t_{h_1}. This approach assumes that the total amount of handling time per food item is not affected by a conflict over this food item, and that there can only be one conflict per prey item.

We assume that fighting takes a constant time t_f. Conflicts in which at least one of the opponents chooses not to use aggression are assumed to be resolved instantaneously.

THE PAYOFF FUNCTION

Knowing the expected consequences in terms of energy and time, as well as the probability of occurrence of each event and action, we can calculate for each strategy the expected payoff $W_{P,\hat{P}}$, whereby the notation indicates that the payoff is associated with a focal forager playing strategy $P = (p_s, p_h)$ in a population of foragers that all play strategy $\hat{P} = (\hat{p}_s, \hat{p}_h)$. As payoff function, we use the ratio of the expected energy consequences over the expected time consequences (the 'long-term average rate of net energy gain'), which is one of the standard payoff functions used in models of foraging animals. In a subsequent section (Section 4.4), we discuss the use of this specific currency in relation to its alternatives.

The long-term average rate of net energy gain equals the ratio of the sum of the energy consequences of each of the paths of the decision tree and the sum of the time consequences of each of the paths, whereby the energy consequences and the time consequences of each path j have to be weighted by the probability $\varphi_j(P, \hat{P})$ of the focal forager passing through that path:

$$W_{P,\hat{P}} = \frac{E_{P,\hat{P}}(G)}{E_{P,\hat{P}}(T)} = \frac{\sum_{j=1}^{n} \varphi_j(P, \hat{P}) G_j}{\sum_{j=1}^{n} \varphi_j(P, \hat{P}) T_j} \tag*{[6]}$$

Determining for each path the summed consequences in terms of energy and time is straightforward; the probabilities $\varphi_j(P, \hat{P})$ of a focal forager taking path j through the decision tree can be found by multiplying the probabilities of all the events and actions in that path (Table 6.4). For ease of representation and interpretation, probabilities involving the same consequence in terms of energy or time can also be grouped into compound probabilities $\zeta_k = \zeta_k(P, \hat{P})$ of reaching consequence k :

$$W_{P,\hat{P}} = \frac{\zeta_v v - \zeta_c c}{t_s + \zeta_{h_0} t_h + \zeta_{h_1} t_{h_1} + \zeta_{h_2} t_{h_2} + \zeta_f t_f} \tag*{[7]}$$

Deriving the compound probabilities ζ_k from the path frequencies φ_j as given in Table 6.4 is straightforward. The compound probability ζ_c of losing c resources, for instance, is the sum of the probabilities φ_j of a focal forager taking each path that leads to the loss of c resources (i.e., the sum of the probabilities of the paths I-1, I-2, III-1 and III-2):

$$\begin{aligned} \zeta_v = {} & \gamma\kappa[p_h \hat{p}_s \alpha + p_h(1-\hat{p}_s) + (1-p_h)(1-\hat{p}_s)\alpha] + \gamma(1-\kappa) \\ & + (1-\gamma)[p_s \hat{p}_h \alpha + p_s(1-\hat{p}_h) + (1-p_s)(1-\hat{p}_h)\alpha], \end{aligned} \tag*{[8]}$$

$$\zeta_c = \zeta_f = \gamma\kappa p_h \hat{p}_s + (1-\gamma) p_s \hat{p}_h \,,$$

$$\zeta_{h_0} = \gamma(1-\kappa),$$

$$\zeta_{h_1} = \gamma\kappa \,,$$

$$\begin{aligned} \zeta_{h_2} = {} & \gamma\kappa[p_h \hat{p}_s \alpha + p_h(1-\hat{p}_s) + (1-p_h)(1-\hat{p}_s)\alpha] \\ & + (1-\gamma)[p_s \hat{p}_h \alpha + p_s(1-\hat{p}_h) + (1-p_s)(1-\hat{p}_h)\alpha] \\ = {} & \zeta_v - \gamma(1-\kappa) = \zeta_v - \zeta_{h_0} \,. \end{aligned}$$

Table 6.4. Summed consequences in terms of energy and time, associated with each of the paths of the decision tree, and the probability of a focal forager taking that path. Path numbers correspond to Figure 6.1.

		Consequences		
Path (j)		Energy (G_j)	Time (T_j)	Probability (φ_j)
I-1	find food, start handling, be discovered, dare, fight, win fight, finish handling	$v-c$	$t_s+t_{h_1}+t_f+t_{h_2}$	$\gamma\kappa p_h\hat{p}_s\alpha$
I-2	find food, start handling, be discovered, dare, fight, lose	$-c$	$t_s+t_{h_1}+t_f$	$\gamma\kappa p_h\hat{p}_s(1-\alpha)$
I-3	find food, start handling, be discovered, dare, win conflict, finish handling	v	$t_s+t_{h_1}+t_{h_2}$	$\gamma\kappa p_h(1-\hat{p}_s)$
I-4	find food, start handling, be discovered, be careful, lose conflict	0	$t_s+t_{h_1}$	$\gamma\kappa(1-p_h)\hat{p}_s$
I-5	find food, start handling, be discovered, be careful, win peaceful contest, finish handling	v	$t_s+t_{h_1}+t_{h_2}$	$\gamma\kappa(1-p_h)(1-\hat{p}_s)\alpha$
I-6	find food, start handling, be discovered, be careful, lose peaceful contest	0	$t_s+t_{h_1}$	$\gamma\kappa(1-p_h)(1-\hat{p}_s)(1-\alpha)$
II	find food, start handling, be undiscovered, finish handling	v	t_s+t_h	$\gamma(1-\kappa)$
III-1	find handler, dare, fight, win fight, finish handling	$v-c$	$t_s+t_f+t_{h_2}$	$(1-\gamma)p_s\hat{p}_h\alpha$
III-2	find handler, dare, fight, lose fight	$-c$	t_s+t_f	$(1-\gamma)p_s\hat{p}_h(1-\alpha)$
III-3	find handler, dare, win conflict, finish handling	v	$t_s+t_{h_2}$	$(1-\gamma)p_s(1-\hat{p}_h)$
III-4	find handler, be careful, lose conflict	0	t_s	$(1-\gamma)(1-p_s)\hat{p}_h)$
III-5	find handler, be careful, win peaceful contest, finish handling	v	$t_s+t_{h_2}$	$(1-\gamma)(1-p_s)(1-\hat{p}_h)\alpha$
III-6	find handler, be careful, lose peaceful contest	0	t_s	$(1-\gamma)(1-p_s)(1-\hat{p}_h)(1-\alpha)$

When the focal forager plays the same strategy as the population, some of these compound probabilities can be simplified:

$$\hat{\zeta}_v = \underbrace{\gamma(1-\kappa)}_{\mathrm{P(no\ conflict)}} + \underbrace{[1-\gamma(1-\kappa)]}_{P(\text{conflict})}\underbrace{[\hat{p}_s\hat{p}_h+(1-\hat{p}_s)(1-\hat{p}_h)]}_{P(\text{opponents same strategy})}\alpha + \underbrace{\gamma\kappa(1-\hat{p}_s)\hat{p}_h+(1-\gamma)\hat{p}_s(1-\hat{p}_h)}_{P(\text{only focal aggressive})} ,$$

$$\hat{\zeta}_c = \hat{\zeta}_f = \underbrace{[1-(1-\kappa)\gamma]}_{P(\text{conflict})} \qquad \underbrace{\hat{p}_s\hat{p}_h}_{P(\text{aggressive fight})} , \qquad [9]$$

$$\hat{\zeta}_{h2} = \underbrace{[1-\gamma(1-\kappa)]}_{P(\text{conflict})}\underbrace{[\hat{p}_s\hat{p}_h+(1-\hat{p}_s)(1-\hat{p}_h)]}_{P(\text{opponents same strategy})}\alpha + \underbrace{\gamma\kappa(1-\hat{p}_s)\hat{p}_h+(1-\gamma)\hat{p}_s(1-\hat{p}_h)}_{P(\text{only focal aggressive})} .$$

FEEDBACK EFFECTS OF THE STRATEGY PLAYED BY THE POPULATION

At this point, we have fully specified the payoff function except for the rate λ_b at which searchers encounter food items owned by handlers and the rate λ_s at which handlers are discovered by searchers. Finding these two rates is somewhat complicated as both of them depend upon the fraction of foragers in one of the behavioural states; foragers will be more likely to find a food item owned by a handler when more foragers are in the handling state, and similarly, handlers will be more likely to be discovered when more of the foragers are searching. To account for this dependency, we have to keep track of the fraction of foragers $\hat{\rho}_i = \rho_i(\hat{P})$ that is in each of the three states i, where the notation indicates that these fractions are assumed to depend on the strategy of the average individual in the population, but not on the strategy of the focal forager. Under this assumption, the rate λ_b at which searchers encounter food items owned by handlers is a simple function of the rate b at which they search for food items owned by handlers, the density of foragers y , and the fraction of foragers in the handling state $\hat{\rho}_H$:

$$\lambda_b = by(\hat{\rho}_{H_0} + \hat{\rho}_{H_1}). \qquad [10]$$

This rate is independent of the fraction $\hat{\rho}_{H_2}$ of foragers handling a food item that has been contested before, because we assume that food items can be the stake of a conflict only once. Similarly, the rate λ_s at which a handler is discovered by searchers equals the product of the rate b at which foragers search for food items owned by handlers, the density of foragers y , and the fraction of foragers in the searching state $\hat{\rho}_s$:

$$\lambda_s = by\hat{\rho}_s \qquad [11]$$

Note that it is through the rates λ_b and λ_s that intake rate depends on the density of foragers.

What remains to be done is to determine the fractions $\hat{\rho}_i$ of foragers in each of the three behavioural states i . At equilibrium, these fractions $\hat{\rho}_i$ will equal the relative amount of time that the average individual in the population of foragers spends in each of the behavioural states. Therefore, the fraction of foragers in each state follows naturally from the expectations on time allocation, which in turn follow from the compound probabilities $\hat{\zeta}_k = \zeta_k(\hat{P})$ of reaching consequence k :

$$\hat{\rho}_s = \frac{E_{\hat{P},\hat{P}}(t_s)}{E_{\hat{P},\hat{P}}(T)} = \frac{t_s}{E_{\hat{P},\hat{P}}(T)} \ , \tag{12}$$

$$\hat{\rho}_{H_0} = \frac{E_{\hat{P},\hat{P}}(t_{h_0})}{E_{\hat{P},\hat{P}}(T)} = \frac{\hat{\zeta}_{h_0} t_h}{E_{\hat{P},\hat{P}}(T)},$$

$$\hat{\rho}_{H_1} = \frac{E_{\hat{P},\hat{P}}(t_{h_1})}{E_{\hat{P},\hat{P}}(T)} = \frac{\hat{\zeta}_{h_1} t_{h_1}}{E_{\hat{P},\hat{P}}(T)} \ ,$$

$$\hat{\rho}_{H_1} = \frac{E_{\hat{P},\hat{P}}(t_{h_2})}{E_{\hat{P},\hat{P}}(T)} = \frac{\hat{\zeta}_{h_2} t_{h_2}}{E_{\hat{P},\hat{P}}(T)} \ ,$$

$$\hat{\rho}_F = \frac{E_{\hat{P},\hat{P}}(t_f)}{E_{\hat{P},\hat{P}}(T)} = \frac{\hat{\zeta}_f t_f}{E_{\hat{P},\hat{P}}(T)} \ ,$$

The expectated time consequences for the average individual in the population resembles the denominator of equation [7], but differs from it because the expected time consequences in equation [12] depend on the compound probabilities $\hat{\zeta}_k$ of reaching consequence k, whereby the compound probabilities depend on the strategy played by the population, but not on the strategy played by the focal forager :

$$E_{\hat{P},\hat{P}}\ (T) = t_s + \hat{\zeta}_{h_0} t_h + \hat{\zeta}_{h_1} t_{h_1} + \hat{\zeta}_{h_2} t_{h_2} + \hat{\zeta}_f t_f \ . \tag{13}$$

MODEL ANALYSIS

To analyze the evolutionary dynamics of interference behaviour we rely on techniques from *Adaptive Dynamics* theory (Dieckmann & Law 1996; Metz et al. 1996; Geritz et al. 1998; Hofbauer & Sigmund 1998; van Doorn et al. 2003a,b). According to this theory, the evolutionary rate of change of a strategy $\hat{P}$ is given by the following dynamical equation (Dieckmann & Law 1996):

$$\frac{\partial \hat{P}}{\partial \tau} = \mathrm{M} \left. \frac{\partial F_{P,\hat{P}}}{\partial P} \right|_{P=\hat{P}} \ , \tag{14}$$

where τ is a measure of evolutionary time. Here, M is a *mutational variance-covariance matrix*, which, in our case, captures the genetic variance in the two strategic components (p_s and p_h), and the covariance between them. The second term on the right hand side of equation [14] is the *selection gradient*, which is the slope of the relationship between the fitness $F_{P,\hat{P}}$ of a mutant playing strategy $P = P(p_s, p_h)$ in a population of individuals playing strategy $\hat{P} = P(\hat{p}_s, \hat{p}_h)$ and the mutant's strategy P, evaluated at the point where the mutant's strategy equals the strategy of the residents (i.e., where $P = \hat{P}$). Here, the appropriate measure of fitness is the long term population growth rate of the mutant population in an environment set by the residents, that is, the *invasion fitness* (Metz et al. 1992; Rand et al. 1994). From equation [14] the full dynamics of evolving traits can be deduced. Evolution will end at *singular points* (Metz et al. 1996), where a change in evolutionary time does not result in a change in the trait value, that is, where equation [14] equals zero. The (invasion and convergence) stability of singular points can be deduced from the second order derivatives of the fitness function (e.g., Matessi & Pascuale 1996; Geritz et al. 1998; van Doorn et al. 2004).

A SPECIFIC IMPLEMENTATION

The approach developed in the preceding paragraphs applies to models of the evolution of interference behaviour in general. In this section, we describe a specific implementation that we developed to illustrate the use of our approach by means of some predictions. In the next section we present these predictions.

As an approximation of invasion fitness, we used the payoff function associated with foraging. Given the complexity of our payoff function (i.e., equation [7]), we refrained from analysing the second order derivatives of our payoff function. Instead, we invoked numerical techniques to find the singular points of interference behaviour. In doing so, we restricted our attention to finding convergence stable endpoints of evolution, that is, endpoints that can be reached by evolution; the specific form of the payoff function used in our model ensures that convergence stable endpoints are also ESSs, that is, that they are stable against invasions (see Appendix).

To determine the convergence stable endpoints of evolution, we evaluated a grid of searcher and handler tendencies to dare (i.e., a grid of p_s and p_h values). For each combination of the strategic parameters in our grid, we studied the performance of mutants playing against a population of residents with that combination of strategic parameters. If the mutant did better than the resident, we adjusted the resident strategy in the direction of the mutant's strategy. For each of the points in our grid we repeated this procedure till the resident strategy converged to a stable endpoint. Practically, this was achieved by solving equation [14] for each point in our grid, using a standard algorithm for the numerical integration of ordinary differential equations; specifically, we used the 'odeint' Runge-Kutta driver with adaptive step size control as described in Press et al. (1992, p719). To exclude evolution towards equilibrium strategies that are sensitive to occasional errors in decision-making, we imposed all strategic parameters to lie within the rage $[\delta, 1-\delta]$, that is, we used the ‘trembling hand’ approach (Selten 1975). For all calculations we set δ equal to 10^{-6}. In our simulations, we used the following implementation of the mutational variance-covariance matrix:

$$M = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}, \qquad [15]$$

assuming that both strategic components are fully subjected to natural selection (i.e., there is no constraint on the genetic variation in either component; the diagonal elements equal 1), and that the two strategic components evolve independent of each other (i.e., there is no covariance; the off-diagonal elements equal zero). The predictions presented below were all generated from a single set of parameters ($c = 1$, $t_f = 2$, $t_h = 1$, $v = 10$, and $\alpha = \frac{1}{2}$).

MODEL PREDICTIONS

EVOLUTIONARILY STABLE INTERFERENCE BEHAVIOUR

We find three evolutionarily stable interference strategies : 1) to always dare (i.e. $p_s = 1$, $p_h = 1$), 2) to always be careful as a searcher and to always dare as a handler (i.e. $p_s = 0$, $p_h = 1$), and 3) to always dare as a searcher and to always be careful as a handler (i.e. $p_s = 1$, $p_h = 0$). Following Mesterton-Gibbons (1992), we refer to these three strategies as the Hawk, the Bourgeois and the anti-Bourgeois strategy, respectively. We do not find stable internal endpoints, and no endpoints on the boundaries of strategy space other than the three corner strategies mentioned above, meaning that no mixed strategy (‘to dare sometimes as a searcher, and to dare sometimes as a handler’) or semi-mixed strategy (‘to dare sometimes either as a searcher or as a handler’) is evolutionarily stable. Also, we do not find the *Dove* strategy (‘to always be careful’) to be evolutionarily stable. We do find that evolution can sometimes lead to alternative stable strategies. Which (combination) of the three evolutionarily stable interference strategies is reached depends on the rate of at which unhandled food is encountered and the rate of competitor encounter by (Figure 6.2).

When the rate at which unhandled food is encountered ax is low, the Hawk strategy evolves, regardless of the rate of competitor encounter by (Figure 6.2) and regardless of the strategic behaviour of the searchers and the handlers originally present in the population (Figure 6.3A). The Hawk strategy does best at this ecological condition because individuals that do not play the Hawk strategy save some time from fighting, but they do not find much food in this time saved from fighting, since the food encounter rate is low.

When the rate of food encounter is intermediate and the rate of competitor encounter is high, evolution can lead to all three of the evolutionarily stable

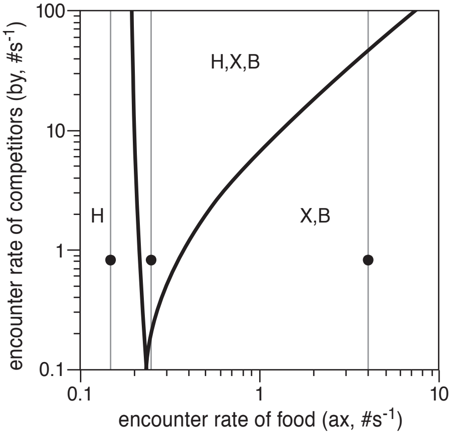

Figure 6.2. The outcome of evolution in relation to the rate at which unhandled food items are found (*ax*) and the rate at which competitors are encountered (*by*).Three regions are predicted that differ in the presence of the Hawk strategy (H), the anti-Bourgeois strategy (X) and the Bourgeois strategy (B) as potential outcomes of evolution. Symbols correspond to the parameter combinations of food encounter rate and competitor encounter rate used in Figure 6.3. Thin grey lines correspond to the food encounter rates for which the interference curves are given in Figure 6.4. Parameters values used: c = 1.00, t_f = 2.00, t_h = 1.00, v = 10.00, α = 0.50 .

interference strategies (Figure 6.2). Which of the three strategies is actually reached does not depend on the ecological conditions; rather, it depends on the strategies originally present in the population, and hence on the history of the population (Figure 6.3B). At most initial combinations of the two strategic components (p_s and p_h) the Hawk strategy evolves. However, if the initial tendency to dare is high for searchers but low for handlers, or if the initial tendency to dare is low for searchers but high for handlers, evolution leads to the anti-Bourgeois and the Bourgeois strategy, respectively. That the Bourgeois and anti-Bourgeois strategies can be evolutionarily stable may come as a surprise. The Bourgeois strategy can be stable, because when the resident population plays the Bourgeois strategy, a mutant that sometimes dares as a searcher ($p_s > 0$) is certain to gain resistance, and thus to lose time an energy to fights, whereas it will be certain not to lose time when finding food itself, given that a Bourgeois strategist never dares as a searcher. Similarly, when the resident population plays anti-Bourgeois, a mutant that sometimes dares as a handler ($p_h > 0$) is certain to lose time and energy to fights, whereas the same individual will be certain not to lose time when it gives away its food item and dares some other individual that owns a food item, given that an anti-Bourgeois strategist never dares as a handler.

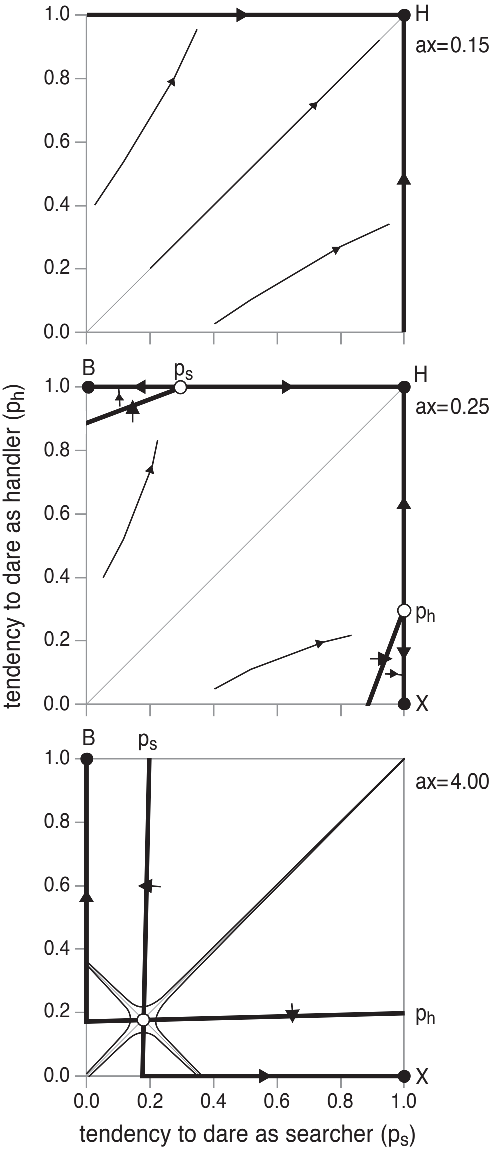

Figure 6.3. Trajectory plots showing how the tendency to dare as a searcher (p_s) and as a handler (p_h) evolve at low ($ax = 0.15$), intermediate ($ax = 0.25$), and high ($ax = 4.00$) rates of food encounter ($by = 0.80$, $c = 1.00$, $t_f = 2.00$, $t_h = 1.00$, $v = 10.00$, $\alpha = 0.50$). Open and filled dots indicate unstable and stable singular points, respectively, whereby the letters indicate the Hawk strategy (H), the Bourgeois strategy (B), and the anti-Bourgeois strategy (X). Thick black lines are isoclines for the tendency to dare as a searcher (p_s) or as a handler (p_h). Thin black lines are examples of evolutionary trajectories. Dotted lines are borders lines of different domains of attraction (separatrices).

When the rate of food encounter is high and the rate of competitor encounter low or intermediate, evolution leads to either the anti-Bourgeois or the Bourgeois strategy (Figure 6.2): any population that starts with a higher tendency to dare as a searcher than to dare as a handler evolves to the anti-Bourgeois strategy, and all other populations evolve towards the Bourgeois strategy (Figure 6.3C). At these ecological conditions, the Hawk strategy is not evolutionarily stable. Apparently, the probability to find and consume food without being discovered is so high, that it does not pay to spend time and energy on fights.

ECOLOGICAL CONSEQUENCES

Knowing the evolutionarily stable interference strategies, we can consider the interference effects that can be expected at the various ecological conditions. To do so, we study the relationship between the payoff of foraging and the rate at which competitors are encountered by, because we think that it is the combination of forager density y and the area of discovery of handlers b, rather than forager density per se, that matters.

When the rate at which unhandled food is encountered is low, only the Hawk strategy is evolutionarily stable (Figure 6.3A). In a population that plays the Hawk strategy, the payoff to foraging decreases with the rate at which competitors are encountered; at higher forager densities, more time is lost on fighting (Figure 6.4A). Even though the Bourgeois strategy and the anti-Bourgeois strategy will yield a higher payoff when played by all members of the population, playing Hawk is the best option for any individual; the Bourgeois strategy and the anti-Bourgeois strategy are not evolutionarily stable with respect to invasion by individuals that plays the Hawk strategy.

When the rate of food encounter is intermediate, the Bourgeois and the anti-Bourgeois strategy are the only stable strategies at low competitor encounter rates. At the higher competitor encounter rates, the Hawk strategy is also evolutionarily stable (Figure 6.3B). Interestingly, the payoff to foraging only decreases with forager density in populations that play the Hawk strategy; in populations that play the anti-Bourgeois strategy or the Bourgeois strategy no such interference effect is present (Figure 6.4B). The reason for this is that in populations that play the anti-Bourgeois strategy or the Bourgeois strategy overt fighting is absent. In a population that plays the Bourgeois strategy or the anti-Bourgeois strategy, non-aggressive conflicts (i.e., conflicts in which only one of the two opponents dares) do take place, but such conflicts are assumed to bear no costs. It is interesting to note that at the higher competitor encounter rates, populations in which all individuals play the Bourgeois strategy or the anti-Bourgeois strategy achieve a higher foraging payoff than populations in which individuals play the Hawk strategy. Nevertheless, the best strategy for an individual in the population where all individuals play the Hawk strategy still is to play the Hawk strategy itself.

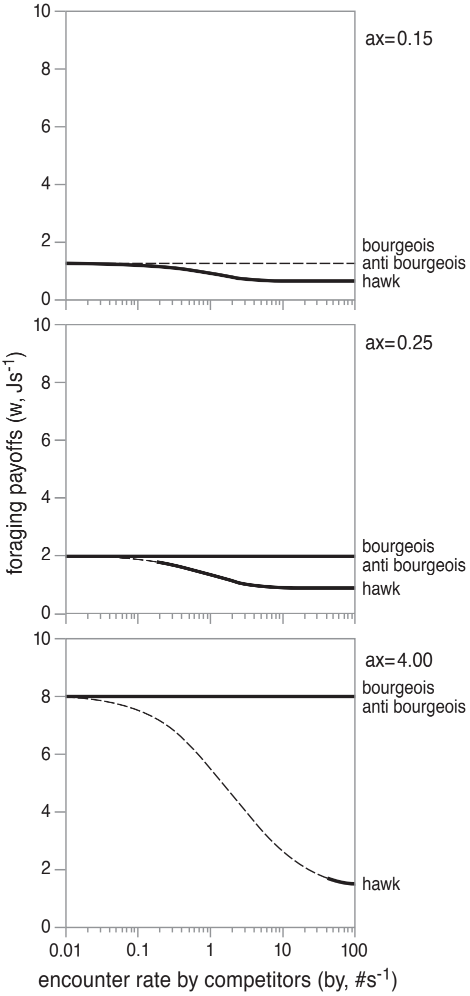

Figure 6.4. Interference curves showing how the foraging payoff ($W\hat{p}$) depends on the competitor encounter rate (by) at low ($ax = 0.15$), intermediate ($ax = 0.25$), and high ($ax = 4.00$) rates of food encounter ($c = 1.00$, $t_f = 2.00$, $t_h = 1.00$, $v = 10.00$, $\alpha = 0.50$), for populations playing the Hawk strategy, the anti-Bourgeois strategy or the Bourgeois strategy. Solid and dotted lines indicate those parts of the interference curves for which the strategy played is and is not among the stable outcomes of evolution, respectively.

When the rate of food encounter is high, results are qualitatively the same as when the rate of food encounter is intermediate, but in populations that play the Hawk strategy the interference effect is much larger, and the Hawk strategy is only evolutionarily stable at high forager densities (Figure 6.4C).

SOME GENERAL CONCLUSIONS

It was the main purpose of this paper to develop a conceptual contribution to modelling the evolution of interference behaviour. For that reason, we do not pretend to give a complete analysis of the model sketched above. Nevertheless, some general conclusions can be drawn regarding the evolutionary stability of interference strategies. First, we predict that evolution does not lead to the Dove strategy (to never dare); foraging animals will always be aggressive, either as a handler (Bourgeois strategy), or as a searcher (anti-Bourgeois strategy) or both as a searcher and as a handler (Hawk strategy). This prediction is not specific to the fact that foraging animals play the Hawk-Dove game repeatedly; given the presence of an asymmetry, the Hawk-Dove game generates the same predictions when it is played as a one-shot game (Maynard Smith 1982). Second, we predict that foraging animals in their role of searcher or handler will either always behave aggressively or never; we find no stable mixed strategies to evolve. When the encounter rate with unhandled food items is high, we do find an internal equilibrium point, but this is a saddle-point; the strategy to dare as a searcher evolves towards this equilibrium point, but the strategy to dare as a handler evolves away from it, so that evolution does not actually lead to this point. Third, we find that under certain ecological conditions, alternative interference strategies can be evolutionarily stable; which of the alternative strategies actually do evolve only depends on the interference strategies present at the start of evolution, and thus on the history of the population. This might explain why ecologically similar species or populations often differ strikingly in their behaviour towards conspecific foragers.

With regard to interference effects, we find that interference effects are only to be expected when populations play the Hawk strategy, that is, when foragers always behave aggressively. In populations that play the Bourgeois or the anti-Bourgeois strategy, intake rate is independent of forager density. These results imply that from an evolutionary perspective, interference effects cannot be taken for granted; at a substantial range of ecological conditions, foraging animals do not suffer from density-dependent effects. These predictions, however, should be interpreted with care, because they rely heavily on the assumption that conflicts in which only one of the opponents behaves aggressively bare no cost, neither in energy nor in time. Introducing a cost to losing a conflict in which only one of the two opponents dares may well make the evolution of the Bourgeois strategy and the anti-Bourgeois strategy less frequent, and it will introduce an interference effect to populations playing either of these two strategies. Although it seems unlikely that conflicts in which only one of the opponents behaves aggressively will be costly for the opponent winning such a conflict, the costs of such conflicts may be substantial for the opponent losing it, for instance, because it spends a considerable amount of time in running away from its opponent. Alternatively, it could be that interference competition among foraging animals is mainly due to 'non-adaptive' interference effects, such as loss of concentration or loss of control over search paths.

ASSUMPTIONS AND PITFALLS

In developing our approach, we have introduced a number of crucial ingredients that, according to us, should feature prominently in all models of the evolution of interference behaviour. These ingredients include (1) the structure of interactions, (2) the constraints that potentially arise through feedback effects of the strategy played by the majority of the foragers, (3) assumptions on asymmetries among foraging animals, (4) the precise form of the payoff function evaluated and (5) the techniques invoked to analyse the evolutionary stability of interference strategies. In this section, we determine how these features have been addressed by each of the models presented in Table 6.1, and where possible, we will relate these characteristics to the predictions generated by these models (Table 6.2).

INTERACTION STRUCTURE

We find the basic structure of the various models to vary considerably (Table 6.5). To identify some of these differences, the decision tree proves very useful. Among others, the decision tree helps to reveal the consequences of constraints imposed deliberately by the various models (the '–' signs). In the models of Dubois, for instance, it is assumed that foragers are always discovered when handling a food item (i.e., path II is excluded from their model). Similarly, Broom et al. (2004a,b) deliberately exclude the paths in which both opponents are careful (i.e., path 5 & 6 of the conflict module). Several of the models also constrain the strategic options of the foragers. Broom and Ruxton (1998, 2003a,b) assume that only searchers have the choice to act aggressively upon encountering a competitor; foragers that are discovered while handling a food item have no option but to respond aggressively to an encounter (i.e., $p_h = 1$). This assumption excludes three of the paths of the conflict module (Figure 6.1: path 3, 5 & 6). Dubois et al. (2003) assume that searchers only dare when their handling opponent does (i.e., path I-3 & I-4 are excluded). Sirot (2000) assumes that foragers apply the same aggressive strategy when in the searcher role as when in the handler role. These constraints on the foragers' strategies implicitly introduce assumptions on the genetics underlying interference behaviour. Assuming that handlers have no choice but to behave aggressively, for instance, implies that there is no variation in the second strategic component. In terms of the mutational variance-covariance matrix this comes down to assuming the lower diagonal element to be zero. Assuming that the tendency to behave aggressively is independent of the behavioural state of foragers implies

Table 6.5. Classification of evolutionary models of interference competition according to our decision tree approach

	I						path† II	III					
reference	1	2	3	4	5	6		1	2	3	4	5	6
Broom & Ruxton 1998	0	0	-	0	-	-	+	+	0	-	+	-	-
Broom & Ruxton 2003 a	0	0	-	0	-	-	0	+	+	-	0	-	-
b	+	+	-	0	-	-	+	+	+	-	0	-	-
Broom et al. 2004	0	0	0	0	0	0	+	+	+	+	+	-	-
Sirot 2000	+	+	+	+	+	+	+	+	+	+	+	+	+
Dubois et al. 2003	+	+	-	-	+‡		-	0	0	0	0	0	0
Dubois & Giraldeau 2003	+	+	+	-	+‡		-	0	0	0	0	0	0
Dubois & Giraldeau 2005	+§		+	+	+‡		-	+§		+	+	+‡	

† Indicated is whether each of the paths of the decision tree is included (+), ignored (0) or excluded by explicit assumptions (-). Latin numbers indicate whether foragers enter the conflict model after having found food themselves (I), after having found handlers (III), or do not enter the conflict model (II). Roman numbers indicate the six paths of the conflict model.

‡ It is assumed that food items are shared among opponents, rather than that there is a peaceful con test between the opponents.

§ It is assumed that food items are shared among opponents, rather than that there is a fight.

full covariance between the two strategic components (the off-diagonal elements of the variance-covariance matrix equal one). Although such constraints can in principle be defended as applying to specific systems, they generally are not defended as such; they more or less just slip into the models. To us, these assumptions seem unnecessary restrictive. Systematic characterisation of a decision tree will have the advantage that constraints imposed on the model have to be motivated explicitly.

Much more important, however, is the role of the decision tree with respect to constraints imposed implicitly on the model; in several models, one or more of the paths through the decision tree is not included in the payoff function (the '0's in Table 6.5). In all cases, the authors apparently are not aware that these aspects can play an important role in their model. In some models, this leads to major inconsistencies in the interaction structure. In the models of Broom and Ruxton (1998, 2003a,b), for instance, focal foragers in the searching state can find handlers to interact with (i.e., path III is included), but they themselves can not be detected by other searchers when handling a food item (i,.e., path I is ignored). Similarly, while Dubois et al. (2003) and Dubois and Giraldeau (2003) assume that focal foragers handling a food item are always detected by other searchers (i.e., path I), the possibility that a focal searcher finds a food item owned by a handler (i.e., path III) is neglected.

FEEDBACK EFFECTS

One of the crucial elements of the approach developed in Section 2 is that we explicitly acknowledge the presence of feedback effects; while the (aggressive) behaviour of a foraging animal depends on the role it plays in a conflict (i.e., searcher or handler), the probability of playing these roles in turn depends on the aggressive behaviour of other foragers, or more precisely, of the resident individuals. We find two such feedback effects. First, the rate λ_b at which searchers encounter food items owned by handlers depends on the fraction of foragers in the handling state. Second, the rate λ_s at which handlers are discovered by searchers depends on the fraction of foragers in the searching state. Indirectly, several other parameters are also affected by the behaviour played by the population. Both the expected time to find either a food item, or a handler t_s and the probability γ of a searcher finding an unhandled food item depend on λ_b. Similarly, both the probability κ of a handler being discovered by a searcher and the expected handling time invested before discovery t_{h_1} depend on λ_s. The reason why these feedback effects feature in evolutionary models of interactions among foraging animals, is that foraging animals interact repeatedly, and that the payoff functions of an interacting foragers depends on the summed outcome of several interactions. This creates the possibility of carryover effects through the fraction of foragers in each of the behavioural states. If each interaction could have been evaluated on itself, feedback effects would not have been an issue.

Several of the evolutionary models of interference competition do not acknowledge any of these feedback effects (Table 6.6); either ignoring them ('0's) or excluding them through explicit assumptions ('-' signs). Some of the other models do realise that λ_b and λ_s depend on the strategy played by the population, but they do not acknowledge that some of the other parameters are indirectly, through their dependency on either λ_b or λ_s, also affected by the population strategy. For instance, Sirot (2000) acknowledges that both the rate at which a handler is discovered by a searcher and the probability that this occurs, depends on the fraction of searchers. However, he does not account for the fact that the time spent handling before being discovered likewise depends on the fraction of searchers; rather he assumes that handlers are discovered after having spent half of the handling time.

Exclusion of any of the feedback effects seems unwanted because the presence of feedback effects can have far-reaching consequences for the outcome of evolutionary games. First, feedback effects can cause supposedly independent parameters to depend (implicitly) on the behaviour of the population of foraging animals. A more subtle, but potentially much more important effect of the feedback effects is that they can introduce non-linearities to payoff function that would otherwise have been linearly dependent on the strategies of both residents and mutants. Indeed, due to feedback effects through λ_b or λ_s, the payoff

Table 6.6. Feedback effects of strategy on various parameters of evolutionary models of interference competition.

reference		feedback effects[†]					
		λ_b	γ	t_s	λ_s	κ	t_{h_1}
Broom & Ruxton 1998		0	0	0	0	0	0
Broom & Ruxton 2003	a	+	0	0	+	0	0
	b	+	+	+	+	+	+
Broom et al. 2004		+	+	+	0	0	-
Sirot 2000		+	+	0	+	+	0
Dubois et al. 2003		0	0	0	-	-	-
Dubois & Giraldeau 2003		0	0	0	-	-	-
Dubois & Giraldeau 2005		0	-	0	-	-	-

[†] Indicated is whether feedback effects of the strategy played by the population through each of six parameters are included (+), ignored (0) or excluded by explicit assumptions (-).

developed in Section 2 is a non-linear function of the strategy played by resident individuals. As much of evolutionary game theory was developed for linear matrix games, an important corollary of this is that insights from evolutionary game theory need no longer apply to the Hawk-Dove game when this is embedded in a foraging context. To give an example, it is a well-known theorem of evolutionary game theory that in the presence of asymmetries, no mixed strategies can evolve (Selten 1980). This theorem, however, was derived under the assumption of a bilinear payoff function (i.e., linear to both the strategy of mutants and the strategy of residents). Given that the payoff to foraging is a non-linear function of the interference strategy played by residents, this theorem cannot be invoked to exclude mixed strategies as possibly evolutionarily stable. In work on territorial animals, the presence or absence of feedback effects has indeed been shown to affect the occurrence of mixed strategies as potential outcomes of evolution. Eshel and Sansone (1995), for instance, who analyzed a Hawk-Dove game with a role-asymmetry, predicted no mixed ESS when feedback effects (of the strategy played by residents on the probability to find an empty territory and the probability to be discovered when owning a territory) were neglected, but semi-mixed ESSs, that is, strategies that were mixed in one of two components, when such feedback effects were acknowledged. Another subtle, but potential highly important consequence of feedback effects is that the choice of the payoff function may become much more important. In the presence of feedback effects, the usefulness of different currencies as approximations of invasion fitness depends strongly on the precise way feedback effects act upon the evolutionary game (Mylius & Dieckmann 1995).

ASYMMETRIES

All models assume opponents in a conflict to differ in their role; foragers enter a conflict either as a searcher or as a handler. In most of the models, foragers are allowed to make their strategy dependent on this role; foragers have a separate tendency to dare as a searcher and as a handler (Table 6.7). Sirot (2000), however, does not allow for this role-asymmetry; interaction games in his model are symmetric, as he assumes foragers to have the same tendency to dare when entering a conflict as a searcher as when entering a conflict as a handler (i.e., $p_s = p_h$). By assuming this, Sirot reduces the strategy space subjected to evolution to a one-dimensional axis (corresponding to the positive diagonal of Figure 6.3), excluding the Bourgeois strategy, the anti-Bourgeois strategy and any semi-mixed strategy as potential outcomes of evolution. This difference between the model of Sirot (2000) and the other models is substantial; from classical evolutionary game theory it is well-known that the introduction of even the most minor asymmetries can drastically change the set evolutionarily stable strategies corresponding to a conflict (Maynard-Smith and Parker 1976; Hammerstein 1981). While the symmetric Hawk-Dove game, for instance, predicts a mixed strategy as a possible outcome of evolution, an evolutionarily stable strategy of an asymmetric Hawk-Dove game can only be obtained in pure strategies (Selten 1980). This might explain why Sirot (2000) predicts a mixed strategy to evolve, whereas no such strategy is predicted to evolve in the model developed in this paper; the stable mixed strategy of Sirot's symmetric game may well correspond to the instable saddle-point found at the high food conditions in the asymmetric model developed in Section 3 (Figure 6.3C).

Table 6.7. Asymmetries assumed in models of the evolution of interference behaviour.

reference		asymmetry role	 RHP[†]	 payoff[†]
Broom & Ruxton 1998		yes	0.5	0
Broom & Ruxton 2003	a	yes	0.5	$f(-)$
	b	yes	0.5	0
Broom et al. 2004	a	yes	0.5	0
	b	yes	$f(-)$	0
Sirot 2000		no	0.5	0
Dubois et al. 2003		yes	$f(fa)$	$f(-)$
Dubois & Giraldeau 2003		yes	0.5	$f(se)$
Dubois & Giraldeau 2005		yes	0.5[‡]	$f(-)$

[†] Indicated is whether the chance of winning a conflict (α) or the finder's advantage (d) is specified, or variable ($f(\,)$). In the latter case it is additionally indicated whether these parameters are a function of either the fighting ability (fa) or the searching efficiency (se) of the focal forager, or independent of any such characteristic (-).

[‡] The probability to win from another individual is fixed at 0.5, but as the number of contestants can exceed two and depends on the population strategy, the realized probability to win a fight is variable.

In addition to a role-asymmetry, several of the models allow the foragers to differ in either their resource holding potential (RHP), in the payoff associated with their behaviour, or in both these aspects. Broom et al. (2004b) and Dubois et al. (2003) introduce a RHP-asymmetry by allowing opponents to differ in their ability to win conflicts (α). Broom and Ruxton (2003a), in their 'apple model' introduce a payoff-asymmetry by assuming that handlers are certain to get a part of the food item proportional to the time they invest in handling. Similarly, in the models of Dubois, a payoff-asymmetry is introduced through the assumption of a finder's advantage d; foragers that find a food item get at least a part of the resource, regardless of the outcome of the conflict. In the model of Dubois and Giraldeau (2003), the payoff-asymmetry is enhanced by individual differences in searching efficiency; efficient searchers receive the finder's advantage more often. All of these asymmetries elaborate the basic Hawk-Dove game; while the symmetrical game is a special case of the role-asymmetric game, games without difference in RHP or with no payoff-asymmetry are but special cases of the RHP-asymmetric and the payoff-asymmetric game, respectively. Introduction of different asymmetries, or different combinations of asymmetries may lead to radically different predictions (Eshel 2005), rendering the models incomparable.

PAYOFF FUNCTION

All models use a short-term currency to approximate fitness. The general justification for this approach is to assume a positive relationship between intake rate and 'real' fitness. Although this assumption is common to most work on foraging animals (Stephens & Krebs 1986), the evidence supporting it is limited (but see Lemon 1991). Moreover, the generality of this assumption has been doubted (Maurer 1996). Moreover, the conditions that the relationship between intake rate and invasion fitness should fulfil in order for intake rate to be a useful approximation of invasion fitness are far from obvious. Determining these conditions, however, is a task on itself; here, we restrict ourselves to noting that a pure monotonous relationship does not guarantee that the same evolutionarily stable interference strategies are found when intake rate is used as when invasion fitness is used. Minimally, the relationship between intake and fitness should be linear (i.e., $F_{P,\hat{p}} \propto W_{P,\hat{p}}$).

The precise currency evaluated differs between the models (Table 6.8). Broom and Ruxton, in all their models, assume that there is no energetic cost to fighting (i.e., $c = 0$). Consequently, in most of their models they evaluate the expected time costs of interference behaviour; only in their apple model (Broom & Ruxton 2003a) they also consider the gains from fighting behaviour. These gains however, can easily be expressed in terms of time, given that there is a linear relationship between invested handling time and gain. Dubois and Giraldeau (2003) assume that both handling and fighting do not involve time

Table 6.8. Assumptions on the energy and time consequences and the currency evaluated in evolutionary models of interference competition.

		energy†	time†		currency
reference		c	t_h	t_f	
Broom & Ruxton 1998		0	$f(-)$	$f(-)$	$E(T)$
Broom & Ruxton 2003	a	0	$f(-)$	$f(-)$	$E(\mathrm{G}/T)$
	b	0	$f(-)$	$f(-)$	$E(\mathrm{T})$
Broom et al. 2004		0	0‡	$f(-)$	$E(\mathrm{T})$
Sirot 2000		$f(-)$	$f(-)$	$f(-)$	$E(\mathrm{G}) / E(T)$
Dubois et al. 2003		0	0	$f(-)$	$E(\mathrm{G}/T)$
Dubois & Giraldeau 2003		$f(-)$	0	0	$E(\mathrm{G})$
Dubois & Giraldeau 2005		$f(-)$	0	$f(-)$	$E(\mathrm{G}/T)$

† Indicated is whether the energetic cost of fighting (c), the time cost of handling (t_h), and the time cost of fighting (t_f) are assumed to be constant (0), or variable and independent of any character ($f(-)$).

‡ Broom et al., (2004) assume the handling time of food items to be zero, but in deriving their model the rely on the results of Broom and Ruxton (1998), who assume handling to cost time, so that some of the findings of Broom et al. (2004) do depend on handling time.

costs (i.e., $t_h = 0$ and $t_f = 0$). Consequently, they evaluate the expected net energy gain of interference behaviour. All other models consider the ratio of net energy gain and time, though in a subtly different way; while Broom and Ruxton (2003a), Dubois et al. (2003) and Dubois and Giraldeau (2005) consider the expectation of the ratio of net energy gain over time ('EoR': the expectation of the ratios), Sirot (2000) studies the ratio of the expectations of net energy gain and time (RoE: the ratio of expectations). The use of these two ratios has led to some ambiguity in the early literature on optimal foraging (see Stephens & Krebs 1986, Box 2.1), resulting from the fact that the average of a function is not necessarily equal to the function of the average (i.e., $E(G/T) \neq E(G)/E(T)$).

Which of these short-term currencies is to be preferred is not obvious. Use of either the expectation of the net energy gain or the expectation of the time costs seems restrictive as it assumes that either the time or the energy consequences are very small or absent. Regarding the two ratios: for biological reasons, it has been argued that the ratio of expectations (RoE) is to be preferred (Bateson & Kacelnik 1995; McNamara & Houston 1997), but the expectation of the ratio (EoR) can also be defended when the short-term performance of foraging animals is critical (Turelli et al. 1982; Stephens & Krebs 1986), or when the mental storage capacity of foragers is limited (Bateson & Kacelnik 1995). Both ratios, however, are rate-maximizing currencies, to which time constraints are implicit (Ydenberg et al. 1994). When foragers are unconstrained, or when they are constrained by energy rather than by time, currencies other than the maximization of net energy gain rate may well be more realistic (e.g., Schmid-Hempel et al. 1985; Ydenberg et al. 1994; McNamara & Houston 1997).

ANALYSIS

Most of the evolutionary models of interference competition use the classical approach to evolutionary game theory (Maynard-Smith 1982); they study the invasion stability of specific strategies by comparing the performance of different strategies when played against each other. In doing so, several of the models exclude certain strategies from analysis. Broom and Ruxton (1998, 2003a,b), for instance, by assuming that handlers always dare (i.e., $p_h = 1$), reduce the strategy space subjected to evolution to a one-dimensional axis (corresponding to the upper border in Figure 6.3). As a consequence, the Dove strategy, any mixed strategy and the anti-Bourgeois strategy are excluded from analysis.

Use of the classical approach would be appropriate for linear games, as in linear games invasion and convergence stability coincide. Due to the feedback effects of strategy on role, the payoff to foraging, however, is a non-linear function of the strategy played by residents. In non-linear games both the invasion and the convergence stability of singular strategies have to be studied, because invasion stable endpoints of evolution need not be attainable (Eshel 1983); in fact, any combination of invasion and convergence stability can occur (e.g., Geritz et al. 1998). The only study that determines whether singular points can actually be reached in the course of evolution, that is, whether they are convergence stable, is the study of Sirot (2000), who numerically evaluates the first order derivative of the payoff function. This implies that the evolutionarily stable interference strategies found by all other models may not actually be attainable in the course of evolution.

CONCLUSIONS AND IMPLICATIONS

By applying our systematic approach to some evolutionary models of interference competition, we showed that modelling interference competition may not be as straightforward a task as it may appear to be at first sight. We found that specific events and actions were easily overseen, that feedback effects of the strategy played by residents on the role of focal foragers in conflicts were generally not accounted for, and that decisions regarding the payoff function used to evaluate the foraging game were often not made explicit. Proper account of these issues yields an approach to modelling the evolution of interference behaviour that is much more complete, but it also introduces the need for more sophisticated techniques of analyses than those generally used by evolutionary models of interference competition. Together, these improvements can drastically change ideas on the evolution of interference strategies.

DIRECTIONS FOR FUTURE RESEARCH

A major assumption underlying our approach is the premise that the payoff to foraging with a certain strategy is linearly related to the invasion fitness of that strategy. Although similar assumptions underlie most work on foraging animals, such will be the case only under the most restrictive assumptions regarding the behaviour of the foraging animals and especially regarding the interaction between that behaviour and the environment (Mylius & Diekmann 1995). A more thorough derivation of the invasion fitness of a mutant strategy would, for instance, require explicit consideration of feedback effects of the strategy played by the animals on the dynamics of the foragers' prey. Although attempts have been made to reconcile game theory with explicit population dynamics (e.g., Rand et al. 1994), accounting for such feedback effects through the environment remains one of the major challenges for future research.

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APPENDIX

The payoff function of the specific implementation of our framework that we consider in the main text (i.e., equation [7]) is a non-linear function of both the resident strategy and the mutant strategy. Due to its specific mathematical form, however, this payoff function behaves as if it were a linear function of the mutant strategy. To see this, it is helpful to rephrase equation [7]:

$$W_{P,\hat{P}} = \frac{\mathrm{E(G)}}{\mathrm{E(T)}} = \frac{\zeta_v v - \zeta_c c}{t_s + \zeta_{h_0} t_h + \zeta_{h_1} t_{h_1} + \zeta_{h_2} t_{h_2} + \zeta_f t_f} = \frac{z_1 + z_2 P}{z_3 + z_4 P} \,, \qquad \text{[A1]}$$

where z_1 to z_4 are parameters that depend on the resident strategy $\hat{P}$, but not on the mutant strategy P. From equation [A1] it is obvious that both the nominator and the denominator of the payoff function are linear functions of the mutant strategy P. As was pointed out by Sirot (2000), the interesting consequence of this linearity in both the nominator and the denominator is that the sign of the selection gradient (i.e., the first derivative of the payoff function with regard to the mutant strategy) is independent of the mutant strategy:

$$\frac{\partial W_{P,\hat{P}}}{\partial P} = \frac{z_1\,(z_3 + z_4 P) - (z_1 + z_2 P) z_4}{(z_3 + z_4 P)^2} = \frac{z_2 z_3 - z_1 z_4}{(z_3 + z_4 P)^2} \,. \qquad \text{[A2]}$$

For a singular point to be invasion stable the second derivative of the payoff function to the mutant strategy should, in the neighbourhood of the singular point $\tilde{P}$, be less than zero:

$$\left.\frac{\partial^2 W_{P,\hat{P}}}{\partial^2 P}\right|_{P=\hat{P}=\tilde{P}} < 0 \,. \qquad \text{[A3]}$$

For our payoff function this criterion is not met, as the second derivative of the payoff function to the mutant strategy equals zero, just as it does in the case of a payoff function that is a linear function of the mutant strategy. This implies that no singular point is invasion stable; at singular points all mutant strategies achieve the same payoff. For our analysis, this is not problematic, as convergence stable singular points will, in the long run, behave as if they were invasion stable. The reason for this is that any time a mutant succeeds to invade a population that is at a convergence stable singular point, natural selection ensures this population to converge back to the singular point.

From a mathematical point of view, the linearity of both the nominator and the denominator of the payoff function is a very special (if not trivial) case. In fact, it can be argued that all linear games are but degenerates of the more complete non-linear games (Rand et al., 1994). An important drawback of this is that the introduction of even the slightest non-linearity with regard to the mutant strategy in either the nominator or the denominator may qualitatively affect our results, for instance by creating the possibility of evolutionary branching (Geritz et al., 1998). Such non-linearities will, for instance, arise when paths through the decision tree contain more than one conflict; such would be the case if the assumption of at most one conflict per food item would be relaxed.

CHAPTER 7

GENERAL DISCUSSION

INTERFERENCE COMPETITION AND THE DYNAMICS OF POPULATIONS

This thesis deals with interference competition among foraging waders as a research topic in itself. In the General introduction, I argued (1) that although competition holds a prominent position in ecology, the process is as yet not well understood, (2) that a proper understanding of the phenomenon requires ideas on the mechanisms of competition and on the evolution of competition-related traits, and (3) that variation between individuals is essential to the mechanisms of competition and to the evolution of competition-related characteristics. This motivated me to study the mechanisms of interference competition among foraging waders. Other students of interference competition among waders have merely been interested in the consequences of interference competition for the dynamics of populations (e.g., Goss-Custard, 1980; Ens *et al.*, 1994; Sutherland, 1996). In this chapter I discuss the link between interference competition and the dynamics of populations. I will explain why I have not touched upon this link in my own research, and I will nevertheless suggest some new directions for further study.

WHY LINKING COMPETITION TO POPULATION DYNAMICS?

Why would students of population dynamics be interested in individuals? The various arguments that have been put forward can be categorized in three groups.

DISSATISFACTION WITH CLASSICAL MODELS OF POPULATION DYNAMICS

A first motivation stems from dissatisfaction with classical models of population dynamics (for a review of these models: see Hastings, 2005; for some examples: see Figure 7.1). These models assume that the dynamics of populations can be described in terms of a single state variable (population density; DeAngelis & Gross, 1992b). This presumes that individuals are all identical, or, if it is acknowledged that they are not, that the dynamics of the population can be described adequately in terms of the average individual (DeAngelis & Gross, 1992b). Additionally, it presumes that individuals are well-mixed, such that their density is the same everywhere, with every member of the population having an equal influence on every other member of that population (Durrett & Levin, 1994). Because of its analogy with physics, this approach can be referred to as the ‘mean field’ approach (Durrett & Levin, 1994).

The use of the mean field approach in classical models of population dynamics was motivated by the success of this approach in physics (Kingsland, 1995). A well-known example of a successful application of the mean field approach

The Pearl-Verhulst logistic equation

$$dN/dt = rN\left(1-N/K\right)$$

with; N: population density, r: per capita innate capacity for increase, K: carrying capacity

The Lotka-Volterra competition equations

$$dN_1/dt = r_1N_1\,(K_1 - N_1 - \alpha_{1,2}N_2)/K_1\ ,$$

$$dN_2/dt = r_2N_2\,(K_2 - N_2 - \alpha_{2,1}N_1)/K_2\ ,$$

with; N_i: density of species i , r_i: per capita innate capacity for increase of species i ,
K_i: carrying capasity of species i , α_{ij}: inter-specific competition coefficient

The Lotka-Volterra predator-prey model

$$dN/dt = N\left(b - aP\right)$$

$$dP/dt = P\left(-d + kaN\right)$$

with; N: prey density, b: prey per capita birth rate, a: predator per capita capture rate,
P: predator density, d: predator per capita death rate, k: predator per capita conversion efficiency

The Nicholson-Bailey parasitoid-host model

$$N_{t+1} = \lambda N_t e^{-aP_t}$$

$$P_{t+1} = cN_t\,(1 - e^{-aP_t})$$

with; λ : host reproductive rate, N_t: host density at time t, a: predator per capita searching efficiency,
P_t: parasitoid density at time t, c: average number of viable eggs laid by a parasitoid

Figure 7.1. Four examples of classical models of population dynamics. Each of these models describes the dynamics of a population by a system of ordinary differential equations or difference equations, whereby the equations are unstructured: they do not account for between-individual differences in, for instance, size or age.

concerns the behaviour of gasses. In principle one might want to describe the behaviour of the whole gas in terms of the movements of all the gas molecules. As it turns out, however, the behaviour of gasses can very accurately be described in terms of the characteristics of the whole gas (Rosen, 1969; O'Neill et al., 1986; Laughlin, 2005). The key rationale underlying the mean field approach, thus, is that variation at the level of individuals averages out to yield highly constant statistical regularities at the level of populations, an idea referred to as collective exactness (Laughlin, 2005).

Dissatisfaction with the classical models of population dynamics originates from the growing awareness that individuals are unique and not mixed homogeneously (see for instance the papers in DeAngelis & Gross, 1992a). Violation of these assumptions is problematic whenever characteristics other than the mean are biologically relevant, or when the aggregated process is non-linear. Non-linearity is problematic for aggregation attempts because the average is not a good description of non-linear processes. Problems can also be expected when the aggregated process is stochastic (DeAngelis & Rose, 1992). In that case, the average may be a bad descriptor if the population size is small and/or if rare events have strong effects. Violation of the mean field assumptions can lead to qualitatively different predictions regarding the dynamics of populations (e.g., Łomnicki, 1988; DeAngelis & Rose, 1992).

Dissatisfaction with classical models of population in essence calls for an approach that accounts for variation between individuals. Any approach that wants to account for between-individual variation has to specify the extent to which it wants to do so but it also has to specify which characteristic of individuals is allowed to vary. Discussion about the first issue has been clarified by Metz and Dieckmann (1986), who identified three classes of models: p(population)-state models, i(individual)-state distribution models and i(individual)-state configuration models. P-state models do not account for differences between individuals. The classical models clearly fall into this class. I-state distribution models do allow individuals to vary; they describe the dynamics of a population by keeping track of the distribution of the characteristic(s) in which individuals vary. Leslie matrix models, for instance, account for variation in age by keeping track of the distribution of individuals over age-classes. I-state distribution models involve some aggregation (for instance, of individuals into age classes), but less aggregation than p-state models. I-state configuration models represent each individual as a separate, discrete, entity. They do not involve any aggregation. The second issue – specifying the characteristic that is allowed to vary - has attracted much less attention than the first one (Murdoch et al., 1992; van der Meer, 1997a). This issue is most apparent for i-state distribution models, where the number of characteristics is most limited. Age, sex, spatial position, size, reserves, nutritional status, behaviour, and genetics are all reasonable candidates that have featured in models of population dynamics. Although in many species (e.g., fish and invertebrates species) especially size will be a characteristic that is of importance for the dynamics of populations. Waders, however, reach adult size within weeks after birth so that size-differentiation is limited.

LINKING THE STUDY OF ANIMAL BEHAVIOUR AND POPULATION DYNAMICS

A second motivation springs from the realization that the field of animal behaviour and population biology have developed largely in isolation of each other. Students of animal behaviour have traditionally shown little interest in the consequences of behaviour for the dynamics of populations. Students of population dynamics have concentrated on the mere determination of demographic parameters (such as population growth rate and carrying capacity) without much consideration on how these parameters result from the behaviour of the members of the population. This situation has let to several pleas for linking the fields of population dynamics and animal behaviour to each other (Hassell & May, 1985; Smith & Sibly, 1985; Goss-Custard, 1985; Sutherland, 1996).

Linking the fields of animal behaviour and population dynamics should enable the interpretation of population-level parameters in terms of the behaviour of individuals (i.e., the members of the population). Thus, the plea to do so essentially is a plea for more mechanistic detail to models of population dynamics. Indeed the advantages that linking the two fields should have are the advantages attributed to mechanistic models in general. First, mechanistic models are thought to be intellectually more satisfying than their phenomenological counterparts, because they (can) provide an understanding of how phenomena come about (e.g., Hassell & May, 1985; Smith & Sibly, 1985). Second, because of this understanding, it is also thought that mechanistic models can be extrapolated to novel conditions, or at least more so than phenomenological models (Sutherland, 1996). Third, because mechanistic models specify how the phenomena under study come about, they provide extra means to select among different models (namely on the basis of the assumed mechanisms; Smith & Sibly, 1985).

INTRINSIC ADVANTAGES TO STUDYING INDIVIDUAL ORGANISMS

A third motivation is found in the conviction that there are advantages intrinsic to studying processes at the level of individual organisms. Several arguments have been invoked to support this conviction. First, individuals are the organizational level upon which selection generally acts most strongly. Therefore, studying processes at the level of individuals provides the best possibilities to embed the study of population dynamics in the theory of natural selection (e.g., Smith & Sibly, 1985; Sutherland, 1996). Second, 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). Third, individuals, unlike units of other levels of organization, come in discrete entities, making individuals the most suitable organization unit (e.g., Łomnicki, 1992; Durrett & Levin, 1994). Fourth, the traditional ecological hierarchies all intersect at least at the level of individual organisms (MacMahon et al., 1978); this suggests that the level of individual organisms may be the most appropriate level to begin to explore commonality and integration in ecology (Pickett et al., 1994). The first of these arguments – that individuals are the organizational level that can be linked most easily to the theory of natural selection – leads to an approach to population dynamics that accounts for between-individual variation, given that between-individual variation is a prerequisite for evolution by natural selection. The other three of these arguments imply an approach to studying population dynamics that is phrased in terms of characteristics of individuals.

HOW TO LINK COMPETITION TO POPULATION DYNAMICS?

Motivated by either of the above-mentioned arguments, several approaches have been developed that account for interference competition while studying the dynamics of populations ('interference-based approaches to population dynamics'). Three examples from the literature on waders are presented in Figure 7.2. The basic notions underlying these approaches are (1) that processes that determine population size may themselves dependent on population size and (2) that interference competition may be the mechanism underlying density-dependence effects. These ideas are merged with the use of the ideal-free-distribution model of Fretwell and Lucas (1970). Based on the assumption that the spatial distribution of food is heterogeneous, this model predicts the distribution of animals over patches of food, while accounting for competition effects on intake rate.

Implemented in the study of wader population dynamics these ideas yield a framework with the following main ingredients. First, processes operating during the breeding season and those operating during the rest of the year are treated separately. During the winter, the main process of relevance for the size of populations is mortality. Mortality may have various sources, including predation, diseases and starvation. Population size is thought to affect mortality through density-dependent starvation. Starvation occurs when body mass (condition) falls below a minimum. Condition is determined by intake rate, which depends on population size through exploitative competition and/or interference competition. The essential relationships underlying these frameworks are 1) the relationship between population density and intake rate, 2) the relationship between intake rate and condition (body mass), 3) the relationship between condition and population density, and 4) the relationship between the population density in one winter and that in the next. At least in the framework presented by Goss-Custard, intake rate may also affect population size directly (a higher intake rate could lead to a reduction in the time spent on dangerous foraging grounds, and therefore in a lower mortality).

ARE ARGUMENTS MET?

To what extent do interference-based approaches to wader population dynamics acknowledge the various arguments to link models of population dynamics to the behaviour and/or the characteristics of individuals?

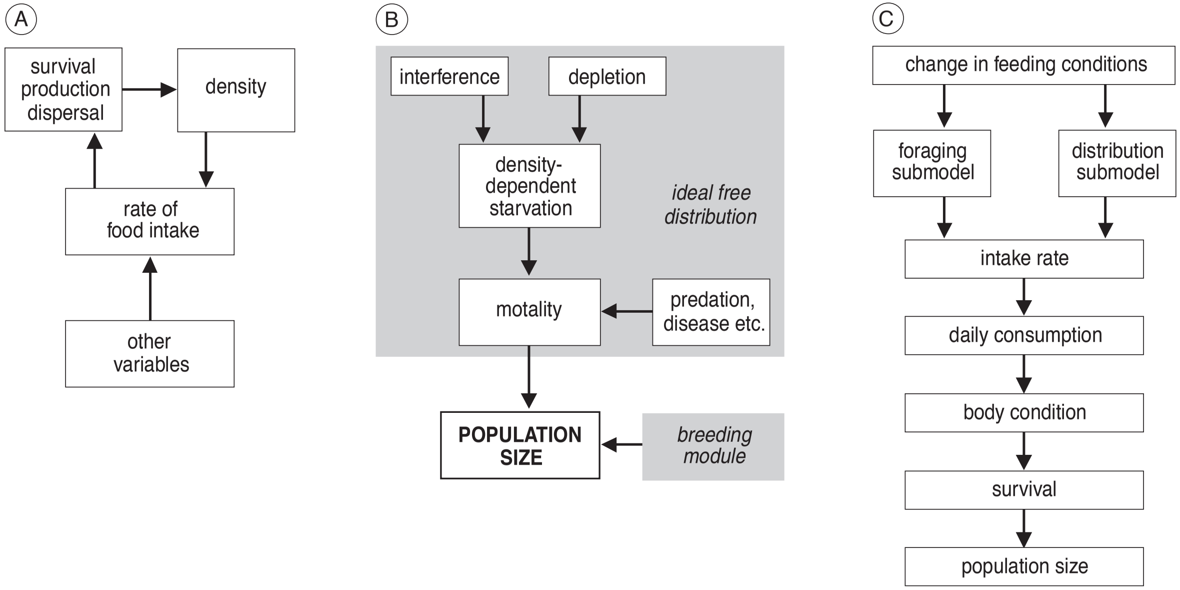

Figure 7.2. Schematic representations of the link between interference competition and population size in three examples. A: the feed-back loop for waders as explored in Goss-Custard (1980). B: the framework for linking interference and depletion outside the breeding season with territorial behaviour in the breeding season to determine population size (from Sutherland, 1996; note that I inserted all processes relevant to breeding in the box 'breeding module'). C: flow chart showing how the behaviour-based model of Stillman et al. (2000) predicts the effect of the winter mussel food supply on the body condition of individual oystercatchers and on the starvation rates of the population. Although competition and the ideal-free-distribution model are not represented explicitly in this flow chart, both play an important role in the model: competition features prominently in the foraging submodel, and the rationale behind the ideal-free-distribution model forms the essence of the distribution submodel.

DISSATISFACTION WITH CLASSICAL MODELS OF POPULATION DYNAMICS

Critics of the classical models of population dynamics made a plea for accounting for between-individual variation. All studies that link competition among foraging waders to changes in wader population size use individual-based simulation models to do so, that is they use an 'i-state configuration approach'. This approach allows for a full account of between-individual variation. It has the advantage that technical difficulties as well as aggregation problems are avoided, but the disadvantage of limited generality (Caswell & John, 1992; DeAngelis & Rose, 1992). Furthermore, the fact that there is no limit to the number of variables that is allowed to vary in i-state configuration models often hampers a proper evaluation of model behaviour. It also makes the question as to which variables are allowed to vary less relevant. Therefore, let me consider the characteristics that should *at least* feature in interference-based models of population dynamics. The use of the ideal-free-distribution model implies that individuals should at least be allowed to vary in their spatial position. The assumption that density-dependence acts through starvation further implies that individuals should also be allow to vary in condition (body mass). Perhaps surprisingly, however, in the absence of a third variable characteristic, it does not suffice to allow these two characteristics to vary. The reason for this is that according to the ideal-free-distribution model individuals all achieve the same intake rate, even though they vary in their spatial position. Therefore, individuals should be allowed to vary in at least one extra characteristic, the most obvious candidates being some characteristic directly related to the competition process, such as dominance status or competitive ability.

In modelling interference competition on itself (rather than its population dynamical consequences), analytical approaches have been used as well as simulation approaches. Van der Meer and Ens (1997) review six models of the generalized functional response. Applied in the context of the ideal-free-distribution model, these models only account for variation in the spatial position of foragers. Even though they all have a clear-cut interpretation in terms of the behaviour of individuals, they can be classified as p-state models in that they aggregate all individuals in a single state variable (forager density). Yet, some of these models of the generalized functional response have been extended to account for variation in dominance status (e.g., Sutherland & Parker, 1985; Parker & Sutherland, 1986), though this is often done in an *ad hoc* manner, whereby individuals are assumed to belong to certain competitive classes (but see van der Meer, 1997b). Such models could count as i-state distribution models, but they do not actually follow the distribution of individuals over the competitive classes. Instead, the proportion of individuals in each of the classes is assumed to be constant. Furthermore, all models that have accounted for between-individual variation in dominance status have made rather arbitrary decisions on how dominance relates to patch choice.

LINKING ANIMAL BEHAVIOUR TO POPULATION DYNAMICS

Above, I have argued that the plea for linking the fields of animal behaviour and population dynamics essentially is a plea for more mechanistic detail to models of population dynamics. In general terms interference-based approaches to wader population dynamics are indeed more mechanistic than classical models of population dynamics; they consider how the carrying capacity of a population comes about.

In more specific terms the interference-based approaches to population dynamics are all phrased in terms of the levels of organization concept, as is, for instance, apparent from the title of the book by Łomnicki (1988; Population Ecology of Individuals) and from the title of the book by Sutherland (1996; From Individual Behaviour to Population Ecology). According to the definition of mechanistic models of population dynamics as models that describe population dynamics in terms of the behaviour of individuals, interference-based approaches of wader population dynamics clearly are mechanistic. For the reasons presented in the first Reflection that follows on this General discussion, however, such may not be the most fruitful way to approach the topic.

Interference-based approaches to wader population dynamics are usually not phrased in terms of the process-rate definition of mechanistic models (as models that describe a phenomenon in terms of processes operating at a rate faster than that at which the phenomenon operates).

If mechanistic is defined as explaining how changes in population size come about while using parameters that are independently measurable, interference-based approaches to the study of population dynamics are not mechanistic. Even though mechanistic models of the generalized functional response exist (e.g., Beddington, 1975; Ruxton et al. 1992), all interference-based models of population dynamics use a phenomenological model, derived from an empirically determined relationship. Thus, all models contain at least one parameter that does not have a clear-cut mechanistic interpretation. This parameter is generally referred to as the interference coefficient ('mystery coefficient' would probably be a more appropriate reference to this parameter, given that it does not have a mechanistic interpretation) and is defined as the regression coefficient of the relationship between intake rate and forager density (several of the phenomenological models only differ in whether they apply log-transformation to intake rate, forager density or both). Although this interference coefficient may capture the interference effect, it does not specify how this effect comes about.

INTRINSIC ADVANTAGES TO STUDYING INDIVIDUALS

Studying processes at the level of individuals was argued to provide the best possibilities to embed the study of population dynamics in the theory of natural selection. In applying the ideal-free-distribution model to describe the distribution of foraging waders, interference-based approaches to population dynamics indeed adopt evolutionary thinking. The ideal-free-distribution model assumes that foraging individuals choose patches such as to maximise their intake rate. this assumption may be best justified through an argument of optimality, namely that natural selection can be expected to have weeded out all individuals that did not behave so as to maximise their intake rate. However, evolutionary considerations remain implicit; no account is made of the dynamics of evolution, nor is the performance of different patch choice strategies evaluated.

Studying processes at the level of individuals was also argued to have the intrinsic advantage that the 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). Although this argument depends on the species under study, it seems to apply to interference-based approaches to wader population dynamics.

Additionally, it was argued that individuals are the most suitable organizational units because they usually come in discrete entities, unlike units of other levels of organization (e.g., Łomnicki, 1992; Durrett & Levin, 1994). This argument would have applied to interference-based approached to the study of population dynamics if these approaches would have been free of any considerations regarding populations. Such, however, is not the case; models are still phrased in terms of characteristics of populations (density), so they still rely on the fuzzy concept 'population'.

LINKING COMPETITION AND POPULATION DYNAMICS; WHY NOT (YET)?

Even though the link between interference competition and the dynamics of populations is a very interesting one, I have not touched upon it in this thesis. Quite deliberately, I have restricted my work to the study of the interference process in itself. Linking these processes to the dynamics of populations seemed (and seems) premature to me, given that understanding of the interference process still is rudimentary. In this section I discuss (1) why I think that it is studies of the interference process that are currently most wanted, (2) what my thesis has contributed and (3) the way to proceed in the study of interference competition and its consequences.

SUBTLE DIFFERENCE WITH STRONG EFFECTS

The decision to focus the work in this thesis on the interference process, rather than on its consequences in terms of population dynamics, or even in terms of the distribution of foraging animals over food patches, mainly stems from the

MECHANISTIC MODELS

The Beddington model

$$W = \frac{ax}{1 + at_h x + 2bt_f y}$$

The Ruxton model

$$W = \frac{ax}{1 + at_h x + \dfrac{2bt_f y}{1 + at_h x}}$$

PHENOMENOLOGICAL MODELS

The Hassell-Varley model

$$W = \frac{a(y/r)^{-m} x}{1 + a(y/r)^{-m} t_h x}$$

The Doublelog model

$$W = \frac{ax}{1 + at_h x} (y/r)^{-m}$$

The Semilog model

$$W = \frac{ax}{1 + at_h x} \left(1 - m\log\,(y/r)\right)$$

The untransformed model

$$W = \frac{ax}{1 + at_h x} (1 - qy)$$

Parameter interpretation

W	$\#s^{-1}$	intake rate
x	$\#m^{-2}$	food density
y	$\#m^{-2}$	forager density
a	$m^{-2}s^{-1}$	area of discovery of food
b	$m^{-2}s^{-1}$	area of discovery of competitors
t_h	s	prey per capita handling time
t_f	s	per capita fighting time
m	–	interference coefficient
q	m^{-2}	interference area
r	$\#m^{-2}$	reference forager density

Figure 7.3. The six models of the generalized functional response reviewed by van der Meer and Ens (1997).

work of van der Meer and Ens (1997). I have already introduced this paper in the Introduction, but I will now present it in more detail.

Van der Meer and Ens (1997) start their paper by showing how the ideal-free-distribution model of Fretwell and Lucas (1970) can be used to derive predictions on the aggregative response from models of the generalized functional response. In general terms, this comes down to using the ‘ideal-free’ prediction that intake rate will be the same at all occupied food patches. Next, van der Meer and Ens (1997) gathered six different models of the generalized functional response from literature on interference competition among foraging waders (Figure 7.3). Two of these models had been derived mechanistically, through an approach resembling reaction kinetics; the other four had been derived phenomenologically. Next, they showed, both analytically and by means of a numerical example, that application of the ideal-free-distribution model to each of the six models of the generalized functional response yielded qualitatively different predictions of the distribution of foraging waders over food patches (Figure 7.4B). While some of the models of the generalized functional response

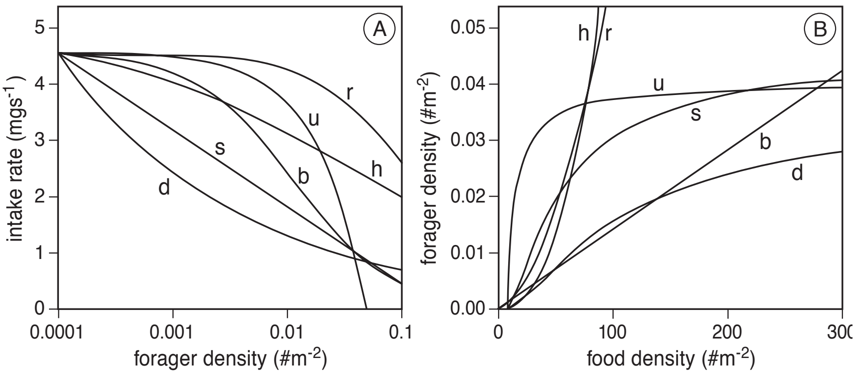

Figure 7.4. The relationship between forager density and intake rate as described by six models of the generalized functional response (A), and the predictions of the ideal-free-distribution model on the aggregative response, that is, the relationship between food density and forager density (B), for each of these six models. Model codes (h, r, b, d, s and u) and parameter values as in van der Meer and Ens (1997).

led to the prediction that forager density would be limited at high food densities (the Doublog, Semilog and Untransformed model), others led to the prediction that foragers choose patches in proportion to the food density at these patches (the Beddington model), or that foragers aggregate in the best food patches (the Ruxton model and the Hassell-Varley model). This result is striking especially because the six models yielded overlapping generalized functional response curves (Figure 7.4A) and because predictions on the aggregative response were all generated in the same way – by means of the ideal-free-distribution model.

What van der Meer and Ens (1997) showed is that predictions of the distribution of foraging waders over patches of food are sensitive to the precise form of the generalized functional response. Had the various models of the generalized functional response yielded more or less identical predictions of the aggregative response, it could have been argued that the details of the interference process did not matter. But such was not the case. Apparently subtle differences between models of the generalized functional response resulted in qualitatively different predictions regarding the aggregative response. This implies that the very choice of a model of the generalized functional response determines predictions of the aggregative response. This makes knowledge of the details of the interference process (the generalized functional response) an essential prerequisite for predictions of the aggregative response. It was this insight that was the motivation underlying my Ph.D. project to study the generalized functional response in more detail and to consider study of its consequence on the distribution of foraging animals and/or the dynamics of wader populations premature. What sense does it make to study the consequences of an arbitrarily selected model of the generalized functional response, if these consequences are sensitive to the very choice of this model?

AN INCONSISTENT FRAMEWORK

Van der Meer and Ens (1997) provided one other argument that convinced me that understanding of the interference process was still wanting. Applied to foraging animals, the ideal-free-distribution model invokes the assumption that foraging animals behave so as to maximize their intake rate. This assumption is generally justified by the idea that such behaviour is the result of natural selection. No such assumption is made in the models of the generalized functional response reviewed by van der Meer and Ens (1997). These models treat foraging animals as 'aimless billiard balls' with no choice but to act aggressively when encountering each other. Whether or not such behaviour is adaptive is not considered. Thus, use of the ideal-free-distribution model in combination with models of the generalized functional response is not quite consistent.

THE NEED FOR MECHANISMS

Given that predictions of the aggregative response are sensitive to the generalized functional response model used to generate them, the obvious question is how to select among models of the generalized functional response. Van der Meer and Ens (1997) argue against the use of phenomenological models, because such models are 'both theoretically deficient and lacking empirical support'. They argue in favour of mechanistic models, because of the 'higher theoretic appeal' of such models. As mentioned above, mechanistic models are indeed generally thought to be intellectually more satisfying than their phenomenological counterparts, because they (can) provide an understanding of how phenomena come about, and because they can be extrapolated to novel conditions, or at least more so than phenomenological models. For the specific case of selection among models of the generalized functional response, a further important argument in favour of mechanistic models is that, because mechanistic models specify how the focal phenomenon comes about, they provide extra means to select among different models; mechanistic models can be selected on the basis of the assumptions regarding the mechanisms. This latter argument is particularly of relevance here, because the qualitatively different predictions of the aggregative response were generated from models that yielded overlapping generalized functional response curves (Figure 7.4A). The overlap in the generalized functional response curves implies that it will probably be very difficult, if not impossible, to select among models on the basis of any goodness of fit criterion. Data sets in ecology are generally so variable that selection of only subtly different models of the generalized functional response may not be possible. This argument seems supported by an as yet unpublished analysis performed by Jeroen Minderman, who fitted the six models of the generalized functional response to the turnstone data of chapter 2. Indeed, in terms of explained variance, the fit was near identical for the various models even though parameter values sometimes differed consideranly.

SOME MARGINAL NOTES

Are these reasons sound? I have come to realize that some marginal notes can be made. With regard to the reasoning that predictions of the aggregative response depend on the details of the generalized functional response, at least three objections can be made. Additionally, a marginal note can be made to the 'inconsistent use of evolutionary thinking' argument, to the 'impossibility to select among phenomenological models of the generalized functional response' argument, and to the very idea that two of the models reviewed by van der Meer and Ens (1997) would be mechanistic.

SUBTLE DIFFERENCE WITH STRONG EFFECTS

First, the methods used by van der Meer and Ens (1997) could be criticized for, in comparing the various models of the generalized functional response, van der Meer and Ens (1997) have used rather arbitrary parameter values. For each of the six models parameter values were chosen in such a way that the models generated overlapping generalized functional response curves. Such an approach seems hard to justify for it makes the comparison between models arbitrary. This point of criticism, however, may not be too important for the conclusions drawn from the analysis, because van der Meer and Ens (1997) also studied the behaviour of the generalized functional response models in qualitative terms, by comparing first and second order derivatives. This qualitative analysis ensures that their results will hold regardless of the specific parameter values chosen in the numerical analysis. To this it can be added that other ways of selecting parameter values are likely to lead to stronger differences in the predictions of the aggregative response, thereby strengthening the conclusion drawn by van der Meer and Ens (1997). In his analysis, Jeroen Minderman found that the six models, when fitted to one and the same data set, yielded generalized functional response curves with sometimes considerably different parameter values. As a result, differences in the predictions of the aggregative response became much more pronounced than those in the numerical example of van der Meer and Ens (1997). Thus, the more precise conclusions to be drawn from their study may be that the choice for a specific generalized functional response model qualitatively affects predictions on the aggregative response, *even when models generate overlapping generalized functional response curves*.

Second, on pragmatic grounds it could be argued that predictions of the aggregative response differ in part of the parameter space, and, thus, that the relevance of the conclusion drawn by van der Meer and Ens (1997) depends on the food densities present and on the number of foragers in the system (van Gils & Piersma, 2004). Although this option cannot be excluded, it seems unlikely in the light of the point made in the previous paragraph that the analysis by van der Meer and Ens was conservative in that it was based on models that generated overlapping generalized functional response curves. The analysis by Jeroen Minderman suggests that when parameter values are selected by fitting the models to one and the same data set, there will not be any parameter range in which the predictions regarding the aggregative response overlap.

Third, it could be argued that the various generalized functional response models yield different predictions of the aggregative response, but that such differences need not to be reflected in changes in population size. At least in principle, it is still possible that the various models of the generalized functional response are irrelevant when these models are linked to models of the dynamics of populations. Whether or not this is the case remains to be studied. The preliminary study by Jeroen Minderman suggests that predictions of the mortality of foraging waders are sensitive to details of the generalized functional response models, but only quantitatively so.

THE INCONSISTENT USE OF EVOLUTIONARY THINKING

The argument that use of the ideal-free-distribution model in combination with models of the generalized functional response is not consistent because only the former assumes hat foraging animals behave in an adaptive manner seems valid to me. Nevertheless, this argument should be treated with caution. Classification of a model being consistent with evolutionary thinking suffers from the same problem as classification of models as being mechanistic: it is a relative concept. Just as it is not possible to derive an entirely mechanistic model, it is not possible to study the evolutionary consistency of all elements of a model. To give an example: although the models presented in chapter 6 do consider the evolution of interference behaviour within the context of a Hawk-Dove game, they do not consider the adaptive value of either this game itself, or of the other model parameters, such as those capturing the foragers' searching behaviour and handling behaviour.

SELECTING AMONG PHENOMENOLOGICAL MODELS

It may be true that selection among phenomenological models of the generalized functional response on the basis of data on the relationship between intake rate and forager density is difficult. This argument, however, does not have to lead to the study of mechanistic models of the generalized functional response. Given that the various models generate different predictions, they may be selected on the basis of these predictions. In general it may be true that models either vary in at least one aspect, in which case it will be possible to select among them, or they do not differ in any aspect, in which case selection among is not relevant. Against this pragmatic line of reasoning it can be argued that there is one drawback to selection among the phenomenological models on the basis of their predictions regarding the aggregative response; such requires the extra assumption that the ideal-free-distribution model (used to generate predictions) holds. Selection of phenomenological models on the basis of data on the generalized functional response would be independent of (ideas on) the distribution of foraging animals, whereas selection on the basis of the aggregative response is not.

INTERFERENCE PARAMETERS NOT YET INDEPENDENTLY MEASURABLE

The interference parameters of phenomenological models do not have a clear-cut mechanistic interpretation. They can only be found by fitting the models to data of the relationship between forager density and intake rate (searching efficiency). Interestingly, the same could be said for the two models assigned as 'mechanistic' by van der Meer and Ens (1997). These two models are very similar; they are both based on the reaction kinetic idea. They only differ in a detailed assumption on the foragers' interference behaviour: while the Ruxton model assumes that foragers in the searching state cannot interact with foragers in the handling state, the Beddington model assumes that they can. The two models contain the same two parameters related to interference competition: the 'area of discovery of competitors' and the 'fighting time'. Fighting time is generally interpreted as either a constant or as the average from an exponential distribution of fighting times, and should be independently measurable. Quantifying the area of discovery of competitors, however, is very difficult, if not impossible. The area of discovery of competitors generally has a 'mechanistic interpretation' as the area searched per unit time for competitors, but this search rate is hard to determine other than by fitting the models to data. This makes this parameter as much a 'mystery parameter' as the interference coefficient used in phenomenological models, at least according to the 'independently measurable' definition of the term mechanistic.

ARGUMENTS OF PRINCIPLE

These marginal notes notwithstanding, I still support the plea by van der Meer and Ens (1997) for studying the mechanisms of interference competition. By now, however, I prefer another argument for doing so. Van der Meer and Ens (1997) come to their plea through a practical argument, namely on the basis of differences in predictions of the aggregative response. The same conclusion can also be reached through an argument of principle. If it is a mechanistic understanding that is the goal of a research program, than mechanistic models are to be preferred regardless of their performance relative to phenomenological models, simply because phenomenological models do not yield a mechanistic understanding. This line of reasoning underlies the statement by Metz and de Roos (1992) that they prefer models based on mechanistic considerations over phenomenological models even if the latter provide a much better fit to data. In fact, this line of reasoning also underlies van der Meer and Ens' argument that use of the ideal-free-distribution model in combination with non-adaptive models of the generalized functional response is inconsistent.

Whether the argument of principle can justly be invoked, depends on the goal of the research project (Reflection I), as well as on the definitions used (Reflection II). If one strives to generate predictions, then predictive ability is the sole criterion for evaluation and it is the practical argument rather than the principle argument that should be used (see Reflection I). If the goal is to understand the distribution of foraging waders or the dynamics of their populations, then the principle argument may be preferred over the practical argument, though this depends on the definition of a mechanistic understanding. In mechanistic studies of the dynamics of populations, the use of phenomenological models of the generalized functional response is justified when either of the two hierarchical definitions of the term mechanistic (see Reflection II) is used, but not when the definition in terms of independently measurable parameters (see Reflection II) is used. In mechanistic studies of the distribution of foraging waders neither definition of the term mechanistic warrants the use of phenomenological models of the generalized functional response. This line of reasoning shows the importance of the specification of research goals.

Thus, by now, I consider the use of generalized functional response curves in mechanistic studies of the distribution of foraging waders and/or the dynamics of populations premature, because understanding of the interference process is still wanting. Models of interference competition account for only few of the mechanisms through which competition may arise, they have not yet led to an ability to generate *a priori*, accurate predictions, even the most mechanistic ones still contain parameters that cannot be measured independent of the model's structure, and attempts to study the evolution of interference parameters are but in their infancy (chapter 6).

WHAT DID THE PROJECT DELIVER?

Having explained why I have focused on the interference process itself rather than on its consequences, let me now address the question what this approach has yielded.

DETERMING THE GENERALIZED FUNCTIONAL RESPONSE

The experiments described in chapter 2 were among the first to study, at experimentally controlled forager densities, effects of forager density on the intake rate of waders. Above all, these experiments convinced me of the limitations to understanding of interference competition. I found that forager density negatively affected the rate at which prey were discovered by both knots and turnstones. Nevertheless, only in turnstones did intake rate decrease with forager density. Knots compensated for the lower rate of prey discovery at higher forager densities by rejecting fewer prey. This conditional rejection of prey hints at the flexibility of behaviour and shows that social interactions may affect foraging success even in the absence of noticeable effects on intake rate. With regard to the mechanisms underlying the interference effects on prey-discovery rate, I found that knots and turnstones were affected in strikingly different ways. In knots, bird density had a complex, nonmonotonic effect on the time spent on vigilance and the time spent searching. In turnstones the main effect of increased bird density was a reduction in the prey-encounter rate, that is, the reward per unit search time. In neither of the two species did interference effects appear to result from an expected increase in time spent interacting. Other unexpected results of these experiments were that the allocation of time was independent of food density, that the dominance status of the focal turnstones did not explain variation in their intake rate, and that kleptoparasitic events were virtually absent in both experiments. Clearly, interference competition occurred for reasons other than those considered in models of interference competition, and the mechanistic basis of effects of forager density was more complex than generally assumed.

AN ALTERNATIVE INTERFERENCE MECHANISM

These findings left me puzzled with the question why knots and turnstones suffer from interference competition. Models of interference competition for food generally assume that interference arises from kleptoparasitism, that is, the stealing of food items. This mechanism can only be expected in systems in which the prey handling time is long (Brockman & Barnard, 1979). Such is usually the case for the bigger species. For many species, however, prey handling time may be so short that kleptoparasitism is not feasible. Knots and turnstones in the experiments described in chapter 2, for instance, swallowed their food very quickly, leaving little time for robbery. This implies that models of interference competition may as yet not be able to explain interference effects in perhaps the majority of cases. Why then do knots and turnstones suffer from interference competition? As the consumption of clumps of food may take time, even when the handling time of individual food items is short, I realized that interactions could potentially concern clumps of food rather than individual food items. This mechanism had been suggested several times before, but it had not gained firm ground in thinking on interference competition. As natural food distributions are often clumped, interactions over food clumps could be quite a general mechanisms of interference competition.

Chapter 3 starts with a review of experiments on the effect of the spatial clumping of food. Although not often considered in studies on interference competition, the idea that the spatial distribution of food can affect the behaviour of foraging animals had achieved ample attention in studies on resource defence. As I came to realise these studies of resource defence differ from studies of interference competition in that their main predictor variable is the distribution of food and not the density of foragers, and in that their main response variable is aggression and not intake rate. As a result, the two fields of study have developed in parallel but quite isolated. Few studies have actually considered the effects of both food distribution and forager density on both aggression and intake rate. The experiment described in chapter 3 does exactly this.

As it turned out, I found that the distribution of food was of prime importance for the extent to which focal turnstones suffered from interference competition. When food was dispersed, focal turnstones did not suffer from the presence of a competitor. When food was clumped, however, the presence of a competitor had a strong negative effect on intake rate, but only if this competitor was dominant over the focal forager. Apparently, dominant foragers could monopolize food but only when this was spatially clumped. This clearly supported the idea that interference effects could arise from interactions over clumps of food. The mechanisms underlying these effects, however, were not quite as we expected. Effects on intake rate were not reflected in the foragers' aggressive behaviour; dominant and subordinate foragers spent about the same amount of time interacting. Apparently, the monopolization of resource took only a few interactions. This, I attributed to the high familiarity among the turnstones. The lesson I drew from this finding was that it may be difficult to predict interference effects from the amount of agonistic behaviour observed; interference effects on intake rate may be unrelated to the amount of aggression. Again, I found that interference effects occurred for reasons other than those considered in models of interference competition.

DOMINANCE STATUS

The most striking result of the experiment described in chapter 3 was the very pronounced effect of the foragers' social dominance status. This effect was especially surprising because I did not find any effect of dominance in the previous turnstone experiment (chapter 2). The two experiments, however, differed strongly in the way I had treated the factor dominance. In chapter 2, I classified turnstones as 'dominant', 'intermediate' or 'subordinate' according to their absolute dominance position in a linear dominance hierarchy. In doing so, I assumed that foragers that have similar positions in a dominance hierarchy have more in common than foragers that take widely different position in the hierarchy. In chapter 3, on the contrary, I treated dominance as a relative characteristic; I made focal foragers 'dominant' or 'subordinate' by letting them forage in the presence of a low-ranking or a high-ranking competitor, respectively. The rationale behind this approach is that foragers that are dominant over their competitor are comparable, even though they may take widely different positions in a dominance hierarchy. What my experiments revealed is that it is the latter approach that may be most appropriate. Apparently what matters for a forager is whether or not it is dominant over its competitor; not by how much it is so.

The importance of the forager's dominant status also made me realize the limitations of intake rate as a measure of fitness. Intake rate is the measure of performance generally used in studies of foraging animals. However, being a short-term response variable, it does not capture long-term processes such as the formation or maintenance of dominance relationships. Yet, such processes may be of prime importance for foraging animals, given that being dominant or subordinate may make all the difference. This implies that establishing dominance relationship may be one of the reasons why foraging animals interact with each other, or at least an important side-effect of agonistic interactions. Accounting for this insight would require a drastic change in the way we model the interference process for it would require considerations of both the short-term and the long-term consequences of interference behaviour.

FREE-LIVING TURNSTONES

The experiment described in chapter 4 concerns the question whether food distribution also affects the aggressive behaviour, intake rate and distribution of free-living turnstones. I found that the distribution of food did affect the wild foragers; when food was spaced out, the foragers were present in higher numbers, they interacted less frequently with each other, but they nevertheless spent about the same time on digging for food, my measure of their intake rate. These results support the finding of chapter 3 that the distribution of food may affect the foraging waders.

The main insight I gained from this experiment, however, is that experiments on free-living foragers differ in an essential way from experiments on captive foragers, so that direct, quantitative comparison between the two types of experiments is not straightforward. The crucial difference is in the treatment of the factor 'forager density'. In the laboratory experiment (chapter 3), I had experimentally controlled the density of foragers; this I did by forcing turnstones to forage on a specific foraging platform. As a consequence I could determine interference effects in the absence of feedback effects through patch choice. In the field experiment (chapter 4), forager density was out of my control; forager density was an uncontrolled response variable. Because free-living foragers can adjust their distribution over food patches, and hence their presence on my experimental plot, in response to, or even in anticipation of interference effects, feedbacks effects through patch choice were present in this experiment. The absence of feedback effects in the laboratory experiment and the presence of such effects in the field experiment means that the two experiments address quite different questions. While the laboratory experiment addressed causal interference effects (the underlying process, so to say), the field experiment addressed observable patterns (the outcome of the interference process).

This insight had a strong effect on the way I analysed my field experiment. Clearly, the statistical design should do justice to the fact that forager density was an uncontrolled response variable and not an experimentally controlled predictor variable. Treating forager density as a response variable, however, implied the use of multivariate statistics, because aggression and intake rate were also affected by my experimental treatment, and because these three response variables could freely affect each other. In reviewing previous field experiments on the effect of food distribution, I realize that these studies generally had not acknowledged the multivariate nature of their data.

THE DIVISIBILITY OF FOOD

Chapter 5 presents another experiment at the intersection between the study of interference competition and the study of resource defence. By going through the publication process of chapter 3, I had come to realize the value of experiments that bridge these two fields of study. Initially, because of its meagre theoretical underpinning, I had not been much impressed by the literature on resource defence. It took me some time to realize that despite its weak theoretical foundation, the literature on resource defence was very valuable for its high number of experiments. This situation is almost the reverse of the situation in the literature on interference competition, where theory plays an important role, but where experiments are rare. Clearly, linking the two fields of study may be to the benefit of both. This motivated me to zoom in on the major differences between the two fields of study. One such difference concerns the way in which food is treated; while the studies of interference competition tend to think of food in terms of individual items, studies of resource defence usually consider food clumps.

In chapter 3 I discuss at some length whether it actually matters what foragers are fighting for; food items or food clumps. If food clumps do not differ from food items in a way essential to the interference process, it will be quite straightforward to adjust models of interference competition in such a way as to account for this alternative interference mechanism. If, on the contrary, the outcome of the interference process does depend on whether interactions are over food items or over food clumps, such requires further considerations. As one of the major differences between food items and food clumps I identified the extent to which they can be divided over multiple foragers, that is, their ‘divisibility’. By definition, food clumps differ from food items in that they are composed of multiple items, and therefore their divisibility is higher. While some models acknowledge the potential importance of the divisibility of resources, few empirical studies have looked into this aspect, and these few studies did not consider its consequences for the interference process, which is the question that is addressed in chapter 5. In this chapter I anticipate that the divisibility of resources will become a crucial factor in future models of interference competition.

As it turns out, the extent to which foraging animals suffer from interference competition does depend on the divisibility of food. In the experiment described in chapter 5, I had manipulated this factor, along with the distance between food clumps and the foragers' dominance status. What I found was that subordinate foragers were able to get a share of the food only when food pits (the experimental devices containing food) were spaced out and when food within pits was divisible. These findings imply that to understand and predict interference competition the detailed characteristics of resources matter, and thus that in linking ideas from literature on resource defence with ideas from literature on interference competition differences in the divisibility of resources may be of special importance. Furthermore, the results of this experiment provided a strong corroboration of the findings of chapter 3, especially with regard to the striking importance of the foragers' relative dominance status. Again, the differences in the success of dominant and subordinate foragers were large and very consistent.

EVOLUTIONARY CONSISTENT

One motivation to focus my work on the generalized functional response was the inconsistency of use of the ideal-free-distribution theory in combination with models of the generalized functional response. The ideal-free-distribution model applied to foraging animals assumes that foraging animals behave so as to maximize their intake rate, and thereby use of the model invokes the idea that animals behave in an adaptive manner. No such considerations were made in the original models of the generalized functional response (van der Meer and Ens, 1997). In the course of my Ph.D. project, several interference models have been published that do consider the evolution of aggressive behaviour. Although these models seem to be very similar, they yield strikingly different predictions regarding the evolutionary stability of various interference strategies. In chapter 6 I compare some of the models of the evolution of interference behaviour. Although these models broadly have the same structure, they differ substantially in their detailed assumptions regarding, among other things, the structure of interactions, the presence of asymmetries and the payoff function. Although these differences may seem of minor importance, they turn out to strongly affect model predictions.

To unify previous approaches, chapter 6 contains a framework that allows for a more systematic approach to the study of the evolution of interference behaviour. I applied this framework to the previous interference models. By doing so, I have come to realize that modelling the evolution of interference behaviour may not be such a straightforward task as it may have appeared at first sight. I found that many important aspects of the foraging game were easily overlooked, and that several important assumptions were not made explicit. Not only were the assumptions made by the various models not consistent with each other, several of the models also were internally inconsistent. That let me to plea for a more systematic approach and for the use of analyzing techniques that are more sophisticated than those generally used by evolutionary models of interference competition.

These suggestions may improve the way the evolution of interference competition is modelled and as such they may change ideas on the evolution of interference strategies. Indeed, preliminary analysis of a model that avoided some of the inconsistencies of previous models, already led to hitherto unpredicted outcomes of the evolution of interference behaviour. What I really learned from this chapter, however, has to do with the limitations of current understanding of the evolution of interference behaviour. Models of the evolution of interference behaviour are still utterly unrealistic with regard to several aspects, including variability of interference behaviour, dynamics of both food and forager density, variation in environmental conditions and differences between individuals, to mention but some. Among these aspects may well be the essence of the interference process. Furthermore, I have come to realize the intrinsic difficulty of linking models of the evolutions of interference behaviour to experiments. The evolutionary process operates at a time scale that cannot be studied experimentally, at least not in studies of foraging waders.

HOW TO PROCEED?

I started the work presented in this thesis with the conviction that understanding of interference competition is so wanting that use of models of interference competition in studies on the consequences of interference competition for the distribution of foraging animals and/or the dynamics of populations would be premature. This motivated me to focus on the competition process itself. As I have argued in the previous section, I think that this thesis presents some contributions to an understanding of the interference process. Above all, however, my work has strengthened my conviction that understanding of the interference process is still rudimentary. Therefore, I would argue that the next step in studying interference competition and its consequences should still concern the generalized functional response. I will now present some suggestions for future work.

SEPARATING INTERFERENCE FROM PATCH CHOICE

The one thing I have come to acknowledge is the difference it makes whether foragers are forced to forage on a specific patch or whether they are able to choose between patches. Being clear about the status of observations on foragers in the absence or presence of patch choice may well help to clarify the study of interference competition. It is in the absence of patch choice that interference competition can best be determined. Observations on foragers that are free to choose between patches provide data on the outcome of the combination of the interference process and the distribution process. To study the basics of the distribution process, it may be equally desirable to initially exclude the interference process. This can be done by studying the patch choice of solitary foragers.

SPATIAL VARIATION AND SOCIAL DOMINANCE

What the experiments in this thesis suggest is that account of the small scale distribution of food and of the foragers' dominance status is an absolute must for models of interference competition among foraging waders.

Heterogeneity in the spatial distribution of food can in principle be included in models of the generalized functional response through statistical distribution functions. Such an approach would, however, be unwanted as it is not understood how such distribution functions come about. Perhaps a more fruitful way to account for heterogeneity in both the distribution of food and the within-patch distribution of foragers is by changing the way foraging behaviour is modelled. The generalized functional response is generally modelled through mean field equations; they are formulated in terms of (mean) food density and forager density. Alternatively, models of foraging animals could start from the movement rules of individual foragers, an approach generally referred to as Lagrangian. Of course, such models have already been developed (e.g., Turchin, 1998), but not often in the context of the social foraging; specifying social movement rules is difficult. The main advantage of such an approach would be that the distribution of food and foragers no longer has to be imposed; rather it follows naturally from the movement rules.

The importance of social dominance has, of course, been emphasized often before, and several models of the generalized functional response for unequal competitors have already been presented (e.g., Sutherland & Parker, 1985; Parker & Sutherland, 1986). The main difficulty in accounting for variation in social dominance position, however, is that it is difficult to do so in a non *ad hoc* fashion. Ideally, account of variation in social dominance status is based on ideas regarding the formation and maintenance of dominance hierarchies. The way to approach this question empirically would be to study groups of unfamiliar individuals. Previously, variation in dominance status has been accounted for by assuming that individuals come in discrete classes, being either dominant or subordinate. What my experiments suggest, however, is that any individual (except the most subordinate one and the most dominant one) is both dominant and subordinate; dominance status depends entirely on the status of the opponent. What varies between individuals is the frequency with which they are in either position. This frequency will follow a uniform distribution. Once variation in dominance status is accounted for it remains to be determined how dominance relates to food intake. As my experiments show, his may well depend on environmental conditions such as the distribution and the divisibility of food.

DISTRIBUTION OVER FOOD PATCHES

Once the desired understanding of the interference process has been reached, it can be considered how interference competition affects the distribution of foraging waders. For this step, I would argue that much the same principles apply as I have been propagating for the generalized functional response. I think it will pay to develop a model that is both mechanistic and evolutionary. The ideal-free-distribution model is neither. It is not mechanistic, as it does not specify how animals choose patches (i.e., how animals gather information, how

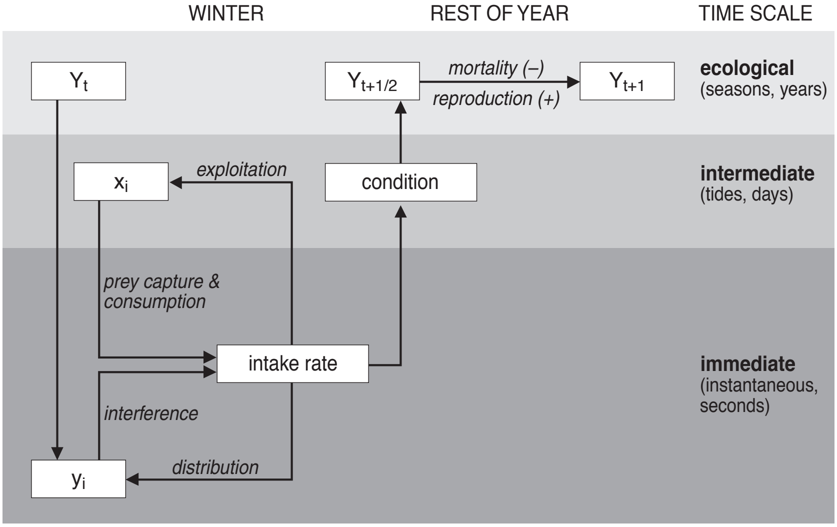

Figure 7.5. A process-rate-based framework to link the foraging behaviour of wintering waders to the dynamics of their population. The essential notion underlying this framework is that various processes operate at different time scales and that they can be separated accordingly. The density of predators (foragers) y_i at food patch i is assumed to change at a faster rate than the density of prey (food) x_i at this patch and than the condition (body mass) of the predators, which in turn are assumed to change at a faster rate than the population density of predators Y at the start of winter Y_t (the subscript j indicates a moment in the annual cycle), $Y_{t+1/2}$ the population density at the end of the winter and Y_{t+1} the population density at the start of the next winter). At the shortest time scale, the main assumption is that intake rate depends on the densities of prey (food) and predators (foragers) at specific food patches. At the longest time scale, it is assumed that the annual cycle contains two, distinct phases – ‘winter’ and ‘rest of the year’ – that are linked to each other only through effects on population density.

they move between patches). It is not evolutionary in that it studies neither the performance of different path choice strategies, nor the evolutionary dynamics of patch choice strategies.

LINKING INTERFERENCE TO POPULATION DYNAMICS

In developing interference-based approaches to population dynamics, I think much can be gained from exploring the linkages between hierarchical levels more systematically. To this end, the process rate based approach of O'Neill et al. (1986) may come in handy. Although hierarchies are generally defined in terms of levels of organization and not in terms of process rates, I think the latter way of looking at interference-based approaches of population dynamics might be illuminating: the dynamics of populations can be seen as the (slow) focal phenomenon and the behaviour of individuals as the underlying, fast process that is invoke to explain the dynamics of populations.

To illustrate this idea, I have slightly modified the frameworks presented in Figure 7.2 to explicitly arrange the various processes according to the time scale at which they operate (Figure 7.5). Specifically, I have assumed that the foraging process, including interference competition and the distribution of foraging animals, operates at a short, 'immediate' time scale, that is, that foraging is a fast process. In line with the definition of standing stock systems as 'systems in which food density changes at a time scale longer than that at which animals forage', I have assumed that the exploitation of resources operates at a somewhat longer, 'intermediate' time scale, being a slower process. Changes in the large scale population density are assumed to operate at an even longer, 'ecological' time scale. Looking at it this way, the essential notion underlying behaviour-based approaches to modelling the dynamics of populations thus is that processes operate at different time scales and that these time scales can be separated (in accordance with O'Neill et al. 1986).

Using this approach based on process rates, it immediately becomes clear that the real challenge for interference-based studies of population dynamics is the linkage between processes at the immediate time scale and processes at the ecological time scale. This can be done by aggregating the interference process in summarizing statistical properties that are preferably derived from the interference process itself (O'Neill et a., 1986; Flierl et al., 1999).

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REFLECTION I –
A CRITIQUE FOR 'A CRITIQUE FOR ECOLOGY'

Ecology is in crisis. There is a lack of scientific rigour, predictive capability is weak, and ecologists fail to harness modern technology. Indications of the poor condition of ecology include, among others, the lack of testable theory, low research budgets, lack of employment opportunities, and the proliferation of uncontrolled, uncoordinated studies. Most of all, however, the weakness of ecology as a science is revealed by our inability to solve ecological problems. While public demand and the practical necessity for attractive, powerful, ecological theory has mushroomed, the science has languished.

The above is the starting point of 'A Critique for Ecology' by Peters (1991), a thought-provoking book that criticises many an aspect of contemporary ecology. In essence, the book expresses the concern that ecologists have got their goals wrong. According to Peters, scientific theories must make testable predictions, so that ecology should be the branch of science that 'seeks to predict the abundance, distributions and other characteristics of organisms in nature'. Peters' major concern is that this is not quite what most ecologists do. Much of, especially academic, ecology is devoted to 'understanding' ecological observations. Understanding seems to have become a goal in itself; many studies do not even intend to make predictions. But, how to know whether something is understood if this cannot be tested? In the absence of predictive power claims of understanding cannot be evaluated independently. This analysis leads Peters to a plea for a 'predictive ecology', in which the focus is on the actual goal of science – making predictions. In principle, there are two kinds of theories that generate predictions and that can thus be used in predictive ecology. Empirical theories, such as statistical models, describe regularities in the world around us and predict likely patterns; explanatory theories predict and that tell why a system behaves as it does and therefore why predictions are valid. According to Peters the key tools of predictive ecology, however, should be empirical theories rather than explanatory theories. Opting for explanatory theories would 'demand too much, too soon'. For now, 'we should develop simple predictive tools that allow us to propose and confirm patterns that are relevant to the biological world. In future, such patterns may lead to more ambitious theory, but at present, they can serve as tool for environmental management, arguably a more pressing and important problem than creating a general field theory for ecology.' For this reason, predictive ecology seeks patterns rather than explains them.

WHAT IF PETERS WERE RIGHT?

If the goal of science were to make predictions, making ecology a predictive science by focussing on empirical theory rather than on explanatory theory might not be such a bad idea. Simply because empirical theory has the sole purpose to predict, whereas explanatory theory also wants to explain, empirical theories can in general be expected to outperform explanatory theories. This expectation is supported by Poole (1978), who states that to make predictions 'statistical models are generally faster, cheaper, simpler and better predictors than their explanatory counterparts that attempt to predict and explain'. Poole bases this statement on experience in economics, where statistical prediction is used extensively. Peters also cites Cartwright (1983), for stating that in physics explanations are provided by general (explanatory) theories, but applied decisions are made with empirically justified calculating tools (empirical theory). Whether or not the same holds true for ecology, however, remains to be seen[1]. Currently, the ability of ecologists to predict the course of everyday events is small regardless of the kind of theories invoked (of course, Peters would argue that this is because ecologists have been addressing the wrong kind of questions, focusing too much on understanding and too little on prediction, and not because ecology is fundamentally different from economics and physics).

There is one common argument against the view that statistical models provide the most efficient means to generate predictions. Statistical models are but interpolations; they have to assume that the future will resemble the past, and therefore they only work if the system is not changed dramatically (O'Neill et al., 1986; Peters, 1991). Often it is claimed that explanatory theory is less sensitive to such changes, because it is based on the processes underlying studied phenomena, and because processes are thought to change less than statistical relationships. Although this argument is appealing, it remains to be seen how often this argument applies; with certain changes explanatory models probably cannot cope any better than empirical models[2]. Furthermore, it should be realized that what constitutes a change in a system depends on the domain of applicability of the statistical model. If the model is fitted on a dataset in which similar changes feature frequently, changes should not form a problem to the model.

WHY ISN'T PETERS RIGHT?

Although many of the concerns raised by Peters should be taken seriously, one might argue about his basic premise that the goal of science is to make predictions. At some point in his book, Peters himself states that 'science lies at the interface between the abstract constructions of our mind and the phenomena of the external world'. Indeed, the general notion (Pickett et al., 1994 and references therein) is that science is about linking ideas (abstract constructs, theories) to observations (empirical stuff, data). This implies that the goal of science is to understanding nature (remember that understanding was defined as 'the match between confirmable natural phenomena and independent predictions derived from conceptual considerations'; chapter 1), not just to predict it. Peters is right in saying that predictive ability is a necessary means to evaluate such understanding; this does not make predictive ability the ultimate goal of science.

WHERE DOES HE GO WRONG?

Peters bases his conviction that science is about making predictions on the ideas that 1) predictive power is what distinguishes science from nonscience and 2) that the goal of science should be formulated in terms of its distinctive characteristics. Let's have a closer look at these ideas. The first is about the demarcation of science. The statement cannot be true, for it implies that anything that has predictive power is science. Peters demarcates science on the basis of its performance, whereas science should be demarcated on the basis of its methods. If that is done, it is obvious that the second idea is equally problematic; the goal of science should not be formulated in terms of its methods. Thus, Peters' statement that science is about making predictions does not have a robust, rational foundation. Rather, I think, it stems from his desire to conserve nature and his conviction that the best way to do so is through predictive ecology[3].

THE COROLLARY

Acknowledging that science is about understanding nature, it is obvious that predictive ability is not the goal of science. But, it could be argued, predictive ability may still be the ideal criterion to evaluate explanatory theories. After all, the proof of the pudding is in the eating, isn't it? Promising as this may look, there are several obstacles. It may be obvious that a match between theoretical predictions and observations does not guarantee understanding (to see this, just remember that statistical models may be very good predictors, even though they do not yield understanding). But there are other reasons why the evaluation of explanatory theories cannot be reduced to tests of their predictive ability. Let me present three of them.

LIMITATIONS TO DATA

First, data are not perfect. We all know that the collection of data is an ongoing process. The data we have today may be the best we can get, but there is no guarantee that it is a good description of nature or that we cannot improve it. More philosophically, the imperfection of data follows from the notion that objective data do not exist (e.g., Ford, 2000). All perceptions involve the brain, and as a consequence all observations depend in part on past experience, knowledge and expectations (Polanyi, 1969; Chalmers, 1982). As Fagerström (1987) puts it, 'rather than reporting what we see we report what we think that we see and this is what is possible to see and what is acceptable to see'. But even if all people could perceive signals in an identical way, observations would still not be objective, as all statements about observations are preceded by theory (observations are 'theory-laden'); what we observe and regard as meaningful depends upon theoretical preconceptions obtained before the activity of observation was begun (Chalmers, 1982; Fagerström, 1987; Haila, 1988). To give an example: measures of the dynamics of populations require a presupposition about what is a population. The corollary of the notion that perfect data do not exist is that a mismatch between theory and data may be due to imperfect theory, but also to imperfect data.

PREDICTIONS TESTING DOES JUSTICE TO NEIGHTER THEORY NOR DATA

Second, theory has an internal structure. Each specific theory consists of several components (Pickett et al., 1994; Ford, 2000), such as facts, concepts, their mutual relationship and their domain of applicability. If a theory does not match a set of observations, it may be that only one of its components needs to be improved (Ford, 2000). Acknowledging this can help to design tests that do more than merely falsify a theory (Loehle, 1988)[4]. To this it can be added that there is an empirical and a logical component to the output of theories (Quine, 1981). Prediction testing involves evaluation of only the empirical output of a theory (its predictions). However, theories can do more than predicting data; theories may help to clarify matters (Levin 1980, 1981; Peters 1991), they may indicate what is possible (Levin, 1980, 1981; Peters, 1991; Odenbaugh, 2005), they may create intuition which may be used as a baseline against which to evaluate observations (Odenbaugh, 2005) and they may provide us with a conceptual framework through which we can conduct experiments and fieldwork (Levin, 1981; Odenbaugh, 2005). These issues are examples of the logical output of theory. It is important to realize that any theory can be evaluated on the value of either its logical output or its empirical output (or both). Note that this implies that even a theory that has limited predictive ability can still be very valuable.

Just as reducing theory to prediction generation does no do justice to the scientific process, it would be short-sighted to consider the evaluation of theories as the only value of data (Haila, 1988). Not all data are suited for that (Loehle, 1987); what, when and where questions, for instance, do not lend themselves easily for falsification. More importantly, not all data need to be used in tests either. Data can also form the basis of existential statements, pattern identification, analytical descriptions, and comparisons (Haila, 1988). An example of this statement is provided by the empirical chapters of this thesis.

THEORIES MATURE

Third, the formation of theory is a process. Theories often start out vague and qualitative. As more work is done on a theory, it matures. This as important implications for the idea of theory testing, because it implies that theories can be tested too early, potentially resulting in the premature rejection of a correct, but incomplete theory (Loehle, 1987). Pickett et al. (1994) identify three axes on which the maturity of theories can be evaluated. Mature theories are complete (domain, assumptions, concepts, definitions, facts, laws, models translation modes, frameworks), have well-developed individual components (exactitude, empirical certainty, applicability, derivativeness) and have well-integrated components. Because it is difficult to test immature theories, it may often be better to invest in increasing the maturity of theories than in trying to prove or disprove the immature theory (Loehle, 1987).

WHERE DOES THIS LEAVES US?

There is but one conclusion that follows from these three issues (the imperfection of data, the internal structure of theory, and the maturation of theories): predictive ability cannot be used as the sole criterion for theory evaluation. Other criteria can be equally important. Peters mentions the following: relevance, immediacy, operationality, accuracy, generality, precision and quantification (these could all be regarded as aspects of predictive ability), economy of effort, practicability, simplicity, consistency with existing views, inspirational or heuristic effect, and elegance. To these I would add internal consistency and especially the reasonability of assumptions (Murray, 1986; Haila, 1988). How are we to combine these different criteria? There may not be an objective way to do so; evaluating theories is an art, whether we like it or not.

NOTES

[1] An example of a biological study that systematically compares the performance of statistical and mechanistic models is provided by Ellner et al. (1998), who analyzed data on measles epidemics in five large cities from the time before vaccination became standard procedure (which began in the 1960s). Ellner and coworkers compared the performance of one mechanistic model (the 'SEIR' model, which is based on the idea that populations contain susceptible, exposed, infective and recovered individuals), two phenomenological models (one based on feed-forward neural networks, the other based on linear autoregression) and a hybrid, semimechanistic model (which combines the mechanistic SEIR model with a regression model). These four models were parameterized and/or fitted on the first half of the data series and applied to predict the second half. As it turned out, the semimechanistic model outperformed both the phenomenological models and the mechanistic model in terms of explained variance, and one of the phenomenological models outperformed the mechanistic model. Thus, this study suggests that it may be hybrid models that do best in terms of predictive ability. However, to draw general conclusions from this study is not straightforward because the conclusions of Ellner et al. (1) apply to the average performance of their models (for specific cases other conclusions could be drawn), (2) may have been highly specific to the models and the data used, and (3) do not account for the amount of time and energy invested in either of the models. Clearly, ecology would benefit from more such systematic 'snapshot comparisons' of the performances of different kinds of models; they provide a clear-cut improvement over verbal claims of superiority.

[2] This is, for instance, clear from the data of the development of the Svalbard barnacle goose population as provided by Pettifor et al. (2000). Using a stochastix matrix model (i.e., an empirical model), Pettifor and coworkers were well able to predict the growth of the Svalbard barnacle goose population over the first twenty years of observation. After that, however, observations started to deviate rapidly from their predictions. Pettifor et al. (2000) mention several explanations for this sudden deviation of observed and predicted population size. Among others, the geese had discovered new, successful breeding grounds. To me, this indicates that dealing with drastic changes may be as problematic for explanatory models as for empirical models.

[3] To be just, let me note that it would also be difficult to defend the idea that science is about linking ideas to observations. The fact that many references claim so may provide an argument of majority or of authority; it does not provide a rationale. Personally, I think there simply is not one a priori specified goal to science. Because this implies that we cannot take the goal of science for granted, it may well pay to be more explicit about our personal motivations so as to avoid endless polemics and much confusion.

[4] It is this point that motivated me to test the assumptions of models of interference competition rather than predictions of specific models; it just seemed inefficient to me to test predictions of models that had dubious, untested assumptions. Although it may seem equally problematic to test assumption as to test predictions, this is not the case. Testing assumptions only implies statistical inference; testing predictions also involves scientific inference. The difference between statistical and scientific inference is that the latter involves explanations, whether the former just concerns patterns (Loehle, 1987).

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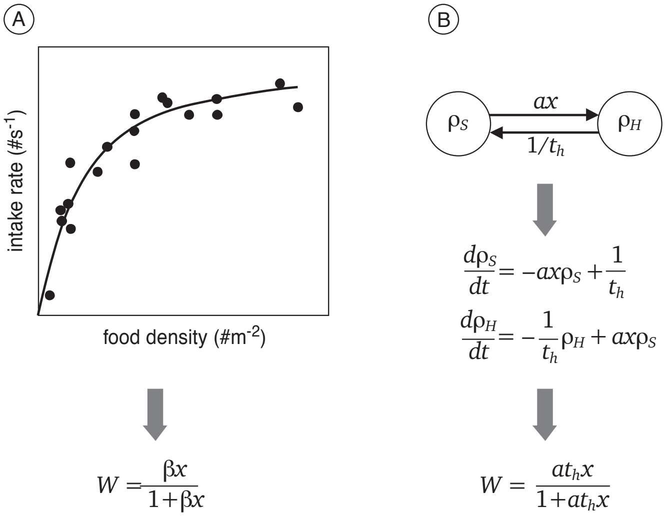
REFLECTION II –
MECHANISTIC VERSUS PHENOMENOLOGICAL

The distinction between mechanistic and phenomenological models has been a recurrent theme in my thinking on interference competition among foraging waders. This distinction is, for instance, of importance for the evaluation of models of the generalized functional response, but it is also of importance for the rationale behind interference-based studies of the dynamics of populations (chapter 7).

In principle, the distinction between mechanistic and phenomenological approaches is straightforward. Phenomenological models merely describe a focal phenomenon, whereas mechanistic models additionally specify how this phenomenon arises. To give an example, while phenomenological models of interference competition consist of an empirically derived relationship between forager density and intake rate, their mechanistic counterparts are based on conceptual considerations of how the negative effect of forager density on intake rate comes about. Let me be more specific. In four of the models reviewed by van der Meer & Ens (1997) the interference effect is caught by a parameter referred to as 'the interference coefficient' (Figure 7.3). This parameter does not have a clear-cut interpretation in terms of the processes leading to interference competition. Instead, it can be found by regression intake rate (or the area of food discovery) against forager density (whereby the models differ in whether they log-transform intake rate and/or forager density). Because these models do not specify how interference effects come about, they are phenomenological. The two other models reviewed by van der Meer & Ens (1997) do specify how interference effects come about. Specifically, they assume (1) that foraging animals can be in one of three mutually exclusive behavioral states (searching, handling and fighting), (2) that two foraging animals enter the fighting state whenever they encounter each other, (3) that foraging animals search the environment for competitors at a constant rate ('the area of discovery of competitors') and (4) that interference competition arises from the loss of time spent fighting. In these two models, interference effects are caught by the area of discovery of competitors and the duration of a fight, two parameters that do have a clear-cut interpretation.

A FIRST COMPLICATION AND ITS SOLUTION

A first complication in distinguishing mechanistic and phenomenological models arises from the fact that phenomenological models can sometimes be given a mechanistic interpretation. Let me give an example by means of the type II functional response, that is, the relationship between food density and intake rate in which intake rate levels off at high food densities. Holling (1959a) first derived this relationship phenomenologically (in accordance with Figure 7.6A)



$$\frac{d\rho_S}{dt} = -ax\rho_S + \frac{1}{t_h}$$

$$\frac{d\rho_H}{dt} = -\frac{1}{t_h}\rho_H + ax\rho_S$$

$$W = \frac{\beta x}{1+\beta x}$$

$$W = \frac{at_h x}{1+at_h x}$$

Figure 7.6. Schematic representation of a phenomenological (A) and a mechanistic (B) derivation of Holling's type II functional response, that is, his 'disc equation'. The phenomenological derivation starts from observations (black dots indicate hypothetical observations) on the relationship between food density x and intake rate W. The observed relationship can be caught analytically to provided a model of the functional response, where β is an unspecified coefficient. The mechanistic derivation starts from the idea that foraging animals are either searching or handling (ρ_S and ρ_H indicate the fraction of foragers in the searching state and in the handling state respectively). After specification of the transition rates (a is the area of discovery of food and t_h the per capita handling time of food items), a set of differential equations can be derived that keeps track of changes in the fraction of foragers in each of the two behavioural states. Assuming that equilibrium is reached, intake rate can be derived by solving the differential equations.

by studying the intake rate of a solitarily foraging deer mouse (*Peromyscus maniculatus*) in relation to experimentally manipulated densities of cocoons of the European pine sawfly (*Neodiprion sertifer*). In a subsequent publication (Holling, 1959b) he showed how this relationship could be derived mechanistically (in accordance with Figure 7.6B), from the assumptions (1) that solitary foraging animals can be in two mutually exclusive behavioural states (searching and handling), (2) that they search for food at a constant rate, and (3) that each food item takes a constant time to handle. This shows that the same equation can sometimes be derived both phenomenologically and mechanistically. Similar examples are provided by Kozłowski (1980), who showed that the logistic equation, which was originally derived phenomenologically, can be given a mechanistic interpretation, and by van der Meer (1997), who presented a mechanistic interpretation of the (phenomenological) Lotka-Volterra competition equations.

This complication can be solved rather easily. For that, we just have to remember that a model can be more than an equation; along with the equation may come a set of assumptions. This implies that the same *equation* may be derived in two different ways, but that the two derivations actually yield different *models*, because they involve a different set of assumptions. In terms of the previous example: derived from observations on foraging deer mice, the type II functional response forms part of a phenomenological model; derived from considerations on the behavioral states of foraging animals, the same equation forms part of a mechanistic model. Thus, while it may not be unambiguous to classify a certain equation as either mechanistic or phenomenological, classifying models as such should not be a problem.

A MORE SERIOUS COMPLICATION

A more serious complication arises from the relative nature of the term mechanistic. Defined as 'specifying how a phenomenon arises' the term mechanistic has an open end. Because this definition does not specify the level of detail required, any mechanistic model (but the one phrased in terms of nature's smallest particles) can be made more mechanistic by the addition of more detail. This implies that any mechanistic model contains phenomenological elements, that is, elements of which it is not specified how they come about. Let me make this clear by means of the mechanistic version of Holling's type II functional response model. This model predicts intake rate to level off at high food densities. To derive this prediction, the model assumes that animals search for food items at a constant rate and that each food item takes a constant time to handle. How these parameters come about, that is, for instance, why it takes a certain time to handle a food item, is not specified by the model. Yet, just as intake rate results from the searching and handling behaviour of foraging animals, these parameters result from certain processes (such as cognitive processes involved in searching and handling or physical processes involved in handling food items). In principle these parameters can therefore also be derived mechanistically. Because they are not, the mechanistic version of Holling's type II functional response is, to some extent, phenomenological.

Failing to acknowledge the relative nature of the term mechanistic is dangerous; it can lead to a practically endless spiral of reduction (Pickett et al. 1994; more whimsically, it can drag one into the 'swamp of reductionism'). Let me give an example of such a spiral. To study the dynamics of populations it can be argued that the underlying mechanisms, such as interference competition, should be studied to achieve a better understanding. While studying interference competition, however, it can subsequently be argued that the underlying mechanisms, such as the duration of fights, should be studied to achieve an even better understanding. What this example shows is that with an open definition of the term mechanistic, there is a high risk of mechanistic studies growing infinitely more mechanistic. The price that is paid for the increased level of detail is that with every level of extra mechanistic detail it gets increasingly difficult to focus on the focal phenomenon.

CLOSING THE TERM MECHANISM

The obvious solution to the danger of infinite regress is to make the term mechanistic absolute. Throughout my Ph.D. project I have considered three different ways to do so. The first two ways are based on the concept of hierarchies; the third way is based on ideas regarding the measurability of parameters. These three ways are not mutually exclusive; especially the third can easily be combined with either one of the two hierarchy-based definitions.

The general idea behind the two hierarchy-based definitions is the same: assuming that natural phenomena can be assigned to levels in a hierarchy, mechanistic studies can be defined as those studies that describe a phenomenon (operating at a certain level in the hierarchy) in terms of processes that operate on a lower hierarchical level (O'Neill et al. 1986). To avoid the swamp of reductionism, it can simply be specified that mechanistic models describe a phenomenon in terms of processes operating *at the one level below* that on which the focal phenomenon operates (Figure 7.7). The two hierarchy-based definitions differ in the way they distinguish hierarchical levels.

I	II	III	example
noise	noise	noise	...
noise	context	noise	communities
context	phenomenon	noise	populations
phenomenon	mechanisms	context	individuals
mechanisms	noise	phenomenon	organs
noise	noise	mechanisms	cells
noise	noise	noise	...

Figure 7.7. Illustration of the relative nature of the terms 'phenomenon' and 'mechanism' (modified from a lecture by Hannu Rita). Assuming that natural processes can be structured hierarchically, the hierarchical level below that of the focal phenomenon contains the mechanisms causing the phenomenon and the hierarchical level above that of the phenomenon forms its context; all other levels can be considered to be noise. Thus, processes at a certain level (in the example, the level of individuals) can be the focal phenomenon (I), the mechanisms of a higher-level phenomenon (II), or the context of a lower-level phenomenon (III).

THE LEVELS OF ORGANIZATION DEFINITION

In ecological literature, hierarchies are usually defined in terms of levels of organization (O'Neill et al. 1986). The classical hierarchy runs from molecules, through subcellular structures, cells, tissues, organs, organisms, populations, communities, and ecosystems to biospheres (Pickett et al., 1994), though various variations are around. In terms of levels of organization, mechanistic models describe phenomena at one organization level (say that of individuals) in terms of processes operating at the one level below (which would be the level of organs). Although the 'levels of organization' concept is very popular, it is not without difficulties. I will mention three of them.

First, identification of levels of organization may not always be unambiguous. The logistic equation, the Lotka-Volterra competition equations and the Lotka-Volterra predator-prey equations (Figure 7.1), for instance, are all generally considered to be population-level models. If population-level means 'containing characteristics that are specific to populations', the logistic equation and the Lotka-Volterra competition equations would indeed count as population-level models. The reason for this is that they contain a parameter K, the carrying capacity, that only has an interpretation as a population characteristic: carrying capacity can be interpreted as the maximum number of individuals that can be sustained in a system. Clearly, individuals do not have a carrying capacity. The growth parameter r of these models, however, can be interpreted either as the intrinsic rate of increase of a population, and hence as a population-level parameter, or as the average net contribution of individuals to the population size, which would make it an individual-level parameter. The way the growth parameter is interpreted does not change the status of the logistic equation or the Lotka-Volterra competition equations as population-level models, because there is only a population-level interpretation to the carrying capacity. However, the Lotka-Volterra predator-prey equations can be interpreted entirely in terms of individual-level characteristics, so that the status of this model as either population-level or individual-level is ambiguous[1].

Second, the classical levels-of-organization hierarchy (and many of its variations) is conceptually problematic, because it is a mixture of concepts of various types (Rowe, 1961). Ecosystems, for instance, have a physical structure, whereas populations and communities are abstract categories without such a structure. To avoid these conceptual problems, MacMahon et al. (1978) distinguish four different hierarchies. The classical levels-of-organization hierarchy is also conceptually problematic, because it assumes that lower level phenomena are nested within higher level phenomena. Allen and Hoekstra (1992) argue that such need not always the case. Treating the human stomach as an ecosystem, for instance, ecosystems can be nested within individual organisms. To emphasize that levels of organization do not necessarily correlate with scale, Allen and Hoekstra (1992) propose a 'layer cake of ecology' model, in which they recognize the same six levels of organization at each spatial scale. These attempts, however, have not yet succeeded to replace the popular, but problematic classical hierarchies.

Third, the levels of organization provide a means of structuring natural phenomena that is both rigid and coarse, and that may not always be operational. Consider, for instance, the negative effect of forager density on intake rate. If this is taken as the focal phenomenon, its mechanisms should be sought at the level of organs (classical hierarchy) or organ systems (MacMahon et al., 1978), assuming that this phenomenon lies at the level of organisms. Intuitively, this does not make much sense to me. Rather, I would look at the behaviour of individuals for a mechanistic understanding of such interference effects. But where does the behaviour of individuals fit in if natural processes are organized according to the levels of organization? Presumably, the behaviour of individuals should be assigned to the level of organisms, just as the negative effect of forager density on intake rate. According to O'Neill et al. (1986) this touches upon an essential problem of the levels-of-organization definition of a hierarchy. Forming a hierarchy on the basis of levels of organization may be intuitive, but it is neither operational, nor functional.

THE PROCESS-RATE DEFINITION

To solve the problems inherent to the levels-of-organization definition of hierarchies, O'Neill et al. (1986) make a strong plea for structuring natural phenomena on the basis of differences in process rates. According to O'Neill et al. each process in nature operates at a specific rate and a specific spatial scale. They give the following example: "... individual tree leaves respond rapidly to momentary changes in light intensity, CO_2 concentration, and the like. The growth of the tree responds more slowly and integrates these short-term changes. Change in the species composition of the forest occurs even more slowly, requiring decades or even centuries."[2]. The variation in process rates and spatial scales allows for an arraying of processes in hierarchical levels, with processes corresponding to higher levels occurring at slower rates and at smaller spatial scales. The fact that variation in process rates occurs naturally gives the structuring of processes in terms of process rates the strong advantage (over, for instance, hierarchies based on levels of organization): the imposed structure is not arbitrary and can be derived empirically. A further advantage of defining hierarchical levels in terms of response times is that it naturally lads to the isolation of hierarchical levels. Generally, lower hierarchical levels communicate only their average responses to the higher levels; in this way each level acts like a filter. Again, O'Neill et al. provide an example of this in terms of trees. Fast changes in light availability affects photosynthesis, which operates a low hierarchical level, but are not reflected in the annual growth response of trees; they are filtered out. Only the average (integrated) response is seen in the growth increment at the level of the tree.

How does this relate to definitions of the term mechanistic? If natural phenomena are assigned to hierarchical levels according to their process rates, mechanistic models can be defined as those models that explain slow processes in terms of faster processes. This sounded rather abstract to me, until I realized that an example of this could be found in interference-based approaches to the study of population dynamics. Essentially what is done when interference is invoked to study the dynamics of populations is to explain a slow phenomenon (population dynamics) in terms of a faster phenomenon (interference competition). I will not elaborate this insight here; it features in chapter 7 of this thesis.

Although I find the idea to define mechanistic in terms of a hierarchy based on process rates intriguing, this is not the definition that I have used throughout my thesis. In part this is because I encountered the idea only recently, but it is also because I am not yet convinced of its applicability. It remains to be seen whether processes in general operate at distinct time scales and whether these time scales can be identified objectively. Furthermore, I am not convinced that this way to define hierarchies provides a fruitful way to close the definition of the term mechanistic either. For that it should be possible to objectively determine which rate is the one operating below the rate of the process of interest; this may well be difficult.

THE INDEPENDENT MEASURABILITY DEFINITION

The third way to make the term mechanistic absolute is based on the definition of the term mechanistic as specifying how a certain phenomenon arises, but extends it by adding the condition that the parameters of mechanistic models should be measurable independently of the structure of the model in which they feature. This extra condition weeds out all models that contain what I refer to as ‘mystery parameters’, that is, parameters that do not have a clear-cut interpretation in terms of the processes through which the focal phenomenon comes about. Mystery parameters cannot be measured but through fitting the model in which they feature to observations on the focal phenomenon. Such is unwanted, because it implies that parameter values only have an interpretation in the context of the model in which they feature and because it requires the assumption that the model in which they feature is correct. Let me give an example. The logistic equation contains one mystery parameter – the carrying capacity. The way to quantify this parameter is to realize that the model predicts population growth to level off at the carrying capacity, to assume that the model is correct, and then to determine the asymptotic population size. Having to assume that the model is correct is very problematic as there are many reasons why the model would not be correct, in which case population growth would level off at a population size other than the carrying capacity. Furthermore, if model parameters cannot be estimated without assuming the model to be correct, there is no independent way to study the correctness of the model. The use of mystery parameters precludes the independent evaluation of models.

Does the condition that model parameters should be independently measurable make the definition of the term mechanistic absolute? I think so, because it provides a clear endpoint to mechanistic studies. If the goal is to model a certain phenomenon mechanistically, this goal is achieved when the first model is developed in which all parameters are measurable independently of the structure of the model in which they feature.

NOTES

[1] This ambiguity can be avoided if the definition of a population-level model is changed from 'containing parameters that can only be understood in terms of population-level characteristics' to 'not accounting for between-individual variation'. The logistic equation, the Lotka-Volterra competition equations and the Lotka-Volterra predator-prey equations are all phrased in terms of the average individual; none of them accounts for variation between individuals, and therefore this new definition would ensure that they all have the same status as population-level models.

[2] O'Neill et al. (1986) find a further example in the work by Sollins et al. (1983), who analyzed soil organic mater accumulation at mudflows on Mt. Shasta, California. Over centuries, major changes in organic matter result from fire-initiated secondary succession. On a finer time scale, that of years, net accumulation of organic matter is due to annual litterfall and decomposition. At the even finer time scale, that of days, organic matter changes due to wind-blown additions and removals and to the action of large decomposer organisms.

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DUTCH SUMMARY – NEDERLANDSE SAMENVATTING

Iedereen weet wat competitie is. We komen het bijna dagelijks tegen. Sporters strijden om een beker, politici winnen stemmen ten koste van anderen, en collega's verdrukken elkaar om schaarse promotieplekken te bemachtigen. Maar ook voorbeelden vanuit de natuur zijn alom bekend. Mannetjes herten die met hun gewei op elkaar in rennen om indruk te maken op vrouwtjes, zangvogels die elkaar verjagen van een voedertafel, meerkoeten die een territorium verdedigen en meeuwen die elkaar om een stuk brood verdringen.

Voor biologen is competitie de strijd om schaarse goederen. Biologen zijn zich al lang van het belang van dit proces bewust; aangezien natuurlijke hulpbronnen vaak schaars zijn, is competitie onvermijdelijk. Dit besef is door niemand zo uitvoerig en overtuigend verwoord als door Thomas Malthus. In 1798 publiceerde hij een essay waarin hij uiteenzette dat omdat elke populatie de neiging heeft harder te groeien dan voedselvoorraden toestaan, competitie om voedsel wel de uiteindelijke grens *moet* stellen aan de grootte van populaties. Dit idee ligt ook ten grondslag aan Charles Darwin's ideeën over evolutie door natuurlijke selectie.

Het besef dat competitie onvermijdelijkheid is heeft er onder meer voor gezorgd dat competitie een prominente plaats inneemt in de ecologie. De ideeën van Malthus en Darwin zijn terug te vinden in de eerste wiskundige modellen van de groei van populaties en deze modellen vormen nog steeds de basis van een belangrijk deel van de ecologie. Theoretisch zowel als praktisch is er buitengewoon veel onderzoek gedaan naar competitie. Zo loopt alleen al het aantal veldexperimenten waarin competitie bestudeerd is in de honderden. Competitie heeft zelfs zoveel aandacht gekregen dat er biologen zijn die verzucht hebben dat er *te veel* aandacht is besteed aan competitie (Peters, 1991).

Gezien al de aandacht voor competitie zou je welhaast verwachten dat biologen het nodige van competitie begrijpen. Toch zijn er biologen die hier aan twijfelen. Paul Keddy bijvoorbeeld, beweert in zijn boek over competitie (Keddy, 2001) het tegenovergestelde: ondanks het vele werk dat in de studie van competitie gestoken is, begrijpen biologen nog maar bar slecht hoe dit proces in elkaar steekt. Volgens hem hebben biologen veel te veel tijd gestoken in het bepalen van *of* competitie plaatsvindt en veel te weinig tijd in het ontrafelen van *de mechanismen* die aan competitie ten grondslag liggen. Om deze bewering op waarheid te kunnen schatten is het belangrijk dat we even nadenken over wat het inhoud om iets 'te begrijpen'. Dit is niet zonder meer duidelijk. Het begrip 'begrip' wordt zo vaak en zo algemeen gebruikt dat de term haast betekenisloos is. Zelf denk ik dat we pas met recht kunnen claimen dat we competitie begrijpen als we (1) ideeën hebben over hoe dit proces tot stand komt en (2) in staat zijn op basis van deze ideeën te voorspellen onder welke omstandigheden en in welke mate dieren van elkaar last hebben. Wanneer ik deze definitie gebruik, denk ik dat Keddy het bij het rechte eind heeft; biologen weten inderdaad maar weinig van hoe competitie tot stand komt (de mechanismen) en waarom dieren in specifieke situaties het elkaar lastig maken (wat de voor- en nadelen hiervan zijn). Ook zijn we nog maar slecht in staat te voorspellen in welke mate dieren last zullen hebben van elkaar.

HET DOEL VAN DIT PROEFSCHRIFT

Gestoeld op de overtuiging dat begrip van competitie nog gebrekkig is, richt dit proefschrift zich op het bestuderen van de mechanismen die aan competitie ten grondslag liggen. Anders dan de meeste eerdere studies aan competitie staat hierbij het gedrag van individuele dieren centraal. Eerder werk heeft competitie beschouwd als eigenschap van populaties, levensgemeenschappen of soorten, maar één van de essentiële inzichten van Darwin was nu juist dat competitie bij uitstek tussen individuen plaatsvindt en dat het de verschillen tussen individuen zijn die er toe doen bij het competitieproces. Nu is ‘de studie van de mechanismen die aan competitie ten grondslag liggen’ een te breed doel voor een proefschrift. Vandaar dat ik me heb beperkt tot het bestuderen van een specifieke vorm van competitie en me heb gericht op competitie bij een bepaalde groep dieren. Om deze keuzes te introduceren zal ik eerst wat dieper in gaan op wat competitie precies is en welke verschijningsvormen kunnen worden onderscheiden.

Strikt gedefinieerd is competitie *het negatieve effect dat het ene individu heeft op een ander individu door het gebruiken, of het ontzeggen van toegang tot een goed dat beide individuen najagen*. Van competitie worden over het algemeen twee vormen onderscheiden. Men spreekt van *exploitatiecompetitie* als nadelige effecten tot stand komen via het uitputten van voorraden. Een voorbeeld hiervan zou zijn dat het ene individu weinig voedsel weet te bemachtigen simpelweg omdat een ander individu het beschikbare voedsel al heeft opgegeten. Men spreekt van *interferentiecompetitie* als nadelige effecten het gevolg zijn van interacties tussen individuen. Een voorbeeld hiervan zou zijn dat het ene individu weinig voedsel weet te bemachtigen omdat een ander individu de toegang tot dit voedsel ontzegt of omdat de ene vogel veel tijd verliest door met een andere individu om voedsel te vechten.

In dit proefschrift richt ik me op *interferentiecompetitie*, omdat deze vorm van competitie het minst goed begrepen is. Interferentiecompetitie kan zowel tússen als bínnen soorten plaatsvinden. Om het simpel te houden kijk ik alleen naar interacties binnen soorten. De groep dieren waar ik me op richt zijn steltlopers die in het intergetijdengebied foerageren (Charadrii; ik zal hier in het vervolg over spreken als *wadvogels*). Er is een aantal redenen waarom interferentiecompetitie juist bij deze groep dieren en in deze habitat goed te onderzoeken is. Zo spenderen wadvogels in intergetijde gebieden een groot gedeelte van hun tijd aan foerageren, zijn het vrij grote en daardoor relatief gemakkelijk waarneembare soorten, waarvan ook het gedrag in het veld te bestuderen is, en is het voedsel van wadvogels relatief gemakkelijk te kwantificeren. Een ander belangrijk voordeel is dat er al veel onderzoek gedaan is aan interferentiecompetitie bij wadvogels.

INTERFERENTIECOMPETITIE BIJ WADVOGELS

De studie van interferentiecompetitie bij wadvogels is begonnen vanuit een interesse om de verspreiding van wadvogels over wadplaten te begrijpen. Door de dynamiek die het getijdengebied eigen is, moeten wadvogels elk tij opnieuw de keuze maken waar ze hun voedsel gaan zoeken. Eén van de factoren die hierbij waarschijnlijk een grote rol speelt, is de hoeveelheid voedsel die op elk van de wadplaten beschikbaar is. Maar ook het aantal vogels op een bepaalde wadplaat kan van groot belang zijn. Stel je eens voor dat alle vogels naar de meest voedselrijke wadplaat gaan. Als dit gebeurt dan zal de vogeldichtheid (het aantal vogels per oppervlakte) op deze wadplaat waarschijnlijk zo hoog zijn dat de vogels veel last van elkaar hebben. Voor sommige individuen kan het dan lonen om naar een minder voedselrijke plek te gaan, waar weliswaar minder voedsel is, maar waar de dichtheid aan andere vogels ook een stuk lager is. Dit voorbeeld laat mooi zien hoe competitie een belangrijke rol kan spelen bij plekkeuze. Theoretisch wordt dit idee gevangen door het 'ideale-vrije-verdelingsmodel' van Fretwell en Lucas (1970). 'Ideaal' en 'vrij' slaan op de basisveronderstellingen van dit model, namelijk dat dieren bij het kiezen van plekken onbeperkte informatie hebben en dat er geen reis- of andere kosten gemoeid zijn bij de keuze voor bepaalde plekken. De essentie van dit model is echter de gedachte dat competitie van groot belang is bij de verspreiding van dieren over voedselplekken.

In de loop der jaren is er veel praktisch werk verricht om de bovenstaande ideeën te onderzoeken. Een aanzienlijk aantal studies heeft onderzocht wat het verband is tussen de dichtheid aan vogels en de opnamesnelheid (het aantal prooien dat per tijdseenheid wordt geconsumeerd) op een bepaalde plek. Ongeveer de helft van de studies vond dat wadvogels een lagere opnamesnelheid behalen op plekken waar de dichtheid aan vogels hoog is, wat wijst op competitie. Daarnaast komt uit deze studies naar voren dat de mate waarin wadvogels last hebben van competitie, verschilt per soort, en binnen soorten afhangt van het gegeten prooitype. Ook blijkt de mate waarin wadvogels last hebben van elkaar te verschillen per individu en bijvoorbeeld afhankelijk te zijn van de dominantiepositie, en leeftijd. Een andere bron van aanwijzingen voor het belang van competitie vormen studies die gekeken hebben naar de volgorde waarin voedselplekken bezet worden door wadvogels. In een aantal studies blijken wadvogels bij lage vogeldichtheden allereerst voor de meest voedselrijke plekken te kiezen. Minder voedselrijke plekken worden pas gebruikt als de vogeldichtheid toeneemt. Ook zijn verschillende interferentiemechanismen ontdekt. Verreweg de meeste aandacht is uitgegaan naar het idee dat vogels last hebben van elkaar doordat ze voedsel van elkaar stelen ('kleptoparasitisme'), maar ook blijken wadvogels voedselplekjes te kunnen monopoliseren, en lijken er nadelige effecten van vogeldichtheid op het zoekvermogen van vogels te zijn.

Theoretisch werk aan interferentiecompetitie bij wadvogels heeft zich voornamelijk gericht op het in wiskundige termen vatten van het verband tussen vogeldichtheid en opnamesnelheid. Daarnaast is er gekeken naar de consequenties van competitie op de verspreiding van wadvogels over voedselplekken. Een belangrijke bijdrage in dit verband is een stuk dat één van mijn begeleiders samen met een collega gepubliceerd heeft (Van der Meer & Ens, 1997). In dit stuk geven zij een overzicht van de verschillende competitiemodellen die er gebruikt zijn in de wadvogelliteratuur. Voor elk van deze modellen laten ze zien wat de verspreiding van wadvogels over voedselplekken zou zijn. Uit deze studie blijkt dat voorspellingen van verspreiding sterk afhangen van het specifieke competitiemodel dat gebruikt wordt. Deze bevinding heeft verstrekkende gevolgen omdat het betekent dat wadvogelbiologen niet 'zomaar' een model kunnen kiezen om de verspreiding van wadvogels te voorspellen.

HOE BRENGEN WE HET BEGRIP VERDER?

Gegeven dat de keuze voor een bepaald competitiemodel zo van belang is voor de (verspeidings-) voorspellingen, hoe valt dan te achterhalen welk competitiemodel het best gebruikt kan worden? Eigenlijk is het antwoord op deze vraag heel eenvoudig. Zodra we weten welke mechanismen leiden tot competitie bij wadvogels kunnen we de modellen schiften op basis van hun aannamen. In dit proefschrift richt ik me dan ook op de mechanismen achter interferentiecompetitie. Ik doe dit op twee manieren.

In het grootste deel van mijn proefschrift hanteer ik een *experimentele aanpak*. Bij het doen van mijn experimenten heb ik groot belang gehecht aan een gedegen proefopzet en een gedegen analyse van de experimentele gegevens. Ik heb hiervoor gekozen vanuit de overtuiging dat ook het verhogen van de kwaliteit van gegevens een belangrijke manier kan zijn om vooruitgang te boeken. Tot voorkort bestond verreweg het meeste praktische werk aan competitie bij wadvogels uit het doen van observaties in ongemanipuleerde (dus niet-experimentele) situaties in het veld. Een dergelijke aanpak heeft het voordeel dat ze informatie over de natuur geven zoals die werkelijk waar te nemen is. Het nadeel van dit type waarnemingen is dat er in de natuur veel factoren tegelijkertijd variëren, waardoor gevonden verbanden mogelijkerwijs vervuild kunnen zijn door effecten van ongecontroleerde factoren. Dé manier om dit probleem te omzeilen is door experimenten te doen, dat wil zeggen: bepaalde factoren te manipuleren. Eerder werk aan interferentiecompetitie heeft weinig gebruikt gemaakt van experimenten om de eenvoudige reden dat het vrij moeilijk is om experimenteel onderzoek te doen aan competitie bij wadvogels. Dat ik in dit proefschrift een experimentele aanpak heb kunnen hanteren is dan ook vooral te danken aan het feit dat ik het voorrecht heb gehad gebruik te kunnen maken van 'de wadvogelunit'; een experimentele faciliteit die speciaal ontworpen is voor het doen van onderzoek aan wadvogels. In dit gebouw kunnen vrij grote aantallen wadvogels gehuisvest worden. Ook is er een kunstwad; een ruimte (± 50 m^2) waarvan de bodem bestaat uit wad en waarin automatisch een getijdenregiem ingesteld kan worden. Deze ruimte is bij uitstek geschikt voor experimenten met foeragerende wadvogels.

In één van de hoofdstukken in dit proefschrift (**hoofdstuk 6**) probeer ik een bijdrage te leveren aan de *theoretische* studie van interferentiecompetitie. Specifiek richt ik me op modellen die zich afvragen welk interferentiegedrag we eigenlijk kunnen verwachten als uitkomst van evolutie. De oorspronkelijke modellen van interferentiecompetitie houden zich niet met deze vraag bezig. Zij nemen simpelweg aan dat als twee individuen elkaar tegenkomen, ze altijd een interactie met elkaar aan zullen gaan. Vanuit evolutionair oogpunt is dit niet zonder meer logisch; onder sommige omstandigheden kunnen een interactie beter uit de weg gaan.

DE EXPERIMENTEN

HEBBEN WADVOGELS LAST VAN ELKAAR?

In de eerste twee experimenten (hoofdstuk 2) heb ik gekeken of wadvogels inderdaad last hebben van elkaar, zoals inmiddels algemeen verondersteld wordt in de literatuur over wadvogels. In deze experimenten heb ik samen met Diederik van Dullemen en een aantal andere studenten het gedrag van twee soorten wadvogels onderzocht: de kanoet (*Calidris canutus*) en de steenloper (*Arenaria interpres*). Beide soorten zijn middelgrote wadvogels die buiten het broedseizoen gebruik maken van de Waddenzee, ofwel om er te overwinteren ofwel om er bij te tanken op doorreis van en naar meer zuidelijk gelegen overwinteringsgebieden. Van beide soorten had de ervaring al geleerd dat ze in gevangenschap te bestuderen zijn. Om het belang van competitie te bepalen hebben we vogels in de wadvogelunit onder verschillende combinaties van vogeldichtheid en voedseldichtheid naar voedsel laten zoeken. Vogeldichtheid hebben we experimenteel bepaald door de vloer van de experimentele ruimte onder water te zetten en slechts één plek, een soort voedertafel, boven het water uit te laten steken. Deze opzet garandeerde dat alle vogels tegelijkertijd op de voedertafel aanwezig waren; ze konden immers nergens anders in de experimentele ruimte landen. Voedseldichtheid hebben we gemanipuleerd door een specifiek aantal prooien op de voedertafel aan te bieden. In het geval van kanoeten betrof dit mosselen (*Mytilus edulis*), die we in een laag zand begraven hebben; in het geval van steenlopers hebben we meelwormen (*Tenebrio molitor*) gebruikt, die we op een stenen plateau aanboden bedolven onder een laag zeewier. In beide experimenten hebben we 300 proefjes gedaan van elk 60 seconden. In elk proefje hebben we het gedrag bepaald van één specifieke vogel; de 'aandachtsvogel'. Het gedrag van deze vogel hebben we met behulp van twee videocamera's vastgelegd. Na afloop van alle proefjes hebben we de videobanden vertraagd afgespeeld om nauwkeurige de tijdsbesteding en de opnamesnelheid van de aandachtsvogels te kunnen bepalen.

De resultaten van deze proef hebben me op meerdere manieren verrast. Allereerst bleek het effect van vogeldichtheid op opnamesnelheid niet vanzelfsprekend. Hoewel kanoeten wel minder voedsel vonden bij een hogere vogeldichtheid, was er geen negatief effect op het aantal prooien dat ze per tijdseenheid naar binnen werkten. Het bleek dat bij lage dichtheden vogels de kanoeten een vrij groot gedeelte van hun prooien weigerden en dat ze bij hogere vogeldichtheid minder kritisch werden. Steenlopers vonden én aten minder prooien al naar gelang ze met meer op de voedertafel waren. Wat me ook verbaasd heeft, is dat hoewel beide soorten minder voedsel vonden als ze met meer waren, deze effecten op zeer verschillende wijze tot stand kwamen. Zo was de tijdsbesteding van kanoeten heel anders dan die van steenlopers. Ook was het verband tussen voedseldichtheid en zoekefficiëntie niet hetzelfde bij de beide soorten. Daarnaast heeft nog één ander aspect me aan het denken gezet. In geen van beide experimenten was het negatieve effect van vogeldichtheid op opnamesnelheid het gevolg van kleptoparasitisme. En dat terwijl het stelen van voedsel juist het interferentiemechanisme is dat in de literatuur de meeste aandacht heeft gekregen.

WAAROM HEBBEN WADVOGELS LAST VAN ELKAAR?

Dat er nauwelijks sprake was van kleptoparasitisme (het stelen van voedseldeeltjes) is op zich best te begrijpen. Het is namelijk bekend dat kleptoparasitisme alleen mogelijk is als de prooidieren enige tijd vergen om 'behandeld' te worden. Zo moeten mosselen door scholeksters (*Haematopus ostralegus*) eerst met de snavel opengebroken voordat het vlees bereikbaar wordt. Gedurende dit 'gehannes' lopen scholeksters het gevaar dat ze hun prooi verliezen aan een concurrent. Kanoeten slikken mossels heel in, zodat er nauwelijks gelegenheid is voor diefstal. Ook de steenlopers, die in het experiment meelwormen aten, konden hun prooien met maar weinig hannestijd naar binnen werken.

Hoewel de afwezigheid van kleptoparasitisme dus niet helemaal onverwacht was, riep deze observatie wel een duidelijke vraag op: waarom spenderen vogels tijd aan onderlinge interacties als dit geen extra (gestolen) voedsel oplevert? Op deze vraag zijn verschillende antwoorden mogelijk. In dit proefschrift heb ik me op één van de mogelijke antwoorden gericht en dat is het idee dat vogels interacties met elkaar aangaan niet om voedsel, maar om voedsel*plekjes* te veroveren. Voedseldeeltjes zijn in de natuur vaak gegroepeerd verspreid. Als interferentiecompetitie ook het gevolg kan zijn van interacties over voedselplekjes, valt opeens van veel meer soorten te verwachten dat ze last van elkaar zullen hebben dan wanneer we ervan uitgaan dat interferentiecompetitie voornamelijk het gevolg is van kleptoparasitisme.

DE RUIMTELIJKE VERDELING VAN VOEDSEL

De vraag of de mate waarin vogels last van elkaar hebben afhankelijk is van de ruimtelijke verdeling van voedsel staat centraal in **hoofdstuk 3**. Dit hoofdstuk begint met een korte literatuurstudie. Hoewel er weinig aandacht aan dit de ruimtelijke verdeling van voedsel besteed is in de literatuur over interferentiecompetitie, blijkt er wel het een en ander aan gedaan te zijn. Enigszins los van de literatuur over interferentiecompetitie bestaat er namelijk literatuur over het verdedigen van voedsel ('resource defence'). Al met al heb ik zo'n dertig experimenten gevonden die al gekeken hadden naar het effect van voedselverdeling op agressief gedrag en op opnamesnelheid. Het verschil tussen deze studies en interferentie-experimenten is dat er in deze studies niet gelet is op het effect van de dichtheid aan foeragerende dieren, terwijl dat juist de factor is die centraal staat in de literatuur over interferentiecompetitie. Samen met Tamar Lok heb ik daarom een nieuw experiment uitgevoerd, waarin we tegelijkertijd gekeken hebben naar de effecten van de ruimtelijke verdeling van voedsel, de vogeldichtheid en de dominantiestatus (de plaats in de pikorde) van aandachtsvogels. Onderzoekssoort in dit (en alle volgende) experimenten was de steenloper. Ik ben me op deze soort gaan richten omdat de experimenten uit hoofdstuk 2 hadden uitgewezen dat interferentie-effecten bij deze soort duidelijker naar voren komen, en daarom wellicht gemakkelijker te onderzoeken zijn, dan bij kanoeten.

De basisopzet van dit experiment was hetzelfde als die van het steenloper experiment dat in hoofdstuk 2 beschreven staat. Wederom hebben we het gedrag en de opnamesnelheid gemeten van aandachtsvogels terwijl deze naar voedsel zochten op de voedertafel in de wadvogelunit. Anders dan in de vorige proef hebben we in dit experiment echter alleen gekeken naar hoe één vogel alleen zich gedroeg en hoe vogels zich met z'n tweeën, dus in de aanwezigheid van één soortgenoot, gedroegen. Daarbij hebben we rekening gehouden met de dominantiestatus van de vogels. Maar de hoofdfactor in deze proef was natuurlijk de verdeling van het voedsel. Deze hebben we gemanipuleerd door dezelfde hoeveelheid meelwormen óf verspreid óf op een kluitje aan te bieden.

De resultaten van deze proef waren verbluffend duidelijk. De mate waarin de aandachtsvogels last hadden van de aanwezigheid van een soortgenoot bleek sterk af te hangen van de combinatie van de dominantiestatus van die aandachtsvogel en van de verdeling van het voedsel. Alleen als voedsel in groepjes verdeeld was en alleen als hun concurrent ondergeschikt was konden aandachtsvogels het voedsel monopoliseren. Dit leert ons drie dingen. Ten eerste ondersteunen deze resultaten het idee dat interacties over voedselplekjes kunnen gaan. Ten tweede laten deze resultaten zien dat het effect van dominantiestatus overheersend kan zijn. Ten derde wordt duidelijk dat het belang van dominantiestatus afhangt van eigenschappen van de omgeving, in dit geval van de verdeling van voedsel. Een belangrijk inzicht dat verder uit deze proef voortvloeit, is dat de maat die we gebruiken om succes te meten – opnamesnelheid – misschien wel niet de meest geschikte is. Gegeven dat de dominantiestatus van de foeragerende vogels zo overheersend is zou de maat die gebruikt wordt om foerageergedrag te evalueren rekening moeten houden met processen zoals de vorming en het onderhouden van dominantiestatus.

VRIJLEVENDE STEENLOPERS

In hoofdstuk 4 maak ik een uitstapje naar het veld. Bewust van de beperkingen die een gecontroleerde labomgeving met zich meebrengt richt ik me in dit hoofdstuk op wilde vogels. De plek die bij uitstek geschikt is om vrijlevende steenlopers te onderzoeken is Delaware Bay (New Jersey, USA). Deze baai is één van de plekken waar nog grote aantallen degenkrabben (*Limulus polyphemus*) voorkomen. In het voorjaar komen deze krabben aan in Delaware Bay land om op de stranden van de baai hun eieren af te zetten. Deze eieren, die ondiep in het zand begraven zijn, vormen een aantrekkelijke voedselbron voor veel wadvogelsoorten. Ook steenlopers komen hier in ongekend hoge aantallen op af, wat de baai zeer geschikt maakt om een veldexperiment uit te voeren.

Samen met Kim Meijer heb ik op de stranden van Delaware Bay een experiment uitgevoerd waarin we bepaald hebben hoe de ruimtelijke verdeling van voedsel het gedrag, en de opnamesnelheid van steenlopers beïnvloedt. In ons experiment hebben we de verdeling van voedsel gemanipuleerd door kuiltjes met daarin krabbeneieren aan te bieden en door de afstand tussen deze kuiltjes te variëren. Anders dan in het laboratoriumexperiment van hoofdstuk 3 hadden we dit keer als onderzoeker niet zelf de controle over het aantal vogels dat op de experimentele plek foerageerde; het ging hier immers om vrijlevende vogels. Ook wisten we dit keer niets van de dominantiestatus van de vogels af. Laat me verder nog even wijzen op de ‘prijs’ die we moesten betalen om een veldexperiment te doen. Waren we in het steenloper experiment in hoofdstuk 2 nog instaat om 300 metingen te verzamelen en het effect van 4 factoren te ontrafelen, in dit veldexperiment bleef de teller steken op 30 metingen en konden we ons slechts richten op het effect van 1 factor - de verdeling van voedsel.

In grote lijnen ondersteunen de resultaten van deze proef het idee dat de ruimtelijke verdeling van voedsel de mate waarin steenlopers last hebben van elkaar beïnvloedt. Dezelfde hoeveelheid voedsel trok minder steenlopers aan als dit voedsel dicht op elkaar lag. En als het voedsel dicht op elkaar lag dan vochten de steenlopers meer met elkaar. In grote lijnen ondersteunen deze resultaten dus de bevindingen uit hoofdstuk 3. De resultaten van ons laboratorium- en ons veldexperiment kunnen echter niet direct met elkaar vergeleken worden, omdat de beide experimenten in te veel opzichten van elkaar verschillen. Vooral het feit dat vogeldichtheid een experimenteel bepaalde factor was in het laboratoriumexperiment, maar niet in het veldexperiment, maakt dat de beide experimenten andere vragen beantwoorden. Alleen in het laboratoriumexperiment konden we de causale verbanden die aan competitie ten grondslag liggen blootleggen. In het veldexperiment is het de uitkomst van competitie die we konden meten; hierbij speelt ook plekkeuze hierbij een grote rol. Natuurlijk moet met dit inzicht ook in de statistische analyse van de gegevens rekening gehouden wordt. Eerdere veldexperimenten hebben dit punt echter over het hoofd gezien. Een belangrijke boodschap van hoofdstuk 4 is dan ook dat het belangrijke is de juiste statistische analyse – in dit geval een multivariate analyse, die rekening houdt met correlaties tussen de verschillende variabelen – te gebruiken.

DE DEELBAARHEID VAN VOEDSEL

Hoofdstuk 5 beschrijft opnieuw een experiment dat zich in de wadvogelunit afspeelt. Dit keer staat de vraag centraal of het nu eigenlijk uitmaakt waar vogels over vechten: voedselplekjes of voedseldeeltjes. Eén wezenlijk verschil tussen deeltjes en plekjes is dat plekjes haast per definitie beter deelbaar zijn dan deeltjes. Van één voedselplekje kunnen meerdere vogels gebruik maken door er tegelijkertijd of na elkaar van te eten. Voedseldeeltjes zijn vaak maar voor één vogel beschikbaar. Dit verschil in deelbaarheid zou wel eens van essentieel belang kunnen zijn voor de mate waarin foeragerende dieren last hebben van competitie, bijvoorbeeld omdat bij gevechten over voedselplekjes ook de verliezer nog een 'graantje' kan meepikken.

Om dit idee te onderzoeken heb ik samen met Dolores Rodriquez en Sjouke Kingma een experiment opgezet waarin we steenlopers naar voedsel hebben laten zoeken dat in kuiltjes in zand begraven was. In elk proefje waren er twee kuiltjes met voedsel, waarbij wij de meelwormen (het voedsel) zo verdeeld hebben dat ze óf allemaal tegelijk, óf één voor één gevonden zouden worden. Om te voorkomen dat de steenlopers onze proefopzet tot soep zouden roeren, hebben we de meelwormen van elkaar gescheiden door carrosserieringetjes. Het kostte wat tijd en moeite om de steenlopers te leren deze ringen met hun snavel weg te wippen, maar na enkele weken waren ze hier meesters in en kon het experiment beginnen. Behalve de deelbaarheid van voedselkuiltjes hebben we in deze proef ook de afstand tussen voedselkuiltjes en de dominantiestatus van de vogels gemanipuleerd, omdat de eerdere experimenten het belang van deze factoren hadden aangetoond. Al met al bevatte dit experiment zes factoren, omdat we naast de vier al genoemde factoren ook rekening gehouden hebben met de dag waarop en de vogel waaraan we gemeten hebben. Ook deze proef hebben we twee keer uitgevoerd.

Net als in de eerdere experimenten lieten de resultaten weinig aan duidelijkheid te wensen over. Enerzijds vonden we net als in hoofdstuk 3 dat de dominantiestatus van de aandachtsvogels van overheersend belang was. Anderzijds werd ook het effect van de afstand tussen kuiltjes uit hoofdstuk 4 bevestigd. Wat deze proef aan de eerdere experimenten toegevoegd heeft is het inzicht dat ook de deelbaarheid van voedsel van invloed is op de mate waarin vogels last hebben van elkaar. In de eerste uitvoering van dit experiment waren ondergeschikte vogels met name in staat een deel van het voedsel te bemachtigen als dit voedsel deelbaar was én zich in plekjes bevond die ver uit elkaar lagen; in de tweede uitvoering waren ondergeschikte vogels alléén onder deze omstandigheden instaat een deel van het voedsel te bemachtigen. Aandachtsvogels die dominant waren konden onder de andere omstandigheden het voedsel te monopoliseren en ze werden hier steeds beter in. Voor modellen over interagerende vogels betekent dit dat de deelbaarheid van voedsel dus inderdaad een wezenlijk verschil kan zijn tussen voedseldeeltjes en voedselplekjes.

CONCLUSIES VAN DE EXPERIMENTEN

Het moge duidelijk zijn dat de experimenten tezamen een zoektocht vormen naar de mechanismen die aan interferentiecompetitie ten grondslag liggen. Netto hebben ze me een idee opgeleverd voor een mogelijk interferentiemechanisme: interacties over voedselplekjes. Zoals ik boven al genoemd heb, denk ik dat dit mechanisme relevant kan zijn voor veel wadvogelsoorten. Uit het bovenstaande overzicht mag ook blijken dat mijn zoektocht veel 'nevenideeën' naar voren heeft gebracht, bijvoorbeeld over het belang van dominantie, over de factoren die bepalen of dominante vogels voedsel kunnen monopoliseren en over de relatieve waarde van veldexperimenten. Ook hoop ik dat mijn experimenten sullen bijdragen aan het samenbrengen van ideeën over interferentiecompetitie en 'resource defence'. In meer abstracte zin hoop ik, dat de nadruk die ik in mijn onderzoek gelegd heb op het doen van experimenten en op het goed doordenken van de opzet en de analyse van experimenten, een nieuwe impuls zal geven aan de studie van interferentiecompetitie bij wadvogels.

DE THEORIE - DE EVOLUTIE VAN INTERFERENTIEGEDRAG

Hoofdstuk 6 gaat over modellen die de evolutie van interferentiegedrag beschrijven. De laatste tien jaar is er een aantal van dit soort modellen gepubliceerd. Anders dan de oorspronkelijke interferentiemodellen nemen deze *evolutionaire* modellen aan dat vogels die elkaar tegen komen alleen een interactie met elkaar zullen aan gaan als dit 'loont', dat wil zeggen als *wel* een interactie aangaan een hogere opnamesnelheid oplevert dan *niet* een interactie aangaan. Het idee achter deze gedachte is dat dieren gedrag vertonen dat hun opnamesnelheid maximaliseert. Onder de aanname dat meten eten bijdraagt tot een hogere fitness (bijdrage aan toekomstige generaties) valt te verwachten dat vogels gedrag vertonen dat het meest loont. Immers, vogels die het meest aan toekomstige generaties bijdragen zullen op de lange termijn namelijk het talrijkst zijn. Om te analyseren welk interferentiegedrag de hoogste opnamesnelheid oplevert, maken alle evolutionaire modellen gebruik van speltheorie. De basisgedachte hierbij is dat elk individu een bepaalde (onveranderlijke) kans met zich meedraagt om bij een ontmoeting een soortgenoot aan te vallen. Deze aanvalskans wordt de ‘strategie’ van de vogel genoemd. Door telkens een aantal vogels met een bepaalde strategie tegen elkaar te laten ‘spelen’ (tegelijkertijd naar voedsel te laten zoeken) kan bepaald worden hoe veel een bepaalde strategie oplevert in termen van opnamesnelheid.

Wat me bij het bestuderen van de verschillende modellen opviel is de aanzienlijke variatie aan voorspellingen die ze genereren, terwijl ze toch in grote lijnen dezelfde opbouw hebben. Dit heeft mij en mijn coauteurs er toe gebracht om een manier te ontwikkelen waarmee modellen van de evolutie van interferentiegedrag op een systematische manier opgebouwd kunnen worden. Deze manier is even simpel als verhelderend. Wat we voorstellen is om voor een bepaalde aandachtsvogel systematisch bij te houden welke gebeurtenissen hem kunnen overkomen, wat de kans op elke gebeurtenis is, en wat de gevolgen van alle mogelijke gebeurtenissen zijn in termen van tijdsverlies en energieopbrengst of -verlies. Een overzichtelijke manier om alle mogelijke gebeurtenissen weer te geven is in de vorm van een ‘beslissingenboom’, een schema dat stapsgewijs weergeeft wat een aandachtsvogel kan overkomen. Aan de hand van een dergelijke beslissingenboom is het vinden van de juiste formule voor opnamesnelheid een kwestie van systematisch boekhouden, zoals we aan de hand van een voorbeeld laten zien. Wat we ons verder gerealiseerd hebben is dat de evolutionaire modellen van interferentiecompetitie vaak niet de meest moderne technieken gebruiken om het foerageerspel te analyseren. Wij sluiten aan bij de hedendaagse theoretische inzichten door bij de analyse van ons voorbeeld gebruik te maken van technieken uit een aanpak die ‘Adaptieve Dynamica’ genoemd wordt.

In de hoop orde te scheppen, hebben we onze methode vervolgens ingezet om bestaande interferentiemodellen onder de loep te nemen. Waar we achter zijn gekomen, is dat bestaande modellen in grote lijnen vergelijkbaar zijn, maar dat ze verschillen in hun aannamen over de details van het foerageergedrag. Zo mogen vogels hun strategische gedrag in sommige modellen wel, en in andere niet, afhankelijk maken van de gedragstoestand (zoeken of hannesen) waar ze zich in bevinden. Dit mag een onbelangrijke detail lijken; het bepaald wel of we kunnen verwachten dat evolutie altijd zal leiden tot ‘pure strategieën’ (altijd of nooit aanvallen) of dat we ook ‘gemengde strategieën’ (slechts in een deel van de ontmoetingen aanvallen) kunnen verwachten. Andere belangrijke ‘details’ betreffen de maat waarin het succes van strategieën wordt geëvalueerd (alleen tijd of ook energie?) en of de analyse zich richt op het daadwerkelijke verloop van evolutie of zich alleen richt op *statische* strategieën. Wat onze analyse laat zien is dat de evolutionaire modellen van interferentiecompetitie op sommige cruciale aspecten van elkaar verschillen. Onze systematische methode kan helpen de modellen op één lijn te krijgen.

DISCUSSIE

In dit proefschrift stond interferentiecompetitie als fenomeen op zichzelf centraal. Andere wetenschappers hebben zich slechts gericht op de consequenties van interferentiecompetitie op de dynamiek van populaties. In **hoofdstuk 7** sluit ik mijn proefschrift af met een discussie over de vraag waarom ik denk dat het van groot belang is dat ook onderzoekers die in eerste plaats geïnteresseerd zijn in de dynamiek van populaties over het interferentieproces nadenken. Het voornaamste argument hiervoor is de bevinding van Van der Meer en Ens (1997), die laat zien dat kleine verschillen in competitiegedrag grote effecten kunnen hebben op voorspellingen van de verspreiding van wadvogels over voedselplekken. De consequentie van deze bevinding is dat competitiemodellen niet zomaar gekozen kunnen worden; dit moet op basis van kennis over het interferentieproces gebeuren. Gaandeweg ben ik me echter ook gaan realiseren hoe belangrijk het is dat we ons afvragen *waarom* we bepaalde dingen eigenlijk willen weten. Wetenschappers die uit zijn op begrip van de dynamiek van populaties kunnen niet zonder ideeën over hoe het interferentieproces in zijn werk gaat, simpelweg omdat dat soort ideeën onderdeel uit maken van het begrip. Dit komt neer op een principeargument; voor mechanistische modellen zijn mechanismen van belang, al hangt dat wel van de definitie van de term ‘mechanistisch’ af.

Ik sluit mijn discussie af met suggesties voor vervolgonderzoek. Mijn experimenten hebben duidelijk het belang uitgewezen van de ruimtelijke verdeling van voedsel en van de dominantiestatus van foeragerende individuen. Logischerwijs denk ik dat het nu tijd is om competitiemodellen te ontwikkelen die zich op deze factoren richten. Hierbij kan het nodig zijn een nieuwe aanpak te ontwikkelen, die zich niet op de *gemiddelde* voedseldichtheid en het *gemiddelde* individu richt, maar waarin expliciet gekeken wordt naar ruimtelijke variatie in de verdeling van voedsel en naar variatie tussen individuen. Wat betreft de link tussen competitie en verspreiding denk ik dat we af moeten van het ideale-vrije-verdelingsmodel, omdat dit model niet echt kijkt naar *hoe* (in termen van gedragsmechanismen) de verdeling van vogels over voedselplekken tot stand komt. Ook denk ik dat het van belang is in verdelingsmodellen expliciet rekening te gaan houden met evolutie. Wat betreft de link tussen competitie en de dynamiek van populaties stel ik een nieuwe manier van naar de vraagstelling kijken voor. Het grote verschil tussen competitie en populatiedynamica is volgens mij namelijk de tijdschaal waarop deze processen opereren. Door expliciet rekening te houden met variatie in de snelheid waarmee processen plaatsvinden, denk ik dat we in het vervolg op een meer systematische manier te werk kunnen gaan. De ware uitdaging komt hierbij te liggen op het koppelen van processen met verschillende snelheden.

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TEXEL

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THREE SPECIAL ACTIVITIES

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Competition is among the most studied topics in ecology, both theoretically and empirically. Nevertheless, understanding of competition is still rudimentary; ecologists are not quite able to tell why, or to predict how much, competing animals suffer from mutual interactions. This thesis strives to contribute to understanding of competition by studying the mechanisms of interference competition among waders (Charadrii), foraging in intertidal areas. It attempts to extend previous work by applying an experimental approach to the empirical study of interference competition and an evolutionary approach to its theoretical study.